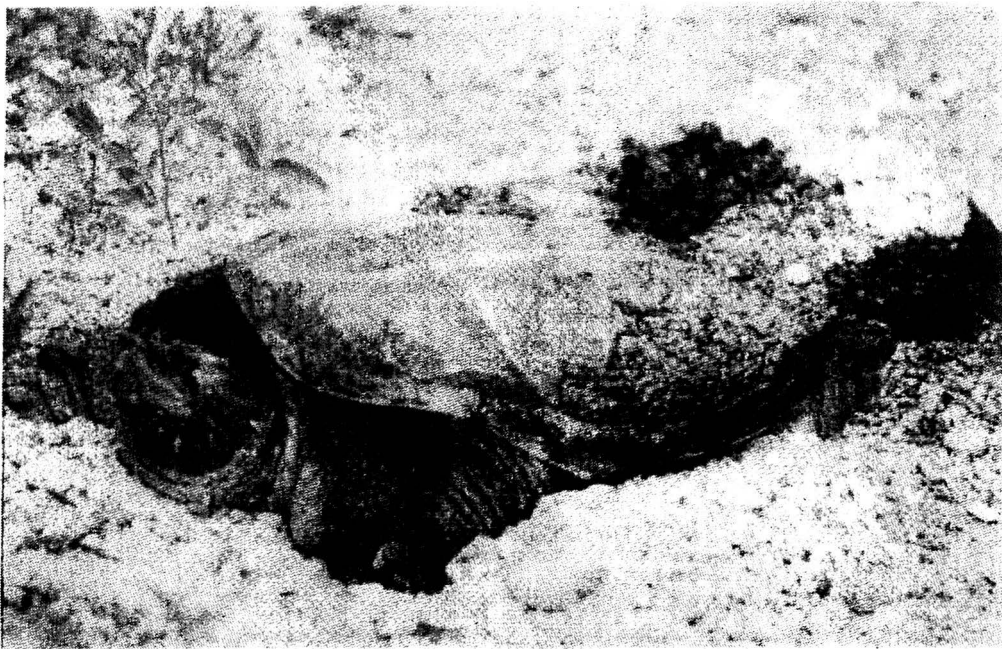


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ANNOUNCEMENTS

OPINIONS FROM THE INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

(A) APRIL 1986

- (i) *Pachycephalosaurus* Brown & Schlaikjer, 1943 and *Troodon wyomingensis* Gilmore, 1931 (Reptilia, Dinosauria): conserved.
- (ii) *Boiga* Fitzinger, 1826 (Reptilia, serpentes): conserved.
- (iii) *Chelydra osceola* Stejneger, 1918 given nonnomenclatural precedence over *Chelydra laticarinata* Hay, 1916 and *Chelydra sculpta* Hay, 1916 (Reptilia, Testudines).

(B) JULY 1986

- (i) *Dromophis* Peters, 1869 (Reptilia, Serpentes): conserved.
- (ii) *Anolis carolinensis* Voigt, 1832 designated as type species of *Anolis* Daudin, 1802 (Reptilia, Sausia).

(C) OCTOBER 1986

- (i) *Rhabdodon* Matheron, 1869 (Reptilia, Ornithischia): proposed conservation by suppression of *Rhabdodon* Fleischmann, 1831 (Reptilia Serpentes).

(D) DECEMBER 1986

- (i) *Liasis* Giray, 1842 (Reptilia, Serpentes): proposed designation of *Liasis mackloti* Dumeril & Bibron, 1844 as type species.

MINI-REVIEW: SEX DETERMINATION AND SEXUAL DIFFERENTIATION IN REPTILES

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ABSTRACT

Sex determination and sexual differentiation in vertebrates have received a great deal of attention in the past few decades. The current view is that gonochorism (separate sexes) in the earliest vertebrates involved environmental control of sex determination and that genotypic sex determination evolved later (*Intersexuality in the Animal Kingdom*, 438, 1975). Concurrent with the establishment of the latter was the gradual evolution of sex chromosome heteromorphism. Reptiles are excellent models for investigations focusing on sex determination and sexual differentiation because they exhibit: (a) both genotypic and environmentally-determined sex determination, (b) various degrees of sex chromosome heteromorphism, (c) both male and female heterogamety (the former also occurs in mammals, the latter in birds), and (d) variations from the typical 1:1 sex ratio predicted by Fisher (*The Genetical Theory of Natural Selection*, 1930). This paper will review patterns of sex determination for the various groups of reptiles and will briefly discuss physiological mechanisms that may be regulating sexual differentiation.

GENOTYPIC VS. ENVIRONMENTAL SEX DETERMINATION

Genotypic sex determination (GSD) refers to a system in which the sex of an offspring is normally irreversibly fixed by its own (or its parent's) genotype. Conversely, environmentally-dependent sex determination (ESD) is a system in which an offspring's sex is determined by the environment it encounters at some time after fertilization. The dichotomy between GSD and ESD is not necessarily absolute, in that an organism may have a genotypic mechanism that operates under some conditions but is subject to environmental control under others.

GENOTYPIC SEX DETERMINATION IN REPTILES

Squamata: Snakes. Snakes are the only group of reptiles in which GSD is ubiquitous. However, few members of this group have been critically examined for the presence of ESD. Regardless of whether ESD is ever found in this group, the study of sex determination in snakes is of interest because it provides a suggestive evolutionary series of sex chromosome heteromorphisms. Snakes are grouped phylogenetically according to skeletal characters. The boids possess the ancestral skeletal condition, the colubrids are derived from the ancestral type, and the viperids are derived from the colubrid condition. Sex chromosomes follow a similar pattern: boids are generally homomorphic (ancestral), colubrids differ only in centromere position, and viperids show female heterogamety. Despite the varying degrees of heteromorphism, the sex chromosomes apparently are

derivatives of a single genotypic sex-determining mechanism ancestral to all snakes.

Besides the suggestive pattern for the evolution of sex chromosome heterogamety, snakes also pose a perplexing problem for those interested in the evolution of sex ratios. Fisher (*ob. cit.*) predicted that the primary sex ratio within a population should evolve to 1:1. However, some species of snake produce offsprings with highly skewed sex ratios (Copeia 1985, 649). The skewing may either be in favour of males or females depending on the species. At present there is no conclusive data indicating the reason(s) for this unexpected finding.

Squamata: Lizards. Unlike the snakes, sex chromosome heteromorphisms which occur in at least seven families of lizards have multiple origins. Except for the family Pygopodidae, the number of species with distinguishable sex chromosomes is a minority of the species that have been karyotyped. The evidence indicates that heterogamety evolved recently in some of species with sex chromosomes. For example, only two species of Gekkonids are known to possess heteromorphism, and in each case, the heteromorphism is not even observed throughout the species' range (Evolution and Reproduction, 55, 1977; Chromosoma 54, 75, 1976). Even though heteromorphism is rare in this group, GSD is apparently the most prevalent method of sex determination (only two species are known to exhibit ESD).

Chelonia. Genotypic sex determination is uncommon in turtles and is apparently of recent origin as both types of sex determination may be observed for different species within the same Family (Copeia 1985, 784). Only three species are known to possess heteromorphic sex chromosomes and in each case it is the male which is heterogametic.

Crocodylia. All species of Crocodylia have been karyotyped and no sex chromosome heteromorphism has been observed (Cytogenetics 9, 81, 1970). Unlike other reptiles, this group has no microchromosomes so the possibility of overlooking a heteromorphism is unlikely. Available data indicate that crocodilians group probably do not exhibit GSD.

TEMPERATURE-DEPENDENT SEX DETERMINATION IN REPTILES

A special type of ESD is temperature-dependent sex determination (TSD). TSD is probably the ancestral form of sex determination for all groups of reptiles (Quart. Rev. Biol. 55, 3, 1980). The first report of TSD in reptiles was made in 1967 by Charnier (Soc. Biol. Quest. Af. 160, 620); however this phenomenon was brought to the attention of the scientific community largely as the result of research performed by C. Pieau and C. L. Yntema. Data indicate that temperature is in fact controlling sexual differentiation of the embryonic gonad rather than causing differential mortality of one sex (Science 206, 1186, 1979).

Not surprisingly, the vast majority of experiments examining ESD in reptiles have focused on the effects of temperature. This narrow focus may be unfortunate because other epigamic factors that may also be affecting sex determination are currently being overlooked (e.g. water potential of the substrate has been shown to influence sex determination in one species (J. Exp. Zool. 226, 467, 1983)). Therefore, while the discussion of ESD in this paper will focus on the effects of temperature, readers are cautioned that temperature may not be the sole environmental factor influencing sex determination.

Patterns for TSD. One surprising observation in the patterns of TSD among groups of reptiles is that male-producing and female-producing temperatures in lizards and crocodilians are the reverse of those found in turtles. Temperatures of 25-27°C produce females in lizards and crocodilians, whereas, the same temperatures produce males in turtles. Whether this is an actual reversal of the sex determining mechanism or simply a phase shift in the response to temperature has yet to be determined. Current data indicate that TSD is ubiquitous in crocodilians, frequent in turtles, rare in lizards, and absent in snakes (Table 1). At present, information is not available for the type(s) of sex determination in the amphisbaenids and the tuatara.

In species with TSD, the biases of sex ratios are dramatic. Over a 1-2°C range the sex ratio will go from almost all male offspring to all female. The temperature at which this shift in sex ratio occurs (the threshold temperature) is species-specific but one threshold generally is found between 28° and 30°C. Previously, it was assumed that there was a single threshold temperature for each species but findings presented by Yntema (J. Morphol. 150, 453, 1976) on snapping turtles (*Chelydra serpentina*) demonstrated that two threshold temperatures were present (*i.e.* females are produced both at high and low temperatures). This spurred the search for a second threshold in other

Order	Family	TSD
Crocodylia	Alligatoridae	+
	Crocodylidae	+
Chelononia	Chelidae	-
	Chelonidae	+
	Chelydridae	+
	Dermochelyidae	+
	Emydidae	+/-
	Kinosternidae	+/-
	Trionychidae	-
Squamata (lizards)	Agamidae	1 sp
	Gekkonidae	1 sp
	Iguanidae	-
	Lacertidae	-
Squamata (snakes)	All	-

TABLE 1: Temperature-dependent sex determination (TSD) in reptiles.

species. Currently, several species have now been found which exhibit two thresholds. We must await critical examination of more species to determine if two thresholds are the normal pattern rather than the exception. One of the problems encountered in this search is that the second threshold temperature, if present, is usually at the extreme range of survivability for incubation at constant temperatures. However this should not dissuade researchers from seeking a second threshold as temperatures within natural nests are often variable and at least occasionally are in the range which would cause mortality if conditions remained constant.

The discrepancy between thermal profiles found in the field and those used in the laboratory has been used to support the argument that TSD is simply a laboratory artifact which does not apply to natural conditions. However, data have now been presented which demonstrate that findings in the laboratory regarding the occurrence and pattern of TSD correlate to those obtained in the field (Ecology 66, 1115, 1985).

Another area of concern for researchers is the permanence of temperature-induced sex (*i.e.* does sex of an individual change as the organism matures?). This question was probably raised as a result of studies involving the influence of steroid hormones on sex determination (see below). Recent work indicates that sex reversal probably does not occur after hatching in species that exhibit TSD (J. J. Bull, in press).

Sensitive periods. An important consideration in the study of TSD is the sensitive period during which temperature affects sex determination. The results obtained from these inquiries are rather perplexing in that the sensitive period apparently varies among taxa and between sexes within the same species (Quart. Rev. Biol. 55, 3, 1980). Some of the confusion regarding the former is undoubtedly the result of different staging criteria used to describe embryological development among various groups of reptiles. For example,

temperature affects sex determination in turtles between stages 17-19 inclusive, while the sensitive period is reported to be between stages 37-39 for lizards. The impression is that sex is determined in turtles earlier in embryogeny than it is in lizards. However, there are only 25 stages described for turtle embryogeny (J. Morphol. 125, 219, 1968); thus apparent variations in the sensitive period for sex determination between turtles and lizards are difficult to interpret. The observation that within a species the sensitive period for male induction may not coincide with the period for female induction may be attributable to the fact that embryological stages are based on gross morphological characters the occurrence of which becomes less and less dependent upon temperature as development progresses (J. Morphol. 125, 219, 1968). Sexual differentiation however is due to physiological processes which are probably temperature sensitive throughout development. Thus two embryos may be at the same morphological stage of development but vary substantially in their physiological stage.

Constraints on TSD in nature. There are at least three circumstances that exclude the occurrence of TSD in nature: (a) the presence of heteromorphic sex chromosomes, (b) live-bearing, and (c) brooding. These constraints are due to theoretical considerations and are consistent with the available data (for a more detailed discussion see Quart. Rev. Biol. 55, 3, 1980).

MECHANISMS OF GONADAL DIFFERENTIATION

The physiology of gonad determination has not been resolved for any vertebrate. The sequence of events leading to gonadal differentiation apparently follows a similar pattern for all gonochoristic vertebrates: germ line cells migrate to the area where the somatic portion of the gonad is developing and then either move into the cortical (centre) or remain in the medullary (outer) regions of gonad. If the cells migrate into the cortex, the gonad develops into a testis, if they remain in the medullary region an ovary develops. At this time the major candidates for the primary inducer of gonadal differentiation are H-Y antigen and steroid hormones.

Early studies on sex determination. Early physiological studies of vertebrate sex determination addressed the possible role of steroid hormones on gonadogenesis. By administering exogenous steroids to larvae and embryos of various species complete or partial gonadal reversal was noted in all vertebrate classes, but functional sex reversals were restricted to anamniotes (for review see *Neuroendocrinology of Reproduction: Physiology and Behavior*, 159, 1981). The failure of steroids to produce functional sex reversals in amniotes coupled with the discovery that testes developed in XY mammals with the mutation 'testicular feminization' (an aberrancy of androgen receptors that prevents incorporation of testosterone into cells) fostered the search for an alternative primary inducer of gonad determination. With the discovery of a substance called H-Y antigen many researchers felt that the search had ended.

H-Y Antigen. The heterogametic sex of birds (female) and mammals (males) have been shown to be H-Y antigen positive. This finding is so consistent within these groups that H-Y antigen has been proposed as the primary inducer of sex in all vertebrates. H-Y antigen has also been noted in reptiles which exhibit TSD, with approximately 50 per cent of the hatchlings being H-Y antigen positive and an equal percentage being negative for this antigen. These percentages hold regardless of incubation temperature (and therefore the sex of individuals examined; Differentiation 22, 73, 1982). This finding has lead researchers to propose that there is a weak genetic sex determining mechanism in organism that have TSD which is simply over-ridden by temperature. However, the above results indicate that H-Y antigen is not the primary inducer of gonadal differentiation in species that exhibit TSD. In addition, recent findings have cast doubt as to the central role of H-Y antigen in gonadal differentiation in species exhibiting GSD as well (e.g. Nature 320, 170, 1986).

Steroid hormones and TSD. Recent discoveries by researchers investigating sex determination and environmental effects on embryogenesis in reptiles that exhibit TSD have lead to the resurrection of the idea that steroid hormones may have a central role in gonad determination (at least in this group). This new-found interest is based on the following information. First, steroid hormones can cause complete sex reversal in turtles if the hormones are applied during certain stages of gonadal development. In species with TSD this time corresponds to the sensitive stages for temperature induction of sex (see above); in species with GSD it is apparently somewhat earlier in development. Second, the application of exogenous testosterone (T) can cause a gonad to differentiate into an ovary. This finding may seem puzzling given the traditional view that androgens cause 'maleness'; but testosterone can be aromatized to an estrogen (E). If during certain stages of development, all embryos have the biochemical machinery to convert T to E (the back conversion, E to T, has never been found in organic systems) then differentiation of a gonad into a testis may simply be by default (*i.e.* a testis is formed if no steroid hormones are present). Note that this explanation would also account for the formation of a testis in organisms with the mutation 'testicular feminization'. A final piece of information concerns a potential source of steroid hormones available to developing embryos. Studies examining the influence of incubation temperature on catabolism of various components in the yolk by embryonic turtles report that at male-producing temperatures (25-28°C), embryos are catabolizing relatively less lipids than embryos at female-producing temperatures (21-23°C and 30-32°C). Because cholesterol (which is a precursor to steroid hormones) is associated with the lipid fraction of the yolk, it may be that embryos at female-producing temperatures are simply converting this cholesterol into steroids thereby inducing the gonad to differentiate into an ovary. While none of the above can be considered conclusive evidence that steroid hormones are the primary inducer of sex in species that exhibit TSD, there is sufficient data to

warrant further investigation as to the possible role of these substances on sexual differentiation.

CONCLUSIONS

Although the study of sex determination and, to a lesser extent, sexual differentiation in reptiles have received a great deal of attention during the past decade, more work is needed to fill large gaps in our understanding of these phenomena in reptiles (and other vertebrates as well). For example, reptiles exhibiting TSD are suitable for studies of geographic and interspecific variations in those parameters which affect sex ratios. Such studies would aid in understanding the coevolution of sex determination, reproductive biology, sex ratio, and biogeography. Further areas of interest include: the determination if factors other than temperature influence sex determination; the type(s) of sex determining mechanism(s)

found in amphisbeanids and the tuatara; differences in the responses to hormone between species exhibiting TSD and those with GSD; and the search for a species that exhibits both GSD and ESD. This small sample of the issues waiting to be resolved indicates that studies of sex determination and sexual differentiation in reptiles will be fertile areas of inquiry for years to come.

ACKNOWLEDGEMENTS

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EFFECT OF EXOGENOUS TESTOSTERONE ON THE EPIDERMAL GLANDS OF *HEMIDACTYLUS FLAVIVIRIDIS*

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ABSTRACT

The influence of exogenous testosterone on the epidermal glands i.e. β -glands and pre-anal glands, of *Hemidactylus flaviviridis* was studied 15 and 30 days post treatment during breeding and non-breeding phases of gonadal cycle. Parameters like length and breadth of pre-anal glands and their cellular and nuclear dimensions, appearance of further development of β -glands were considered. In general, it was found that the changes observed 30 days post treatment were more obvious, however, 15 days of treatment did influence both the glands studied, to some extent. Also the exogenous hormone showed pronounced effect during non-breeding period than during the breeding period.

INTRODUCTION

Sexual dimorphism in terms of holocrine epidermal specialization in gekkonines has been confirmed by Maderson and others (Maderson, 1970; Maderson and Chiu, 1970; Menchel and Maderson, 1971, 1975). It has also been observed by Chauhan (1985) that only males of *Hemidactylus flaviviridis* possess the epidermal glands, i.e. pre-anal glands and β -glands and females do not possess any of these. It was also observed that pre-anal glands' activity varied with respect to testicular cycle (Chauhan and Chauhan, 1985). The pre-anal glands are holocrine structures which open on

the ventral femoral side through pores, whereas β -glands are nothing but glandular cells developed within the epidermal cell layers.

The effects of sex steroids (chiefly the androgen) on the epidermal glands of different gekkonid lizards have been extensively studied (Maderson and Chiu, 1974; Chiu *et al.*, 1970, 1975 and Maderson *et al.*, 1979). Their findings suggested that only males have pre-anal glands and not females. It was also proposed that the differentiation of epidermal glands involved a synergistic action between androgens and hormones responsible for shedding.

There was no such study reported on the influence of androgens in the epidermal glands of a gekkonid lizard, *Hemidactylus flaviviridis*, with the observations during breeding and non-breeding phases separately. Therefore, it was deemed worthwhile to see the influence of exogenous testosterone on the epidermal glands, during breeding and non-breeding phases of the gonadal cycle.

MATERIAL AND METHODS

The adult lizards (*H. flaviviridis*) of both the sexes were obtained twice during the year, once around mid-February and secondly in the beginning of July, i.e. during the breeding and non-breeding periods respectively from a local dealer (Baroda, India). They were maintained on the diet of cockroach-nymphs. Water was provided *ad libitum*. Prior to experimentation, lizards were allowed a week's acclimatization to the cage conditions. Sloughing cycle was followed for every lizard to decide stages of sloughing cycle. It was observed that the interslough period on an average was of 22 days. Lizards were treated on the day after sloughing, i.e. having either stage-0 or stage-I (for details on stages, see Maderson, 1966) for the purpose of β -gland studies. The animals of the same weight group (18-20 gms) were then isolated in two groups as follows:

Group 1: Males (*H. flaviviridis*).

Group 2: Females (*H. flaviviridis*).

Each group was made up of seventy animals. Ten lizards were sacrificed at the beginning of experiments and designated as untreated normals at zero day (N^0). From the remaining animals, one third of each group, i.e. 20 lizards, served as experimental controls (EXC), 20 lizards as experimentals (EX), and rest 20 as the normal controls (NC). The 'EX' lizards were given intramuscular injections of testosterone propionate (Sigma, st. Louise, USA) (200 μ g of testosterone in 1 ml of 0.9 per cent saline), on alternate days, each time 0.05 ml per 20 gms of body weight of hormone was given. 'EXC' animals were injected with 0.05 ml of 0.9 per cent saline only and no hormone per 20 gms of body weight, 'NC' animals were not treated in any manner.

The experimental and control animals were sacrificed at the end of 15 days (EX^{15} and EXC^{15} respectively), and 30 days (EX^{30} and EXC^{30} respectively), under hypothermy.

The gross morphometric observations, i.e. pore diameter, length and breadth of pre-anal glands were made using a micrometer fitted to an ocular eyepiece of stereozoom dissection microscope.

The histological preparations for pre-anal glands and β -glands were obtained as described earlier (Chauhan, 1985). The nuclear and cellular diameters were measured with the help of calibrated ocular micrometer at considerably higher magnifications. Student 't' test was performed for all these parameters and 'P' values were derived to record statistical significance. Increase in terms of percentage was calculated for pore diameters. All these results have been recorded in respective tables.

RESULTS

I. OBSERVATIONS DURING NON-BREEDING PHASE OF GONADAL CYCLE:

Group 1:

(a) Pre-anal glands:

The exogenous hormonal treatment for 15 days did not reveal significant alterations in pre-anal gland length, breadth and nuclear diameter (Table 1), however, cell diameter showed considerable change ($P < 0.05$). While treatment for 30 days showed statistically significant changes in gland length and diameters of cells and nuclei. It was interesting to note that gland breadth remained unaffected even after treatment for 30 days. Pore diameter increased after 15 and 30 days of treatment (Table 1). Thus the microscopic structure of pre-anal gland proper showed a proliferation due to exogenous hormonal treatment. This was clearly evident, especially in germinal cells (GC) and inner differentiating cells (IDC) (Fig. 2) of treated lizards when compared to normal/control ones (Fig. 1). Mitotic figures were also common in GC and IDC of treated animals (EX^{30}), indicating active proliferation. Eosinophilia of differentiating cells in glands of EX^{30} lizards also increased simultaneously. In short, the pre-anal glands of EX^{30} animals, even during non-breeding phase assumed that state of development which resembled to those of recrudescence phase of gonadal cycle of normal lizards.

(b) β -glands:

Normally β -glands in the epidermal layers are found to develop during the breeding period. However, the treatment with testosterone during the non-breeding period resulted in the development of β -glands. It was observed that the development of β -glands. It was observed that the development of β -gland was dose-dependent.

Group 2:

(a) Pre-anal glands:

These are normally absent in this group and the treatment did not allow the development of pre-anal glands.

(b) β -glands:

β -glands are also absent in this group, however, exogenous testosterone resulted in the development of β -glands. It was found that the glandular development was dose-dependent.

II. OBSERVATIONS DURING BREEDING PHASE OF GONADAL CYCLE:

Group 1:

(a) Pre-anal glands:

There was not much difference in the pre-anal glands of normal controls (Fig. 3) and treated ones (Fig. 4), except for the fact that cell diameter showed significant difference. Rest of the parameters namely pre-anal glands' length breadth and nuclear diameters did not show statistically significant changes when compared to those of controls (Table 1).

(b) β -glands:

β -glands also did not show any significant variation in the treated animals when compared to the controls.

Group 2:

(a) Pre-anal glands:

As stated earlier, pre-anal glands are absent in this group and could not be induced to develop with exogenous hormone treatment.

(b) β -glands:

β -glands are also absent in this group (Fig. 5) but the treatment with testosterone was found to induce their development. The development of β -glands was dose dependent (Fig. 6 and 7).

Since the development of β -glands due to exogenous testosterone, in this group was similar during breeding as well as non-breeding periods, illustrations for only during breeding period are provided.

	Non-breeding phase					Breeding phase				
	Length	Breadth	Pore diameter	Nuclear diameter	Cellular diameter	Length	Breadth	Pore diameter	Nuclear diameter	Cellular diameter
	(mm)	(mm)	(μ)	(μ)	(μ)	(mm)	(mm)	(μ)	(μ)	(μ)
N ⁰	1.1 $\pm$ 0.1	1.0 $\pm$ 0.3	170	4.7 $\pm$ 0.1	9.1 $\pm$ 0.5	3.1 $\pm$ 0.6	1.3 $\pm$ 0.6	185	6.3 $\pm$ 0.6	11.5 $\pm$ 0.2
NC ¹⁵	1.1 $\pm$ 0.1	1.1 $\pm$ 0.0	173	4.8 $\pm$ 0.1	9.3 $\pm$ 0.4	3.1 $\pm$ 0.4	1.3 $\pm$ 0.7	186	6.8 $\pm$ 0.8	11.6 $\pm$ 0.5
EXC ¹⁵	1.2 $\pm$ 0.5	1.1 $\pm$ 0.1	173	4.7 $\pm$ 0.3	9.3 $\pm$ 0.1	3.2 $\pm$ 0.7	1.4 $\pm$ 0.5	185	7.0 $\pm$ 0.6	11.8 $\pm$ 0.4
EX ¹⁵	1.2 $\pm$ 0.0	1.1 $\pm$ 0.1	174	4.9 $\pm$ 0.0	10.2 $\pm$ 0.1	3.2 $\pm$ 0.3	1.5 $\pm$ 0.0	188	6.9 $\pm$ 0.4	11.9 $\pm$ 0.4
Significant at the level*	NS	NS	2.35**	(P<0.10) NS	P<0.05	NS	NS	1.62**	NS	NS
NC ³⁰	1.3 $\pm$ 0.3	1.2 $\pm$ 0.4	178	4.8 $\pm$ 0.5	9.3 $\pm$ 0.3	3.2 $\pm$ 0.5	1.5 $\pm$ 0.4	189	7.0 $\pm$ 0.5	11.9 $\pm$ 0.0
EXC ³⁰	1.3 $\pm$ 0.2	1.2 $\pm$ 0.0	177	4.8 $\pm$ 0.6	9.4 $\pm$ 0.0	3.2 $\pm$ 0.6	1.5 $\pm$ 0.6	188	7.3 $\pm$ 0.1	11.9 $\pm$ 0.3
EX ³⁰	1.8 $\pm$ 0.3	1.4 $\pm$ 0.1	180	5.4 $\pm$ 0.0	10.7 $\pm$ 0.2	3.3 $\pm$ 0.1	1.6 $\pm$ 0.1	190	7.6 $\pm$ 0.3	12.7 $\pm$ 0.4
Significant at the level*	P<0.05	NS	5.88**	P<0.001	P<0.01	NS	NS	2.70**	(P<0.10) NS	P<0.05

* P values refer to differences between N⁰ and EX¹⁵; N⁰ and EX³⁰ periods. The student's 't' test was used to analyze differences in means. NS means non-significant (i.e. P<0.05).

** Depicts per cent increase, values of EX¹⁵ and EX³⁰ compared with N⁰.

TABLE 1: Effects of exogenous treatment of testosterone in various components of pre-anal glands of male *Hamidactylus flaviviridis*. Mean value $\pm$ S.E.M.

DISCUSSION

The present observations explain the involvement of an androgen (testosterone) in the development of epidermal glands in gekkonid lizards and its effect is dose-dependent. The development of β -glands in case of females and also in males during the non-breeding period with hormone treatment is suggestive of the fact that the germinal epithelium of these scales (epidermis) respond to androgens by producing glandular elements and this development is dose-dependent. This kind of response could be better expressed in presence of sufficient androgenic stimulus.

The development of β -glands but not the pre-anal glands in case of treated females is suggestive of the fact that the β -glands are more responsive than pre-anal glands to androgens. Thus, it seems that germinal

epithelium of epidermal layers responded to the androgenic stimulus but not that of pre-anal glands. Probably, the germinal layer of pre-anal gland would respond, if optimum levels of androgens for enough duration are maintained.

In the males, the pronounced effect of exogenous testosterone was evident only during non-breeding period, while during breeding period it seemingly had no effect. It could be realized from these observations that beyond certain level, testosterone exerts no additive influence either due to a feedback mechanism or due to a specific maximum threshold sensitivity of these target organs to such sex steroids. Thus, a direct effect of exogenous testosterone on epidermal glands appears to support the views expressed by Maderson, Chiu and others (Maderson and Chiu, 1970, 1981; Maderson *et al.*, 1977, 1979).

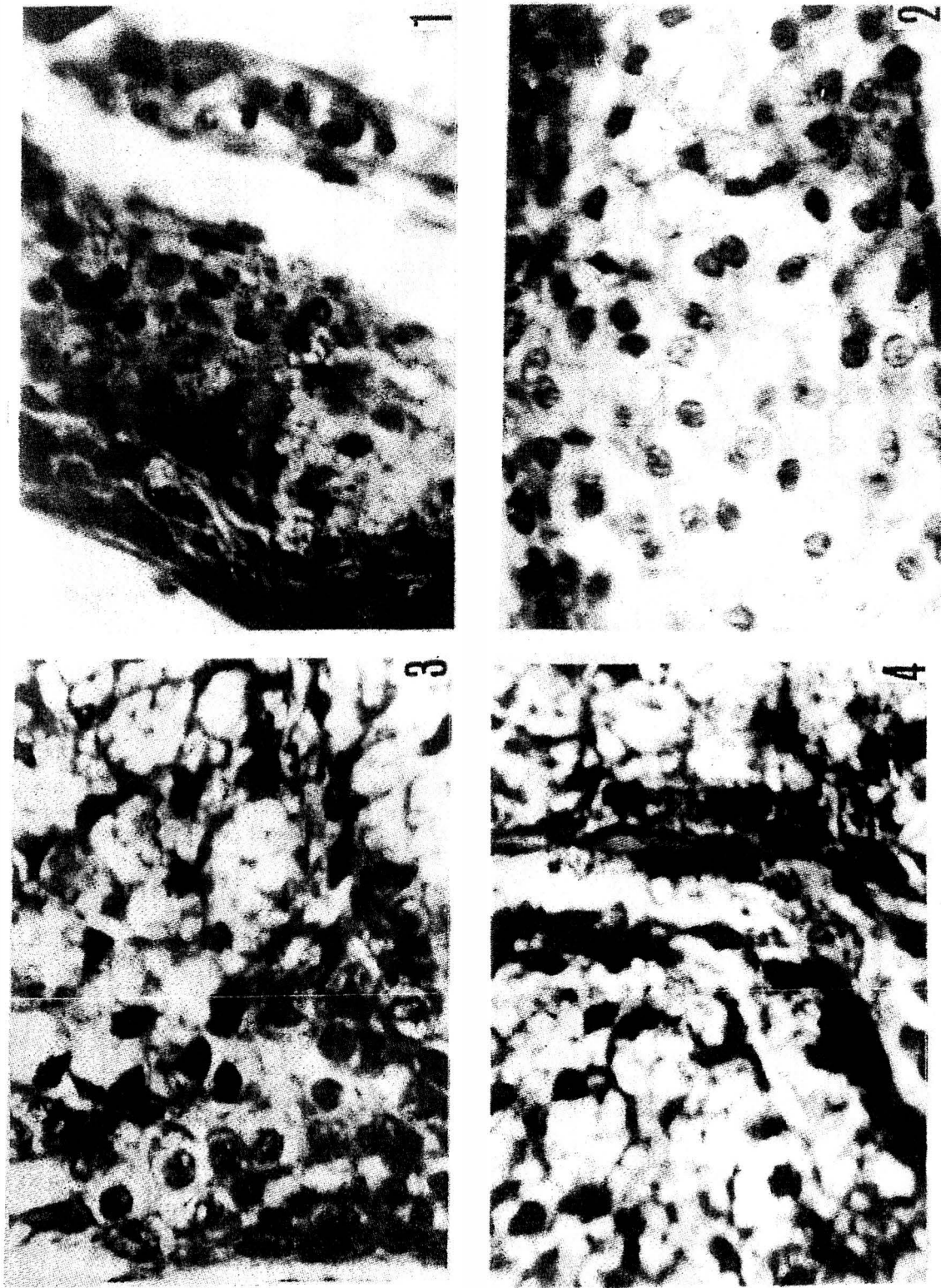


PLATE 1 Photomicrographs of the pre-anal glands of male *H. flaviviridis*

Fig. 1 Pre-anal gland of normal lizard during non-breeding period. Note smaller cells with healthy nuclei; gland as such was also of smaller size.

Fig. 2 Pre-anal gland of testosterone treated (for 30 days) lizards during non-breeding period. Note increase in cell size and glandular mass. Some of the nuclei are unhealthy and cells having them are very large. Gland shows characters similar to that of breeding phase.

Fig. 3 Pre-anal gland of normal lizard during breeding period. Note the hypertrophy of the gland. Compare it with Fig. 2.

Fig. 4 Pre-anal gland of testosterone treated (for 30 days) lizards during breeding period. Note that the gland structure does not differ much than that observed during breeding period of untreated lizards, i.e. Fig. 3.

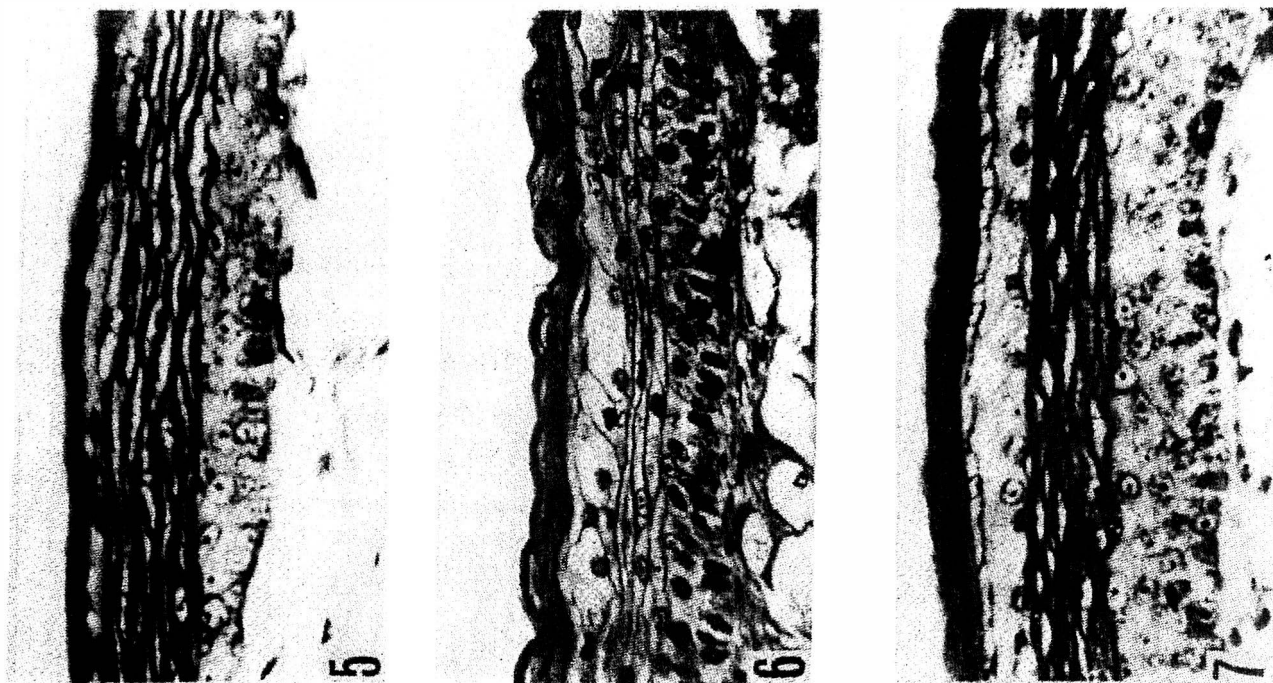


PLATE 2 Photomicrographs of the epidermis of female *H. flaviviridis*.

Fig. 5 Epidermis of the untreated (normal) lizard (decapitated after 30 days, along with treated lizards for 30 days). Note the absence of β -gland, but epidermis is in stage-4 of sloughing cycle.

Fig. 6 Epidermis after 15 days of testosterone treatment. Note moderately developed β -gland.

Fig. 7 Epidermis after 30 days of testosterone treatment. Note well developed β -gland.

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ASPECTS OF THE POPULATION ECOLOGY OF *MAUREMYS CASPICA* IN NORTH WEST AFRICA

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ABSTRACT

Field observations have been made on a North African population of *Mauremys caspica leprosa*. Measurements on 73 animals has provided information on population structure and morphometrics. In a sample of 67 terrapins measured in September carapace lengths ranged from 22-186mm although the majority (59.7 per cent) were below 80mm. Body masses ranged from 4-906g but most animals (71.6 per cent) were below 100g. Females grow larger than and outnumbered males by 2.12:1, terrapins above one year outnumbered hatchlings by 4.15:1. Equations have been produced relating growth annuli (age) to carapace length. These indicate that females grow faster than males but that males outlive females. A general equation predicts that large animals (>200mm C. length) may attain at least 26 years in field populations. Younger animals predominated in the population and 68.1 per cent were aged less than seven years. Equations defining the relationship between body mass and the principal dimensions of the shell have indicated sexual dimorphic trends in shell morphometry during growth. *M. caspica* were found with leeches, shell damage and algal growth on the carapace.

INTRODUCTION

The striped-necked terrapin *Mauremys caspica* is a well known emydid of the Mediterranean region where it is found as three subspecies, *M.c. caspica*, *M.c. rivulata* and *M.c. leprosa* (see Busack and Ernst, 1981). Although certain aspects of the ecology of *M. caspica* in Israel (Gasith and Sidis, 1983; 1984; 1985. Sidis and Gasith, 1985) and North Africa (Meek, 1983) have been described, there is little information on the age structures, and life spans of *M. caspica*. The absence of information concerning these important life history attributes may in part be a result of difficulties involved in long term field studies of a species known to attain a relatively long life span (Bouler, 1977). Growth annuli on the shell can be used to age individuals in certain chelonians (Bruce Bury, 1979) but *M. caspica* is an aquatic species often living in flowing water where the annuli may be worn smooth rendering direct counting difficult or impossible. Therefore, methods for aging terrapins in these circumstances would be a useful tool in order to add to the understanding of their population dynamics. This paper is partly about an attempt to develop a method for aging *Mauremys caspica*; it is also about population structure and morphometrics. The most westerly occurring race of *M. caspica* is *M.c. leprosa* which ranges over southern France, Spain and North Africa (Arnold, Burton and Ovenden, 1978; Street, 1979). The observations in this paper are concerned with this subspecies and were made on a population found near the south western most limits of the species range in North Africa.

METHODS

Measurements on 67 *M. caspica* were made in September 1981 with six animals measured for body mass and carapace length in May 1980. The population was found at an irrigation channel which flowed through a desert area in southern Morocco. The channel originated from a dam which lay 2km southwest of the study site. An area of approximately 1km of the channel was sampled, which was about 1m deep and 2m wide with the water pH 7.2. The channel was man-made being constructed of concrete but sand from the surrounding area had blown into and settled on the concrete base providing a growth medium for clusters of pond weed (*Potamogeton sp.*): three *M. caspica* were observed feeding on this plant. Terrapins were relatively easy to locate here since the water was clear and only small areas colonized by the *Potamogeton*. Animals were collected by hand after entering the water and moving against the current. They were then marked with Tippex fluid for future identification.

BODY MEASUREMENTS

Carapace length. A straight line between the leading edges on the nuchal and supracaudal scutes.

Plastron length. A straight line between the leading point on the junction between the gular scutes and the base of the anal notch.

Shell height. A straight line from the base of the plastron to the highest point on the carapace.

Carapace width. A straight line between the furthest points on the marginals.

Body mass. This was measured by using a set of pan balance scales.

Growth annuli. Determined by counting the number of annuli on the coastal scutes with each distinct annulus regarded as one years growth.

Discernible annuli were found in 22 terrapins (6 males, 12 females, 4 unsexed) with 32 animals with indistinct annuli. The remaining captures (13) were hatchlings with no complete rings (i.e. <1 year). Thus 35 terrapins could be aged directly.

ASSESSING SEX

Terrapins were sexed by the position of the cloaca on the tail which is located in a more posterior position in males. Males may also have a more concave plastron.

PHYSICAL CONDITION

Records were made of major shell damage, flaking scutes and the presence of algal growth or leeches on the shell. Some of these were photographed for later analysis.

METHOD OF ANALYSIS

From inspection of the data it was apparent that both age related and relative growth could be described as a logarithmic process and subsequently regression analysis was applied to the data after transformation to logarithmic form (Sokal & Rohlf, 1981). Age related growth can be described by the equation,

$$\log y = \log a + b \log x$$

where age y is determined from the length of the carapace x ; a and b are constants. This can be rewritten as,

$$y = ax^b \quad (\text{model 1})$$

which treats age y as dependent on the length of the carapace x .

When determining relative growth where no variable can be truly regarded as independent (although body mass represents the whole animal this measurement may be subject to error (Schmit-Neilson, 1984)) values of y and x can be related by,

$$y/y_0 = (x/x_0)^b \quad (\text{model 2})$$

where y_0 and x_0 are the geometric means of y and x respectively. The values of y_0 and x_0 have the same values in the two regression models but a and b may be different. The intercept can be calculated as,

$$a = y_0 x_0^{-b}$$

with b the exponent for either regression model. When there is a high correlation between y and x the models produce only slightly different exponents. A model (2) exponent can be derived from a model (1) by,

$$b_2 = (1/r)b_1$$

where r is the correlation coefficient, b_2 the exponent in model (2) and b_1 the exponent in model (1) (Alexander, Jayes, Maloiy and Wathuta, 1979). Therefore if, for example, r has a value of 1.0, the two methods are in agreement. Lines representing model (2) equations on the graphs in this paper have been calculated from,

$$y = [y_0/(x_0^b)]x^b$$

using the constants from the appropriate equation. The various shell dimensions have been analysed in arithmetic form using regression analysis and the relationships described by,

$$y = mx + b$$

where y and x are related by the slope m and the y intercept b .

Confidence intervals have been calculated for all equations at $n-2$ degrees of freedom using the t -distribution (Bailey, 1981). For b in the allometric equations or m in the regression equations they are the $\pm$ type but for y_0 in the allometric equations they are the $x/\div$ type. Tests for significant differences between equations or significant departures from geometric similarity have been made using the t -distribution at $n-2$ degrees of freedom by the method described by Bailey (1981).

RESULTS

POPULATION STRUCTURE

Size frequencies based on carapace length and body mass are shown in Fig. 1. The distributions were skewed towards smaller animals with 59.7 per cent having carapace lengths below 80mm and 71.6 per cent less than 100g body mass. Females had longer carapace lengths (range 49-186mm, $\bar{x} = 97.1$, S.D. = 37.9) than males (range 54-149mm, $\bar{x} = 82.06$, S.D. = 22.5) and also attained greater body mass (range 17-906g, $\bar{x} = 198$, S.D. = 230) than males (range 23-536g, $\bar{x} = 103$, S.D. = 118). Analysis of the population size structure showed that there was no significant difference ($P > 0.1$) in the lengths of the carapace or body mass between males and females up to 7 years. However, there was a significant increase in female carapace lengths ($F(1,20) = 7.43$, $P < 0.025$) and body mass ($F(1,20) = 4.32$, $P < 0.1$) above 7 years. Hatchling terrapins (i.e. animals with no complete growth rings) had carapace lengths from 22-32mm ($\bar{x} = 26.9$) and body masses from 4-7g ($\bar{x} = 5.5$). In general, the population sample favoured females by 2.12:1 with adults and subadults outnumbering hatchlings by 4.5:1.

AGE MODELS

There is a highly significant correlation between the number of growth rings on the costal scutes and carapace length in males ($r = 0.96$) and females ($r = 0.97$). Fig. 2 is a graph of the data plotted on logarithmic coordinates, Table 1 the allometric equations derived from the measurements. The equations for males and females have each been calculated using the information from unsexed juveniles on the assumption that at this stage no differences exist in the relationship.

There is a significant difference between the exponents in equation (1) for males and (2) for females ($t = 1.92$, 24 d.f., $P < 0.1$) indicating that females grow faster than males with a major departure at 5-7 years. Equation (1) predicts that the largest male in the field sample may have been >23 years, equation (2) that the largest female was >20 years. The maximum carapace

length for *M. caspica leprosa* is over 200mm (Arnold et al., 1978), equation (3) predicts that animals of this size would be at least 26 years.

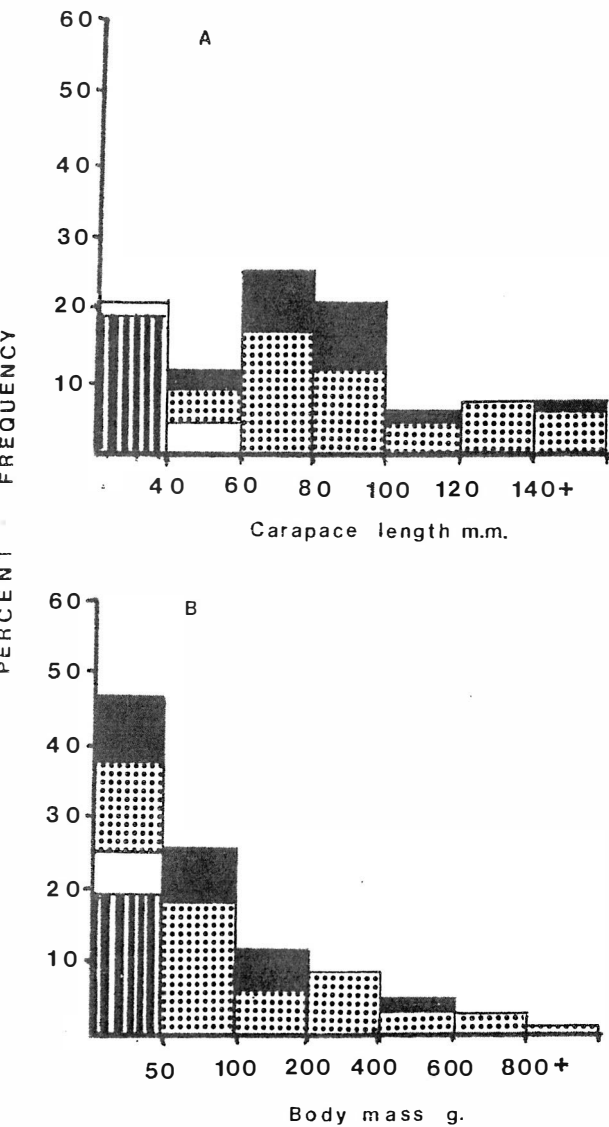


Fig. 1 Histograms of size frequencies of *M. caspica* carapace lengths (A) and body masses (B) expressed as percentages of the total sample in September (n = 67). Vertical bars represent hatchlings, open bars immatures, solid bars males and stippled bars females.

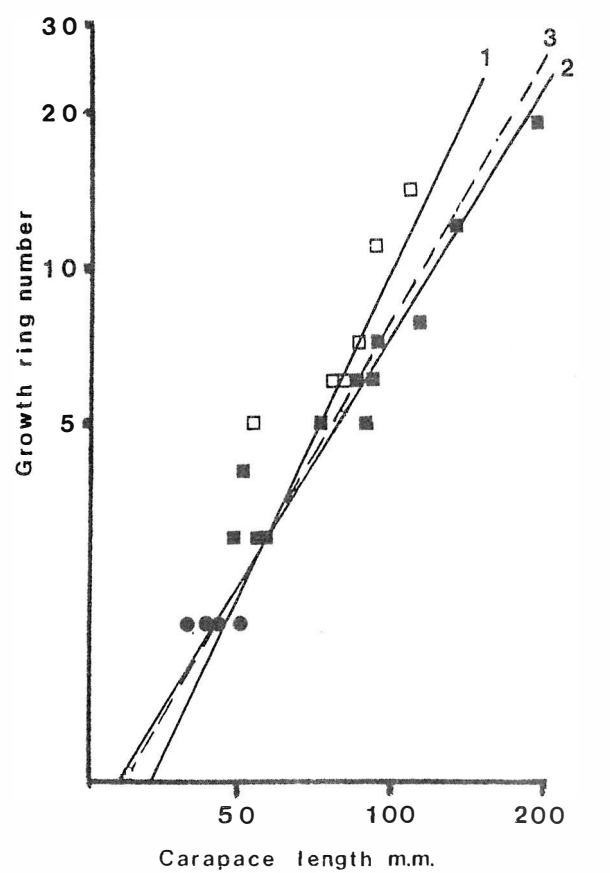


Fig. 2 A graph on logarithmic coordinates of growth ring number plotted against carapace length. The lines taken through the data are derived from the equations in Table 1. The symbols represent males (□), females (■) and unsexed juveniles (●). Sample sizes are given in the text.

AGE STRUCTURE

An important problem in presenting a valid statistical analysis of age structure was that many adults could not be aged accurately because of worn growth rings. Fig. 3b is a histogram of age frequencies of animals aged by direct counting (n = 35) with the age classes shown as a percentage of the total sample (n = 67). Fig. 3a shows these data in addition to terrapins aged by using equations (1) and (2) in Table 1. An obvious feature of the histograms is the high proportion of hatchling terrapins, but these

Eqn. No.	a	b	b ₂	r	n
(1) males	0.0009	2.03 ± 0.32	2.12	0.95	10
(2) females	0.0068	1.53 ± 0.21	1.57	0.97	16
(3) pooled	0.0057	1.59 ± 0.27	1.68	0.94	22

TABLE 1: Allometric equations of the form $y = ax^b$ relating the number of growth annuli on the costal scutes y with the length of the carapace x in mm from the exponent b and intercept a; 95 per cent confidence intervals have been calculated for b. Exponents for model 2 regression (b₂) are also given. The equations for males and females have been calculated by including the data from immatures.

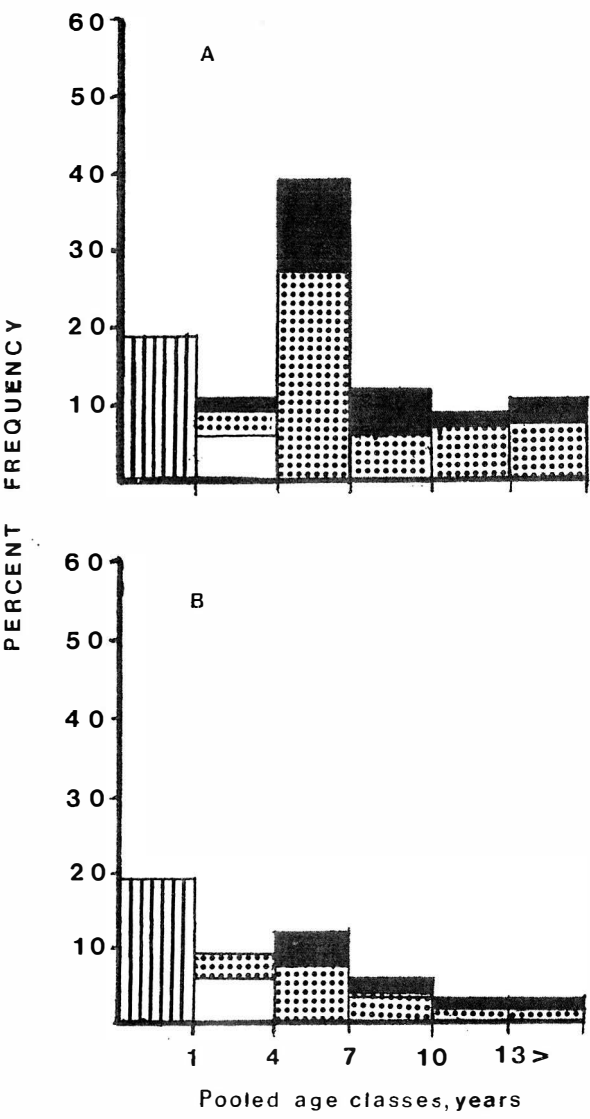


Fig. 3 Age frequency histograms of *M. caspica* expressed as percentages of the total number of animals in the September sample (n = 67). Fig. 3a is based on animals aged by direct growth ring count in addition to animals aged by equations (1) and (2) in Table 1. Fig. 3b is based only on animals aged by direct counting (n = 35) but with the cell sizes represented as per cent frequencies of the total sample (n = 67). Other details as for Fig. 1.

would probably not be expected to be present in such numbers at other periods of the year as a result of mortality. Therefore, it appears that the major age classes in this population were between 4-7 years. In Fig. 3a the majority of terrapins were below 7 years (68.1 per cent) although 10.4 per cent exceeded 13 years.

SHELL CONDITION

Examination of the shell in 67 *M. caspica* showed that eight individuals (11.9 per cent) had flaking scutes on the carapace. Flaking scutes are believed to result from algal growth but in fact no individuals with this condition had any signs of such growth, although growths of algae were observed in a further 4.5 per cent of the sample. Leeches (unidentified) were observed on the carapace, plastron and limbs of 4 (5.9 per cent) of terrapins. In only one animal was there serious shell damage. This involved three of the marginal scutes which were absent. Table 2 is a summary of these data.

MORPHOMETRY

Fig. 4 is a graph on logarithmic coordinates of body mass plotted against the shell dimensions; Table 3 gives allometric equations derived from the data. Exponents for model (1) and model (2) regression have been calculated but only model (2) equations will be discussed here since all the correlation coefficients for the data sets are high and therefore there is little difference between the two methods. It will be convenient to consider the calculated exponents in relation to a hypothetical animal maintaining geometric similarity during growth and therefore also its shape. This requires that the lengths of the corresponding elements are proportional to body mass^{0.33}, exponents above 0.33 imply that the linear dimensions are becoming relatively longer. If elastic similarity is to be maintained during growth (McMahon, 1973) an exponent of 0.25 is required, indicating relatively shorter elements with increasing size.

The exponents for carapace length are significantly higher than 0.33 (males $t = 3.2$, $P < 0.01$; females $t = 9.8$, $P < 0.001$) therefore the almost circular shell shape (i.e. length vs width) of hatchlings develops into a more elongate adult condition, as confirmed by the equations for shell width where the exponents are lower than 0.33. The height of the shell is not

	n	Flaking scutes	Shell damage	Algal growth	leeches
males	16	2	1	2	1
females	34	6	0	1	3
juveniles	4	0	0	0	0
hatchlings	13	0	0	0	0
per cent total		11.9	1.5	4.5	5.97

TABLE 2: Observations on the shell condition in *Mauremys caspica* from data on September captures (n = 67).

maintained during growth in males ($b = 0.29$, $t = 2.6$, $P < 0.02$) but in females, although the exponent is < 0.33 , there is no significant departure from geometric similarity ($t = 0.98$, $P > 0.1$) thus females have higher shells than males which is similar to the condition found in some other terrapins, e.g. *Chrysemys picta* (Iverson, 1982).

The relationship between carapace length and plastron length is shown in Fig. 5. A significant difference ($t = 2.5$, $P < 0.02$) has been found between the equations relating carapace length (x) in mm to plastron length (y) in mm in males,

$$y = 0.84 \pm 0.03X - 0.98 \quad (r = 0.99, n = 33) \quad (12)$$

and females,

$$y = 0.89 \pm 0.02X - 2.43 \quad (r = 0.99, n = 51) \quad (13)$$

and also between the equations relating carapace length (x) in mm to carapace height (y) in mm ($t = 2.23$, $P < 0.05$) in males,

$$y = 0.27 \pm 0.01X + 4.92 \quad (r = 0.98, n = 33) \quad (14)$$

and females,

$$y = 0.30 \pm 0.02X + 3.37 \quad (r = 0.98, n = 51) \quad (15)$$

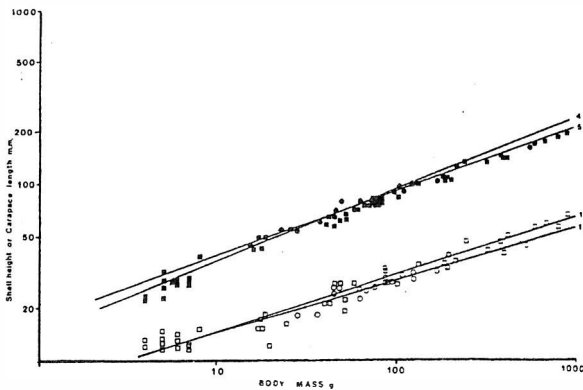


Fig. 4 A graph on logarithmic coordinates of body mass plotted against carapace length and shell height. The lines taken through the data represent equations given in Table 3. Solid symbols represent carapace length, open symbols carapace height; circles represent males, squares females.

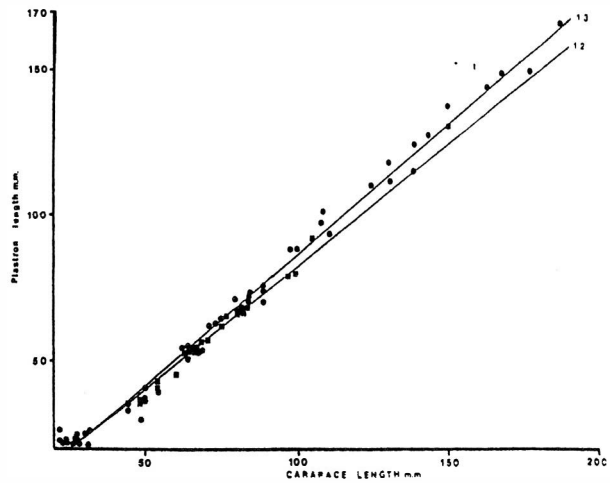


Fig. 5 A graph on arithmetic coordinates of carapace length plotted against plastron length. The lines represent equations given in the text. The square symbols represent males, circles females and juveniles.

However, no significant sexual dimorphic trends were evident from the relationship between carapace length and carapace width ($t = 0.58$, $P > 0.1$) with the pooled data defined as,

$$y = 0.63 \pm 0.2X + 9.66 \quad (r = 0.99, n = 67) \quad (16)$$

where y is the width of the carapace in mm and x the length of the carapace in mm.

DISCUSSION

The information in this paper indicates that in southern Morocco *M. caspica* has a potential long life span, females grow larger than males with sexual dimorphic trends in shell morphometrics. Fig. 3a suggests that the population had a high proportion of animals aged between 4-7 years. There are several possible explanations for this the most likely are: 1. sampling error; 2. if Fig. 3a does indeed

Eqn. No.	Shell dimensions	b_1	b_2	y_0	x_0	r	n
(4)	Carapace length (males)	0.38	0.41 ± 0.05	$48.14x / \div 1.06$	20.20	0.94	33
(5)	Carapace length (females)	0.38	0.38 ± 0.01	$62.67x / \div 1.04$	44.23	0.99	51
(6)	Plastron length (males)	0.39	0.39 ± 0.02	$40.08x / \div 1.02$	21.66	0.99	33
(7)	Plastron length (females)	0.39	0.39 ± 0.01	$53.13x / \div 1.02$	44.23	0.99	51
(8)	Carapace width (males)	0.31	0.31 ± 0.02	$40.69x / \div 1.02$	21.66	0.99	33
(9)	Carapace width (females)	0.31	0.31 ± 0.01	$51.01x / \div 1.02$	44.23	0.99	51
(10)	Carapace height (males)	0.28	0.29 ± 0.03	$18.52x / \div 1.02$	21.66	0.97	33
(11)	Carapace height (females)	0.31	0.32 ± 0.02	$23.04x / \div 1.02$	44.23	0.97	51

TABLE 3: Allometric equations of the form $y/y_0 = (x/x_0)^b$ relating shell dimensions y in mm with body mass x in grammes. Exponents for model (1) (b_1) and model (2) (b_2) regression are given. The values of y_0 and x_0 are the geometric means of y and x respectively, r the correlation coefficient and n the number of observations on which the equations are based; 95 per cent confidence intervals for b and y_0 are also given. The equations for both males and females have each been calculated using the data from hatchlings and unsexed juveniles.

approximate reality then it may be that the population has a widely fluctuating recruitment and/or survivorship from year to year, possibly suggesting favourable breeding success between 1974-77; 3. the sample represented part of a migratory population which would imply that such behaviour is largely confined to certain age classes. Migratory behaviour has been observed in several species of freshwater chelonians (Bruce Bury, 1979) and could also explain the large difference in capture success between May when the number of sightings were low, and September when sightings were frequent. The high proportion of hatchlings recorded during the study period is probably dependent on season since although terrapins produce high numbers of eggs annually (6-8 in *M. caspica*; Pritchard, 1979) nest destruction and high mortality of the hatchlings due to the relatively soft shell, greatly reduces recruitment into the juvenile age class (Bruce Bury, 1979) and therefore a rather different size distribution might be expected to be found at other periods of the year.

A number of methods of aging terrapins in field populations have been developed. Several are based on the assumption that growth annuli are indicators of age in temperate species and have included counting plastron annuli (Sexton, 1959), plastron length and recent growth history (Wilbur, 1975) and the number of annuli on the left pectoral plate which was used to establish a relationship with plastron length in older individuals (Gibbons, 1968). In general, these methods take into account differential growth rates but inevitably all incur some degree of error. Although high correlations have been found for the information concerning carapace length and growth ring number in *M. caspica* it should be noted that the equations derived from the data are also based on the assumption that growth rings are age indicators. However given that this assumption is valid a useful statistic for determining the reliability of the equations and the subsequent error involved in their predictions are the confidence intervals attached to the exponents. These have values of 0.32 and 0.21 in the equations for males (1) and females (2) respectively which are errors of 15.7 and 13.6 per cent, although further error might be expected as a result of the observers counting error since some secondary rings with no annual deposition rate could have been inadvertently recorded with major annuli. This would be most likely to occur in older animals or in those showing greater shell wear.

Estimates of life spans for freshwater chelonians have indicated maximum ages of less than 30 and 35 years for *Pseudemys scripta* (Gibbons and Semlitsch, 1982) and around 40 years for *Chrysemys picta* (Wilbur, 1975) which are in approximate agreement with the age spans estimated for *M. caspica* in this paper.

Berry and Shine (1980) examined sexual size dimorphism in chelonians and observed that in most aquatic 'swimmers' females (as found here for *M. caspica*) attained greater size than males. To explain this they suggested that in addition to larger size enabling increased female fecundity, smaller males could also be actively favoured since it may allow for

increased mobility to locate females. Smaller males could also simply result from males devoting energy to locating females rather than to growth. Growth studies in chelonians have included a number of freshwater species (e.g. Dunson, 1967; Meek, 1982; Long, 1983; Iverson, 1982, 1984). These works have indicated a consistent trend towards a low profile shell design in highly aquatic species ($b > 0.33$). Iverson (1984) suggested that there may be an adaptive ontogenetic trimming of body mass in terrapins during growth by a reduction in shell height and width. The data presented here for *M. caspica* agree with this prediction, which might be expected since a streamlined shell design would have advantages for a mobile swimmer. However the trend is less evident in female *M. caspica* where there is a retention of a more bulky shape. This appears to be a further adaptation (in addition to attaining greater absolute size) to increase fecundity. A high exponent (0.41) relating shell length to body mass has been found for *Emys orbicularis* (Meek, 1982) a species often sympatric with *M. caspica* and with a similar general appearance and life style (Arnold et al., 1978).

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GROWTH IN THE SMOOTH NEWT (*TRITURUS VULGARIS*) DURING THE AQUATIC PHASE OF THE ANNUAL CYCLE

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ABSTRACT

Growth during the aquatic phase of the annual cycle (measured as change in snout-vent length) was investigated in a natural population of smooth newts (*Triturus vulgaris*) at a pond in southern England in 1983. Two types of data were collected: growth at the population level (quantified as changes in mean snout-vent length) and growth in individual, recaptured newts. For the population as a whole, significant growth was detected during the aquatic phase. At the level of individual newts, rate of growth during this period was negatively correlated with snout-vent length at entry to the pond; such a relationship is common in the Amphibia. The average growth rate of adult newts observed during the present field study (1.1-1.5mm) agrees closely with an independent estimate (about 1.5mm) obtained during a previous, skeletochronological investigation (Verrell and Francillon, 1986).

INTRODUCTION

Despite the widespread occurrence and distribution of European newts in the genus *Triturus*, little is known about the growth of individual newts. A common assumption in the amphibian literature is that growth is indeterminate in these animals, but in many taxa, growth rate shows considerable individual variation, and body size is a poor predictor of individual age (see review by Halliday and Verrell, in press). The few published data which are available indicate that growth follows a similar pattern in the smooth newt, *Triturus vulgaris* (Hagstrom, 1977, 1980; Harrison, Gittins and Slater, 1984), the crested newt, *T. cristatus* (Hagstrom, 1977, 1980; Glandt, 1981), the alpine newt, *T. alpestris* (Smirina and Rocek, 1976) and the marbled newt, *T. marmoratus* (Caetano, Castanet and Francillon, 1985).

In the natural environment, growth can be measured at either the level of the population (by comparing the average body sizes of the same groups of animals at different times) and/or at the level of individuals (by marking and then recapturing known animals over time). The interval of time between episodes of measurement can be relatively short (within-years) or long (across-years). The best data for *Triturus* published to-date are for growth across, not within, years.

In a previous study (Verrell and Francillon, 1986), preliminary information on average annual growth rate in adult *Triturus vulgaris* was obtained during a skeletochronological investigation of the relationships between individual body size, age and investment in reproduction. In the present paper, field data are presented on growth in body size in a population of *T. vulgaris* visiting pond in southern England. Growth

is considered during the aquatic phase of the annual cycle, at both the population and individual levels.

METHODS

The study pond, near Soulbury, Buckinghamshire, has a surface area of approximately 120m² and is a deep, permanent pond situated on private farmland. It is a breeding site for smooth newts, crested newts, common frogs (*Rana temporaria*) and common toads (*Bufo bufo*).

From February 1983 to May 1984, the pond was completely encircled by a polythene drift fence, 25cm high and buried in the soil to depth of at least 5cm; plastic pitfall traps were sunk along the outside of the fence at intervals of about 8m. Every two or three days, smooth newts were collected from the pitfall traps and from the ground adjacent to the fence. The sex of each newt was recorded, together with its snout-vent length (SVL) measured to the nearest 0.5mm. Newts are notoriously difficult to measure when held in-the-hand, due to their frantic wriggling. The latter was reduced by suspending each newt up-side down by its pelvic area for a few seconds before SVL was measured. This appears to induce a quiescent state in the animals, resembling a condition known as tonic immobility. Individuals caught on the outside of the drift fence (i.e. entering the water) were marked by removing phalanges to show date of capture; each combination of phalanges removed was unique for a period of four days in duration (this method of marking was devised by Malkmus, 1980, during a study of *T. boscai* populations in Portugal). In addition, any characteristics such as limb deformities were noted, to aid in the identification of individuals at

recapture. After measurement and marking, all newts were released onto the opposite side of the drift fence to that on which they were caught.

In addition to this field-work, a laboratory study was conducted in order to determine the precision with which SVL can be measured. Seven adult smooth newts (two males and five females) were brought into the laboratory in 1984 and, over the course of two days, the SVL of each was measured to the nearest 0.5mm (as described above) on eight, randomly-assigned occasions.

RESULTS

Before considering the field data obtained during this study, it is pertinent to consider the precision with which SVL can be measured in adult smooth newts; few authors address the important issue of precision in morphometric studies (but see Bell, 1977; Lee, 1982). The results of the precision study conducted in the laboratory are summarised in Table 1, and indicate that SVL can be measured quite precisely. However, it should be noted that the margin of error of measurement (0.5-1.0mm) corresponds to the change in SVL recorded for the majority of newts recaptured in the field (see below). Two lines of evidence suggest that the changes in SVL of these recaptured newts were due to real growth and not mere error of measurement. First, as discussed below, no recaptured individuals showed a decrease in SVL in the interval between entry to and exit from the pond. Secondly, as shown in Table 1, 42 (75 per cent) of the 56 SVL measurements taken from the captive newts scored as 'same' within individuals. However, it is clear that data on apparent growth should be treated with some caution, especially if the precision of measurement is either low or unknown.

In 1983, I recorded the SVLs of adult *T. vulgaris* entering ($N=321$, March to June) and leaving ($N=176$, June to December) the study pond. Summary statistics of the SVLs of these two classes of newts are given in Table 2. Sexual dimorphism in mean SVL was not apparent for either class ($P>0.1$ for both intersexual comparisons, Student's *t*-test). Within 1983, mean SVL was significantly greater in adult newts leaving the water than in newts entering (for males, $t=2.8$,

$P<0.05$; for females, $t=4.15$, $P<0.01$, Student's *t*-test). These data indicate that, taking the adult newt population as a whole, both males and females increased in SVL by an average of 1-1.5mm during their period of residence in the water.

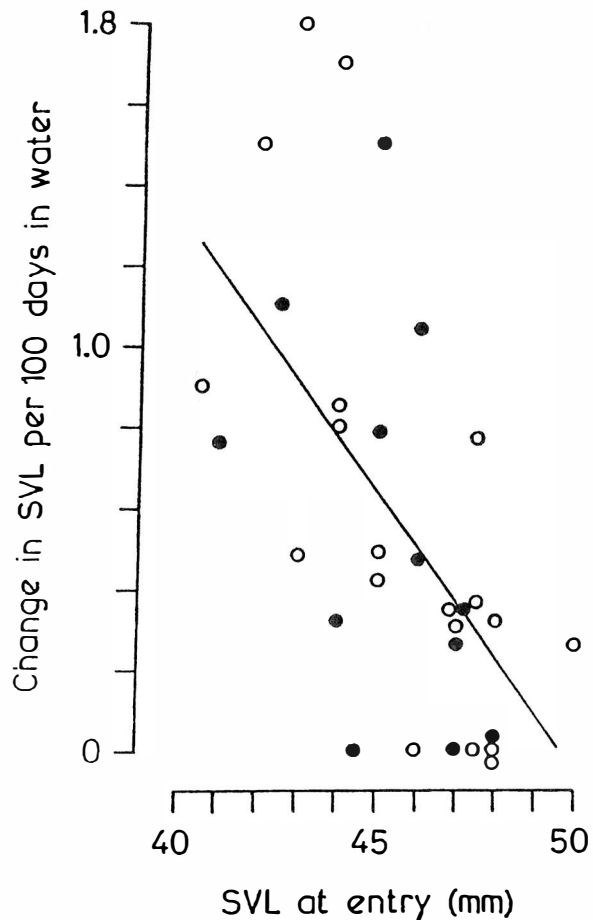


Fig. 1 Growth in 31 adult *Triturus vulgaris*, measured at entry to the study pond and recognised as individuals at exit from the pond; open circles are males ($N=19$), closed circles are females ($N=12$). Each circle represents change in snout-vent length per 100 days in water as a function of snout-vent length at entry to the pond. The regression equation is: $y = -0.139x + 6.88$. See text for further details.

Sex	Number of 'same' scores	Variance	Min	Max	Range
Male	6	0.140	40.0	41.0	1.0
Male	6	0.130	41.0	42.0	1.0
Female	6	0.071	41.5	42.5	1.0
Female	5	0.053	44.0	45.0	1.0
Female	7	0.030	46.0	46.5	0.5
Female	6	0.071	46.5	47.5	1.0
Female	6	0.053	50.0	50.5	0.5

TABLE 1: Number of 'same' scores, variances, minima, maxima and ranges for snout-vent length measurements taken on eight, randomly-assigned occasions from each of seven adult *Triturus vulgaris*. See text for further explanation.

Data on changes in SVL for individual smooth newts are available for 19 males and 12 females. These newts bore easily recognisable marks, and it proved possible to extract their individual SVL records at entry to and exit from the pond from the records for the population as a whole. The total amount of time that these newts spent in the water ranged from between 55 and 205 days (mean = 129 days). Seven newts did not change in SVL during their stay in the water, and no newts showed a decrease in SVL during this period, as mentioned above (such a decrease was observed by Glandt, 1981, who called it 'negative growth'). Twenty-four newts (77 per cent of the total) exhibited an increase in SVL during their stay in the water and of these, 19 (79 per cent) changed in SVL by either 0.5 or 1.0mm (as noted above).

These data for the 31 recaptured newts were then analysed in order to examine the relationship between growth rate and body size. As shown in Fig. 1, change in SVL per 100 days in the water was negatively correlated with SVL at entry to the pond ($r = -0.61$, $P < 0.001$). Mathematically, this relationship can be defined thus: Change in $SVL_{(mm)}$ per 100 days in water = $6.88 - 0.139 \cdot SVL_{(mm)}$ at entry. Growth rate was thus a decreasing function of body size, as predicted by the general growth model of von Bertalanffy (see Bertalanffy, 1957; Andrews, 1982). However, note that SVL at entry accounts for only 37.2 per cent of variance in growth rate.

DISCUSSION

It is clear from Table 2 that adult *T. vulgaris* increased in SVL by an average of 1.1mm in males and 1.5mm in females during that part of the annual cycle spent in water; previous work has revealed that, during this time, the newts both breed and feed (Verrell, 1985; Verrell and Halliday, 1985; Griffiths, 1986). These data, obtained for the population as a whole, mask considerable variability in the growth rates of individual newts. As shown in Fig. 1, growth rate was negatively correlated with SVL at the beginning of the aquatic phase of the annual cycle. Such a relationship seems to be common in the Amphibia (for anuran studies see Ryan, 1953; Jameson, 1956; Bellis, 1961; for urodele studies see Stebbins, 1954; Hendrickson, 1954; Taber, Wilkinson and Topping, 1975). It must be stressed that this relationship between growth rate and size cannot be taken as evidence for a similar relationship between growth rate and age. Despite the common assumption that growth is indeterminate in the Amphibia, there is now mounting evidence that body size is a poor predictor of individual age in these animals (see review by Halliday and Verrell, in press).

To my knowledge, the data presented in this paper are the first to document growth in SVL in a natural smooth newt population within a single year; studies of growth in the genus *Triturus* are few in number, and all are connected with growth across, not within, years. Many of the studies available have combined mark-release-recapture and skeletochronological methods to determine patterns of growth. In skeletochronology,

	Males	Females
Entry to pond	44.5±2.7 37.5 – 51.0 (N = 105)	44.2±2.7 37.0 – 52.5 (N = 216)
Exit from pond	45.6±2.7 38.0 – 50.0 (N = 81)	45.7±2.9 37.0 – 52.0 (N = 95)

TABLE 2: Summary statistics (mean ± standard deviation, range and sample size) of snout-vent measurements (mm) taken from male and female *Triturus vulgaris* caught entering and leaving the study pond in 1983. Statistical analyses of these data are presented in the text.

histological sections of long bones (either humerus or femur) are examined for 'lines of arrested growth'; these lines record periods when no bone growth occurs, such as winters in species living in temperate areas (see Smirina, 1972; Francillon, 1979, 1980; Gibbons and McCarthy, 1983; Francillon and Castanet, 1985). The number of lines of arrested growth in a bone should therefore record the age of the individual in years. Hagstrom (1977, 1980) has studied growth in populations of *T. vulgaris* and *T. cristatus* in Sweden. He found that, after the attainment of sexual maturity, growth rate slows and body size and age become poorly correlated; presumably, this reflects the diversion of resources from somatic growth to reproduction. In addition, rate of growth across years appears to decrease with body size. Similar data have been obtained by Glandt (1981) and A. Bielinski (unpublished data) for populations of *T. cristatus* in Germany and southern England, respectively.

I have no data on growth across years for the population described in this paper, largely as a consequence of phalangeal regeneration preventing the recognition in 1984 of newts marked in 1983. However, independent evidence obtained during a skeletochronological study of smooth newts revealed that, between the ages of two and six years, the mean annual change in SVL was approximately +1.5mm (Verrell and Francillon, 1986). This value is comparable with the average change in SVL observed between entry to and exit from the pond in the present study (Table 2). I tentatively interpret this similarity as indicating that most, if not all, growth in any one year occurs during the aquatic phase of the annual cycle (although physiological processes, such as the yolking of oocytes, continue during the winter: see Verrell, Halliday and Griffiths, 1986).

In summary, growth in SVL in *T. vulgaris* occurs during the time that the population spends breeding and feeding in the water; on average, males grow by 1.1mm and females by 1.5mm. These estimates mask considerable variation in the growth rates of individual newts; rate of growth is negatively correlated with body size. These field data were derived from a single

population studied over a relatively short period of time. There is considerable evidence that growth patterns in amphibians and reptiles vary over both space and time (e.g. Schoener and Schoener, 1978; Van Devender, 1978); thus, further research is needed in order to confirm that the growth pattern of *T. vulgaris* conforms to the pattern outlined above. A study in which a cohort of individuals of known age (such as newly-metamorphosed young-of-the-year) are marked and then frequently recaptured over long intervals of time would undoubtedly yield valuable information on growth in these animals.

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FOOD AND FEEDING RELATIONS OF COMMON FROG AND COMMON TOAD TADPOLES (*RANA TEMPORARIA* AND *BUFO BUFO*) AT A POND IN MID-WALES

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ABSTRACT

The guts of frog tadpoles in Llysdyman Pond, 1983, frequently contained detritus (partially decomposed macrophyte tissue) and other items associated with the pond's sediment (the tests of rhizopod protozoa, pollen grains, fungi), suggesting that the frog tadpoles fed directly on the sediment. The guts of toad tadpoles from Llysdyman, 1984, however, contained high frequencies of rotifers (*Keratella*) and motile algae (Dinophyceae) and little detritus, suggesting that the toad tadpoles fed mainly in mid-water. Evidence of both mid-water and sediment feeding was observed in samples of toad tadpoles from other ponds. Samples of frog tadpoles from other ponds, however, showed only the sediment feeding mode.

INTRODUCTION

As Altig and Kelly (1974) point out, feeding mechanisms in anuran tadpoles have been studied in considerable detail (e.g., Dodd, 1950; Savage, 1952; Kenny, 1969; Wassersug, 1972; Seale and Wassersug, 1979) but there is less detailed information concerning the food ingested either by common frog (*Rana temporaria*) or common toad (*Bufo bufo*) tadpoles. Data on the food taken by these tadpoles is confined mainly to the observations of Savage (1952) and Scorgie (1980). Although such studies give useful insights into the food taken by tadpoles, they are mainly qualitative and yield little information on the importance of the various items in the diet.

The aim of the present study, therefore, was to describe in a semi-quantitative way the food taken by frog and toad tadpoles in Llysdyman Pond, mid-Wales. The gut contents of tadpoles collected from several other localities in mid-Wales were also described. Together, these investigations give an insight into both the food of the tadpoles and also their modes of feeding, and suggest possible differences in feeding behaviour between frog and toad tadpoles.

METHODS

Samples of tadpoles were netted from Llysdyman Pond, Newbridge-on-Wye, mid-Wales (described in detail by Harrison, Gittins and Slater, 1983). Frog tadpoles were collected from 30.3.83 to 7.6.83 and toad tadpoles from 4.5.84 to 7.6.84 for examination of their gut contents. Direct yearly comparisons could not be made because toad tadpoles were not present in the pond in 1983 (due to high spawn mortality) and the frog tadpoles were present for a short period only in 1984 (due to habitat desiccation — Harrison, 1985).

Immediately following collection from the pond, tadpoles were preserved in 70 per cent alcohol. At a later date, 5mm of foregut from each tadpole was removed, mounted in a drop of water on a glass slide and examined microscopically. Inspection of the slides showed that many guts contained items which did not occur in discrete categories, such as filamentous green algae (which were present in filaments of just a few cells to very large colonies), and detritus, such as fragments of partially decomposed macrophyte tissue, which varied greatly in size. The usual numerical methods of analysis, therefore, were unsuitable (Hyslop, 1980). As an alternative the occurrence method was used. Here the number of guts containing a particular food category is expressed as a proportion of the total number of guts containing food. This method does not relate information concerning the numerical importance of items in the diet, nor on the contribution of each item to the bulk of the diet. It does, however, yield a crude quantitative picture of the most frequent types of food ingested by tadpoles.

In addition to the samples taken from Llysdyman Pond, the gut contents of small samples of frog and toad tadpoles from a number of other mid-Wales localities, collected during 1983 and 1984, were examined.

RESULTS

DIET OF FROG AND TOAD TADPOLES IN LLYSDYMAN

In total, 67 frog tadpoles and 80 toad tadpoles were taken from Llysdyman Pond. Many were very young tadpoles, at or just following the external gill stage (Gosner, 1960 stages 21-25) and showed little evidence of any ingested food material. The following analysis, therefore, is based on the guts of 34 frog tadpoles and 38 toad tadpoles which contained food. The range of

size (total length) in the samples was 14-43mm (frogs) and 12-18mm (toads).

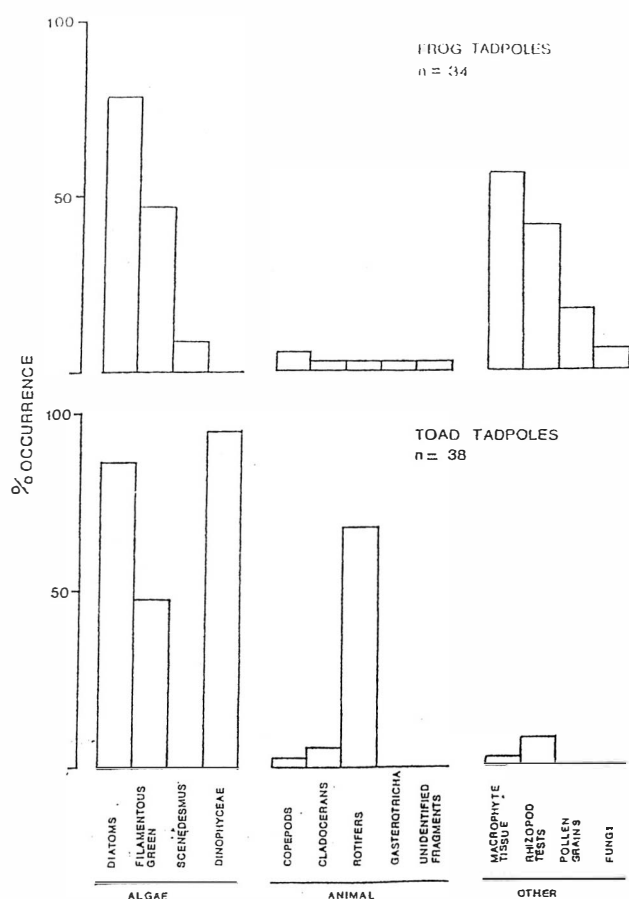


Fig. 1 Items recorded from the guts of frog tadpoles (from Llysdyndam Pond in 1983) and toad tadpoles (from Llysdyndam Pond in 1984).

Diatoms and filamentous green algae were observed frequently in the guts of both frog and toad tadpoles collected from Llysdyndam Pond (Fig. 1). Additionally, the frog tadpole guts frequently contained items associated with the pond's sediment (partially decomposed macrophyte tissue, tests of rhizopod protozoa, pollen grains, fungi) but rarely contained items usually present in mid-water (motile algae — Dinophyceae, planktonic rotifers — *Keratella*). However, the reverse trend was apparent in the sample of toad tadpole guts (Fig. 1). This difference in gut contents suggests that the frog tadpoles may have been feeding predominantly on the pond's sediment whereas the toad tadpoles fed mainly in mid-water.

DIETS OF TADPOLES FROM OTHER MID-WALES LOCALITIES

The gut contents of frog tadpoles from Royal Welsh Show Pond and Buftons Pond (Table 1) contained large amounts of detritus suggesting that the tadpoles were feeding mainly on sediment. This manner of feeding was also apparent in samples of toad tadpoles

from Dyfnant and Llandrindod Quarry (Table 1). The toad tadpoles from Builth Quarry, however, contained little detritus and were dominated by microscopic algae, indicating that they fed mainly in mid-water (Table 1).

DISCUSSION

Although the present study is based on small sample sizes and utilises only a semi-quantitative analysis of gut contents, the results indicated the presence of two modes of feeding in populations of frog and toad tadpoles: (1) feeding on the pond's sediment; (2) feeding on planktonic organisms in mid-water. Moreover, the data indicated that the mid-water feeding mode was more prevalent in populations of toad tadpoles (recorded in two of four populations sampled) than in frog tadpoles (not recorded). Further research is necessary to determine whether this trend is indicative of possible interspecific differences in feeding habits between frog and toad tadpoles, or merely reflects conditions in the study ponds at the time of sampling (high concentrations of micro-organisms, for example).

In common with most families of anuran tadpoles, Ranidae and Bufonidae possess the filter feeding apparatus which enables them to remove small particles from suspension, and also the keratinized mouth-parts allowing them to bite and scrape at surfaces (Savage, 1952; Kenny, 1969). Thus both species have the necessary morphology to perform both modes of feeding. Any possible interspecific differences in feeding habits, therefore, are likely to result from differences in behaviour rather than morphology.

The present study showed that detritus was a frequent component of the diet of the frog tadpoles in Llysdyndam Pond in 1983. Fragments of partially decomposed macrophyte tissue found in guts were typically large (mean length = 1.3mm, SD = 0.73, n = 21; maximum = 3.5mm) suggesting that such organic detritus formed an important constituent of the diet. The growth rate of the frog tadpoles in 1983 was 72.7mg per week (Harrison, 1985). The frog tadpoles diet, therefore, was evidently capable of supporting growth. Berrie (1976) suggested that animals which consume detritus are utilising the microorganisms attached to the detritus, which are an easily digestible high grade food, rather than the detritus itself.

The habit of ingesting large amounts of detritus was apparent in all three frog tadpole populations and in two of the four toad tadpole populations which were sampled by this study. Similarly, detritus was recorded in the guts of frog and toad tadpoles by both Savage (1952) and Scorgie (1980). It may be better, therefore, to describe sediment feeding tadpoles as opportunistic detritivores rather than herbivores.

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	Site	Size mean total length $\pm$ SE	Items Associated with Sediment	Algae	Animal	Possible Mode of Feeding
FROG TADPOLES	Royal Welsh Show Pond	33.0 $\pm$ 1.7 (n = 5)	Many inorganic particles	Diatoms Desmids <i>Scenedesmus</i>	None	On sediment
	Buftons Pond	39.6 $\pm$ 2.7 (n = 3)	Decomposed macrophyte tissue. Inorganic particles	Diatoms Chrysophyceae	Cladoceran	On sediment
TOAD TADPOLES	Dyfnant	19.2 $\pm$ 1.1 (n $\pm$ 4)	Many inorganic particles	Diatoms	None	On sediment
	Llandrindod Quarry	27.2 $\pm$ 0.6 (n = 5)	Many inorganic particles	Diatoms <i>Dinobryon</i>	None	On sediment
	Builth Quarry	22.2 $\pm$ 1.2 (n = 5)	Little detritus	Many algae Diatoms Chrysophyceae Dinophyceae <i>Scenedesmus</i> <i>Dinobryon</i>	None	In mid-water

TABLE 1: The gut contents, and possible modes of feeding, of frog and toad tadpoles from a number of sites in mid-Wales, collected in 1983 and 1984.

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FOOD CONSUMPTION, THERMOREGULATION AND ECOLOGY OF THE SKINK *CHALCIDES BEDRIAGAI*

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ABSTRACT

Chalcides bedriagai were found to live under rocks, mostly at body temperatures between 25-35°C, and were active between mid-March and mid-October. Population density (excluding juveniles) was 42 Ha⁻¹ in an abandoned field habitat, 990 Ha⁻¹ in the utilised sub-habitat. Larger females had more young (overall range 1-6 per year), but offspring size and relative clutch mass (mean 0.37) were independent of maternal size. Escape success was linearly related to substrate temperature (T_s), ranging from 0 at 17°C to 0.5 at 37°C. Pregnant females were found under rocks with higher T_s than other adults, and had reduced food intake. Food consumption of adults in summer was estimated from the production of urates as 12mg dry weight.g live weight⁻¹.day⁻¹. This is similar to that of a cool temperate lacertid and a tropical nocturnal gecko, but only half that of a warm temperate lacertid. Energy expenditure on hibernation, maintenance and activity was estimated from the annual temperature profile and values of metabolic rate. Estimates were also made for energy used in reproduction, growth and sloughed skins. The total annual budget suggested an average daily food intake only half of that estimated in summer, and half of that expected from a general relation for active lizards in warm climates.

INTRODUCTION

Although studies of the thermoregulation of lizards are common, the inconspicuous burrowing and litter dwelling forms have been neglected (Avery, 1982). This is even more true of energetics: despite the evolution of powerful (Nagy and Shoemaker, 1975) and simple (Avery, 1971) techniques of measuring food consumption there are still few data for lizards, and none for burrowing or semi-fossorial (living in litter or under rocks) forms. We took advantage of a convenient population of the semi-fossorial skink *Chalcides bedriagai* to obtain data on these points.

METHODS

SITE DESCRIPTION

The study was made in a 3.5 Ha area of abandoned vine fields at Calpe, Spain (41° N, 0° E) from July 1981 to September 1983. The sandy soil was divided into small fields by dry limestone walls, from which rocks had fallen which provided cover for the skinks. The area was completely enclosed, on two sides by hotels, by a major road and by the sea. 1.6 Ha of the area had been spoilt before the study by excavation of sand and

dumping of rocks, possibly as a foundation to building. This spoilage continued during the study, increasing during 1983. The long term prospects for the area, which appeared to be a prime site for hotel development, are doubtful.

The fallen rocks were mostly within 0.5m of the walls, the fields being occupied by old vines, a sparse (less than 5 per cent) cover of grasses and herbs, and a few low shrubs (*Cysticus* and *Thymelea* sp). Reproductive data is included from a few skinks in the nearby Jalon valley; these lizards were larger than those from Calpe.

THERMOREGULATION

The site was visited in all months from March to October inclusive (in different years), at all times of day. On each visit most of the rocks were turned over (and replaced). They were recorded into the categories large (>30cm greatest dimension), medium (20-30cm) and small (<20cm or <5cm thick). Substrate temperature (T_s) was measured in the soil under every rock where a skink was found, and a sample of others from each size category. The skinks were always just under the rocks, sometimes partially buried in the soil but always partly visible. On many occasions we stirred up soil under rocks, but did not locate any skinks in this way.

Body temperatures (T_b) were measured by a 0.5mm diameter thermistor probe inserted into the cloaca within 30s of capture. T_b of juveniles could not be measured. In July 1981 the thermal environment was studied intensively, so that the T_s under rocks of each size could be described in 1.5 hour periods throughout the day in both sunny and changeable weather (Rose, Pulford and Hailey, MS).

ECOLOGY

Lizards were measured snout-vent length SVL and tail length, and weighed with a Pesola scale to 0.1g. They could not be sexed repeatedly, even by probing for hemipenes (females may have a sac in this region, as do *C. ocellatus*; Wilson, 1984), nor could regenerated tails be reliably differentiated from complete ones.

From June to August 1983 all lizards were retained in 10cm plastic petri dishes at room temperature (21–28°C) for seven days, and the faeces and urates produced were collected. The lizards were given water twice during this period. Afterwards those thought to be pregnant were kept in 15 x 10cm sandwich boxes with 2cm of sandy soil at room temperature, and fed on wild crickets until the young were born. Mothers and young were weighed within 12 hours of birth. In view of the site development the skinks were transported elsewhere: this enabled a trap-out density estimate to be made.

ENERGETICS

Food consumption was estimated from the production of faeces and urates after Avery (1971). Ten lizards (4.7 ± 1.0 g (SD)) were kept in 15 x 10cm plastic arenas in a cage heated to 28–30°C by a 60W light for 10 hours a day, falling to 20°C at night. They were fasted for seven days, then fed small mealworms at different constant rates for 14–20 days. The lizards were then kept for seven days at temperatures fluctuating between 20 and 25–28°C, and the faeces and urates produced were collected. This was done three times, with three week intervals of feeding on wild insects in a large cage between trials.

Faeces and urates were dried in a desiccator and weighed to 0.1mg. The faeces produced during and after each of the three feeding trials were pooled, powdered, and the energy content was determined with a Phillipson micro bomb calorimeter (two pellets for each trial). A sample of mealworms were dried at 70°C, powdered, and their energy content determined. Absorption efficiency ((consumption-faeces)/consumption) of energy and of dry weight was calculated for mealworms.

Absorption efficiency was also measured for hard-bodied prey, woodlice. Ten lizards were kept in a 50cm diameter plastic arena, with a lamp for thermoregulation 10 hours a day and folded paper shelters. They were fed woodlice for ten days, uneaten food and faeces being collected daily. Faeces were collected for ten days after feeding. Woodlice and faeces were dried, powdered, and their energy content measured as above.

RESULTS

ECOLOGY

Several trips round the site revealed no lizards in mid-March (1982 and 1983) and late October (1982). Fig. 1 shows the sizes of lizards captured between these periods, with the growth curve estimated from them. Lizards with SVL under 45mm formed a distinct group and were termed juveniles in the field, and it is probable that this size is reached in the July after birth. Lizards of SVL 45–55mm formed a less distinct group, termed subadults; 55mm is probably reached in the second July after birth. Thereafter there were no distinctions, and all were termed adults. Lopez-Jurado, Jordano and Ruiz (1978) recognised four size groups in a field study of this species.

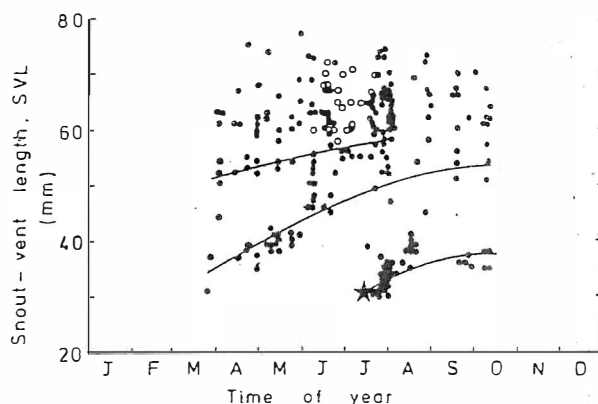


Fig. 1 Sizes of *Chalcides bedriagai* recorded during the annual activity period, with estimated growth curves. The star shows the mean size at, and date of, birth. Open circles are pregnant females.

Without dissection, the only way to distinguish the sexes was in the reproductive season when females were pregnant. Thirty-seven adults were captured in June and before 18 July 1983 (when the first juvenile was seen), and 21 of these later gave birth, suggesting an even sex ratio with breeding every year. Pregnant females had a mean SVL of 68mm, range 57–75mm (two pregnant females from Jalon measured 73 and 84mm).

Offspring size was independent of maternal size (Fig. 2). Mean offspring size was 0.423g (SD = 0.056, correlation with maternal SVL $r = 0.26$, $n = 47$, $P > 0.05$) and 30.4mm (SD = 1.3, $r = 0.16$, $n = 49$, $P > 0.05$). These sizes are similar to those given by Salvador (1981). The number of young increased with maternal size (Fig. 3a), the regression being

Number of young = $0.114 \text{ SVL (mm)} - 5.2$
($n = 22$, $F = 18.7$, $P < 0.001$).

The mean number of young was 2.15 per female (2.41 including the two females from Jalon). Relative clutch mass RCM was calculated as total offspring weight/maternal weight after birth (Shine, 1980). This was independent of female size (Fig. 3b);

$$\text{RCM (\%)} = -0.343 \text{ SVL (mm)} + 60$$

($n = 20$, $F = 0.73$, $P > 0.5$).

Mean RCM was 37 per cent (SD = 11). After birth of the young, females were on average 0.99g lighter than when they were captured, and they produced on average 1.04g of offspring. Thus the females plus young did not increase in weight during the time the female was in captivity. Females ate the placentae after birth. There was no relationship between time in captivity and mean weight of offspring ($n = 20$, $F = 1.2$, $P > 0.25$).

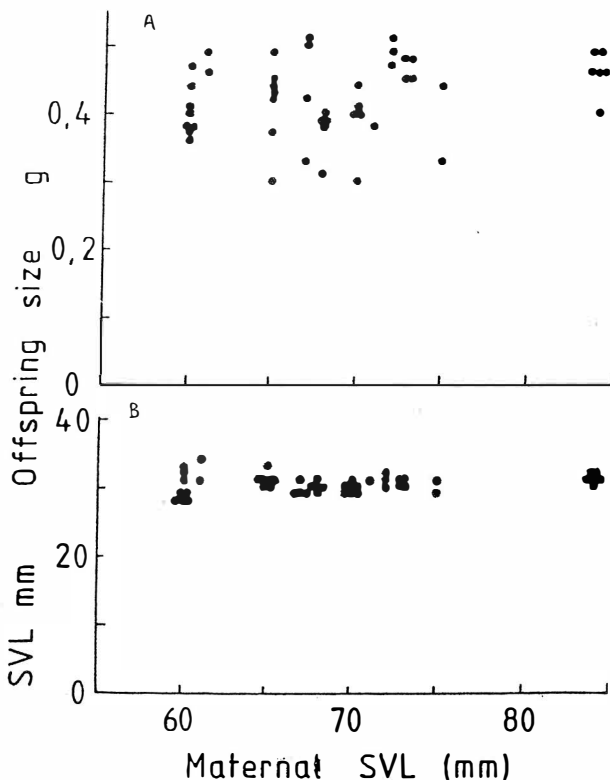


Fig. 2 Independence of (a) offspring weight and (b) offspring length with maternal size.

The trap-out estimate for adults and subadults in this closed population is shown in Fig. 4. This is the intercept of the regression on the abscissa in Fig. 4b (Southwood, 1978), which is 79. This is similar to the minimum population size (the number removed), 77. The crude density (Odum, 1959) was thus 42 lizards Ha^{-1} in the undisturbed 1.9 Ha of the site, similar to densities reported for other small skinks (Turner, 1977; Barbault, 1983). The lizards only used the rocks in the areas around the bases of the walls, extending for about 0.5m on each side of the wall. The ecological density (Odum, 1959) was therefore much higher,

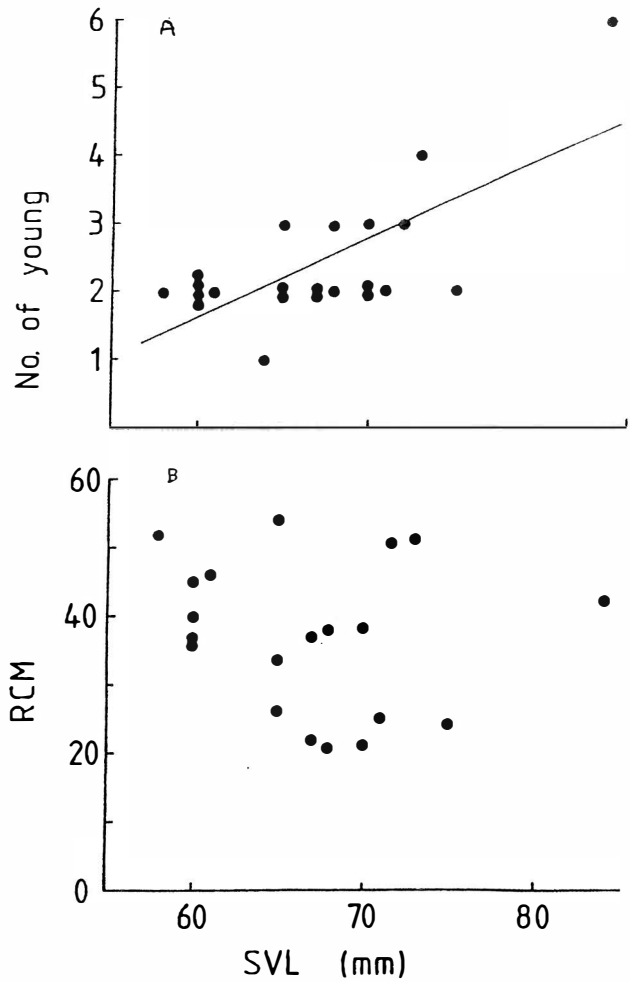


Fig. 3 Relations between maternal size and (a) number of young and (b) relative clutch mass (%).

990 Ha^{-1} in the 0.08 Ha of their base-of-wall habitat (calculated from an area 0.5m on each side of the wall).

ENERGETICS

The weight dependence of production of faeces and urates in the seven days after capture (pregnant females excluded) was described by the equations

$$F = 6.76 W^{1.00 \pm 0.19} \quad (n = 59, r^2 = 0.33, P < 0.01) \quad (1)$$

$$U = 3.98 W^{0.66 \pm 0.13} \quad (n = 59, r^2 = 0.31, P < 0.01) \quad (2)$$

where F and U are dry weights of faeces and urates respectively in mg and W is live weight in g. Hard parts identified in the faeces included the remains of beetles, woodlice, spiders, cockroaches (a small wild species), and orthopterans. The 0.66 exponent for urates is similar to the 0.65 for standard metabolic rate of *C. ocellatus* (Bakker and Andrews, 1984).

Pregnant females produced less faeces and urates than other lizards (Fig. 5). The smallest pregnant female weighed 2.19g; the mean weight-specific production (with SD) of faeces and urates of all lizards of this weight or more was

	Pregnant ($n = 21$)	Non-pregnant ($n = 32$)
Faeces mg.g^{-1}	4.1 (2.4)	9.1 (5.6)
Urates $\text{mg.g}^{-0.66}$	2.9 (1.8)	4.7 (2.3)

As the variability increased with the mean in these data, they were log transformed for t tests. The non-pregnant and pregnant means were significantly different for both faeces and urates ($t = 3.80$ and 3.18 , $P < 0.001$ and $P < 0.01$, respectively).

$F = 0.33 C - 0.9 \quad (n = 30, r^2 = 0.47, P < 0.01) \quad (3)$
 $U = 0.15 C + 4.5 \quad (n = 30, r^2 = 0.35, P < 0.01) \quad (4)$
where C is dry weight of mealworms consumed per day (all quantities in mg). The correlation between U and C was not increased by taking account of body weight (i.e. using U expressed as either mg.g^{-1} or $\text{mg.g}^{-0.66}$, rather than mg), presumably due to the small size range of lizards used in these trials. The dry weight, energy content and absorption efficiencies (AE) of mealworms and woodlice were

	mealworms	woodlice
Dry matter (%)	34	33
Energy (KJ.g dry W ⁻¹)	23	15
AE energy (%)	92	91
AE dry weight (%)	85	81

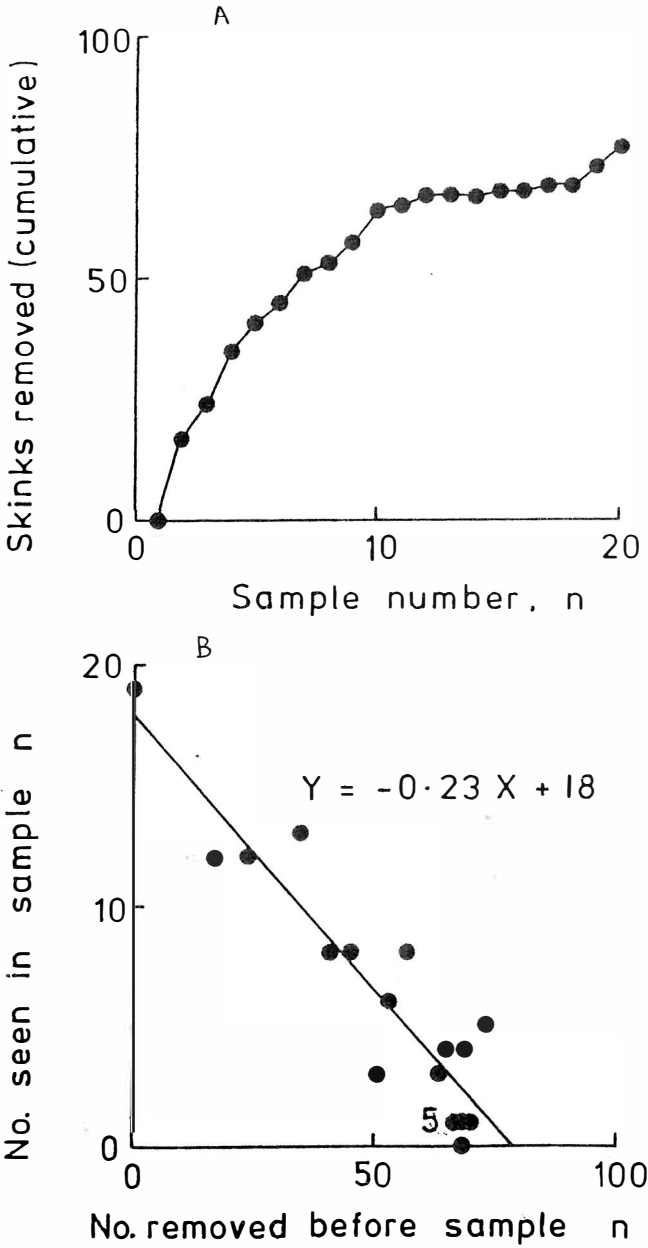


Fig. 4 A trap-out estimate of the total population size of adults and subadults in the study area. (a) The cumulative number of skinks removed in each visit to the site. (b) The relation between the number seen on each visit and the number removed prior to that visit. The regression fit is shown, which estimates the population size as 79 (the intercept on the x axis). The group labelled 5 has five superimposed points.

The production of faeces and urates in seven days after feeding were related to food consumption by the regression equations

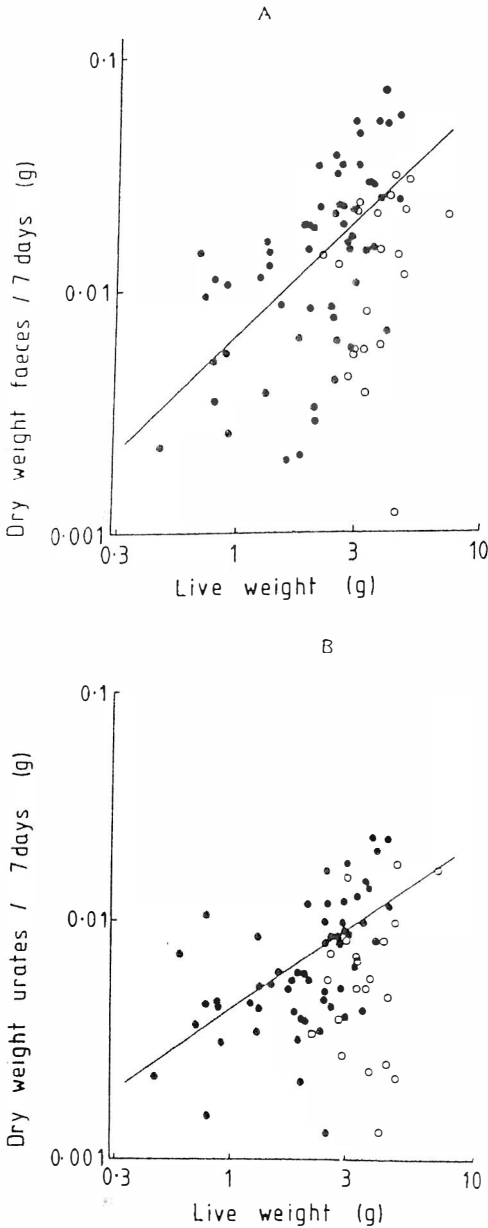


Fig. 5 The relationship between live weight and (a) faeces and (b) urates produced in seven days after capture, all log scales. Open circles are pregnant females. Regression fits (excluding the pregnant lizards) are described in the text.

During one of the feeding trials (a total of about 44 skink-weeks including the FU collection period) eight shed skins were removed from the plastic arenas. This suggests that the lizards shed approximately every 4.5 weeks. Six dried skins had a mean weight of 44mg (SD = 17).

THERMOREGULATION

98 per cent of all lizards were found beneath rocks. In addition they may have inhabited the walls themselves. The open areas were too hot to be used in summer ($T_s > 55^\circ\text{C}$), and were always exposed. Bushes covered a very small area compared to the rocks. Body temperatures were similar to the T_s under the rock from which the lizard came (Fig. 6, $r = 0.89$). The regression of T_b on T_s was significantly different from $T_b = T_s$ (ANCOVA $P < 0.05$), but the differences between T_b and T_s were small ($< 4^\circ\text{C}$) and easily attributable to warming in the hand. The small size and overlapping anal scales of this species made rapid measurement of T_b difficult. As the lizards spent much of the time beneath rocks and at the same temperature as the soil under them, description of under-rock T_s will provide a good guide to the T_b s experienced by *C. bedriagai*.

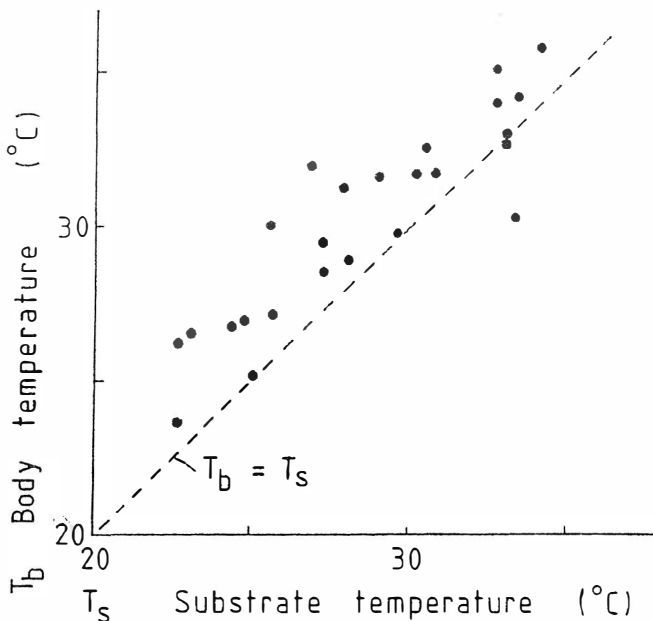


Fig. 6 The relationship between body temperature and the temperature of the substrate under the rock where the lizard was found.

The thermal niche of *C. bedriagai* is shown in Fig. 7. This is the proportion of times spent at different T_s (and by implication T_b), and is used both in the calculation of metabolic costs (below) and in interpretation of temperature-performance relations (Hailey, in prep.) Fig. 7a,b shows T_s experienced during the night and day, respectively, from data on T_s at different times of day in each month, and assuming a linear fall in T_s at night. Substrate temperatures from rocks under which

adult and subadult lizards were found are shown in Fig. 7c. This is a less good measure of their thermal niche during activity, since sampling was not evenly distributed over the yearly and daily activity period. Mean and SD these T_s are 28.5 and 4.22°C ($n = 250$).

Substrate temperatures selected by pregnant females are compared with those selected by other adults from 7 June to 20 July. Mean T_s of the pregnant females, 31.2°C , SD = 3.84, $n = 21$ was significantly different from that of the other adults, 28.0°C , SD = 3.20, $n = 20$ (t test, $P < 0.01$). T_s selected by juveniles are compared with those selected by adults and subadults in the period after the birth pulse (5 July to 1 September). There was no significant difference: juveniles mean 30.2°C , SD = 3.92, $n = 72$; others mean 29.5°C , SD = 3.57, $n = 94$ (t test, $0.3 > P > 0.2$).

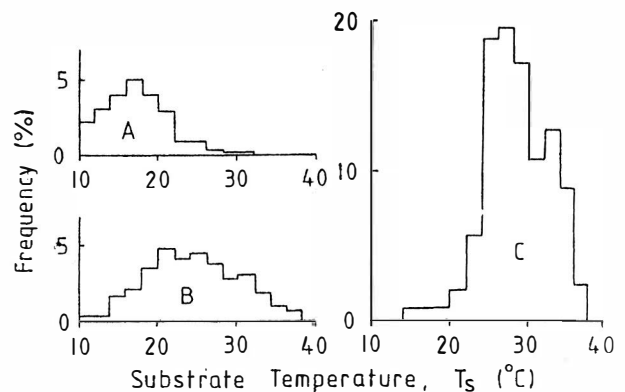


Fig. 7 Frequency distributions of T_s . (a) Activity season, night. (b) Activity season, day. (c) All rocks under which a lizard was found (all daytime).

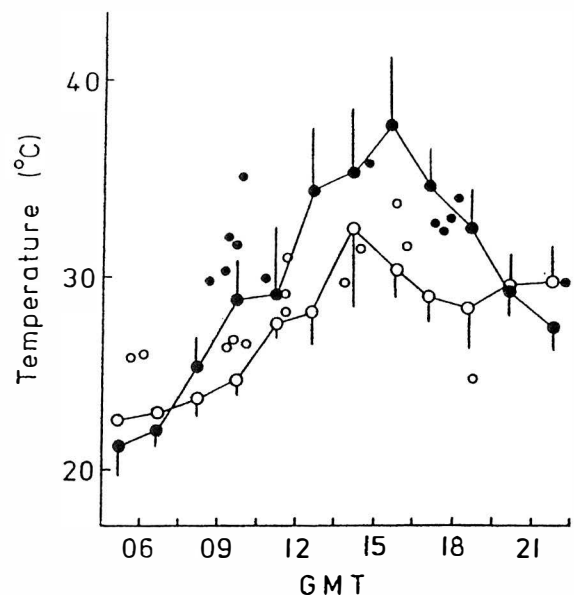


Fig. 8 The effect of weather on environmental and body temperatures at different times of day in July. Dots are for sunny days, open circles for days with broken cloud cover. Small symbols are T_b s, large joined symbols are mean T_s (+ or - 1 SD).

Fig. 8 shows the effect of weather on the thermal environment and T_b s in July. In changeable weather T_s were significantly lower than on sunny days, and all observed T_b s were lower than those found at similar times on sunny days. Mean T_b recorded on sunny July days was 32.6°C , significantly different from the mean of 29.1°C for changeable days (F test, $P < 0.001$).

Pregnant females captured early in June gave birth after those captured later in the season, so that the date of birth was dependent on the time that the female had been in captivity (Fig. 9a). This could be an artifact, since females giving birth early could not have been in captivity as long as those giving birth later. The dotted line in Fig. 9a shows the earliest possible birth date for any period in captivity, i.e. points could not occur below this line. The absence of data in this area does not seem responsible for the correlation observed, suggesting that it is a real phenomenon.

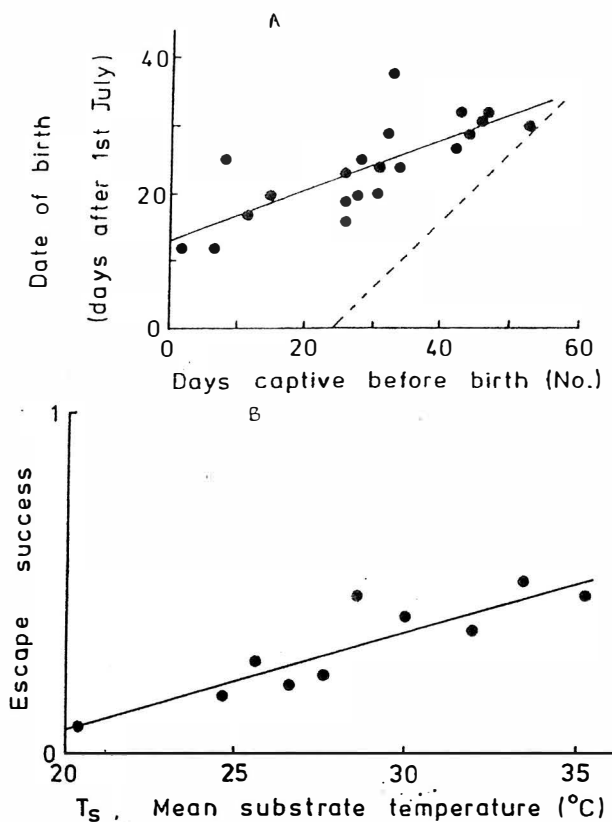


Fig. 9 Two probable thermal effects. (a) Pregnant females held for longer in captivity (at lower T_b than they would experience in the wild) gave birth at a later date than those held for shorter periods. The dashed line shows the earliest date of birth for each period in captivity. (b) The temperature dependence of escape success. Each point is the mean T_s and escape success of 25 lizards.

This is probably a thermal effect, since the females were kept at a lower temperature (daytime maximum $25\text{--}28^\circ\text{C}$) than they would have experienced under rocks (mean 31.2°C). The regression for the relationship between time in captivity and date of birth (days after 1 July) was:

Date of birth = 0.37 days in captivity + 13 ($n = 21$, $F = 26.3$, $P < 0.001$). This predicts that the mean birth date in the wild in 1983 was 14 July.

The similarity of T_b to T_s allows an unusual opportunity to estimate the T_b of the lizards that escaped as well as those that were captured. The effect of temperature on escape success (number which escaped/number encountered) can thus be shown in the wild (Fig. 9b). The 250 recorded T_s for adults and subadults were ranked and divided into ten successive groups: the mean T_s and escape success were then calculated for each group. The regression fit is

$$\text{Escape success} = 0.029 T_s - 0.50$$

($n = 10$, $F = 30.1$, $P < 0.001$). This predicts that at 17°C and below all lizards would be captured, and that at the maximum observed T_s (37°C) about half would escape.

Fig. 10 shows habitat selection in terms of the sizes of rocks occupied at different times of year: lizards preferred larger rocks in summer. The association between rock size and month is significant (September and October combined, G test, $P < 0.001$). This is probably because the soil under the smaller rocks became too hot, although there may have been additional effects of humidity or food investrebrates. On sunny days in July maximum T_s was reached in the 15.00-16.30 GMT periods: the means ($^\circ\text{C}$, with SD) for different rock sizes were

Small	41.0 (1.1)
Medium	38.3 (2.7)
Large	34.0 (2.1)

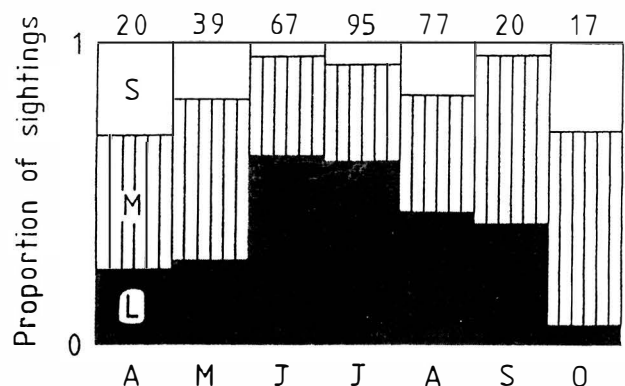


Fig. 10 Habitat selection (small, medium or large rocks) in different months. Numbers show the sample size for each month.

DISCUSSION

ECOLOGY AND THERMOREGULATION

The thermal relations observed during July were very similar to those found by Lopez-Jurado, Jordano and Ruiz (1978) in a study of this species on Tabarca Island, Alicante Province. Body temperatures of 72 'active' lizards on Tabarca were in the range $24\text{--}35^\circ\text{C}$, mean 30.5°C ; at Calpe, July T_b s were in the range $23.6\text{--}35.8^\circ\text{C}$, mean 30.6°C . The mean T_s of eight refuges was 28.1°C on Tabarca; T_s of 125 rocks under which skinks were found at Calpe was 29.8°C ($\text{SD} = 3.6$).

Lopez-Jurado et al (1978) also noted a close correlation between T_b and T_s . This repeatability of results suggests that the thermal relations of *C. bedriagai* have been accurately described.

There is some doubt, however, about the habits of this species and the level of thermoregulation it can achieve. Salvador (1974) suggested that *C. bedriagai* is usually only active in the early morning, when it sets out on a food search, then spends the rest of the day in its hiding place. Lopez-Jurado et al (1978) note that T_b is greater than T_s between 06 and 10 h, and that T_b is independent of air temperature: they suggest that *C. bedriagai* basks in the morning.

Observations at Calpe suggest that this lizard is very seldom active on the surface, and forages under rocks throughout the day. All those disturbed under rocks were alert, rather than sleepy as observed at night in captivity. We found no direct evidence of basking in the field at any time, and attributed the elevation of T_b above T_s to warming during measurement. It is possible that skinks select the warmest position under an individual rock. It is admitted, however, that skinks basking near a rock would be inconspicuous and may retire under it before discovery. This type of basking has been seen in *C. ocellatus* (Coborn, 1981), although this species seems to be more active above ground than *C. bedriagai* (Arnold and Burton, 1978). On two occasions a skink from under a cool rock moved faster than it was expected to from previous experience, and this may be evidence for basking. It is unlikely that *C. bedriagai* spend long periods basking in the wild as they will in captivity, but possible thermoregulation must be taken account of in the calculation of metabolic expenditure.

Pregnancy has been found to affect thermoregulation other skinks (Shine, 1980), though as an increase in basking rather than by selection of microclimate. The latter is probably less costly in terms of the time which has to be used thermoregulating, and in the risk of predation. However, another 'cost' of reproduction, reduced food intake, is high in *C. bedriagai* (below).

FOOD CONSUMPTION

Two independent estimates may be made of the food consumption of a 4.7g *C. bedriagai* (the mean size of animals used in the calibration of F and U production) in summer, based on faeces and urate production, respectively. The weight-specific amount of faeces and urates produced by non-pregnant adults, 9.1 mg.g⁻¹ and 4.7mg.g^{-0.66} respectively convert to 43mg faeces and 13mg urates for a 4.7g lizard. These values would be expected from food consumption of 133 and 57mg dry weight. day⁻¹ from equations 3 and 4, respectively.

Estimates of faeces and urates produced by a 4.7g lizard from equations 1 and 2 (32 and 11mg, respectively) are lower. This is because the regressions are for log-transformed data, in which the effect of the high values is reduced (Sokal and Rohlf, 1981).

Two factors may contribute to the estimate from faeces being higher than that from urates.

- (a) Lizards in the field may ingest sand and dirt with their food, which will pass into the faeces: lizards in clean arenas do not have this problem. This is likely in *C. bedriagai* which lives in sand; Bosca (1880) noted particles of sand in the gut.
- (b) Natural prey may be less easy to digest than mealworms. This may have two effects. Firstly, if the food takes longer to digest, there will be more in the gut at any time. If the gut is evacuated during the seven day period, more faeces will be produced from material with a long passage time. Secondly, if there are hard parts which cannot be digested then more faeces will be produced from a given amount of food (Avery, 1978). This is also likely in *C. bedriagai*, which has previously been found to take at least 50 per cent of prey having hard exoskeletons (beetles) or mineral armour (woodlice) (Table 1). The important measure here is the efficiency of producing faeces, i.e. (100-AE). This was 15 per cent for mealworms and 19 per cent for woodlice on a dry weight basis, which would cause an estimate from faeces to be 25 per cent greater than one from urates.

The value 57mg dry weight.day⁻¹ from urates is thus preferred. This may be compared to estimates for other lizards using this technique, all calculated for a 4.7g lizard (summer or dry season values, mg dry weight.day⁻¹):

<i>Lacerta vivipara</i>	68	(Avery, 1971)
<i>Podarcis muralis</i>	95	(Avery, 1978)
<i>Hemidactylus brookii</i>	46	(Avery, 1981)

Thus food intake of *C. bedriagai* is similar to that of the active cool temperate *L. vivipara* and the tropical nocturnal sit-and-wait *H. brookii*. It is only one half that of the active *P. muralis* from an area of similar climate.

In order to make the estimate of food consumption comparable with a wider range of data for lizards, it may be converted to utilisable energy, using the value 21 KJ.g dry weight⁻¹ for energy content of small invertebrates and an assimilation efficiency of 90 per cent (Turner, Medica and Kowalewsky, 1976). This gives a 4.7g *C. bedriagai* a utilisable energy intake of 1.08 KJ.day⁻¹ in summer, similar to the 1.11 KJ.day⁻¹ calculated for a 4.7g lizard from equation (29) of

	Beetles	Woodlice	Spiders	Other	N
Valverde (1967)	56	19	11	14	73
Mellado et al (1975)	35	22	20	23	40
Seva and Escarre (1976)	47	4	15	34	338

TABLE 1: Published analyses of the diet of *Chalcides bedriagai*. Values are the percentage of N prey items.

Turner et al. (1976). This equation was, however, based on data for average daily intake throughout the active season.

The effect of reproduction on food intake was estimated from the weight-specific production of faeces and urates by pregnant females, 4.1 mg.g⁻¹ and 2.9 mg.g^{-0.66} respectively. These give estimates of food intake of 61 and 24 mg dry weight.day⁻¹ for a 4.7 g lizard, respectively 46 per cent and 42 per cent of the calculated intake of a non-pregnant lizard of this size.

Part of this reduction might be an artifact of the weight of the young, if these did not contribute to maternal production of faeces or urates. This effect would be greatest if the young were of maximum size, when it would lead to an estimate only 73 per cent (1/1.37) of the real value. The observed reduction is twice as large as this, suggesting that it is real.

ENERGY BUDGET

An estimate of annual energy turnover in an adult *C. bedriagai*, comparable to the data used by Turner et al (1976), may be made from estimates of expenditure on respiration and production.

The cost of respiration is estimated from the body temperature profile and the metabolism-temperature relationship. Values of standard metabolic rate SMR are from Patterson and Davies (1978): over the interval 5-37°C SMR increases exponentially with temperature according to the equation

Log SMR = 0.0431 T + 0.88 (5) (Hailey, in prep.) where SMR is in μlO₂.g⁻¹.h⁻¹ and T is °C. Over the activity T_b range 20-37°C active metabolic rate AMR is related to temperature by

Log AMR = 0.0335 T + 1.83 (Hailey, in prep.) giving a mean factorial scope for maximum activity of 4.7 times (range 4.1 at 30°C to 5.9 at 20°C).

The cost of maintenance was estimated from the T_s profiles in Fig. 7, equation (5), and the conversion 1 ml oxygen consumed = 20 J (Morrison and West, 1975) (Table 2). The frequency distribution of under-rock T_s in the hibernation period (not shown) was extrapolated from values in October, December and March.

Two estimates were made of the cost of daytime maintenance:

- 1) Using the daytime T_s profile (Fig. 7b).
- 2) Using the T_s profile for rocks under which lizards were found (Fig. 7c).

The former is a minimum estimate, and assumes that the lizards do not thermoregulate under any

conditions. The latter is a maximum estimate, and assumes that under any conditions the lizards can reach a preferred body temperature of 25-35°C (distribution 7c is not significantly different from temperatures selected in a thermal gradient — Hailey, in prep.).

Estimating the extra cost of activity depends on the T_b profile during activity, and the value of routine factorial scope. Three activity T_b profiles have been used, 1) and 2) as for maintenance above, corresponding to diurnal activity with minimum or maximum thermoregulation, respectively. A third T_b distribution was added:

- 3) Combining the T_s profiles of Fig. 7a and 7b, including night T_s > 20°C and excluding day T_s < 20°C.

This takes account of the 20°C minimum voluntary temperature for activity (Hailey, in prep.), and includes crepuscular or nocturnal activity where T_s is high enough.

Routine scope in lizards has been measured as about 2.5-3.5 times SMR during the activity period:

<i>Sceloporus occidentalis</i>	2.5-3.1	(Bennett & Nagy, 1977)
<i>Cnemidophorus murinus</i>	3.4	(Bennett & Gleeson, 1979)
<i>Sceloporus graciosus</i>	3.1	(Congdon & Tinkle, 1982)

Turner et al (1976) used a value of 2.5 in their model; here, following Congdon, Dunham and Tinkle (1982), estimates are given for different values between 1.5 and 3.5 (Table 3). A value in the middle of this range may be most realistic in view of the low scope for maximum activity in *C. bedriagai* (4.7 compared to a mean of about 8 for lizards in general — Kamel and Gatten, 1983).

The cost of producing sloughed skins was estimated as: 0.22 skins per week over a 31 week annual activity period, each skin weighing 44 mg, energy content 23.4 KJ.g⁻¹. The latter value is from sloughed snake skins (Smith, 1976). This comes to 7.0 KJ year⁻¹ for an adult *C. bedriagai*.

The cost of reproduction was estimated from the RCM of 37 per cent and an energy content of the young of 5 KJ.g live weight⁻¹, totalling 8.7 KJ.year⁻¹ for a 4.7 g lizard. In addition there will be a cost associated with development of the young. This may be estimated for the viviparous skink *Sphenomorphus quoyii*, from the chemical composition of the egg and embryo at the start and end of development (Figs. 3d and 5e of

	Hibernation	Night	Day (1)	Day (2)
% of year	41	23	35	35
Mean T _b (°C)	10.1	17.4	24.4	28.5
Mean SMR (μl.g. ⁻¹ .h ⁻¹)	21	47	105	146
Maintenance (KJ.year ⁻¹)	7.3	9.1	30.3	42.1

TABLE 2: Estimates of annual maintenance costs of a 4.7g. *C. bedriagai* from standard metabolic rate and temperature profiles. The two estimates of daytime maintenance (1,2) are from the temperature profiles in Fig. 7b and 7c, respectively (see text).

Thompson, 1981), plus values for the energy content of fat, protein and carbohydrate (Dowgialls, 1975). In *S. quoyii* an average egg contains 7.4 KJ at the start of development, and the offspring contains 5.7 KJ. Thus 1.7 KJ is used during development, 30 per cent of the energy content of the offspring when born. Applying this to *C. bedriagai*, a 4.7g female would spend 2.6 KJ.year⁻¹ on the young for their development, and their total cost would be 11.3 KJ.year⁻¹.

Expenditure on growth of a 4.7g adult lizard may be given minimum and maximum estimates. The former is zero growth, 0 KJ.year⁻¹. The latter is that it will grow to the maximum observed size of 6.3g, with the 1.6g of new tissue having an energy content of 5 KJ.g⁻¹, giving 8.0 KJ.year⁻¹.

These components of the annual energy budget are listed in Table 4, and give an estimate of utilised energy of 81-171 KJ.year⁻¹ for a 4.7g *C. bedriagai*. This large range mostly results from uncertainty about the annual cost of activity, particularly the value for routine factorial scope; this has much more effect than

differences between differences between temperature profiles (Table 3). In view of the low scope for maximum activity in *C. bedriagai*, a routine scope of about 2.5 seems likely, giving an annual cost of activity of about 52 KJ.year⁻¹. Using mean values for the other components, the annual energy utilisation of a 4.7g *C. bedriagai* is 126 KJ.year⁻¹.

This energy must be obtained during the 31 week activity period, giving utilisable energy intake of 0.58 KJ.day⁻¹. This is only 54 per cent of the estimated 1.08 KJ.day⁻¹ utilisable food intake in summer, probably reflecting reduced food intake during cool weather, and during pregnancy. 0.58 KJ.day⁻¹ is 52 per cent of the utilisable intake estimated for a 4.7g lizard from the equation of Turner et al (1976), which is also for average daily intake over the activity season. This data was mostly for lizards of active habits (except *Anolis*, *Sauromalus* and *Egernia*) from warm climates (except *L. vivipara* and *L. agilis*). Thus average daily utilisable energy intake of *C. bedriagai* is only half that expected for an active diurnal lizard from a warm climate.

Temperature profile	Routine factorial scope				
	1.5x	2.0x	2.5x	3.0x	3.5x
1 Daytime T _s	15	30	45	61	76
2 Observed T _s	21	42	63	84	105
3 All T _s >20°C	16	31	47	63	79
Mean	17	34	52	69	87

TABLE 3: Estimates of the annual cost of activity of a 4.7g *C. bedriagai* from different values of routine scope and temperature profiles. Values are KJ.year⁻¹.

		KJ.year ⁻¹	Range	%
Respiration,	Hibernation	7		5
Respiration,	Maintenance, night	9		7
Respiration,	Maintenance, day	36	(30-42)	29
Respiration,	Activity	52	(17-87)	41
Respiration,	Reproduction	3		2
Production,	Skin	7		5
Production,	Reproduction	9		7
Production,	Growth	4	(0-8)	3
Total		126	(81-171)	

TABLE 4: Estimates of annual energy budget components for a 4.7g *C. bedriagai*.

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SHORT NOTE:

DIURNAL SPAWNING BEHAVIOUR IN THE NATTERJACK TOAD *BUFO CALAMITA*

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INTRODUCTION

Reproductive behaviour in the natterjack toad *Bufo calamita* is primarily a nocturnal activity, unlike the more diurnal common toad *B. bufo*. Spawning has occasionally been recorded in bright sunshine (Beebee, 1983) but the factors influencing such events have not been reported. Whilst investigating the population dynamics of this species at the Ravenglass dunes nature reserve it was noticed that diurnal spawning occurred more frequently at the beginning of the spawning season. Therefore during 1983 and 1984 attempts were made to quantify this observation and to relate it to climatic conditions prevalent at that time of year.

METHODS

The breeding pools were monitored on a regular basis, and the number of fresh spawn depositions recorded. The number of pairs still engaged in spawning behaviour during the day were also recorded. Water temperature data were obtained by placing a max-min thermometer at the edge of the most important spawning pools, with the results being gathered daily where possible. As this was not always attainable further climatic data (air temperatures) were obtained from the local meteorological station — Eskmeals. Statistical methods were carried out according to Bishop (1980) and Bailey (1983).

RESULTS

During both years diurnal spawning did occur, with some pairs still engaged in this activity at 15.00 hours on 18.4.1984. Fig. 1 shows that this behaviour was restricted to the beginning of the spawning season. Maximum temperatures at this time were low, but as they increased so the number of daytime spawnings decreased. Although similar data for 1983 were less complete, no natterjacks were observed spawning after 25.4.1983. On those days when water temperature data were available, combining the results for both years, there was a significant negative correlation between the percentage of spawn strings laid diurnally each day, and the maximum water temperature for the previous day ($r = -0.842$, $df = 13$, $P < 0.001$ (after arcsin transformation)). There was no such relationship with minimum water temperatures for the night on which spawning occurred ($r = 0.182$, $df = 13$, $P > 0.1$).

DISCUSSION

Diurnal spawning only occurred at the beginning of the spawning season, and was clearly related to low maximum water temperatures of the previous day. A likely scenario would seem to be that the males gathered around the breeding pools before water temperatures became warm enough to permit calling. At this site males arrive at the breeding pools some time before calling commences. During 1983 the first males were present on day 76, 20 days before the first calling was heard (unpublished personal observations). Reproductive behaviour is dependent on water temperatures and in Poland Kowalewski (1974) stated that spawning did not occur when water temperatures were below 14°. At the start of the season the water temperature on an evening was just warm enough to allow calling for a short period, attracting a few females to the pool. After the animals paired up water temperatures dropped rapidly, preventing any further calling or spawning activity. The resulting pairs of toads were therefore unable to spawn until the following day when water temperatures began to rise again. Fig. 1 indicates that four days after the start of the 1984 spawning season maximum air temperatures increased greatly allowing spawning to be completed during the night.

There are advantages in breeding as early as possible, and at this site a majority of the females spawn at the beginning of the season (Banks and Beebee, 1986). Natterjack breeding sites are typically ephemeral (Beebee, 1979), and so the earlier the spawn is laid the greater the chances of the tadpoles metamorphosing before the pool desiccates. This advantage is partially offset by an increase in the risk of fungal infestation, which is more virulent during periods of cool weather (Beebee, 1979). In addition to this the adult toads themselves may suffer a greater risk from diurnal predators. On the north-west coast of England disembowelment by sea-birds has been reported to be a common cause of mortality to adult natterjacks during the spring (Beebee, 1979). This form of predation may be greater for pairs of natterjacks spawning during the day, as during early morning the torpid pairs of toads in their typically shallow unvegetated pools would be easy prey.

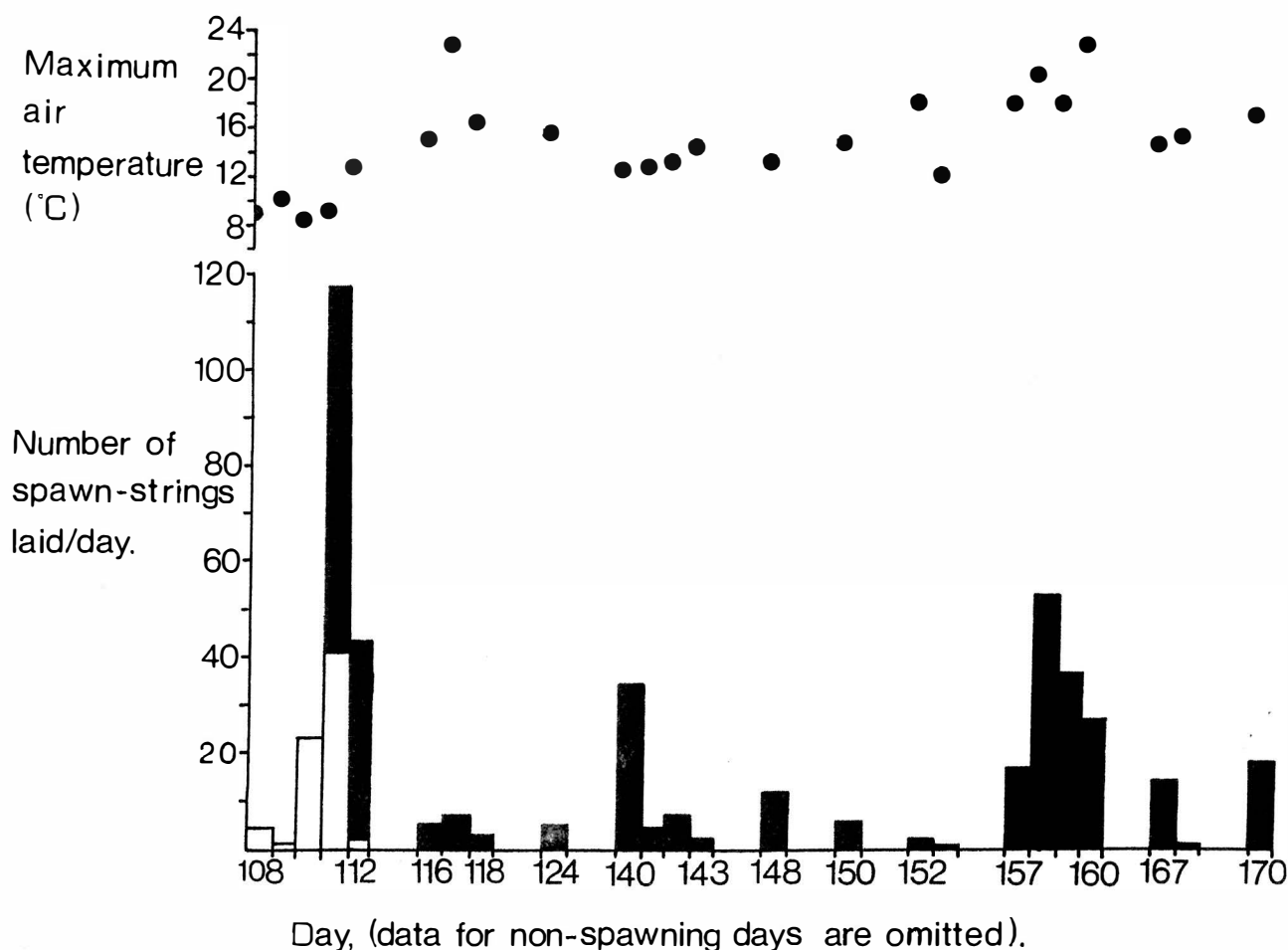


Fig. 1 Frequencies of diurnal and nocturnal spawning by *B. calamita* in relation to maximum air temperatures.

■ Number of nocturnal spawnings.

□ Number of diurnal spawnings.

● Maximum air temperatures.

Day number = day of the year, i.e. day 108 = 18.4.1984.

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SHORT NOTE:

BIONOMICS OF THE ROCK GECKO *CYRTODACTYLUS SCABER* IN QATAR

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INTRODUCTION

Whilst Visiting Professor to the University of Qatar during March and April, 1986, I took the opportunity on a number of evenings to walk around the grounds of the Doha Sheraton Hotel, where I was staying, in order to determine the population density of the nocturnal rock geckos (*Cyrtodactylus scaber*) there, and to ascertain the extent to which this species might be territorial. It was immediately apparent that the animals were only to be found in anything but negligible numbers on certain illuminated concrete paths between the flower beds of the garden, and on the walls of the north-eastern corner of the hotel, which were floodlit.

POPULATION DENSITY

Numbers were assessed using the modified version of the standard capture/recapture method (based upon recognition of individual lizards in the same places on different evenings) that I employed in a study of *Agama agama* at Nsukka, eastern Nigeria (Cloudsley-Thompson, 1981a). A sketch map of the area to be monitored was made, and the positions of the geckos marked on it daily, with notes of recognisable characters such as sizes, postures, and broken tails. A single specimen of *Hemidactylus flavicaudis* which appeared about 6m up the hotel wall approximately every other evening, was not counted. The results obtained were as shown in Table 1 (n = 12):

	On the walls (40m)	On the paths (210m)
Mean ($\pm$ SE)	4.8 $\pm$ 0.65	3.6 $\pm$ 0.45
Maximum observed at one time.	9	8
Maximum calculated on recognition (after 24 h)	10	24

TABLE 1: Summary of observations.

The area monitored nightly comprised some 40m of wall and 210m of pathway. Although occasionally seen at higher elevations, the geckos on the walls of the hotel were nearly always within 3m of the ground — as noted by Arnold (1984), most of whose records were

less than 0.5m from the ground. It was therefore assumed that the area of walls, with the narrow flower beds at their bases, represented approximately 120m². The paths were about 2.5m in width, and the beds between them not more than 4m wide. I therefore calculated that the area of pathways and flower beds surveyed comprised 210 x 4.5 = 945m². The maximum density of geckos on the walls was therefore about 83ha⁻¹. These figures compare with maximum densities of 78.3ha⁻¹ on walls, and 40ha⁻¹ on paths of *A. agama* at Nsukka (Cloudsley-Thompson, 1981), and of 16.2ha⁻¹ and 56.7ha⁻¹ on walls and paths respectively at Ibadan, Nigeria (Harris, 1964).

The similarity in the population densities of *C. scaber* and *A. agama* is remarkable, especially when the crudity of the method adopted for measuring lizard numbers is taken into consideration. Since *A. agama* is a much larger species than is *C. scaber*, however, the biomass of the former must be considerably greater. Differences between the densities of *A. agama* in Nsukka and Ibadan were tentatively ascribed to the fact that there are no vultures at Ibadan, although kites are plentiful, whereas hawks are scarce and hooded vultures numerous in Nsukka. It was postulated that vultures may be less efficient predators of *A. agama* than are hawks and kites (Cloudsley-Thompson, 1981a). *C. scaber* appeared to feed entirely upon insects: I saw both moths and beetles taken. Furthermore, insects are really the only potential food for lizards foraging on walls, and I never saw geckos feeding upon vegetable matter as *A. agama* frequently does.

The geckos began to appear punctually at sunset each evening. On 7 April, for instance, the first geckos were seen; both in the garden and on the walls of the hotel, at 18.08h (local time), 12 min after the Maghreb (sunset) prayer time — before the floodlights were switched on (at 18.13h), and while the animals could easily be seen by the light of the setting sun. By 16.20h it was completely dark, and a total of 14 geckos was then counted. Unusually few geckos were initially observed on evenings when the wind was blowing strongly but, later on, they came out in larger numbers — especially on the walls of the hotel.

TERRITORIALITY

On two occasions only were any of the geckos seen closer to each other than 1m and on one of these a baby, no longer than 3.5cm, was involved. It seems, therefore, that like *Tarentola annularis* (Cloudsley-Thompson, 1972), *Hemidactylus brookii* (Cloudsley-

Thompson, 1981b) and *Tarentola mauritanica* (Cloudsley-Thompson, 1984), *C. scaber* exhibits Stamps' (1977) Type 3 spacing pattern.

DAY-TIME REFUGES

During the daytime, *C. scaber* was found in irrigated oases and agricultural stations underneath rocks and in the axils of palm fronds. Presumably they passed the day in similar situations in the grounds of the Doha Sheraton, but I felt that destruction of the ornamental trees in the interests of herpetology would not be regarded with approval by the hotel authorities. The rocks were all rather small and I did not discover any geckos beneath them.

SUMMARY

Maximum densities of *C. scaber* recorded in Doha were 83ha⁻¹ on walls, and 25ha⁻¹ on pathways. These compare with densities of *A. agama* of 78.3 and 16.2ha⁻¹ on walls, and of 40 and 56.7ha⁻¹ on pathways at Nsukka and Ibadan respectively. *C. scaber* exhibits Stamps' (1977) Type 3 spacing pattern.

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SHORT NOTE:

NOTES ON THE DIETS OF SOME LIZARDS IN THE STATE OF QATAR

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INTRODUCTION

The diet of free-living lizards has been recorded by numerous authors (Angelov, et al. 1966; Itamies and Koskela, 1971; Sadek, 1981; Quayle, 1983; Arnold, 1984). In contrast, relatively little has been published about the diet of lizards of the Arabian desert (Arnold, 1984). Qatar State is a Peninsula, projecting in the north western central coast of the Arabian Gulf. It is an extension from the Arabian Peninsula measuring exactly 11, 437km². The land is mostly pale desert approaching sea level in most places, and the highest peak is 103m above sea level (Clavelier, 1970).

The present work records the diet of 10 lizard species from 4 families. The diet was determined by analysis of alimentary canal contents.

MATERIALS AND METHODS

100 lizards were collected from the desert and from areas of lush vegetation comprising plantations and gardens, virtually all of which were dependent on artificial irrigation. These lizards were collected during August and September 1985. The alimentary canal contents were extracted and stored in 90 per cent ethanol. They were analysed under 120X, 140X and 400X magnifications. The formula of Quayle (1983) was used to calculate the percentage of prey in each category, for every lizard species. The percentages have been rounded off to the nearest whole number.

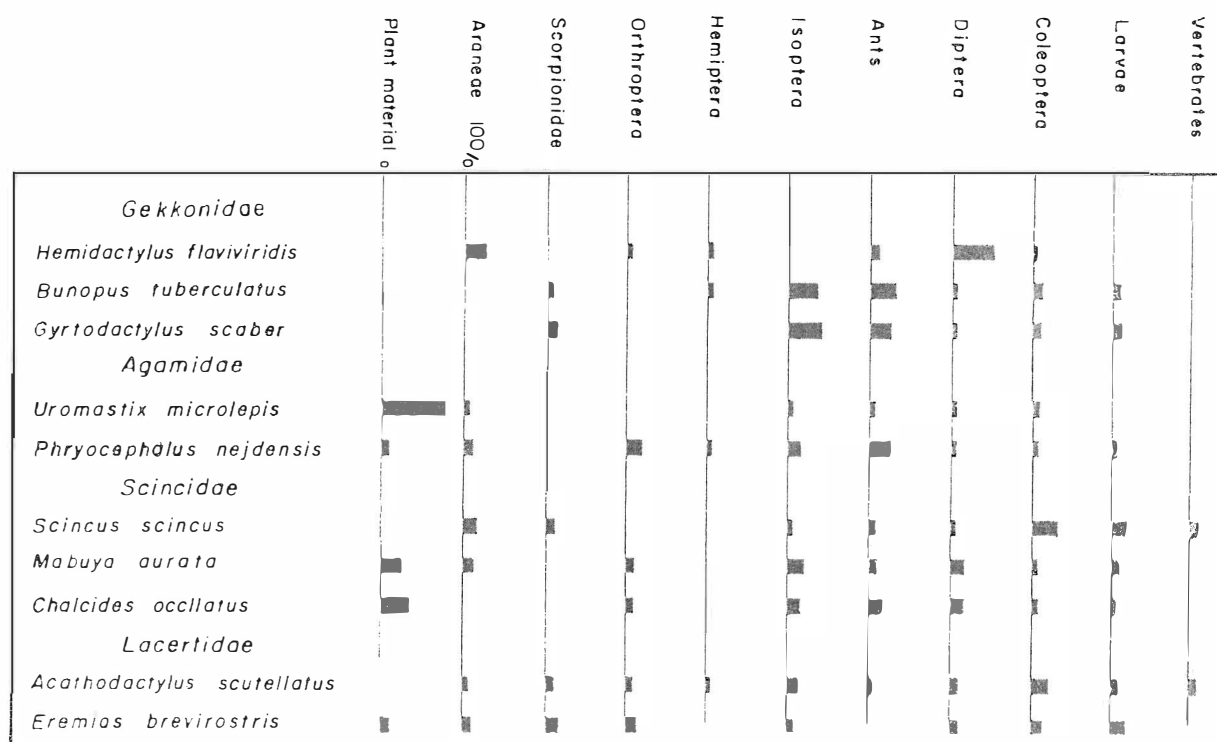


TABLE 1: The percentage of prey in each category for every Qatari lizard species. Every column is based on the average of 10 individual lizards.

RESULTS

The results are given in Table 1, which shows these percentages. The diet of all the species is largely or entirely made up of a wide variety of arthropods, apart from *U. microlepis* and *C. ocellatus* which also ingest significant amounts of plant material. *S. scincus* and *A. scutellatus* were found to have eaten small vertebrates but at the same time had taken substantial quantities of beetles and insect larvae. On the other hand, of the nocturnal geckos, *H. flaviviridis* ate the highest proportion of Diptera, while *B. tuberculatus* and *G. scaber* consumed high proportions of ants and termites. Lepidopterus scales were found among the stomach contents of most species but no identifiable fragments were observed.

DISCUSSION

Of the Gekkonidae, *B. tuberculatus* and *G. scaber* were found mainly under stones whilst *H. flaviviridis* frequented the walls of buildings. These behavioural differences were reflected in their diets, the former species eating mainly Isoptera and ants while *H. flaviviridis* ate mostly flying insects and spiders. Ecological differences between *B. tuberculatus* and *G. scaber* were not apparent in this study since both species were found together and ate similar food. Differences may be apparent in other parts of their range. In the eastern United Arab Emirates, Arnold (1984) showed that *B. tuberculatus* is superficially like *C. scaber* and probably resembles it in many aspects of its ecology, but *C. scaber* lives in moist places. Also, unlike *Bunopus*, it climbs on rocks and walls. When disturbed, it runs rapidly to hide in holes or vegetation.

The remainder of Qatari lizards are day-eating species. Only three of them ate larger quantities of

plant material viz. *U. microlepis*, *C. ocellatus* and, to lesser degree *M. aurata*. *P. nejdensis*, which inhabits regions of gravel, ate more Orthoptera, Isoptera and ants while *S. scincus*, *A. scutellatus* and *E. brevirostris* ate more larvae and Coleoptera. This may reflect their natural distribution in rocky and sandy areas. In general, therefore, it can be seen that, although there is some selection of food materials, the diets of most species is influenced by the fauna of their normal habitats- and other words, they are opportunistic feeders.

ACKNOWLEDGEMENTS

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THE HERPETOLOGICAL JOURNAL

Volume 1, Number 4

June 1987

CONTENTS

Mini-Review

- | | | |
|--|-----------------|-----|
| Sex determination and sexual differentiation in reptiles | W. H. N. GUTZKE | 122 |
|--|-----------------|-----|

Full Papers

- | | | |
|---|------------------------------------|-----|
| Effect of exogenous testosterone on the epidermal glands of <i>Hemidactylus flaviviridis</i> | N. B. CHAUHAN | 125 |
| Aspects of the population ecology of <i>Mauremys caspica</i> in North West Africa | R. MEEK | 130 |
| Growth in the smooth newt (<i>Triturus vulgaris</i>) during the aquatic phase of the annual cycle | P. A. VERRELL | 137 |
| Food and feeding relations of common frog and common toad tadpoles (<i>Rana temporaria</i> and <i>Bufo bufo</i>) at a pond in mid-Wales | J. D. HARRISON | 141 |
| Food consumption, thermoregulation and ecology of the skink <i>Chalcides bedriagai</i> | A. HAILEY, C. A. ROSE & E. PULFORD | 144 |
| <i>Short Notes</i> | | |
| Diurnal spawning behaviour in the natterjack toad <i>Bufo calamita</i> | B. BANKS & T. J. C. BEEBEE | 154 |
| Bionomics of the rock gecko <i>Cryodactylus scaber</i> in Qatar | J. L. CLOUDSLEY-THOMPSON | 156 |
| Notes on the diets of some lizards in the state of Qatar | M. B. H. MOHAMMED | 157 |