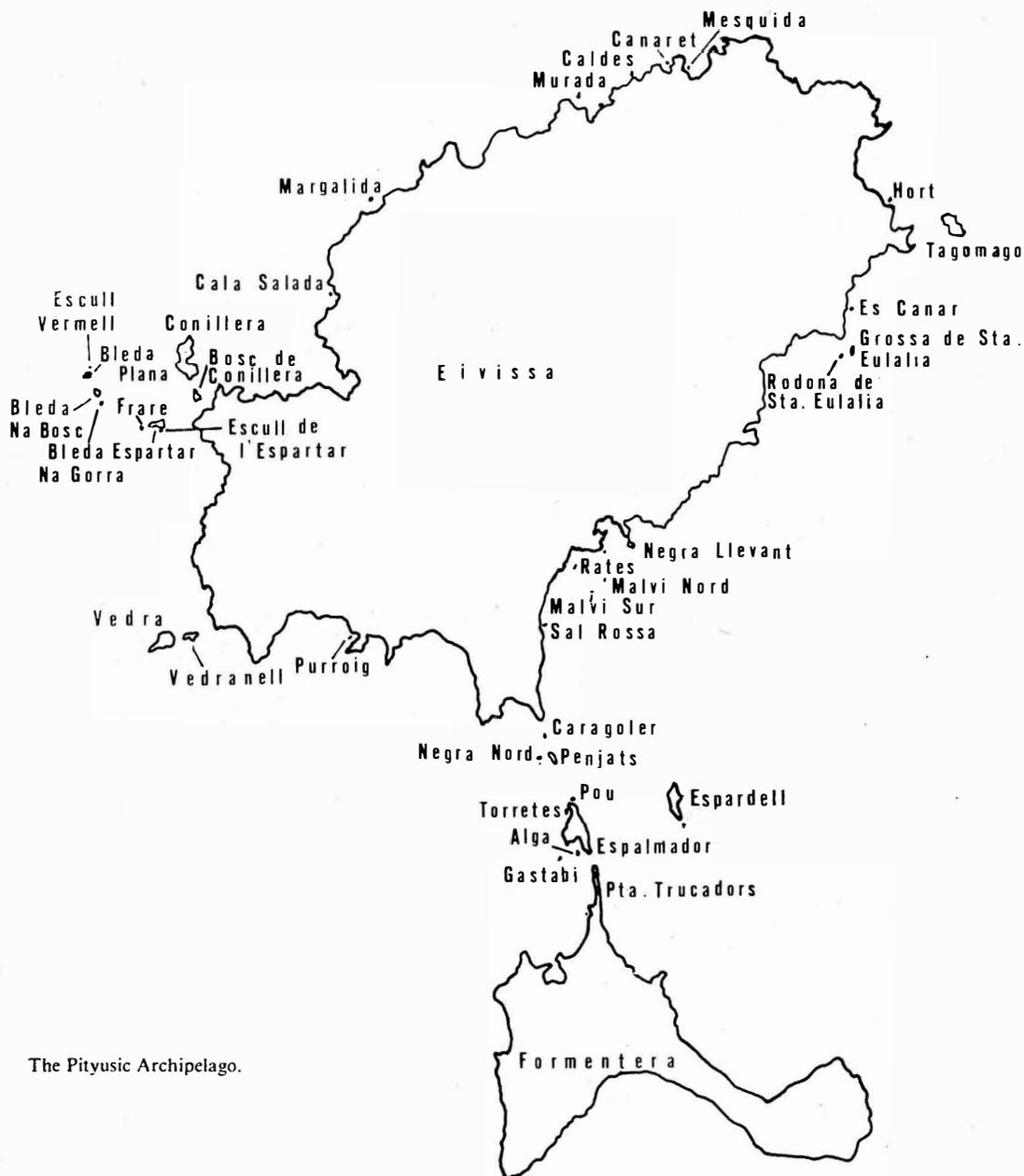


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ANNOUNCEMENTS

APPLICATIONS PUBLISHED IN THE BULLETIN OF ZOOLOGICAL NOMENCLATURE.

Case 2684 *Haplocanthosaurus* Hatcher, 1903 (Reptilia, Saurischia): proposed conservation

Spencer G. Lucas & Adrian P. Hunt

New Mexico Museum of Natural History, P.O. Box 7010, Albuquerque, New Mexico 87194, U.S.A.

Abstract. The purpose of this application is the conservation of the Jurassic dinosaur name *Haplocanthosaurus* Hatcher, 1903 by suppression of the unused senior objective synonym *Haplocanthus* Hatcher, 1903.

Case 2691 *Atheris* Cope, 1862 (Reptilia, Serpentes): proposed conservation, and proposed confirmation of *Vipera chlorechis* Pel, [1851] as the valid name of the type species

Donald G. Broadley

Natural History Museum, Centenary Park, Selborne Avenue, Bulawayo, Zimbabwe

Abstract. The purpose of this application is to conserve the name *Atheris* Cope, 1862 for a genus of African tree or bush vipers. It is threatened by the unused senior subjective synonym *Chloroechis* Bonaparte, 1849. The name of the type species of *Atheris*, *Vipera chloroechis* Schlegel, 1855, is a junior subjective synonym of *V. chlorechis* Pel, [1851], and the valid specific name of the type species is thus *chlorechis* and not *choroechis*.

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POPULATION ECOLOGY AND CONSERVATION OF TORTOISES: DEMOGRAPHIC ASPECTS OF REPRODUCTION IN *TESTUDO HERMANNI*

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ABSTRACT

Female *Testudo hermanni* at Alyki, northern Greece were sexually mature at a mean straight carapace length of 150mm, based on the frequency of finding eggs by X-ray or oxytocin injection during the nesting season. Oxytocin-induced egg laying behaviour is described. Egg width ($r = 0.49$), shape ($r = -0.32$) and weight ($r = 0.30$) were all significantly related to body size. Hatchling wet weight was strongly related to egg weight. Hatchlings of *T. hermanni* were lighter than those of *T. graeca* and *T. marginata* in terms of dry weight/egg weight. This pattern reflects the low energy content of *T. hermanni* eggs, and is possibly a consequence of the use of more productive habitats by this species. Clutch size and clutch mass were weakly related to body size; reproductive potential declined in the largest females. Simple and stratified calculations gave similar estimates of the total reproductive potential of adult females in two populations at Alyki. There were, in round numbers, 250 adult females on the main heath producing 1,700 eggs per year, and 65 adult females on the salt works heath producing 450 eggs per year. Nest predation was low at Alyki, judging from the rarity of destroyed natural nests. This was confirmed by burying chicken eggs to stimulate tortoise nests. About 90 per cent of nests probably remain undisturbed during the incubation period.

INTRODUCTION

Reproduction in chelonian species is known to vary between geographic regions (Tinkle, 1961), populations (Gibbons and Tinkle, 1969), individuals (Turner, Hayden, Burge and Roberson, 1986) and years (Schwarzkopf and Brooks, 1986). Information about reproduction used in a study of population dynamics should therefore be drawn from that population, and should cover as large a range of individuals and years as possible. We have previously (Hailey and Loumbourdis, 1988) compared reproduction of the three species of tortoise in Greece, including three separate populations of *T. hermanni*. The aim of the present study was to describe reproduction in more detail in one of these populations (Alyki in northern Greece), as part of a continuing study of tortoises at that site.

METHODS

FIELD OBSERVATIONS

The Alyki site has been described by Stubbs, Swingland, Hailey and Pulford (1985). Data from the whole site are pooled in this study. Females collected for X-ray examination or for oxytocin treatment were mostly from the salt works heath and the northern end of the main heath (sectors 1, 2, 3, 4, 7 and 10). These were the areas of highest population density, and had convenient enclosures where tortoises could be collected together.

General handling techniques have been described by Stubbs, Hailey, Pulford and Tyler (1984). Apart from urine, which is usually lost on handling, the body weight of a female tortoise may be increased by mature eggs, developing follicles and gut contents. The following measures are used here; *Field weight* is the gross weight of a tortoise as measured in the field. *Body weight* is the net weight of a female after laying a clutch of eggs, but including any developing follicles and gut contents. Note that a third measure (*cleaned soma weight*, excluding eggs, follicles and gut contents) is more appropriate for discussion of reproductive effort (Hailey and Loumbourdis, 1988).

OXYTOCIN-INDUCED EGG-LAYING

Eighty two individual females ranging from 139-198mm SCL were collected on eight days between 15 May and 1 June 1986. On each occasion the tortoises were found in the morning and the early evening, and held in a shaded empty drinking trough in sector 2, or in overturned skips in the salt water heath — the latter were transferred to disused rain collecting pans before oxytocin injection. A 1ml ampoule containing 5 IU oxytocin in saline (G. A. Pharmaceuticals) was diluted in a 5ml ampoule of 0.9 per cent sterile saline. Each tortoise was given an intramuscular injection of about 1.5 IU.kg⁻¹ between 18:00 and 19:00 local time. Tortoises laid their eggs on the floor of the arena, the first after about 20 minutes. Eggs were removed immediately, and labelled with pencil. The tortoises were released in the sector of capture in the

late evening, two hours after oxytocin treatment. Seven females were recaptured after 1-2 weeks and given a second oxytocin treatment.

Ninety seven females ranging from 113-207mm SCL were collected on nine days between 18 May and 1 June 1988. They were collected throughout the activity period, and held in a shaded trough or disused water tank before transport to Thessaloniki for X-ray analysis (below). Tortoises were kept for one to three nights in the arenas, which were liberally supplied with vegetation for shelter; those kept for a whole day or more were fed with tomatoes. Tortoises shown to have eggs by X-ray were placed in cleaned arenas and injected with undiluted oxytocin in saline, at a dose of about 3 IU.kg⁻¹, at either about 11:00 or 18:00 local time; the other tortoises were released immediately. The time of injection was noted for each tortoise, as were the times of each egg laid, all to the nearest minute. Tortoises were released 30 minutes after laying all the eggs identified by X-ray; rectal temperatures of some females were measured after egg-laying with a mercury thermometer.

X-RAY EXAMINATION

Tortoises were taken to Thessaloniki for X-ray examination, with the 70kv Atomscope portable X-ray generator used previously (Hailey and Loumbourdis, 1988), but with different film (loose Kodak X-Omat S 18 x 24cm films, cat. 501 6704). Machine power was reduced to 20mA, and exposure time increased to 5s. The generator was 70cm above the film, which was held in a standard X-ray-transparent metal cartridge. Two tortoises were placed side by side on each film.

The presence of two animals and the longer exposure time gave more chance of movement during the exposure, and so each tortoise was immobilised by wrapping plastic parcel tape around the carapace to cover the legs. One tortoise of each pair was identified by placing a key or paper clip next to it. Tortoises were kept in wooden cages in Thessaloniki for one to three days, before transport to Alyki for oxytocin treatment and/or release.

NEST PREDATION

An experiment on egg predation was carried out by burying chicken eggs (Swingland and Stubbs, 1985) in early June 1986. 100 eggs from a market (probably a few days old) were buried, 20 in each of five locations (Fig. 1);

A) Dry heath near the salt works, around a dump of rusted salt skips. This was the area most likely to house rats, which have been seen around the salt works.

B) Open dry heath where there were several burrows of the suslik ground squirrel (*Citellus citellus*), a possible excavator of tortoise nests.

C) Grassy heath around a small pool on the salt works heath.

D) Grassy heath around patches of brambles on the main heath, an area where opened tortoise nests were observed in autumn.

E) Dry heath on firm sandy soil on the main heath, in an area of regenerating hawthorn bushes.

These locations were chosen as having a range of habitats, and different potential nest predators. The 20 eggs at each location were buried individually, with

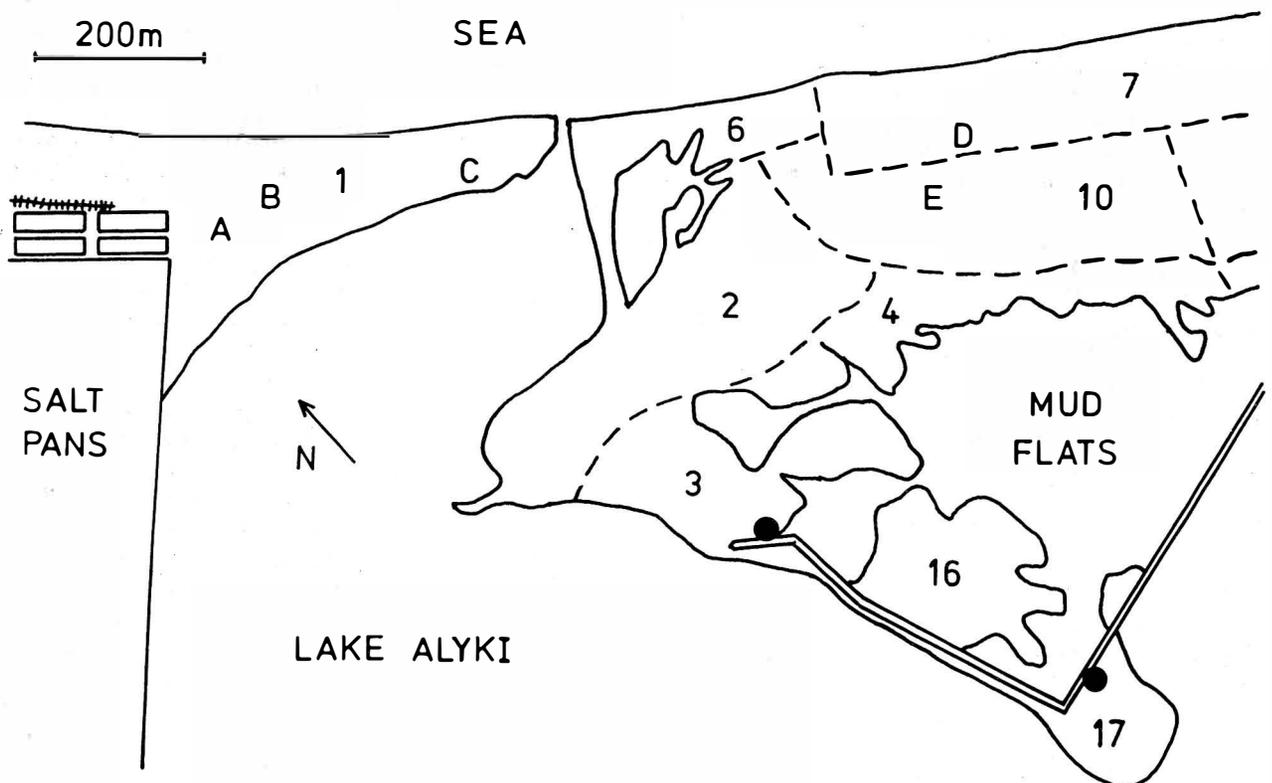


Fig. 1 The salt works heath (sector 1) and the northern end of the main heath at Alyki, showing location of the five areas where hens eggs were buried in 1986 (A-E). The position of burrows in the banks of the new dyke is also shown (●).

about 5m between each egg. The egg was covered by 3-5cm of soil, and disguised with fragments of vegetation. The location of each 'nest' was marked by a 5cm square fragment of roof tile from the salt works. This was placed 50cm to the north of the 'nest', not directly above it, to prevent a predator finding the egg by the marker. The areas where eggs were buried were searched through the summer, sufficiently to note broken eggs on the surface but not to check each buried egg. This was initially done every 2-3 days, but it was soon apparent that egg removal was infrequent and the interval between searches was increased to 10-14 days. The experiment lasted until early September, when an attempt was made to retrieve each buried egg.

EGG MEASUREMENT AND INCUBATION

The length and width of eggs were measured with vernier callipers to 0.1mm. Both maximum and minimum widths were recorded. Eggs were weighed on an electronic balance the day after being laid.

196 eggs of *T. hermanni*, *T. graeca* and *T. marginata*, collected during the study of Hailey and Loumbourdis (1988), were incubated in 3cm deep trays of sand. Eggs were placed in these trays within 24h of being laid, and just covered with sand, which was moistened every week. The trays were placed in two constant temperature cabinets (31°C and 35°C) and in a shaded room fluctuating between 22°C and 27°C, for an experiment designed to test the relation between temperature, sex determination, incubation period, and hatchling size and energy reserves. However, few

hatchlings were obtained; these were weighed and measured within 12h of emergence, and then frozen. They were subsequently dissected to examine yolk remnants, then dried to constant weight at 70°C in an oven.

The 59 eggs collected during 1988 were incubated in two series, to determine whether low hatching success in 1985-86 was due to the incubation technique, or to non-viability of eggs laid after oxytocin injection. 32 eggs were incubated by Dr Theodora Sofianidou using a previously successful technique, in unheated boxes of soil. The other 27 eggs were left in a bare plastic box, also unheated.

Statistical analysis: values in the text are ± 1 S.D. Polynomial, exponential, and geometric regressions (IBM user group) were fitted to curved lines, and the model explaining the most variation (in terms of r^2) was used.

RESULTS

OXYTOCIN-INDUCED EGG LAYING

Details of the timing of oxytocin-induced egg laying were recorded for 25 females, and are given for comparison with natural nesting. Fig. 2 shows a raster plot of laying times for 24 females; the other had not started to lay after 100 minutes, and was given an additional injection. The solid line shows the cumulative proportion of females which had started laying. The first egg was laid after 13 minutes; the last first-egg after 68 minutes. Body temperatures

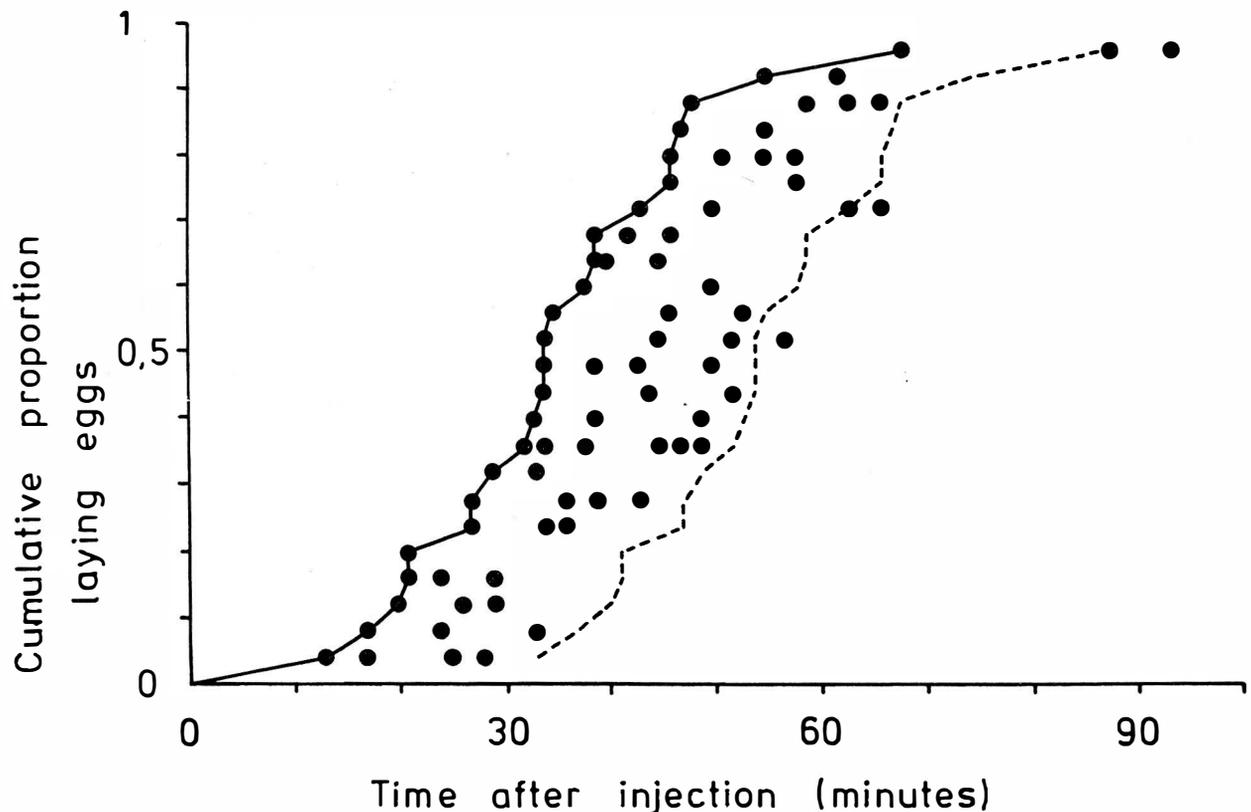


Fig. 2 The timing of egg laying after oxytocin injection. Each horizontal row shows eggs laid by one female, females ranked in order of laying. The solid line shows the cumulative proportion which had begun laying. The dashed line shows a period of 20 minutes after laying the first egg, during which most egg laying was completed.

measured immediately after laying ranged from 26.3-30.3°C. The mean time to the first egg was 35 ± 13 minutes ($n = 24$); the mean time for all eggs was 43 ± 15 minutes ($n = 75$) (Fig. 3). An individual female laid her eggs at intervals of 1-20 minutes, mean 6.2 ± 3.6 ($n = 51$; Fig. 3c), the most common interval being 3-5 minutes. The length of the laying period was much less variable than the latency before laying the first egg. Most eggs were produced within 20 minutes of the start of laying (Fig. 2).

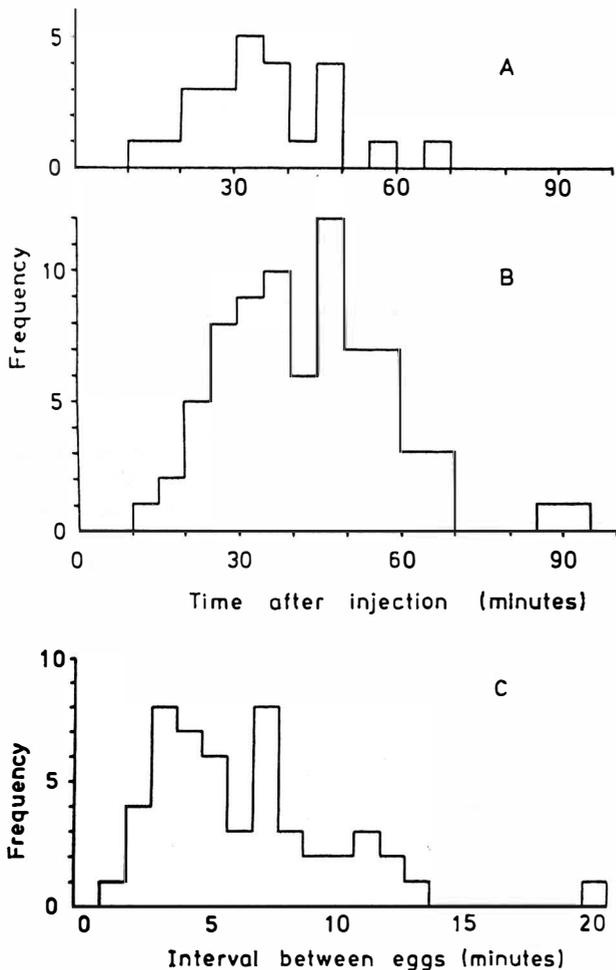


Fig. 3 Frequency histograms of the timing of egg laying after oxytocin injection. a) First eggs, b) all eggs. c) Interval histogram of the time between successive eggs.

Induced egg laying behaviour was stereotyped. The female walked rapidly around the arena in a normal gait after injection. The tail dropped after a few minutes, from the usual horizontal position to vertical, and was trailed along the ground while the female continued to investigate the arena. The female then assumed a posture with the head and forelegs withdrawn, and the front of the plastron resting on the ground. The hind legs were stretched out to raise the posterior of the body, and the tail was pointed horizontally backwards. The female moved away shortly after laying the egg. Females were kept for 30 minutes after laying the full complement of eggs observed by X-ray, but none laid any additional eggs.

SEXUAL MATURITY IN FEMALES

The size of females confirmed to be mature ranged from 142mm to 199mm SCL (Fig. 4a). However, only one (SCL 149mm) of the 13 females in the 140-149mm size class which were examined by X-ray or oxytocin had eggs, compared to 40-60 per cent of females larger than 150mm (Fig. 4b). Females of 150mm SCL or larger are therefore considered to be adults. In total, 146 females of this size were examined by X-ray or oxytocin injection in 1986 and 1988, and 57 of them (39.0 per cent) had calcified eggs. The proportions did not differ significantly between the two years; 28/78 in 1986 and 29/68 in 1988 ($X^2 = 0.44$, $P > 0.05$). In addition, 14 females injected with oxytocin in 1986 laid firm eggs with uncalcified shells (similar to the parchment shells of snake eggs), which would not be visible in X-ray photographs; these eggs were discarded.

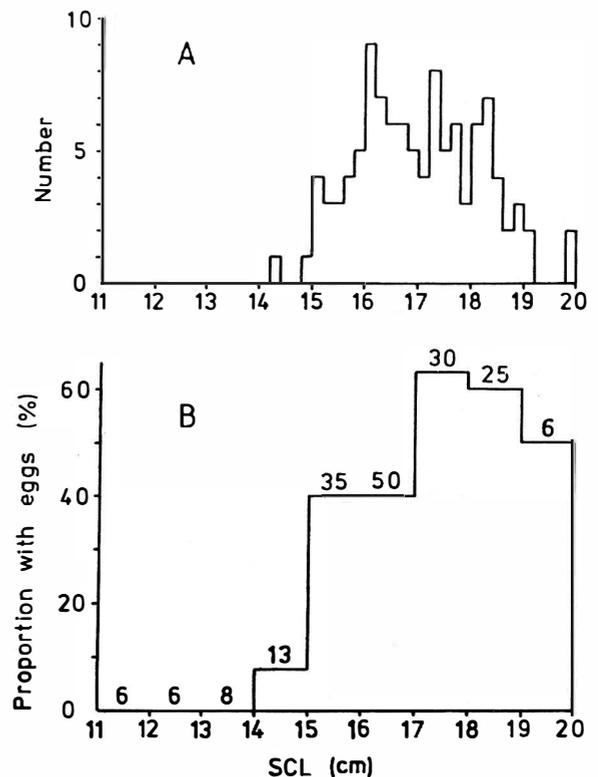


Fig. 4 The size at sexual maturity in females. a) Straight carapace length of all females from Alyki known to be mature, based on X-ray examination, oxytocin-induced egg laying or natural nesting. b) The proportion of females of different size which had eggs on X-ray examination or oxytocin injection. Sample size shown for each 1 cm class.

The field weight of females with eggs was compared to that of other females, in case the lightest females could be eliminated from future studies. The weight-length regression of females of 150mm or more handled in July (all years) was used as the standard:

$$2.785 \pm 0.144$$

$$\text{Weight (g)} = 0.354 \text{ SCL (cm)} \quad (1)$$

($n = 230$, $r = 0.93$). Results from July were used as this marks the low point of the female reproductive cycle, after eggs have been laid and while next years follicles are still small. Field weight, as a percentage of that

	1988	Total
SCL (mm)	171 ± 12 (30)	170 ± 12 (106)
Egg weight (g)	16.4 ± 3.1 (20)	15.5 ± 2.7 (66)
Egg length (mm)	37.2 ± 3.1 (20)	36.6 ± 2.7 (66)
Egg width (mm)	27.1 ± 2.0 (20)	27.0 ± 1.6 (66)
Clutch size	3.10 ± 1.03 (30)	3.59 ± 1.30 (59)
Clutch mass (g)	50.4 ± 17.3 (20)	54.5 ± 18.3 (41)
RCM (%)	5.52 ± 1.79 (20)	6.09 ± 2.00 (35)

TABLE 1: Egg and clutch size parameters for female *T. hermanni* from Alyki. Results for 1988, and pooled results 1983-88, shown as mean ± 1 S.D. (with number of tortoises).

expected from equation 1, was only slightly higher in females producing eggs compared to other females, in both years (with n):

	1986	1988
With eggs	104.2 ± 7.2 (42)	102.6 ± 6.7 (29)
Others	103.1 ± 7.5 (32)	102.0 ± 5.9 (39)

(Four injected females without eggs were not weighed in 1986.)

EGG SIZE AND CLUTCH SIZE

The results for 1988 are shown in Table 1, together with the pooled results for all years to show the mean reproductive pattern of Alyki females. The 1988 results are most similar to those from 1985-86 (Hailey and Loumbourdis, 1988); females laid more (clutch size 4-6) but smaller (mean egg size 12.9g) eggs in 1983 (Swingland and Stubbs, 1985). The average adult female at Alyki measured 170mm SCL, and laid a clutch of about 3.6 eggs, each weighing 15.5g. The measure of relative clutch mass in Table 1 is calculated as clutch weight/body weight, rather than field weight (as used in some studies).

Egg size and shape varied with body size in the Alyki population in 1985-86 (Hailey and Loumbourdis, 1988). The overall results including 1983 and 1988 are generally similar. The regression equations relating egg width (mm), egg shape (the ratio of length/mean width), and egg weight (g wet weight) to female SCL (cm) for the total sample (n = 66) are:

$$\text{Width} = 15.5 + 0.677 \text{ SCL} \quad (r = 0.486, P < 0.001) \quad (2)$$

$$\text{Shape} = 1.78 - 0.0252 \text{ SCL} \quad (r = -0.321, P < 0.01) \quad (3)$$

$$\text{Weight} = 3.24 + 0.728 \text{ SCL} \quad (r = 0.300, P < 0.05) \quad (4)$$

The correlation coefficients for width and for weight are similar to those reported previously, although the latter is now significant because of the increased sample size. The correlation between egg shape and

SCL is lower than the value ($r = -0.53$) found in 1985-86, because of additional unexplained variance from the particularly short eggs found in 1983.

The relation between weight, length and width of eggs from Alyki was investigated by multiple linear regression. The best fit was obtained using length (L), mean width (W)², and the difference between minimum and maximum width (dW):

$$\text{Weight} = 0.437L + 0.0200W^2 + 0.158dW - 14.7 \quad (5)$$

where dimensions are in mm (n = 59, r² = 98.8 per cent). However, the extra information provided by the difference between minimum and maximum widths did not produce a significantly better fit (P = 0.081); the other coefficients were significant at P < 0.001. The simpler equation:

$$\text{Weight} = 0.435L + 0.0203W^2 - 14.7 \quad (6)$$

(r² = 98.7 per cent) may be used to predict egg weight from linear dimensions.

Clutch size (CS) was weakly related to female body size (Fig. 5). The regression equations for the 1988 results and for the overall sample were:

$$\text{1988: CS} = 0.208 \text{ SCL} - 0.5 \quad (n = 30, r = 0.240, P > 0.05) \quad (7)$$

$$\text{Total: CS} = 0.277 \text{ SCL} - 1.1 \quad (n = 59, r = 0.266, P = 0.05) \quad (8)$$

Body size therefore accounts for only about 7 per cent of the variation in clutch size. Clutch sizes ranged from 1 to 6, with a mode of three eggs (Fig. 5c). The clutches derived by oxytocin injection in 1986, and not confirmed by X-ray, were not included in this analysis as they may have been incomplete (Congdon and Gibbons, 1983). These clutches were smaller (mean 2.74 ± 0.88) than full clutches measured by X-ray or nesting, and were not related to body size:

$$\text{CS} = 0.029 \text{ SCL} + 2.3 \quad (n = 43, r = 0.04, P > 0.1) \quad (9)$$

This includes the clutch produced by one of the seven females given a second oxytocin treatment.

	22-27°C	31°C	35°C
<i>T. hermanni</i>	67, 67, 67, 72	56, 56	58, 58
<i>T. graeca</i>	—	56	66, 68
<i>T. marginata</i>	—	—	61, 61
Mean	68	56	62

TABLE 2: The time from laying to hatching at different incubation temperatures. Each value is the incubation period of one egg, in days.

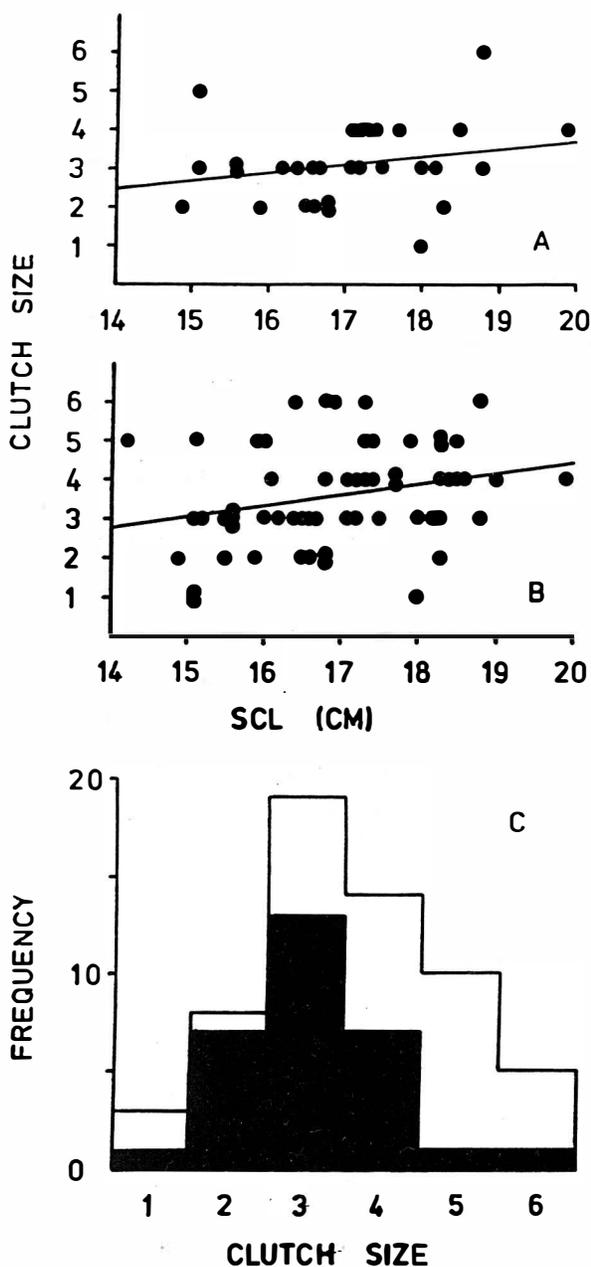


Fig. 5 a, b) The weak positive relationship between female size and clutch size (equations 7 and 8). a) X-ray examination in 1988. b) All complete clutches observed at Alyki. c) Frequency distribution of the sizes of complete clutches; data from 1988 are shaded.

Clutch mass was significantly related to female body size ($r = 0.326$, $n = 41$, $P < 0.05$), with a slightly higher correlation than for clutch size ($r = 0.266$) or egg weight ($r = 0.300$). A slightly improved fit ($r = 0.379$) was given by a polynomial regression rather than a linear model, which showed maximum clutch mass (CM) in intermediate sized females (Fig. 6):

$$CM = 7.9 SCL - 0.022 SCL^2 - 644 \quad (10)$$

where clutch mass is in g and SCL in mm.

INCUBATION

In total 196 eggs were incubated in 1985-86, including 30 *T. graeca* and 20 *T. marginata*. Only 13 of

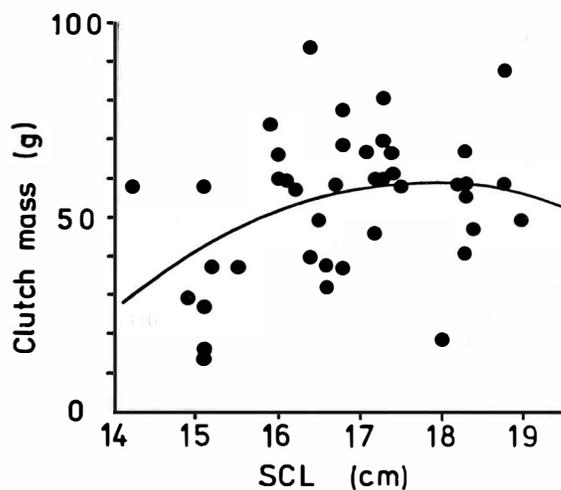


Fig. 6 Relation between clutch mass and female body size. The polynomial regression is given in the text (equation 10).

these hatched, after incubation periods from 56 to 72 days, 8-10 weeks (Table 2). Hatchling body weight (HW) and egg weight (EW) were strongly related, according to the equation:

$$HW = 0.574 EW + 0.79 \quad (11)$$

where HW and EW are wet weights in g ($n = 13$, $r = 0.87$, $P < 0.01$). The hatchling was on average 62.1 ± 5.6 per cent of egg weight. Hatchling size relative to the egg was similar in the three species for wet weight, but not for dry hatchling weight. The mean values, as percentages of egg weight, of the hatchlings incubated at 35°C ($n = 2$ for each species) were:

	Wet	Dry
<i>T. hermanni</i>	63.2	12.9
<i>T. graeca</i>	61.7	18.0
<i>T. marginata</i>	60.5	17.6

Wet weight for all temperatures was 62.2 ± 6.8 in *T. hermanni* and 61.9 ± 3.7 in the other species (t test, $P > 0.9$). The values for dry weight were 14.8 ± 2.3 in *T. hermanni* and 17.4 ± 1.1 in the other species ($t = 2.34$, 11 d.f., $P < 0.05$). Hatchling *T. graeca* retained large yolk sacs, which were partly external. Yolk remnants were smaller in *T. marginata*, and absent in *T. hermanni* incubated in these conditions. Mean hatchling SCL of the three species was:

<i>T. hermanni</i>	33.4mm
<i>T. graeca</i>	34.9mm
<i>T. marginata</i>	34.5mm

The *T. hermanni* eggs which hatched were from Litochoron and Deskati, and were slightly larger than eggs from Alyki.

Incubation was much more successful in 1988. The first group of eggs, laid from 19-28 May, were incubated in soil, and 30 out of 32 hatched before 29 July, after about 60 days incubation. The second group, laid from 31 May to 3 June, were incubated in a bare plastic dish, and 12 out of 27 hatched in late July and early August. Six of these eggs were laid on 31 May, and hatched from 25-29 July, after 55-59 days incubation. These six hatchlings weighed 9.6 ± 1.4 g,

61.3 ± 6.2 per cent of the wet weight of the eggs from which they hatched. Overall hatching success in 1988 was 71 per cent, compared to 6.6 per cent in 1985-86. Some of the 1988 hatchling *T. hermanni* from Alyki retained an external yolk sac. These hatchlings were all kept for growth and subsequent release, so the extent of yolk remnants and dry weight were not examined.

EGG PREDATION

The buried chickens eggs remained undisturbed in four of the five areas; only those in area B were disturbed. Five of the twenty eggs in this area were dug up, and were found intact on the surface. In the other areas, a few eggs were exposed or smashed within the hole, but the majority were recovered:

	A	B	C	D	E	Total
Removed from hole	1	5	0	1	0	7
Exposed in hole	0	0	2	1	0	3
Broken in hole	0	1	1	2	3	7
Recovered intact	19	14	17	14	16	80
Unable to locate	0	0	0	2	1	3

The eggs broken in the hole may have exploded after rotting, and so may not represent interference. The proportion remaining undisturbed through the incubation season was between 80 per cent (recovered intact) and 90 per cent (including eggs lost or broken within the hole).

Only one nesting female was observed at Alyki during the present study, and she did not complete her nest. The eleven nesting females found by Swingland and Stubbs (1985) were not grouped into any particular areas, and nests are thought to be widely dispersed over the heath. A few opened nests with fragments of eggshell were found, all of them in autumn rather than during the May-June nesting season. They are thus thought to result from successful hatching rather than nest predation.

Some large burrows, of fox or badger, were seen in the bank along the new dyke in sector 17 in 1984-86, and in 1988 a new burrow system was seen further along the dyke in sector 3 (Fig. 1). Many small holes, 10-15cm wide and deep, were found in grass within 50m of the burrows, but no fragments of eggshell were found in these holes. Tortoise nests which have been opened by predators at other sites in Greece and in France were always marked by eggshell. It is not known whether there was a localised nest predator in this area, or whether the animal was digging for roots or insects or, if a badger, making latrines (Bang and Dahlstrom, 1974).

Tortoises in the first few years of life were rarely seen at Alyki; animals with 0-3 growth rings made up only 2.6 per cent of all observations. Tortoises with 1-3 growth rings were seen throughout the year, with a similar seasonal pattern to that of larger animals (Fig. 7). The first hatchlings were seen in August, and remained active until November. They were relatively frequently seen in October and November, compared to larger animals, although this pattern is based on a small sample. Hatchlings with 0 growth rings were also seen in spring. They disappeared by June, presumably

as a result of growth of the first ring and incorporation into the 1 growth ring class.

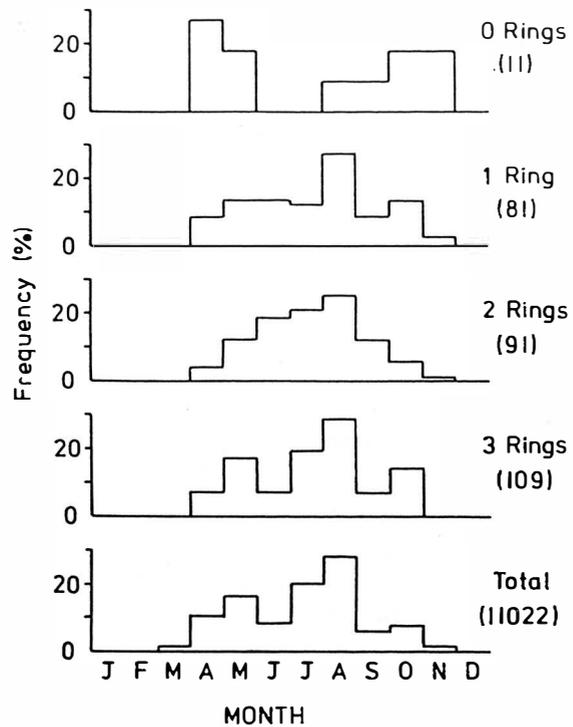


Fig. 7 Seasonal abundance of sightings of *T. hermanni* of different ages at Alyki. Each part shows the percentage of the total in each category (sample size at right) recorded in each month.

DISCUSSION

MATURITY AND EGG PRODUCTION

Female *T. hermanni* of 150mm are sexually mature at Alyki. This value represents the mid point of size at maturity, rather than the size of the smallest mature individual. Females between 100 and 149mm are termed subadults; they may be sexed by external characters (principally relative tail length; Stubbs *et al.*, 1984), but are not mature. Swingland and Stubbs (1985) noted that the smallest size of courting female *T. hermanni* at Alyki was 130mm. However, courtship of a female is not an indication of maturity, as male tortoises often court anything that moves; the smallest female seen being courted at Alyki was 108mm long. This is the reason for the large difference between 'mean adult size' (156mm) and mean size of nesting females (171mm) found by Swingland and Stubbs (1985).

The average reproductive parameters in Table 1 are provided for modelling purposes. The only parameters for which a large sample is not available are clutch frequency and reproductive potential. These are difficult to measure unless females can be restrained in enclosures or located by radio tracking throughout the whole nesting season. The alternative method based on dissection and counting eggs, follicles and corpora lutea (Gibbons, 1968) is only suitable for small samples of the protected *Testudo* species. Hailey and Loumbourdis (1988) used this method, which

suggested that reproductive potential (clutch size \times clutch frequency) was greatest in intermediate sized *T. hermanni* from Alyki, and declined in large females.

Although additional measurements of clutch frequency were not made here, the proportion of females with eggs is an indication of *relative* clutch frequency. This was greater in females of 170-189mm than those of 150-169mm (Fig. 4b), with a decline in the largest size class (which however was based on a small sample). Clutch mass also showed a slight decrease in the largest females (Fig. 6). The lack of a clear relationship between size and reproductive parameters within this population is perhaps not surprising in view of the small size variation of adult female chelonians, compared to other groups of reptiles (Hailey and Davies, 1987). Body size explains (in terms of r^2) only about 5-15 per cent of the variation in reproductive parameters, and is likely to be of little importance in practical models of population dynamics.

Females with eggs weighed on average only 0.5-1.0 per cent more than females without eggs, so that field weight provided no indication of a female's reproductive status. It was expected that females with eggs would weigh about 6 per cent more, i.e. the mean relative clutch mass in the population (Table 1). It is probable that total body volume is constrained by the carapace; eggs are tightly packed within the body (see Fig. 6 of Hailey and Loumbourdis, 1988). This would lead to space for eggs being provided by reduced volume of some other part of the body, most probably by reduced gut contents.

INCUBATION

The low hatching success in 1985-86 was originally thought to result from non-viability of eggs laid after oxytocin treatment. For example, a maturational process within the oviduct may not have been completed, as suggested by Iverson's (1980) failure with oviducal eggs of the gopher tortoise. However the high success in 1988 indicates that the incubation conditions were at fault, possibly too high moisture level in the sand. The 71 per cent hatching rate in 1988 compares favourably with other studies of tortoises, such as 61 per cent in *Gopherus berlandieri* (Judd and McQueen, 1980).

When eggs of the three species were incubated together, hatchling *T. hermanni* had low dry weight compared to *T. marginata* and especially *T. graeca*, the eggs of which have a higher energy content (Hailey and Loumbourdis, 1988). The energy reserves of hatchlings are available to cover non-feeding periods, which may be due to hatchling behaviour or to fluctuating food supply. Reserves of hatchling sea turtles must supply them while digging out of a deep nest and then locating the nursery ground (Kraemer and Bennett, 1981). Many Chelydrid, Emydid and Kinosternid turtles delay emergence from the nest from autumn hatching until the following spring (Gibbons and Nelson, 1978). Hatchling *Geochelone gigantea* remain in their nests for a few weeks (Bourn, 1977), and *Testudo sulcata* are inactive and fast for 1-2 weeks after hatching (Cloudsley-Thompson, 1970). Hatchling *T. hermanni* were first found in the field in August, at about the

same time as eggs hatched in captivity. Prolonged delayed emergence from the nest therefore does not seem to occur at Alyki.

More work will be necessary to show whether the pattern of hatchling energy reserves in *Testudo* is truly species-specific, or whether this varies between populations as well. At present, it is suggested that the greater yolk remnants found in *T. graeca* and *T. marginata* are related to the occupation of less amenable habitats (differences in hatching times are another possibility — Willemsen, personal communication). In coastal areas in north-eastern Greece, *T. graeca* uses arid open heath habitat where *T. hermanni* occupies woodland or scrub (Wright, Steer and Hailey, 1988; Willemsen, 1988). *Testudo hermanni* becomes restricted to productive cultivated or riparian habitats inland at the extreme east of its range (Scholte, Helmer and Strijbosch, MS). The typical habitat of *T. marginata* is unproductive thorny scrub, while *T. hermanni* in southern Greece is largely restricted to more fertile cultivated areas (Willemsen, MS; Willemsen and Hailey, 1989).

Larger hatchlings emerged from larger eggs, with the hatchling being on average 62 per cent of egg weight. The loss of weight is not accounted for by the shell, which makes up about 13 per cent of egg weight in *Testudo* (Hailey and Loumbourdis, 1988), but rather reflects the metabolism of the embryo. This provides the simplest explanation of the higher relative clutch mass of oviparous compared to viviparous reptiles. Other factors being equal, RCM should be about 40 per cent lower in a species producing live young rather than eggs. There is therefore no need to invoke greater costs of reproduction in viviparous species, such as transporting the young or reduced food intake of the mother (for example, Seigel and Fitch, 1984).

No predation of natural nests was observed during the summer, and most buried chicken eggs remained undisturbed. Nesting success is usually about 20-30 per cent in apparently stable populations of tortoises and terrapins (Landers, Garner and McRae, 1980; Christens and Bider, 1987; Congdon, Breitenbach, van Loben Sels and Tinkle, 1987), but values up to about 70 per cent have been reported (Tinkle, Congdon and Rosen, 1981). The present study is directly comparable to that of Swingland and Stubbs (1985) on *T. hermanni* in France, where 71 per cent of chicken eggs suffered predation in the first two days after burial, and less than 10 per cent of natural nests were successful. Such differences in reproductive success must have important consequences for population dynamics; the French population was thought to be declining (Stubbs and Swingland, 1985), while the Alyki population is stable or increasing.

POPULATION REPRODUCTION

The reproductive potential of an animal population may be estimated using the size at maturity in females and the mean reproductive potential of adults, or the abundance of size or age classes and the reproductive potential of each class (for example, Table 9 of Turner and Berry, 1984). This section compares simple and stratified estimates at Alyki to assess the reliability of

SCL (mm)	Reproductive potential (1)	Clutch size	Clutch frequency	Reproductive potential (2)	Females	Main Heath		Salt Works Heath		
						Eggs (1)	Eggs (2)	Females	Eggs (1)	Eggs (2)
140s	-2.9	2.9	0.3	0.9	67	0	58	16	0	14
150s	4.6	3.2	1.6	5.0	88	402	440	21	96	105
160s	8.5	3.5	1.6	5.5	65	553	355	21	179	115
170s	8.9	3.7	2.5	9.2	58	517	532	15	134	138
180s	5.8	4.0	2.4	9.4	34	196	320	6	35	56
190s	-0.9	4.3	2.0	8.4	3	0	25	2	0	17
Total						1668	1730		444	445

TABLE 3: Estimates of the total reproductive capacity of *Testudo hermanni* on the main heath and on the salt works heath, by two methods (see text).

the simple method, and to provide gross measures of reproductive potential in the main heath (post-fire) and salt works heath populations.

A mark recapture study estimated the total number of females (of 100mm or larger) to be 478 in the main heath and 135 in the salt works heath (Table 1c and 1a of Stubbs *et al.*, 1985). This number was divided among 10mm size classes according to the relative frequencies shown in Fig. 3 of Stubbs *et al.*, (1985). Reproductive potential for the mid-point of each size class was calculated by two independent methods (see Table 3).

1) Using the polynomial regression of reproductive potential on carapace length given in Fig. 4 of Hailey and Loumbourdis (1988).

2) Clutch size was calculated from equation 8 above. Relative clutch frequency was taken from the data shown in Fig. 4b, with a maximum value of 1.0 for the 170s mm class. The average relative clutch frequency for the 146 females of 150mm or larger was then 0.767. Average clutch frequency for adult females at Alyki was 1.9 (Hailey and Loumbourdis, 1988). Relative clutch frequency was therefore converted to clutch frequency by multiplying by 2.48 (= 1.9/0.767). The product of clutch size and clutch frequency gave the reproductive potential of each size class.

248 of the 478 females estimated to live on the main heath were of 150mm or larger. The simple estimate of population reproduction is therefore (248 x 1.9 x 3.59) = 1,692 eggs per year. This value is similar to the two stratified estimates (1,668 and 1,730 eggs per year), and together give an estimate with a standard deviation only 1.8 per cent of the mean (1697 ± 31). 65 of the 135 females estimated to live on the salt works heath were of 150mm or larger, with a simple estimate of 443 eggs per year. The three estimates for the salt works are even closer (443, 444 and 445 eggs per year); surprisingly close in view of the crudity of the calculations. The main conclusion is that these methods are robust enough for use in models of the dynamics of the Alyki populations.

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ANALYSIS OF THE STRUCTURE OF AN AMPHIBIAN COMMUNITY IN THE CENTRAL SYSTEM OF SPAIN

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ABSTRACT

This study examines the structure of an Amphibian community, composed of 10 species in the Central System of Spain. We studied resource partitioning in the main dimensions of the niche (food, space and time), the overlap in each dimension and the overall overlap. From a multidimensional scaling analysis (MDS) of the overlap matrices we inferred that the spatial dimension is the main factor responsible for species segregation. Overlap along the time and food dimensions was significantly correlated. The community is structured into three guilds formed, respectively, by the aquatic anurans, the terrestrial anurans together with a terrestrial salamander, and the newts.

INTRODUCTION

Studies on the structure of herpetological communities have mainly been based on lizards (see reviews in Schoener, 1974 and Toft, 1985). Amphibian communities have received less attention and have essentially been studied in frogs of tropical ecosystems (e.g. Inger, 1969; Inger and Colwell, 1977; Toft and

Duellman, 1979; Toft, 1980a and b; 1981; 1985) and in salamanders of the temperate regions of Europe (Avery, 1968; Griffiths, 1986) and North America, principally the studies of Jaeger and Hairston (see reviews in Toft, 1985 and Hairston, 1987).

Regarding the Iberian Peninsula, studies on herpetological communities have been restricted to the work of Valverde (1967), the recent studies of different

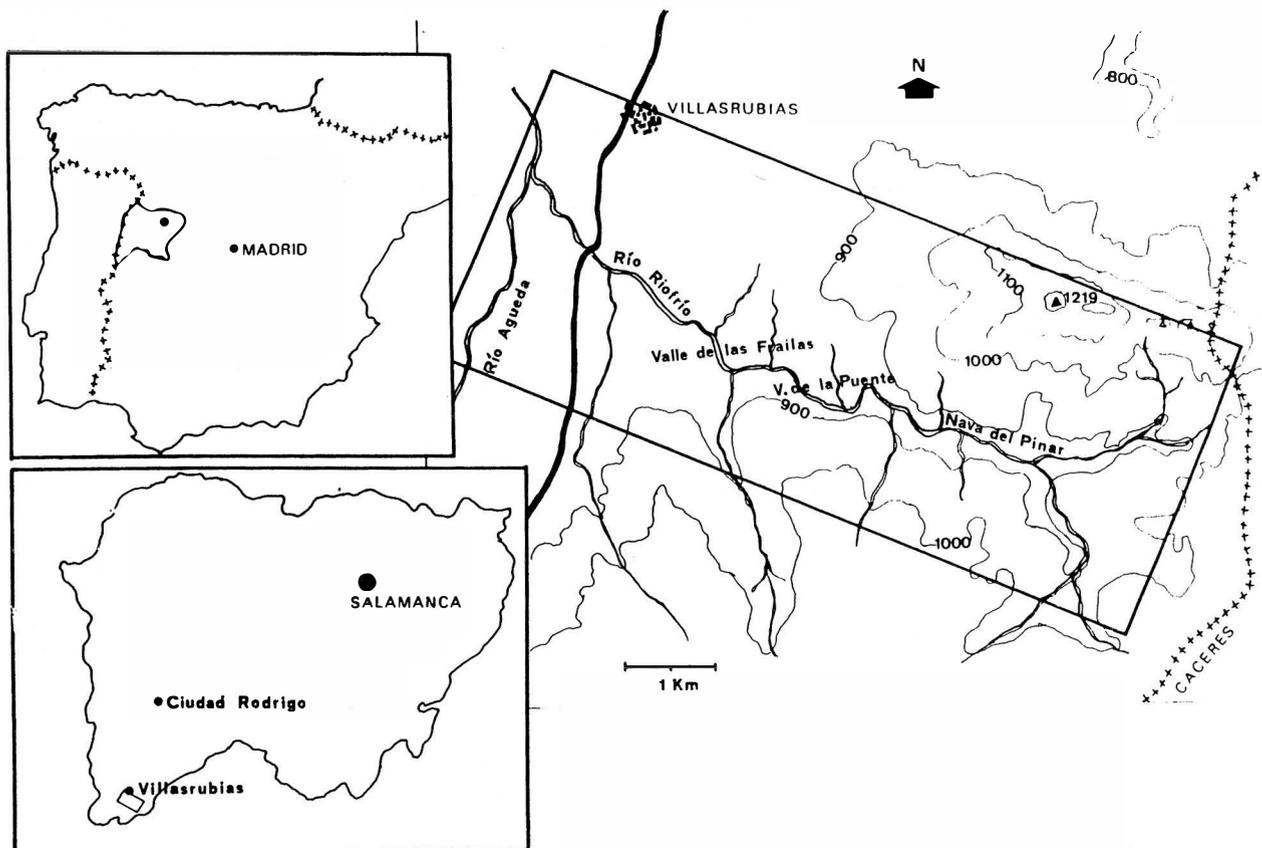


Fig. 1 Geographical location of the study area.

taxocenoses of Sauria, mainly the Lacertidae (Mellado, *et al.*, 1975; Pérez-Mellado, 1982; Seva, 1982 and Braña, 1984), and one study of a complete herpetological community (Bas, 1982). Finally, Díaz Paniagua (1979, 1982, 1983, 1988) studied the interactions within communities of larval amphibians.

The aim of the present study is to offer new data on the resource partitioning in an amphibian assemblage in a European temperate region. This will permit a comparison with other communities of salamanders and frogs that have been studied more extensively.

MATERIAL AND METHODS

STUDY AREA

The field work was carried out at Villasrubias (UTM 29TQE0366) located in the Southwest of the province of Salamanca on the northern slopes of the Spanish Central System (Fig. 1). Samples were taken over an area of approximately 8 x 3.5 km, at altitudes ranging between 800 and 1200 metres. All the aquatic habitats and the terrestrial habitats in their proximities were investigated.

The mean annual rainfall of the zone is 943.15 mm, and the area is subject to both Atlantic and Continental climatic influences. The dominant vegetation is the grade *Genista florida-Quercus pyrenaica*; characterised by oak forests and bushes of *Erica spp.* There are also plantations of *Pinus pinaster* and *P. sylvestris* (Bellot, 1966; Rico, 1978).

Periodic visits were made to the study area, usually twice a month, from November 1982 to February 1984. On each occasion all the habitats of the zone were sampled. For each animal observed, we noted species, habitat type and hour. We sampled terrestrial amphibians by searching in the vegetation, on the banks of aquatic environments, under stones, trunks, etc. Animals that were found inactive, were not taken into account in the analysis of daily and seasonal activity patterns, but were included in the analysis of habitat utilisation and diet composition.

We used netting methods to capture newts and other aquatic species in their aquatic environments. The number of terrestrial amphibians observed and the number of aquatic species observed, usually newts, were corrected in the same way for the time employed in searching. Observations were made and samples were taken during all hours of the day and night.

We calculated hourly and monthly activity indices (I_{ij}) by the formula (see also Lizana, *et al.*, in press):

$$I_{ij} = \frac{n_{ij}}{T_i \%}$$

where I_{ij} = corrected frequency of species j in time category i (months or hours); n_{ij} = number of observations of species j in time category i ; $T_i\%$ = percentage of the time spent sampling in time category i . This was then converted to a percentage using the formula:

$$I_{ij} \% = \frac{I_{ij}}{\sum I_{ij}} \times 100$$

Methods used in the analysis of diet composition and habitat use are detailed in Lizana *et al.*, 1986 and in press).

We studied resource partitioning along the three main niche dimensions: habitat, food and time (Pianka, 1973, 1986; Schoener, 1974), considering the subdimensions of seasonal and daily activity for time and the subdimensions of prey type and prey size for food. Niche overlap was calculated by the index of Pianka (1973):

$$S = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum (p_{ij})^2 (p_{ik})^2}}$$

where p_{ij} and p_{ik} are proportions of species j and k in the resource i . Overlap was calculated for each of the dimensions and subdimensions considered.

The resulting overlap matrices were analysed by the multidimensional scaling technique (MDS) using the Kruskal algorithm (Kruskal, 1964) with the Systat package. Plots were made on the plane defined by the first two dimensions since reasonably small stress (and high goodness-of-fit) were found on each (Schiffman, *et al.*, 1981).

This technique has several advantages that justify its use in the study of communities. First, it uses the distances or similarities between populations (in this case, species) as starting values, so that one can construct a similarity matrix with the overlap values found. Factor analysis and other multivariate techniques have several important premises in their application, among which perhaps the most important is the existence of linear relationships between the starting variables. The MDS does not feature this limitation. Finally the results obtained with the MDS technique are easier to interpret since they are based on the Euclidean distances between the points, while interpretation of the factor analysis must be based on results expressed as angular values between vectors (Schiffman, *et al.*, 1981).

We also analysed the correlation between the overlap values for each of the dimensions and subdimensions considered, using Spearman rank correlation coefficients (Siegel, 1956).

RESULTS AND DISCUSSION

The amphibian community in the study area considered of 10 species, in a zone of high herpetological diversity (Pérez-Mellado, 1983). Seven of them were anurans: *Rana iberica*, *Rana perezi*, *Discoglossus galganoi* (using the taxonomy proposed by Capula, *et al.*, 1985), *Alytes obstetricans*, *Hyla arborea*, *Bufo Bufo* and *Bufo calamita*. The latter species and *H. arborea* were very rare. The other three species encountered were urodeles: *Salamandra salamandra*, *Triturus boscai* and *Triturus marmoratus*.

Feeding Habits

The species are situated along a continuum that ranged from an exclusively terrestrial to an aquatic diet. At the latter end were *Triturus marmoratus* and *T. boscai*, that almost exclusively consumed aquatic

PREY ITEMS	SPECIES	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
BIVALVIA		—	—	—	—	—	—	—	—	2.06	—
GASTROPODA		0.08	—	—	0.19	—	—	—	—	0.19	—
CLADOCERA		—	—	—	—	—	—	—	—	1.27	0.82
OSTRACODA		—	—	—	—	—	—	—	—	25.39	82.66
COPEPODA		—	—	—	—	—	—	—	—	2.55	1.46
ISOPODA		0.45	0.05	0.27	—	—	—	—	—	—	—
OLIGOCHAETA		0.02	—	0.54	—	—	—	—	6.66	—	—
MYRIAPODA		0.99	0.50	2.19	0.38	—	0.45	—	8.88	—	—
PSEUDOESCORPIONES		0.24	0.05	—	—	—	—	—	—	0.29	—
SOLIFUGAE		—	—	—	0.38	—	—	—	—	—	—
OPILIONES		0.53	—	1.64	0.38	—	—	1.96	2.22	—	0.02
ARANEAE		10.49	5.35	7.39	6.58	4.99	0.91	5.88	2.22	0.19	0.05
ACARI		2.26	0.25	1.36	13.95	—	—	—	—	3.34	0.05
COLLEMBOLA		1.88	1.16	1.36	4.06	—	—	—	—	3.83	0.11
DIPLURA		0.13	—	—	—	—	—	—	—	—	—
ODONATA		0.08	0.75	—	—	—	—	—	—	0.19	0.32
EPHEMEROPTERA		0.80	0.45	0.27	0.19	—	0.09	—	—	9.44	2.46
PLECOPTERA		2.58	2.89	—	—	—	—	—	—	1.18	—
EMBIOPTERA		0.02	—	—	—	—	—	—	—	—	—
ORTHOPTERA		0.59	1.21	0.82	1.16	1.66	1.09	—	—	0.19	—
DERMAPTERA		0.32	0.65	0.54	—	—	—	3.92	8.88	—	—
BLATTODEA		0.13	0.15	1.36	—	—	—	—	—	—	—
PSOCOPTERA		0.16	—	—	—	—	—	—	—	0.09	—
HOMOPTERA		4.23	7.89	7.39	0.96	3.33	0.27	1.96	—	0.39	0.08
HETEROPTERA		3.10	3.03	0.54	3.87	—	0.27	—	—	0.09	0.11
UNID. HEMIPTERA		0.13	—	—	—	—	—	—	—	—	—
THYSANOPTERA		0.18	—	—	—	—	—	—	—	—	—
NEUROPTERA		0.08	0.05	—	—	—	—	—	—	0.19	—
COLEOPTERA		17.85	18.32	18.90	26.35	9.99	6.10	52.94	33.33	2.55	1.38
HYMENOPTERA		4.31	9.66	11.78	1.74	1.66	0.36	1.96	4.44	0.29	0.02
FORMICIDAE		4.47	11.77	16.98	33.72	75.00	88.50	25.49	15.55	—	—
TRICHOPTERA		3.82	1.87	—	0.38	—	0.09	—	—	3.34	0.11
LEPIDOPTERA		1.07	1.26	1.09	2.13	—	0.27	3.92	4.44	0.49	0.02
DIPTERA		36.16	31.00	24.10	2.13	1.66	0.36	1.96	6.66	40.25	9.66
UNID. HEXAPODA		1.29	0.55	0.54	0.38	1.66	—	—	2.22	0.98	0.26
UNID. HEXAPODA LARVAE		0.86	1.06	0.82	0.77	—	0.27	—	4.44	0.88	—
UNID. ARTHROPODA		0.67	0.05	—	0.19	—	—	—	—	—	—
VERTEBRATA		—	0.10	—	—	—	—	—	—	—	0.02
— NUMBER OF PREY		3708	1981	365	516	60	1098	51	45	1016	3403
— NUMBER OF INDIVIDUALS		424	199	43	39	8	8	2	4	60	58

TABLE 1: Percentage of prey groups predated by the species of the community. Abbreviations: R. ibe: *Rana iberica*, R.per: *Rana perezi*, D.gal: *Discoglossus galganoi*, A.obs: *Alytes obstetricans*, H.arb: *Hyla arborea*, B.buf: *Bufo Bufo*, B.cal: *Bufo calamita*, S.sal: *Salamandra salamandra*, T.bos: *Triturus boscai*, T.mar: *Triturus marmoratus*. ("unid." means unidentified prey).

SPECIES Size class/	% R.ibe	% R.per	% D.gal	% A.obs	% H.arb	% B.buf	% B.cal	% S.sal	% T.bos	% T.mar
0- 2mm	5.94	7.72	13.09	15.97	—	—	—	—	38.31	86.00
2- 4mm	42.98	34.55	47.35	43.58	10.00	46.58	—	2.32	23.99	2.33
4- 6mm	28.50	27.15	17.27	23.47	73.33	43.47	39.21	38.53	25.02	4.02
6- 8mm	12.45	14.58	9.74	13.21	13.33	4.50	39.21	18.60	9.78	5.25
8-10mm	5.46	5.48	5.57	1.77	—	1.24	15.68	18.60	2.16	0.96
10-12mm	2.74	3.24	2.50	0.98	1.66	0.46	3.92	16.27	0.51	0.52
12-14mm	1.35	3.30	0.83	0.59	1.66	0.46	1.96	4.65	0.10	0.40
14-16mm	0.39	1.22	0.83	—	—	1.24	—	—	—	0.52
16-18mm	0.17	0.85	1.67	0.19	—	0.77	—	—	0.10	0.02
18-20mm	0.07	0.37	—	—	—	0.15	—	—	—	—
20-22mm	0.07	0.31	—	0.19	—	0.46	—	—	—	—
22-24mm	—	0.26	—	—	—	0.15	—	—	—	0.02
24-26mm	0.03	0.15	—	—	—	0.46	—	—	—	—
26-28mm	—	0.05	—	—	—	—	—	—	—	—
28-30mm	—	0.05	—	—	—	—	—	—	—	—
30-32mm	0.07	0.37	1.11	—	—	—	—	—	—	—
32-34mm	—	0.05	—	—	—	—	—	—	—	—
34-36mm	—	—	—	—	—	—	—	—	—	—
36-38mm	—	—	—	—	—	—	—	—	—	—
38-40mm	—	—	—	—	—	—	—	—	—	—
40-50mm	—	0.15	—	—	—	—	—	—	—	—
>50mm	—	0.05	—	—	—	—	—	—	—	—
N. of Prey	2810	1861	359	507	60	644	51	43	971	3375
N. of Ind.	424	199	43	39	8	8	2	4	60	58

TABLE 2: Percentage of size classes of prey predated by the species of the community.

prey such as crustaceans (Ostracoda, Copepoda) and aquatic larvae of insects (Table 1). *Rana iberica*, *R. perezi* and *D. galganoi* occupied an intermediate position with preferential consumption of terrestrial prey, although they also consumed a large portion of aquatic items, such as larvae of insects (Lizana, *et al.*, 1986). *Alytes obstetricans* was the first species with a mainly terrestrial diet. The large number of Formicidae consumed by *Hyla arborea*, pointed to the importance of terrestrial prey in its diet. *Bufo bufo*, *Bufo calamita* and *Salamandra salamandra*, had an exclusively terrestrial diet.

In general, trophic generalists predominated in the community, although certain species such as *B. bufo* or *H. arborea* showed a pronounced preference for Formicidae, while *B. calamita* and *S. salamandra* seemed to prefer large, rather non-sclerotised preys (Table 1 and 2; see data on prey availability and electivity in Lizana, *et al.*, 1986).

The most euryphagous species were those, such as the ranids, that occupied aquatic environments and

their neighbourhoods. In some species there existed an important relationship between the degree of trophic specialisation and the use of terrestrial habitats (Lizana, *et al.*, in press).

Habitat Use

We considered sixteen habitat categories (see description in Table 3 and in Lizana, *et al.*, in press) that were used by at least one species, and described according to their proximity to the aquatic habitats. Three species of anurans were seen to be linked more tightly to the aquatic environments or their proximities. *Rana iberica* occupied a large variety of terrestrial biotopes, although the species was always present close to water. It was segregated from *R. perezi* through its use of habitats with a stronger water current and lesser depth, while *R. perezi* occupied sluggish water (Lizana, *et al.*, 1987 and in press). *Discoglossus galganoi* seemed to prefer more terrestrial environments than *R. perezi* and was usually found on the banks of streams or in flooded meadows (Table 3).

SPECIES	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar	
H A B I T A T S —AQUATIC— —TERRESTRIAL—	A	—	—	—	—	—	—	—	—	0.82	
	B	0.29	—	—	—	—	—	—	—	—	
	C	3.42	—	—	—	—	—	—	—	—	
	D	1.34	—	3.12	14.28	8.82	—	—	4.00	0.71	2.47
	E	0.59	1.78	10.41	16.07	8.82	41.66	40.00	36.00	2.14	4.95
	F	1.34	—	5.20	—	—	—	—	12.00	—	—
	G	—	—	—	3.57	—	—	—	—	—	—
	H	—	—	3.12	55.35	2.94	16.66	—	—	0.71	—
	I	2.38	—	2.08	—	—	—	—	8.00	2.85	2.47
	J	2.53	2.67	34.37	—	8.82	8.33	60.00	—	0.71	—
	K	14.45	20.77	7.29	5.35	58.82	—	—	—	35.71	37.19
	L	4.32	—	—	—	—	—	—	40.00	3.57	—
	M	28.76	15.43	21.87	—	8.82	33.33	—	—	19.28	2.47
	N	—	17.80	1.04	—	2.94	—	—	—	18.57	49.58
O	37.85	10.68	10.41	5.35	—	—	—	—	—	—	
P	2.68	30.86	1.04	—	—	—	—	—	15.71	—	
	%	%	%	%	%	%	%	%	%	%	
1	2.53	2.67	34.37	—	8.82	8.33	60.00	—	0.71	—	
2	33.97	64.68	15.62	5.35	20.58	8.33	—	12.00	91.42	87.60	
3	63.48	32.64	50.00	94.64	70.58	83.33	40.00	88.00	7.85	12.39	
N. of Obs.	671	337	96	56	34	12	5	25	140	121	

TABLE 3: Percentage of observations performed for each species in different habitats of the study area: A: Woodland, B: Sandy areas, C: Dry stream beds, D: Bushy meadows (with shrubs), E: Open meadows (grasslands), F: Litter floor (on dead leaves), G: Stony areas, H: Under large stones (stony areas used for refuge), I: Slopes next to streams, J: Flooded meadows, K: Temporal pools, L: Temporal streams, M: Permanent streams, N: Permanent pools, O: Zones of rivers and streams with rapid current, P: Zones of rivers and streams with slow current.

Class 1 represents the percentage of observations in flooded zones, Class 2 the percentage in water masses and Class 3 the percentage on solid ground, including those carried out in terrestrial habitats and those on the shores of aquatic habitats.

SPECIES	%	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
January	1.70	—	—	—	—	—	—	—	—	7.38	—
February	5.57	2.50	1.86	—	11.44	—	—	—	6.52	27.80	25.40
March	4.78	18.87	16.05	53.66	26.67	—	61.34	94.30	68.56	19.26	10.76
April	1.36	2.94	6.09	—	11.72	—	—	—	—	6.15	—
May	12.74	16.68	10.57	3.49	6.25	40.93	—	—	—	4.92	—
June	8.59	6.75	8.19	5.83	3.69	39.29	—	—	4.22	3.40	5.23
July	16.78	10.50	12.84	1.32	5.69	3.65	20.38	—	2.14	4.24	16.86
August	5.35	5.23	9.29	5.20	—	11.46	18.26	—	—	0.77	19.23
September	8.19	9.04	12.15	11.57	5.83	—	—	—	—	2.55	8.63
October	13.20	13.95	14.60	16.05	18.11	4.64	—	—	—	2.21	8.27
November	19.63	5.61	5.26	2.83	10.55	—	—	5.60	18.54	8.95	5.57
December	2.04	7.86	3.04	—	—	—	—	—	—	12.31	—
Total Sampling	%	%	%	%	%	%	%	%	%	%	%
Time (Minutes)	8785	561	468	137	58	34	15	5	22	163	142
NUMBER OF OBSERVATIONS											

TABLE 4: Percentage of corrected frequencies of the number of observations carried out in each month for each species. The first column details the percentage of minutes sampled each month with respect to the total of the study period.

The other anurans, together with *S. salamandra* has almost exclusively terrestrial habits, except during the reproductive season. They occupied habitats that were generally differentiated by the type and density of vegetation. *T. boscai* and *T. marmoratus* were almost always present in water masses, with no defined terrestrial phase (Lizana, *et al.*, in press), and were differentiated from one another by the presence or absence of aquatic vegetation, the depth of the water and the speed of the current (Table 3).

Activity

Rana iberica and *R. perezi* were active throughout the year except in January (Table 4). The same held for *Triturus boscai* and to a lesser extent for *T. marmoratus*. In these species there was a clear relationship between their use of aquatic habitats and their broad seasonal activity patterns (Lizana, *et al.*, in press). The other anurans and *S. salamandra* showed a more seasonal activity pattern, which was particularly limited by the occurrence of rainy periods in spring and autumn, coinciding in most species with the reproductive period.

Both ranids were active throughout all the hourly segments sampled (Table 5), although *R. iberica* showed the greatest nocturnal activity. *D. galganoi* showed its greatest activity after sunset. The terrestrial anurans and *S. salamandra* were almost exclusively crepuscular and nocturnal except during rainy periods. *T. boscai* and *T. marmoratus* seemed to exhibit a mainly diurnal activity, although our method of sampling the aquatic habitats may have biased their activity estimates (Lizana, *et al.*, in press).

Overlap

The overlap values for the three dimensions of the niche and for the overall overlap are shown in Appendices 1 to 9. As overlap values were highly correlated between subdimensions for food and time (see further), the arithmetic mean of these two subdimensions was also calculated. The highest overlap values were obtained for food and the smallest for habitat.

A fundamental aspect in studies dealing with communities is the degree of dependence between the niche dimensions considered (e.g. Pianka, 1986),

SPECIES HOUR	%	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
1- 2	0.56	—	—	—	—	—	—	—	—	29.70	—
2- 3	—	—	—	—	—	—	—	—	—	—	—
3- 4	0.68	13.33	4.90	—	—	16.69	—	—	—	—	—
4- 5	0.17	17.77	9.90	—	—	—	—	—	—	—	—
5- 6	—	—	—	—	—	—	—	—	—	—	—
6- 7	0.62	1.20	4.10	5.60	—	—	—	—	25.80	—	—
7- 8	0.68	4.40	11.20	10.29	—	—	—	—	—	—	—
8- 9	0.85	3.50	3.90	—	—	—	—	—	—	—	—
9-10	4.26	6.50	7.50	9.00	7.91	5.33	—	—	—	5.80	3.12
10-11	7.39	1.02	4.10	8.00	—	—	—	—	—	4.10	1.70
11-12	8.93	5.50	2.20	—	—	—	—	—	—	7.40	11.90
12-13	6.54	4.80	2.00	—	—	—	—	—	—	3.30	9.50
13-14	4.43	4.26	2.40	3.10	—	2.56	—	—	—	6.20	15.00
14-15	7.17	7.60	3.70	1.95	7.05	—	—	—	—	13.10	6.80
15-16	8.25	4.00	2.60	2.90	—	6.88	—	—	—	4.70	1.07
16-17	10.41	5.20	2.50	4.37	—	4.36	—	—	—	2.90	8.90
17-18	9.84	3.20	4.60	6.40	—	4.61	—	—	1.62	1.40	4.50
18-19	6.77	4.40	6.20	3.10	—	5.03	10.15	—	—	3.60	13.70
19-20	4.66	2.10	3.20	3.75	3.61	4.87	29.51	—	—	2.30	5.71
20-21	4.09	—	4.50	0.85	20.62	2.77	—	—	—	4.70	1.08
21-22	3.92	5.70	7.70	12.50	12.91	5.79	17.54	19.50	28.60	2.80	4.50
22-23	5.17	3.70	4.20	16.20	19.58	6.58	19.94	29.50	27.90	1.60	1.70
23-24	3.01	0.49	6.10	11.60	16.81	11.31	22.84	50.80	15.90	1.80	4.40
0- I	1.47	0.51	1.10	—	11.47	23.17	—	—	—	3.70	6.00
Total Sampling		%	%	%	%	%	%	%	%	%	%
Minutes: 8785		NUMBER OF OBSERVATIONS									
		561	468	137	58	34	15	5	22	163	142

TABLE 5: Percentage of corrected frequencies of the number of observations carried out in each hourly segment for each species. The first column details the percentage of minutes sampled in each hourly segment with respect to the total study period.

which is our case were analysed by correlations. In the first place, this analysis showed that there was no correlation between the degree of overlap in time (Appendix 6) and habitat (Appendix 7; $r_s = 0.29$, $P > 0.05$) or between habitat and food (Appendix 3) ($r_s = 0.23$, $P > 0.05$). However, there was a statistically significant correlation between the overlap in time and food ($r_s = 0.41$, $P < 0.05$), suggesting that the consumption of similar prey types was due to similar activity rhythms. A species diet composition would hence be related directly to its activity patterns and those of its prey (Lizana, *et al.*, 1986).

The correlation of the overlap values was highly significant between the trophic subdimensions of prey type (Appendix 1) and prey size (Appendix 2), ($r_s = 0.49$, $P < 0.001$), and also between the temporal subdimensions of annual (Appendix 4) and daily (Appendix 5) activity ($r_s = 0.48$, $P < 0.01$). This supports the hypothesis that in amphibian communities, owing to their strict ectothermy, differences in activity produce a pronounced segregation in diet composition (see also Schoener, 1974 and Toft, 1985).

Similar conclusions have been reached in studies on lizard communities, although the relationship between both dimensions has not proved to be as tight as would be expected for ectotherms with a greater thermoregulatory capacity (Pérez-Mellado, 1982). Only in the case of strongly stenophagous species such as *Bufo bufo*, food seems to be a sufficient segregating factor. It is striking that, in general, the food specialists in ectotherm communities eat ants (e.g. Mellado, *et al.*, 1975; Barbault, *et al.*, 1978; Toft, 1980 a and b; 1981; Pérez-Mellado, 1982, Pianka, 1986). As has been pointed out elsewhere, prey size seems to be of greater importance in intraspecific segregation than among the different species of the community (Lizana, *et al.*, 1986).

Multidimensional Scaling

MDS analysis shows that in the trophic dimension (Fig. 4) both newts were clearly separated from the other species, and were opposed to another group formed of *B. bufo* and *H. arborea*. The former consisted of quasi-specialists in aquatic prey and the

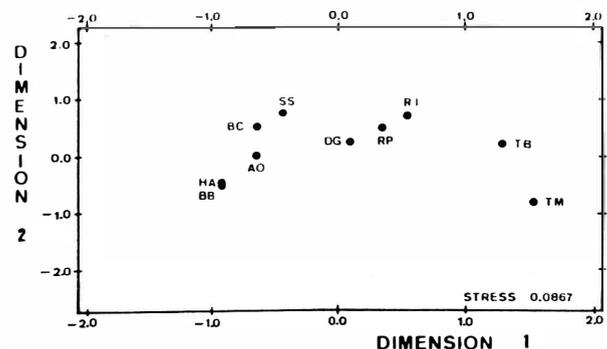


Fig. 2 Euclidean distances between the species according to an analysis of multidimensional scaling (MDS) for the overlap values in the trophic dimension, prey type subdimension. The value of stress for the final configuration is also given. Abbreviations: RI *Rana iberica*, RP *Rana perezi*, DG *Discoglossus galganoi*, AO *Alytes obstetricans*, HA *Hyla arborea*, BB *Bufo bufo*, BC *Bufo calamita*, SS *Salamandra salamandra*, TB *Triturus boscai*, TM *Triturus marmoratus*.

latter of myrmecophagous species. The analysis of prey type and prey size (Fig. 2 and Fig. 3 respectively) revealed a similar pattern, although it was possible to

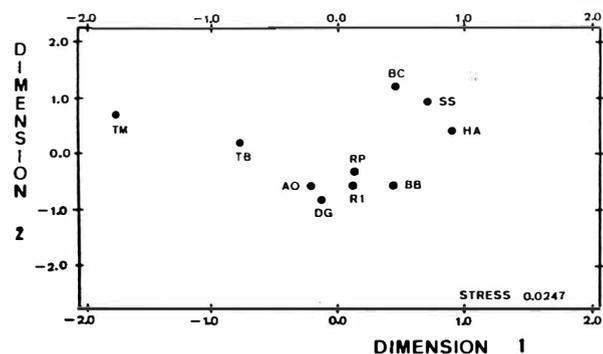


Fig. 3 MDS for the trophic dimension, prey size subdimension.

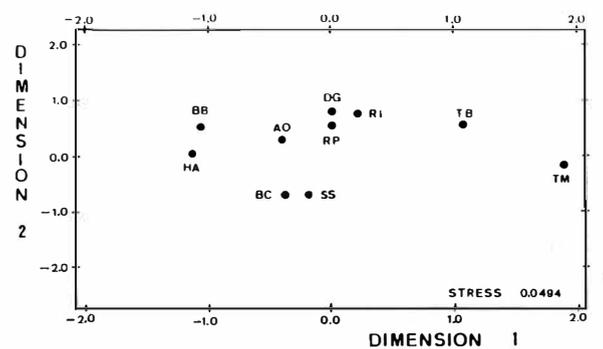


Fig. 4 MDS for the trophic dimension, arithmetic mean of the subdimensions.

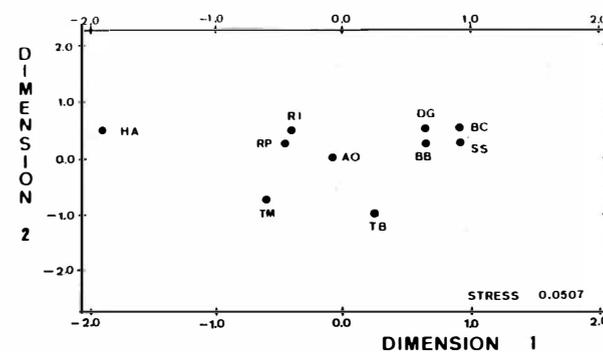


Fig. 5 MDS for the temporal dimension, annual activity subdimension.

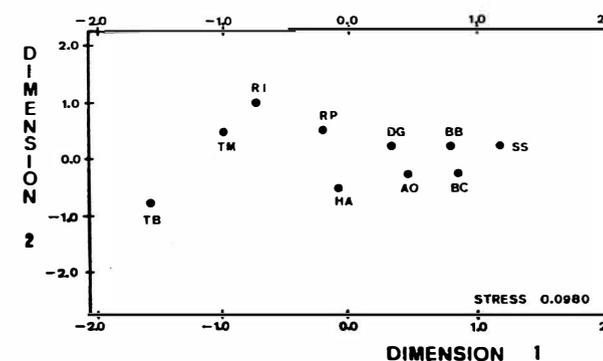


Fig. 6 MDS for the temporal dimension, daily activity subdimension.

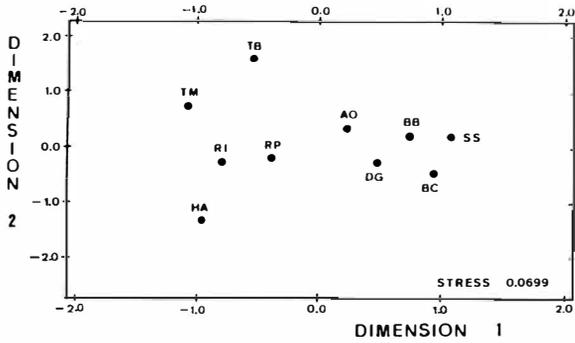


Fig. 7 MDS for the temporal dimension, arithmetic mean of the subdimensions.

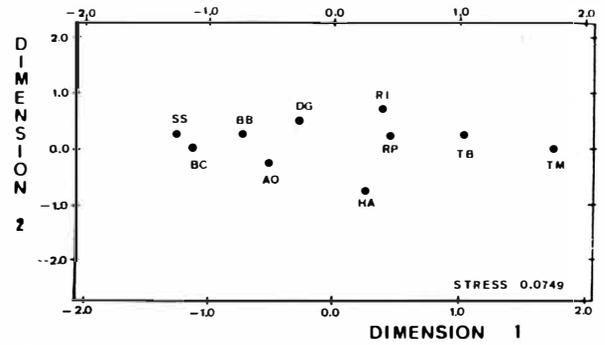


Fig. 9 MDS for the total overlap, arithmetic mean of the dimensions.

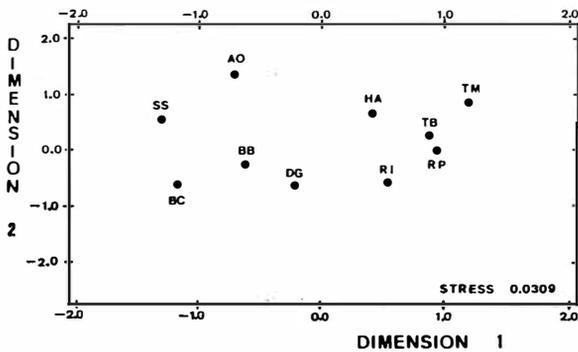


Fig. 8 MDS for the spatial dimension.

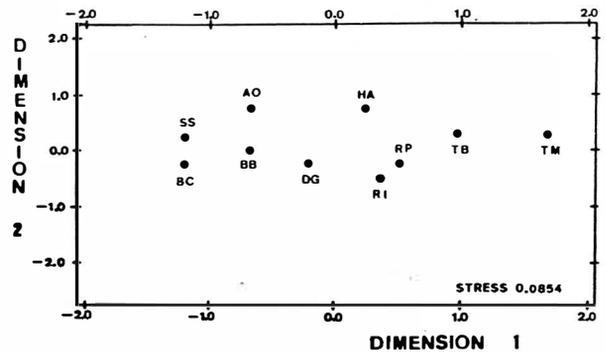


Fig. 10 MDS for the total overlap, multiplication of the dimensions.

appreciate the separation of *S. salamandra* and *B. calamita*, which consumed relatively large terrestrial prey.

Regarding the annual activity pattern (Fig. 5), the plane of the first two components divided the community in two groups: a central one with species, such as ranids and newts, that remained active throughout most of the year, and another to the right of the plane, which basically exhibited activity during autumn and spring. Regarding daily activity rhythms (Fig. 6), a central group of crepuscular species was observed, flanked to the right, by species that was increasingly nocturnal, and to the left by species with activity during almost all hourly segments.

The general plane of activity (Fig. 7) revealed relatively large Euclidean distances between species, indicating that this dimension, more than could be deduced from the overlap values alone (Appendix 6), contributed to a large extent to the interspecific segregation, specially by separating the nocturnal species that were situated to the right of the plane.

The plane corresponding to habitat (Fig. 8) revealed noteworthy large euclidean distances between virtually all species, with a clear trend towards terrestrial habits at the lower values of the first dimension. The planes corresponding to total overlap between the dimensions, calculated by arithmetic means (Appendix 8, Fig. 9) and multiplication (Appendix 9, Fig. 10) (see Pianka, 1974, 1986; May, 1975), again showed that habitat was the main dimension responsible for species segregation in the community studied. In this sense it is interesting to observe the strong correspondence of axis X in Fig. 8 with that in Figs. 9 and 10.

CONCLUSIONS

Habitat seems to be the main dimension responsible for species segregation in our community, with a strong correlation between activity rhythms and food composition of the species. Most species segregate due to the interaction of the three dimensions considered.

Our results agree reasonably well with those that have appeared in recent reviews on the mechanisms of resource partitioning in herpetological communities (Schoener, 1974; Heatwole, 1982; Toft, 1985) and point to the great importance of habitat in species segregation. In snake and larval amphibian communities, segregation seems mainly be due to food and activity rhythms, respectively (Heyer, 1976; Toft, 1985).

The structuring of the community studied seems to be a result of the interrelationship between the dimensions considered, in such a way that the more terrestrial species show basically nocturnal activity and are, in general, markedly seasonal, probably due to limiting factors such as environmental temperature and humidity. The more aquatic species show broader diel and seasonal activity patterns, probably as a result of the buffering effect of their aquatic environments (Brattstrom, 1970; Schoener, 1974; McFarland, *et al.*, 1979; Stevenson, 1985 a and b; Duellman and Trueb, 1986).

This conclusion was also held by Toft (1985) who indicates that 'in single communities, the resource partitioning patterns result from two or more factors that may operate independently, interactively, or both'.

Three main guilds can be distinguished in the community. The first is composed of terrestrial anurans and *S. salamandra*; their activity is overtly seasonal and nocturnal, and they have an exclusively terrestrial diet. The second group is formed by the anurans with aquatic or mixed habits, that are crepuscular or have a broad daily activity period, and that are generally euryphagous. A third guild contains *Triturus boscai* and *T. marmoratus*, which are aquatic and active over almost the whole year and in almost all the hourly segments. Note that for the total overlap, both species of *Triturus* appear separated from each other, to the same extent that *T. boscai* is separated from other the aquatic anurans.

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APPENDIX

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal.	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.95	—								
D.gal	0.88	0.96	—							
A.obs	0.42	0.55	0.68	—						
H.arb	0.19	0.38	0.53	0.81	—					
B.buf	0.13	0.32	0.47	0.78	0.99	—				
B.cal	0.47	0.58	0.67	0.84	0.54	0.49	—			
S.sal	0.55	0.64	0.73	0.77	0.49	0.43	0.92	—		
T.bos	0.73	0.66	0.55	0.09	0.02	0.009	0.07	0.18	—	
T.mar	0.10	0.09	0.07	0.01	0.004	0.001	0.01	0.03	0.61	—

TABLE 1: Overlap matrix in the trophic dimension; prey-type subdimension.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.98	—								
D.gal	0.96	0.94	—							
A.obs	0.97	0.96	0.98	—						
H.arb	0.66	0.71	0.46	0.57	—					
B.buf	0.96	0.94	0.88	0.90	0.77	—				
B.cal	0.54	0.63	0.37	0.47	0.78	0.51	—			
S.sal	0.59	0.66	0.41	0.48	0.84	0.60	0.90	—		
T.bos	0.74	0.70	0.77	0.84	0.55	0.66	0.46	0.48	—	
T.mar	0.17	0.22	0.29	0.35	0.06	0.05	0.07	0.06	0.77	—

TABLE 2: Overlap matrix in the trophic dimension; prey-size subdimension.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.97	—								
D.gal	0.92	0.95	—							
A.obs	0.69	0.76	0.83	—						
H.arb	0.43	0.54	0.50	0.69	—					
B.buf	0.55	0.63	0.67	0.84	0.88	—				
B.cal	0.51	0.60	0.52	0.65	0.66	0.50	—			
S.sal	0.57	0.65	0.57	0.63	0.66	0.52	0.91	—		
T.bos	0.73	0.68	0.66	0.47	0.29	0.33	0.26	0.33	—	
T.mar	0.13	0.16	0.18	0.18	0.03	0.02	0.04	0.04	0.69	—

TABLE 3: Overlap matrix in the trophic dimension; arithmetic mean of the subdimensions.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.95	—								
D.gal	0.74	0.72	—							
A.obs	0.82	0.82	0.82	—						
H.arb	0.54	0.49	0.15	0.21	—					
B.buf	0.63	0.62	0.87	0.66	0.07	—				
B.cal	0.55	0.48	0.92	0.69	0.001	0.91	—			
S.sal	0.59	0.53	0.90	0.75	0.04	0.88	0.97	—		
T.bos	0.59	0.52	0.51	0.72	0.16	0.48	0.50	0.60	—	
T.mar	0.57	0.67	0.41	0.60	0.22	0.50	0.27	0.36	0.70	—

TABLE 4: Overlap matrix in the temporal dimension: annual activity subdimension.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.79	—								
D.gal	0.40	0.75	—							
A.obs	0.24	0.50	0.66	—						
H.arb	0.44	0.47	0.44	0.57	—					
B.buf	0.21	0.44	0.65	0.60	0.42	—				
B.cal	0.13	0.38	0.69	0.69	0.74	0.71	—			
S.sal	0.21	0.44	0.74	0.60	0.30	0.60	0.70	—		
T.bos	0.29	0.30	0.24	0.27	0.21	0.13	0.08	0.08	—	
T.mar	0.48	0.50	0.39	0.29	0.42	0.36	0.19	0.16	0.43	—

TABLE 5: Overlap matrix in the temporal dimension: daily activity subdimension.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.87	—								
D.gal	0.57	0.74	—							
A.obs	0.53	0.66	0.74	—						
H.arb	0.49	0.48	0.29	0.39	—					
B.buf	0.42	0.53	0.76	0.63	0.24	—				
B.cal	0.34	0.43	0.80	0.69	0.37	0.85	—			
S.sal	0.40	0.48	0.82	0.68	0.17	0.74	0.83	—		
T.bos	0.44	0.41	0.37	0.49	0.18	0.31	0.29	0.34	—	
T.mar	0.53	0.58	0.40	0.44	0.32	0.43	0.23	0.26	0.56	—

TABLE 6: Overlap matrix in the temporal dimension; arithmetic mean of the subdimensions.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.54	—								
D.gal	0.55	0.37	—							
A.obs	0.10	0.07	0.17	—						
H.arb	0.36	0.51	0.38	0.20	—					
B.buf	0.35	0.23	0.59	0.46	0.22	—				
B.cal	0.04	0.07	0.77	0.14	0.19	0.53	—			
S.sal	0.09	0.02	0.18	0.27	0.10	0.47	0.35	—		
T.bos	0.47	0.86	0.36	0.09	0.80	0.27	0.03	0.09	—	
T.mar	0.19	0.60	0.16	0.08	0.63	0.08	0.04	0.05	0.78	—

TABLE 7: Overlap matrix in the spatial dimension.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.79	—								
D.gal	0.68	0.69	—							
A.obs	0.44	0.49	0.58	—						
H.arb	0.43	0.51	0.39	0.43	—					
B.buf	0.44	0.47	0.68	0.64	0.45	—				
B.cal	0.30	0.37	0.70	0.50	0.41	0.62	—			
S.sal	0.35	0.38	0.52	0.53	0.31	0.57	0.70	—		
T.bos	0.55	0.65	0.46	0.35	0.42	0.30	0.19	0.25	—	
T.mar	0.28	0.45	0.25	0.23	0.32	0.18	0.10	0.12	0.68	—

TABLE 8: Total overlap matrix calculated by arithmetic mean of the dimensions.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.46	—								
D.gal	0.29	0.26	—							
A.obs	0.03	0.03	0.11	—						
H.arb	0.07	0.13	0.05	0.05	—					
B.buf	0.08	0.08	0.31	0.25	0.04	—				
B.cal	0.008	0.01	0.32	0.06	0.04	0.22	—			
S.sal	0.02	0.008	0.08	0.12	0.01	0.18	0.27	—		
T.bos	0.15	0.24	0.09	0.02	0.04	0.02	0.002	0.01	—	
T.mar	0.01	0.05	0.01	0.006	0.006	0.001	0.001	0.001	0.30	—

TABLE 9: Total overlap matrix calculated by multiplication of the dimensions.

TEMPORARY PONDS AS BREEDING SITES OF AMPHIBIANS AT A LOCALITY IN SOUTHWESTERN SPAIN

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ABSTRACT

Breeding habitats of 10 amphibian species were investigated and classified by their physical characteristics. The relative larval abundance of the species was analysed in 15 temporary ponds, resulting in positive correlations with the area of the ponds, whereas negative correlations were found between species diversity and the persistence of the ponds. Regarding the use of their habitats, one species was not correlated with any one, and among the others, two groups of species were differentiated because of their negative associations.

INTRODUCTION

Breeding sites are of great importance for amphibian reproduction, and therefore play a decisive role in the conservation of the species (see e.g. Cooke and Ferguson, 1976, Beebee, 1983). Some general characteristics of the breeding habitats of several Iberian and European amphibians have been listed in fieldguides (e.g. Boulenger, 1897-98, Smith, 1954, Fretey, 1975, García Paris, 1985). More details have been given of the breeding habitats of newts by Cooke and Frazer (1976) and De Fonseca and Jocqué (1982) in Belgium, and in Norway by Dolmen (1980). The habitats of natterjack toads have been described in several papers (Beebee and Griffin, 1977, Andrén and Nilson, 1985a, b) and those of tree frogs were described by Stumpel and Hanekamp (1986) in Holland. Other works have been published on the characteristics of the breeding sites used by the amphibian communities from different localities. Beebee (1977, 1979, 1980, 1983, 1985) and Banks and Laverick (1986) have made an inventory of the breeding sites of amphibians in England, comparing the occurrence of different types of ponds and analysing their characteristics. Strijbosch (1980) related the breeding of several anuran species in the Netherlands to physicochemical variables and to the plant communities of the ponds. The amphibian community examined in this present paper was also the subject of a previous study made of the abundance of larval amphibian species in relation to pond features (Díaz-Paniagua, 1983).

In this study some physical characteristics of breeding sites were investigated, in an area where 10 species occurred. These were seven anurans: *Pelobates cultripipes*, *Discoglossus galganoi*, *Bufo bufo*, *Bufo calamita*, *Rana perezi*, *Pelodytes punctatus*, *Hyla meridionalis*, and three urodeles: *Pleurodeles waltl*, *Triturus marmoratus* and *Triturus boscai*. The relative abundance of larvae and the coexistence of the different species breeding in the ponds are considered.

STUDY AREA

The Biological Reserve of Doñana is located in Southwestern Spain between the Atlantic Ocean and the marshes formed by the mouth of Guadalquivir River. This area has been described in detail by several authors (Allier, *et al.*, 1974, García Novo, *et al.*, 1978, Amat, *et al.*, 1979).

The climate is Mediterranean with an Atlantic influence, characterised by hot, dry summers, and rains that occur mainly in autumn. Winter temperatures do not commonly reach negative values (a description of the variation of temperature and rainfall during the study period is given in Díaz-Paniagua, 1986).

Temporary ponds in the area are commonly flooded by the autumn rains. A great number occur in an extensive sandy zone of the Reserve, where the predominant vegetation is the scrub of *Halimium halimifolium* and *Erica scoparia*; isolated specimens of *Quercus suber* and small groups of *Pinus pinea* constitute the arboreal vegetation. Numerous temporary ponds in an area bordering the marsh are also flooded. Slow-moving currents of water flow from these into the marsh during the autumn and winter months but later in the year they remain as still ponds, locally known as 'caños'. Some extensive lagoons constitute the permanent waters of the Reserve and these have not been included in this study, but the numerous temporary ponds in the meadows that surround them are included.

METHODS

This study was conducted during the amphibian breeding season 1984-85. In autumn 1984, 15 temporary ponds were selected for sampling larval amphibian populations. These samples were taken by means of a dipnet, during daytime, at different locations in each pond, where the numbers of larvae of



PLATE 1: Two temporary ponds included in this study: CHT (left) and PIN (right).

each species were recorded. This was carried out once every two weeks in the first two months. Later on, samples were taken monthly until no more larvae were found in ponds. A detailed description of some of the ponds has been given in a previous paper (Díaz-Paniagua, 1983). For this study, only physical characteristics were taken into account for the classification of the ponds (Table 1):

The persistence of water in the ponds was calculated in relation to the length of the amphibian breeding season (see description in Díaz-Paniagua, 1986), which is considered to be from the time the first species started breeding to the end of metamorphosis of the last larvae in the ponds. The following categories were considered: A) Ponds that persisted before and after the amphibian breeding season (flooded with autumnal rains and dried up in late summer). B) The breeding season was equivalent to the time of water persistence (flooded with autumnal rains and dried up in early summer). C) Ponds that were flooded once the breeding season had started but persisted up to the end (flooded in winter and dried up in summer). D) Ponds that were

flooded once the breeding season had started and dried up before it had finished (flooded in winter and dried up in spring). E) Ponds that flooded and dried up intermittently during the breeding season.

Area was calculated by measuring the length and width of each pond and by its approximation to an ellipsoid. The areas given in Table 1 correspond to this measurement recorded in December 1984.

Maximum depth: Although fluctuations during the whole study period were registered, only values in December were considered.

Relative depth was calculated by relating the two parameters described above (after Wetzel, 1975).

A classification of the ponds based on these physical characteristics was made by means of a cluster analysis of variables, calculating Euclidian distances as measures of similarity (BMD PIM, Dixon, 1985).

A description of the breeding sites of the species was also made from personal observations recorded in different locations of the study area during the last seven years.

<i>Ponds</i>	<i>Persistence</i>	<i>Area (m²)</i>	<i>Relative Depth</i>	<i>Maximum Depth (cm)</i>	<i>Number of Species</i>	<i>Diversity</i>	<i>Relative Abundance (larvae/sample)</i>
ORF	A	626	1.66	47.0	2 + 2	0.901	3.240
DS	A	1246	2.65	22.5	3 + 3	1.242	2.340
GAN	A	—	—	—	4 + 1	0.774	2.780
MAR	A	491	5.40	85.0	5 + 2	1.513	2.310
MP	B	48	6.01	47.0	1 + 2	0.856	2.500
BRE	B	1295	2.59	21.0	1 + 2	0.218	0.244
CM	B	491	1.85	17.5	4 + 1	0.818	2.160
NSO	C	214	1.44	16.0	6 + 1	1.520	1.637
DOM	D	104	1.17	15.0	2 + 2	0.623	6.579
PIN	D	204	2.01	32.0	2 + 1	0.924	0.918
ACM	D	1200	2.48	20.0	4 + 0	1.136	1.970
CHT	B	1769	3.23	14.0	4 + 2	2.170	0.982
JH	E	406	1.10	24.0	3 + 2	0.760	3.000
ODU	E	304	1.57	16.0	3 + 2	0.761	5.730
NT	E	831	1.89	14.0	2 + 0	0.668	8.000

TABLE 1: Main physical characteristics of the ponds sampled besides number of species (anurans + urodeles), diversity and total relative abundance. (For explanation of codes of persistence: see the text).

Larval communities were described on the basis of relative abundance, considered as a ratio of the numbers of larvae of each species recorded to the number of samples taken. However, for calculating Shannon-Wiener diversity indexes, the frequency of individuals of each species over the total number recorded in each pond was considered. The same diversity index was considered as a measure of niche breadth for each species according to their presence in the different ponds. Multivariate factor (BMD P4M, Dixon, 1985) and cluster analysis (SPSS, 1986) were carried out on larval relative abundance matrix in order to analyse interspecific associations according to the use of their habitats. Non parametric correlation was employed to relate some physical variables characterising the ponds to other parameters of the larval community, such as diversity and relative abundance.

RESULTS

The physical characteristics of the ponds are described in Table 1. Flooding of the more persistent ponds occurred in early November. While the drying up of some was recorded from late March onwards, others persisted as smaller pools into the summer. Maximum depths of the ponds did not reach high values, all were under 100cm; relative depth gave some information on the morphology of the basin, the highest values corresponded to those ponds which have been modified by human activity (MP, MAR) while natural formations were usually shallower.

There was a wide variety in the area of the ponds studied, even though previous selection excluded very extensive stretches of water. The smallest pond measured 48m² (MP), with small fluctuations during

most of its flooded period, whereas the others that reached larger dimensions exhibited broad variations between initial flooding and drying up.

The classification of the ponds based on the results from a cluster analysis is shown in Fig. 1 (because of the lack of some data, GAN was not included). Maximum and relative depths were the main variables contributing to the first grouping of the cases, thus one cluster included the ponds with the largest values and the other cluster included all the remaining ponds. In this second group, ponds were clustered mainly because of differences in their persistence.

The larval species in the ponds

Ten species bred in the study area, their presence and relative abundance in the ponds sampled are shown in Fig. 2, and commented on the following paragraphs:

Pelobates cultripes: This species commonly bred in very large water bodies such as the nearby marsh in the study area, but it also frequently used small temporary ponds and tadpoles were found in most of them. Its early breeding precluded it from using ponds that flood later in the season. This early occupation of temporary ponds, however, could produce mass mortality of the eggs or tadpoles, because of the great fluctuations in water level in the early phases of some ponds which may dry out and refill repeatedly (see Díaz-Paniagua, 1986).

Discoglossus galganoi: Its common breeding sites in the study area were small muddy ponds in meadows close to extensive stretches of water. The largest larval abundance detected corresponded to a small, shallow, intermittently flooded pond (ODU). Its ability to spawn repeatedly during the breeding season (Knoepfpler, 1962) and to metamorphose at a very

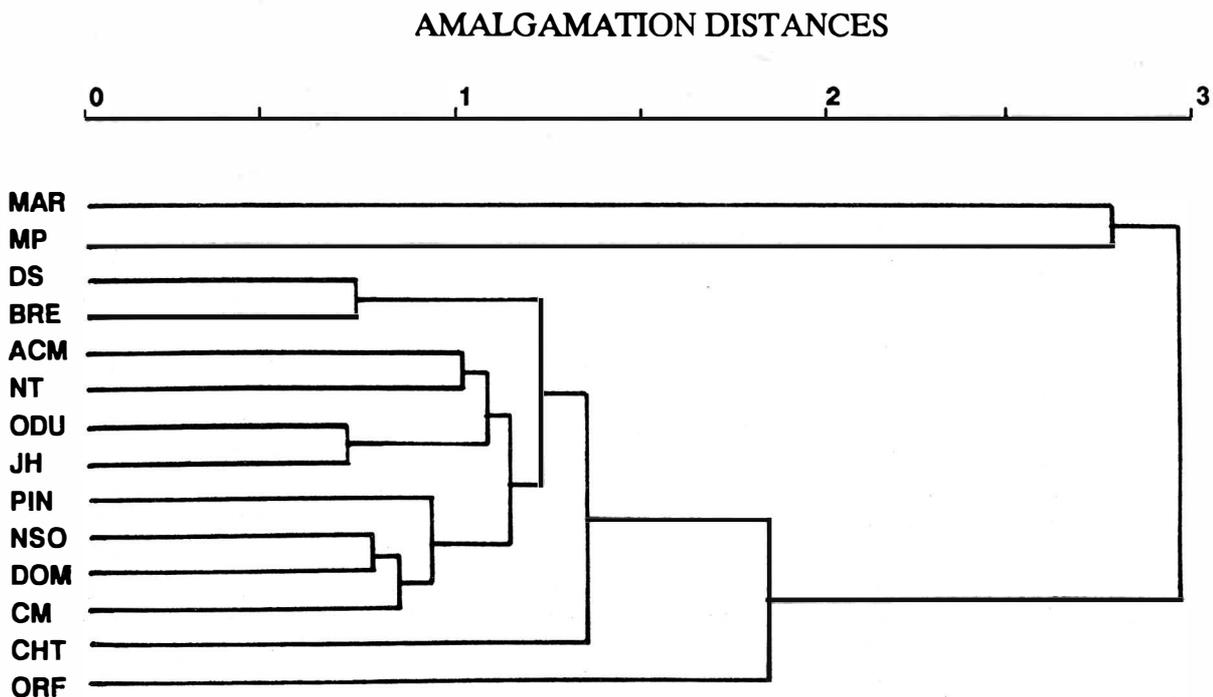


Fig. 1 Dendrograms showing combine distances for 14 temporary ponds based on their physical characteristics. Similarity was measured by Euclidean distances.

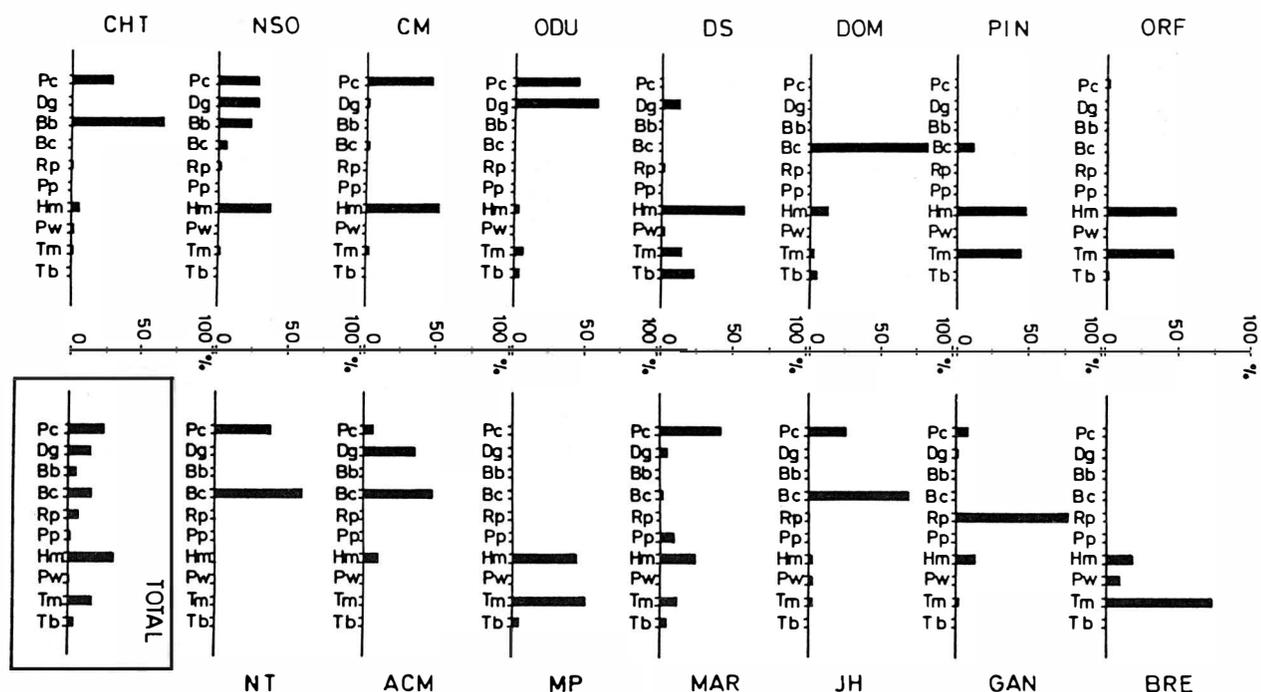


Fig. 2 Relative abundance of each species in the 15 ponds, expressed as percentages over the value of total relative abundance in each pond (see Table 1). (Abbreviations of specific names correspond to the initials of their scientific names.)

small size (Díaz-Paniagua, 1988) enabled this species to breed successfully in such temporary ponds.

Bufo bufo: Breeding of this species in the study area was clearly restricted to a zone characterised by the occurrence of permanent and extensive lagoons (not included in this study). The proximity of the two ponds where tadpoles were detected to large areas of water might have been an important reason for their occupation rather than any other physical characteristic.

Bufo calamita: The short duration of the larval period of this species allowed it to breed successfully in ephemeral pools. Its typical breeding sites in Doñana were small, shallow ponds, but it also has been found to breed in the shallow margins of large ones. This species was abundant in those ponds showing the lower values of relative depth (DOM and JH, see Fig. 2). Even ephemeral puddles have sometimes been observed as breeding sites for this species.

Rana perezi: Adults of this species were common in most areas of water in the study area (temporary ponds, permanent ponds and marshes). High larval abundance was only recorded in GAN, a large pond which persisted much longer into the summer than the others. The characteristic late onset of reproduction in this species (Díaz-Paniagua, 1986, 1988) probably limited its breeding sites to those ponds still in existence in late spring and summer.

Pelodytes punctatus: Breeding of this species in the study area typically occurred in the nearby marsh; where it was found during the autumn. Occasionally it was observed in temporary ponds surrounding this habitat (MAR).

Hyla meridionalis: This species had the largest relative abundance of all the species observed (see also Díaz-

Paniagua, 1983) and its presence in most of the ponds sampled suggested that it may breed in a wide variety of temporary ponds. Their tadpoles were recorded in every pond, with the exception of NT where the breeding season of this species did not coincide with the period of flooding of the pond (see Díaz-Paniagua, 1986, for a description of the breeding season).

Triturus marmoratus: This species typically bred in most temporary ponds in the area, although it was not found in two of the ponds studied. In one of these the reason was the drying up of the pond before the onset of the breeding season of these newts.

Triturus boscai: These newts seemed to have the same requirements for breeding sites as the species above (see Díaz-Paniagua, 1983). The low numbers found may be due to the difficulty in finding their larvae in the ponds.

Pleurodeles waltl: This was an abundant species in the area, breeding mainly in the nearby marsh, although small numbers were detected in the temporary ponds.

The larval communities in the ponds

A general view of the composition of larval communities in each pond, expressed after the relative abundance of each larval species is given in Fig. 2. The maximum number of species occupying one pond was seven, while for anurans the maximum number of species in a pond was six, and for urodeles it was three (all). However it should be noted that in several cases larvae did not utilise the space coincidentally (Díaz-Paniagua, 1988). The highest number of species coexisting was therefore lower than that of species using the ponds.

	Persistence	Relative Depth	Area
Diversity	-0.585* (n = 15)	-0.267 (n = 14)	0.089 (n = 14)
Total Relative Abundance	-0.213 (n = 15)	0.267 (n = 14)	-0.634* (n = 14)

TABLE 2: Spearman correlation coefficients calculated between variables describing physical characteristics of the habitats and variables regarding to the occurrence of larval amphibians (*:P<0.05).

Species	Number of Ponds	Niche Breadth
<i>P. cultripipes</i>	10	1.857
<i>D. galganoi</i>	7	1.122
<i>B. bufo</i>	2	0.549
<i>B. calamita</i>	8	1.480
<i>H. meridionalis</i>	14	2.081
<i>R. perezi</i>	4	0.128
<i>P. punctatus</i>	1	0
<i>T. marmoratus</i>	13	1.646
<i>T. boscai</i>	6	1.225
<i>P. waltl</i>	4	1.332

TABLE 3: Number of ponds in which each species was recorded and values of niche breadth calculated after the Shannon-Wiener diversity index.

The relative abundance of all the species was negatively and significantly correlated to the area of the ponds (Table 2) which affected the measurement because the larvae tended to be more concentrated in smaller ponds. Also a significant negative correlation existed between species diversity in the ponds and their duration, although large diversity values were also obtained for some long-lasting ponds. No significant correlation was found for relative depth between either

species diversity or total relative abundance in the ponds.

The presence of one species in the ponds and the diversity index calculated for each species according to its frequency of occurrence in the ponds (used as niche breadth index) were used to compare the spatial requirements of the species (Table 3). *Hyla meridionalis* was the most generalist species, being found in 14 of the 15 ponds, and presenting the largest value of diversity. At the other extreme, species such as *Bufo bufo* and *Rana perezi* were restricted to small numbers of ponds and presented low niche breadths whereas high abundance was only reached under particular conditions. Results obtained for *Pelodytes punctatus* and *Pleurodeles waltl* were not considered because of the small numbers found (see Fig. 2) thus suggesting that these are not their most characteristic breeding sites.

A cluster classification of the larval density of species in ponds is represented in Fig. 3, and the results obtained from a factor analysis (Table 4) contributed to its clarification. There did not seem to be a high association of species. Three main clusters appeared. A group with only one species, *Rana perezi*, which was not correlated with any of the others, high density only occurring in ponds where other species are not very abundant (see Fig. 2). The second cluster included the urodeles and two species of anurans: *Bufo calamita* and *Hyla meridionalis* which, being widely distributed, was negatively associated with the other four species of anurans. These last four species constituted the third cluster, including species negatively or not associated with those in the other groups.

DISCUSSION

The persistence of the temporary ponds may be considered as a limiting factor for the development of communities therein. For amphibian communities, the unpredictability of these habitats is compensated for by the flexibility of the breeding season (Diaz-Paniagua, 1986) and of the larval life duration with a

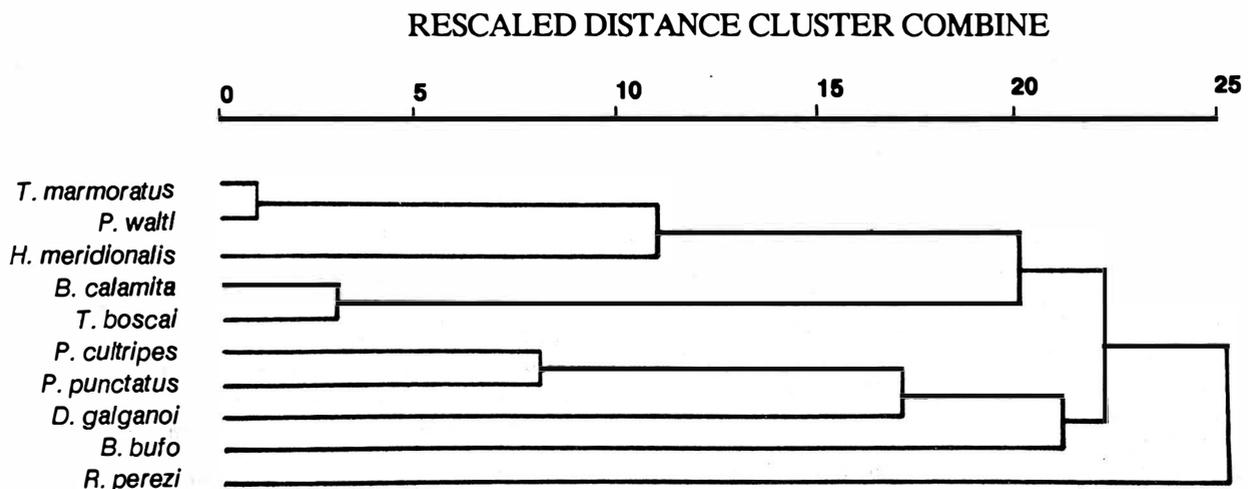


Fig. 3 Dendrogram showing cluster combine distances for the larval species based on their relative abundance in the ponds. Cosine of vectors of variables is used as distance coefficient, rescaled in the figure in a range 1 to 25.

	F1	F2	F3	F4	F5
<i>P. waltl</i>	0.868	-0.281	—	—	—
<i>T. marmoratus</i>	0.803	0.467	—	—	—
<i>D. galganoi</i>	-0.557	—	-0.340	—	—
<i>H. meridionalis</i>	—	0.916	—	—	—
<i>T. boscai</i>	—	—	0.848	—	—
<i>B. calamita</i>	—	-0.439	0.810	—	—
<i>P. punctatus</i>	—	—	—	0.909	—
<i>P. cultripipes</i>	-0.347	-0.431	—	0.668	—
<i>R. perezi</i>	—	—	—	—	0.920
<i>B. bufo</i>	—	-0.466	-0.383	—	—
VP	1.907	1.780	1.751	1.394	1.148

TABLE 4: Rotated factor loadings resulting from a factor analysis based on the relative abundance of the species in each pond, and the proportion of variance (VP) accounted for by the common factors. (Loadings less than 0.250 are not shown.)

wide range of body sizes at metamorphosis (Wilbur and Collins, 1973).

Temporal reproductive patterns of the species studied have been described in a previous study, where a segregation in time was found to be of great importance (Díaz-Paniagua, 1988). In this study, differences in the occupancy of the available breeding habitats were also found, which may contribute to the segregation of the species. On the basis of larval abundance in the ponds, the amphibian community studied may be considered as composed of: a) species breeding mainly in temporary ponds, commonly persisting from winter to early summer (*Hyla meridionalis*, *Triturus marmoratus*, *Triturus boscai*); b) species which usually breed in very temporary ponds (*Bufo calamita*, *Discoglossus galganoi*); c) species breeding mainly in permanent or extensive waters, although they may also occur in temporary ponds (*Pelobates cultripipes*, *Bufo bufo*, *Rana perezi*, *Pelodytes punctatus*, *Pleurodeles waltl*).

The high proportion of species in the group (c) was remarkable. Their larval life histories seem to be better suited to different habitat conditions from the temporary ponds although they can achieve an acceptable level of breeding success in them. The use of such ponds by these species provides another example of the flexibility of the breeding season of amphibians and probably this contributes to increasing the probabilities of success in reproduction under uncertain physical conditions.

The capability of inhabiting a great number of widely differing types of pond and of metamorphosing a large number of individuals may be considered as an indication of a species' ability to breed successfully in such kinds of ponds. In the same way, important variations in relative larval abundance are observed for some species depending on their coexistence with other larval species, resulting in negative associations, which seems to imply differences in competitive ability. Thus, some species appeared to occupy a great number of ponds and they were usually very abundant (e.g. *Hyla meridionalis*, *Triturus marmoratus*, *Pelobates cultripipes*). Others appeared to be restricted to a particular kind of pond and only reached high

numbers when those more common species were not so abundant, as was the case with *Bufo calamita* and *Discoglossus galganoi* in intermittently flooded or ephemeral ponds.

No overriding relationships among the larval species were found in a previous work (Díaz-Paniagua, 1983), but a temporal segregation was found (Díaz-Paniagua, 1988). Habitat partitioning also contributed to a decrease in the overlap among the larval species, suggesting that interspecific relationships might have had an influence on the community organisation. This may also be confirmed by a decrease in larval density of some widely distributed species when they have to share their habitats with other species. As Heyer (1976) argued, it is possible that factors contributing to those segregations might have been important 'historically' and that interspecific competition is not an important factor in the organisation of the larval amphibian communities at present because of the occurrence of the temporal and habitat partitioning.

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IDENTIFICATION OF CLOSELY-RELATED ANURAN EARLY LIFE-STAGES BY ELECTROPHORETIC FINGERPRINTING

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ABSTRACT

- (1) Protein electrophoretic patterns from early life stages of two anurans, *Bufo bufo* and *Bufo calamita*, were compared. Samples were taken from two widely-separated populations of each species.
- (2) Spawn jelly of the two toads could be distinguished reliably by the difference in molecular weight of a single major component (30,000 in *B. bufo*, 35,000 in *B. calamita*).
- (3) Small tadpole total proteins could be distinguished by the presence (*B. bufo*) or virtual absence (*B. calamita*) of two characteristic proteins of Mr 49,000 and 53,000.
- (4) Large tadpole tailfin proteins also differed in a species-specific way; *B. bufo* exhibited a strong band of Mr 62,000 that was almost absent in *B. calamita*, while the latter species had a doublet (Mr 57,000 and 58,000) instead of the single 57,000 Mr polypeptide seen in *B. bufo*.

INTRODUCTION

Molecular analyses offer great improvements in many areas of taxonomic biology where, in the past, there has been almost total reliance on morphological criteria. The more precise molecular approach has many possible uses, including service to field studies in cases where there are difficulties in recognising closely-related species. A good example of this situation arises within the amphibia; in Britain the two species of toad *Bufo bufo* and *Bufo calamita* are readily distinguished as adults, but with much greater difficulty as eggs and larvae. Morphological criteria for spawn and tadpoles do exist (e.g. see Smith, 1951; Beebee, 1983) but are notoriously unreliable. Larvae of both species, for example, are uniformly black and of very similar shape; identification is currently based on difficult measurements of mouth-width or tooth patterns, or on the appearance later in development of a white 'chin patch' in *B. calamita*. The first two of these criteria are very time-consuming on large samples, and all three have substantial error rates (e.g. Mathias, 1971; Beebee, 1977).

In this paper I describe a novel molecular approach to the identification of toad eggs and larvae that, for the above two species, has proved completely reliable.

MATERIALS AND METHODS

MATERIALS

Small samples of spawn and tadpoles of both toads were collected (that of *B. calamita* under licence) from two widely separated sites (Hampshire and Cumbria) in England; development was sustained thereafter in the laboratory (Beebee and Beebee, 1978). Routine chemicals, including electrophoresis-grade acrylamide, were from BDH (Poole, UK) and molecular weight marker proteins (range: 29,000-205,000) were from Sigma (Poole, UK).

SAMPLE PREPARATION

0.5-1.0ml batches of spawn jelly were cut and detached from spawn strings using scissors and forceps, and stored until needed at -20° . Each sample was then lyophilised overnight, dissolved in 100-200 μ l loading buffer (LB = 50mM Tris-HCl pH 6.8, 0.15M mercaptoethanol, 1% SDS, 10% glycerol, 0.001% phenol red) and immersed in a boiling water bath for 5 minutes. 50 μ l were used immediately after cooling for electrophoretic analysis. Small (<12mm) tadpoles were killed by flash-freezing, suspended in 100 μ l LB and treated as above prior to electrophoresis of 10-50 μ l aliquots. Sections of dorsal tailfin were rapidly excised from large (12-25mm) larvae laid on a damp tile, using a razor to cut as shown in Fig. 1. Tadpoles were returned to the tanks, and the fin sample suspended in 100 μ l LB followed by the same treatment employed for entire small tadpoles.

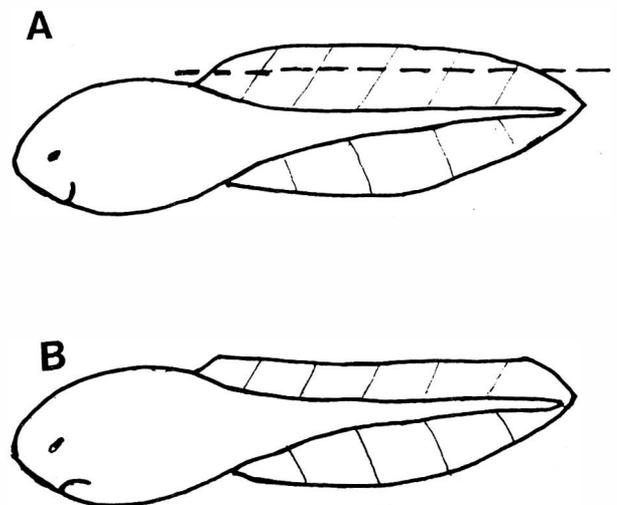


Fig. 1 Tailfin clipping regime.

ELECTROPHORESIS

This was carried out under strictly denaturing conditions. Separating slab gels contained 7.5-12% acrylamide, 0.2-0.35% bis acrylamide made up in 0.33M Tris-HCl pH 8.8, 0.1% SDS. A stacking gel of 5% acrylamide, 60mM Tris-HCl pH 6.8, 0.1% SDS was used and a running buffer of 50mM Tris, 0.38M glycine, 0.1% SDS pH 8.3. Electrophoresis was normally for about 6 hours at 100V. Staining was for 1-2 hours in 0.1% Coomassie blue in 10% acetic acid, 50% ethanol, followed by overnight destaining in 10% acetic acid. Gels were then photographed and, if required, scanned densitometrically using a LKB ultrascan with laser beam.

RESULTS

Examples of spawn jelly protein separations are shown in Fig. 2. All *B. calamita* samples showed strong bands at or about Mr 35,500 (band A on figure) whereas *B. bufo* spawn always showed a band of higher mobility (Mr around 30,000 position B). These were the strongest bands visible in the jelly extracts, and could be seen easily even in old spawn at the point of hatch (i.e. up to 14 days after deposition) although there was evidence of substantial degradation at these later times. The distinction was highly reliable, with similar patterns evident in spawn samples from

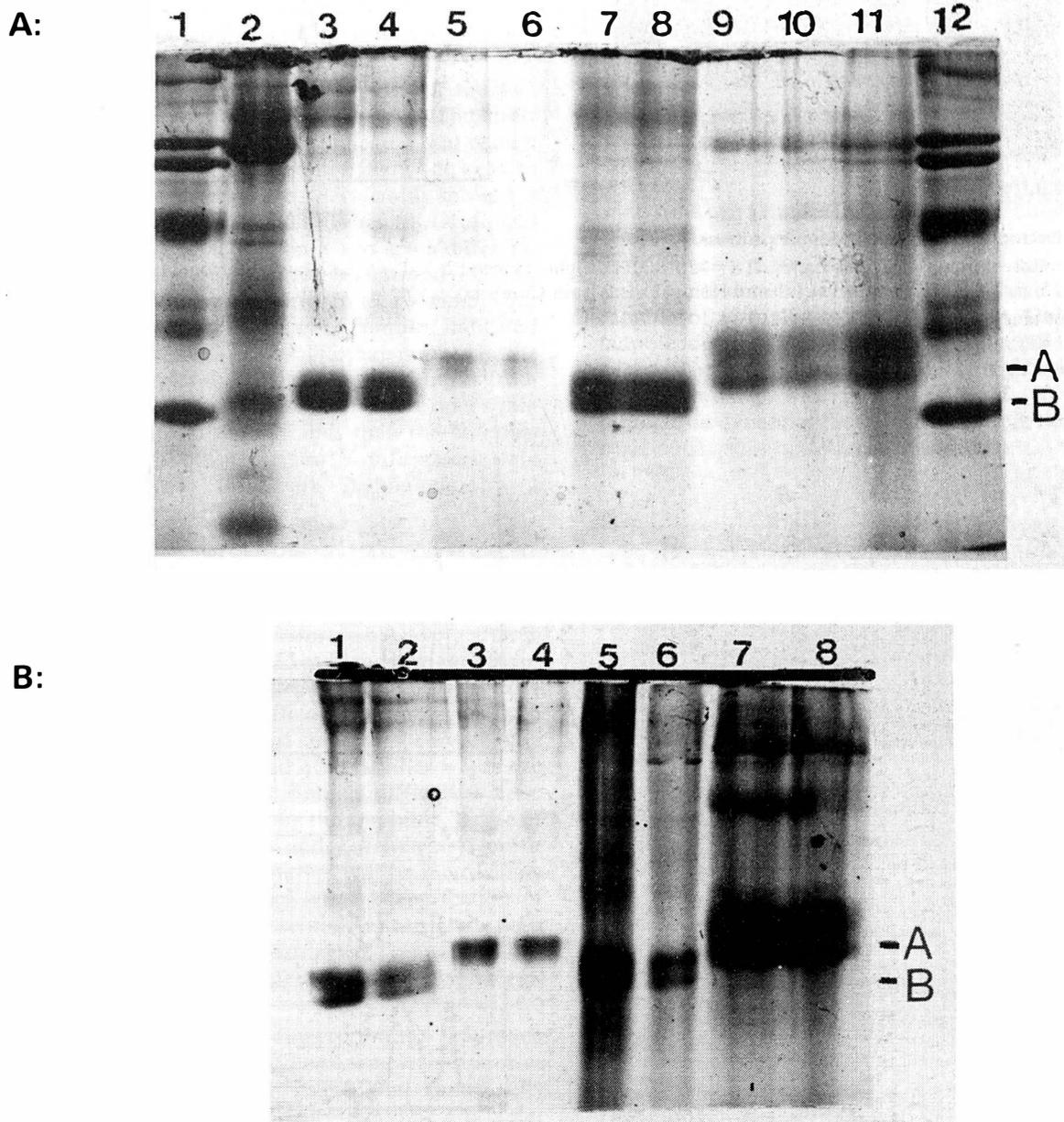


Fig. 2 Electrophoresis of spawn jelly proteins.

A: Samples from Hampshire populations on a 10% acrylamide gel. Lanes: 1, 12 = molecular weight markers; 2-*Rana temporaria*; 3-4 = fresh laid *B. bufo* spawn; 5, 6 = fresh laid *B. calamita* spawn; 7, 8 = *B. bufo* spawn at point of hatch; 9, 10, 11 = *B. calamita* spawn at point of hatch.

B: Samples from Cumbria populations on 12% gel. Lanes: 1, 2 = fresh *B. bufo* spawn; 3, 4 = fresh *B. calamita* spawn; 5, 6 = hatching *B. bufo* spawn; 7, 8 = hatching *B. calamita* spawn.

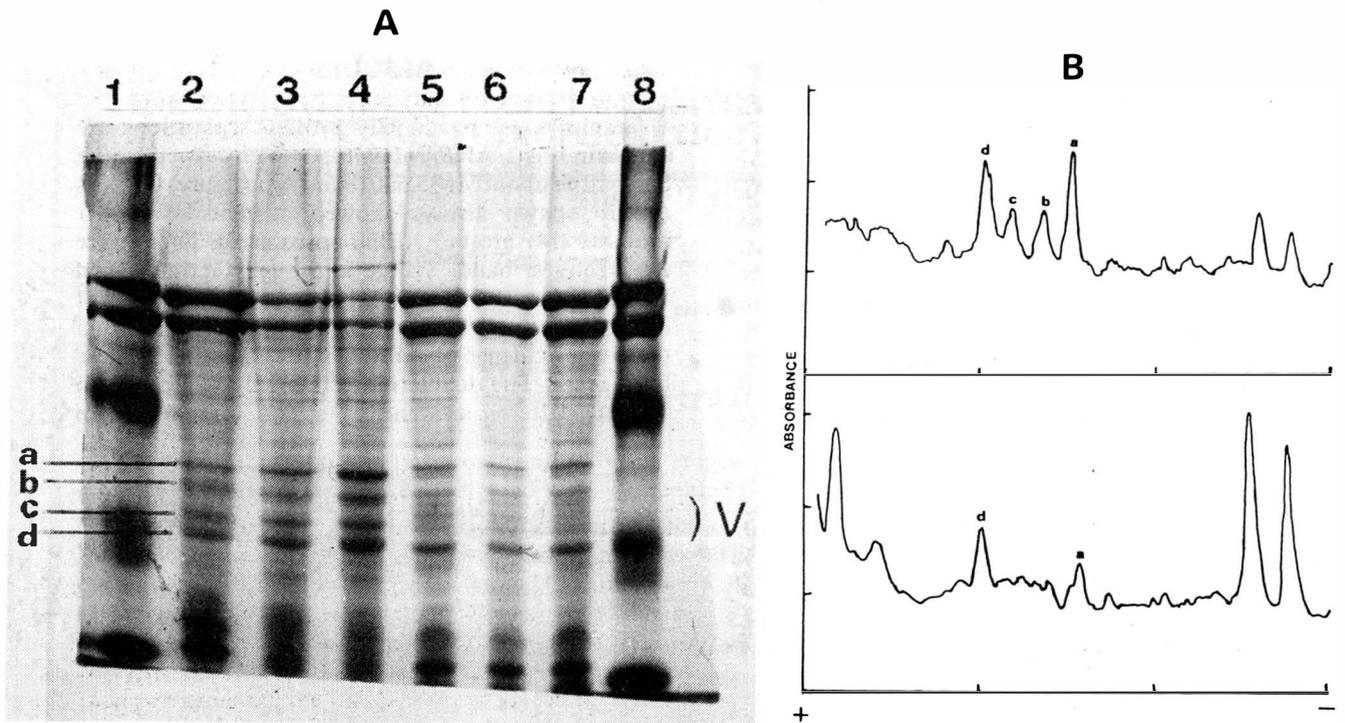


Fig. 3 Electrophoresis of small tadpole proteins.

A: Electrophoretogram (7.5% gel). Lanes: 1, 8 = Molecular weight markers; 2, 3, 4 = *B. bufo* larvae (2 from Hampshire, 1 from Cumbria); 5, 6, 7 = *B. calamita* larvae (1 from Hampshire, 2 from Cumbria).

B: Scans of lanes 4 (above) and 5 (below).

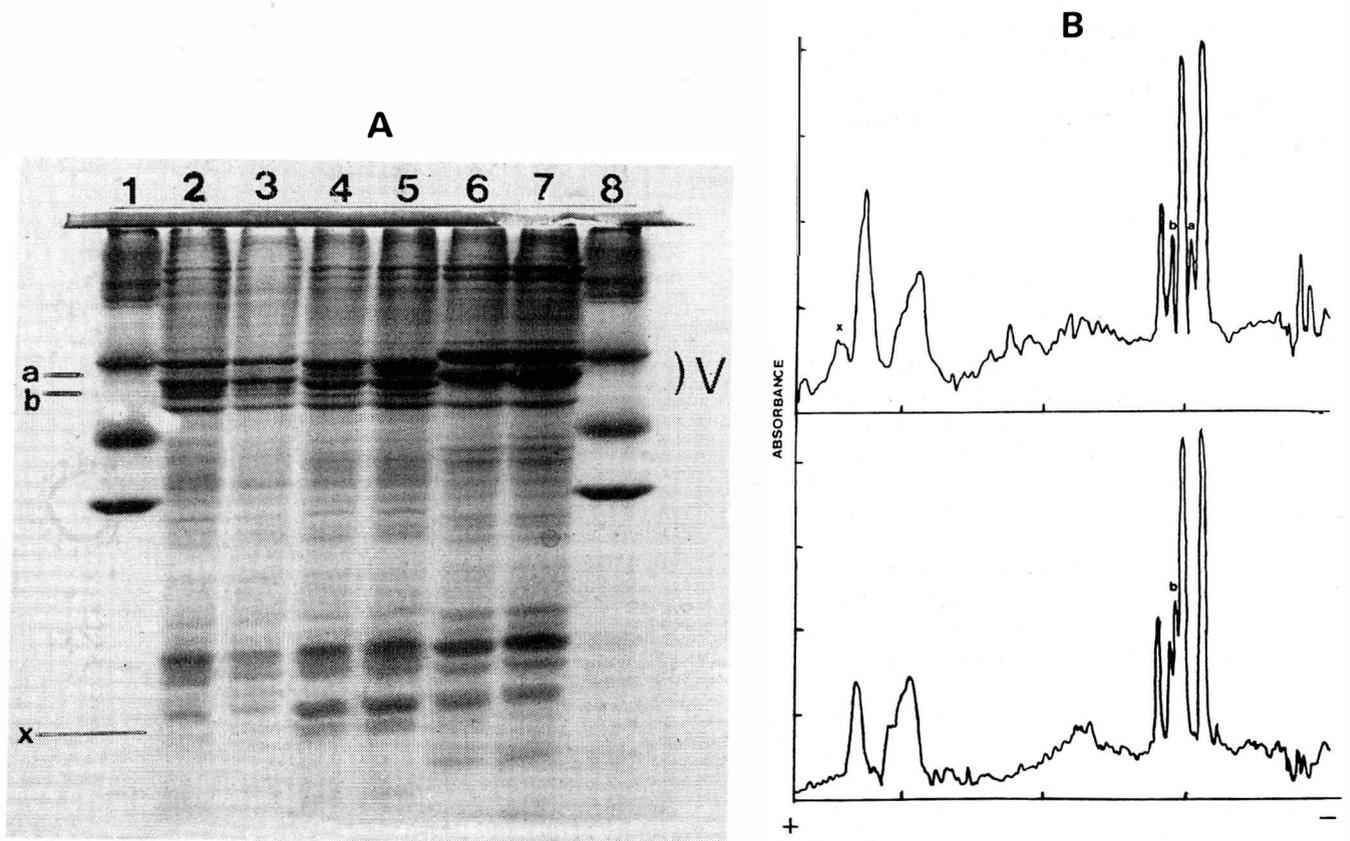


Fig. 4 Electrophoresis of large tadpole tailfin proteins.

A: Electrophoretogram (12% gel). Lanes: 1, 8 = Molecular weight markers (different from those used in Figs. 2 and 3); 2, 3 = *B. calamita* tailfins; 4, 5 = *B. bufo* tailfins; 6, 7 = *R. temporaria* tailfins. In each case one specimen was from Hampshire and the other from Cumbria.

B: Scans of lanes 4 (above) and 3 (below).

northern and southern England. Spawn jelly from a more distantly related anuran, *Rana temporaria* (lane 2) was quite different and showed a more complex banding pattern than the bufonid material.

Total protein patterns from three *B. bufo* and three *B. calamita* small tadpoles are shown in Fig. 3A. Again the patterns were generally reproducible, though the relative intensities of the high molecular weight proteins (90,000-120,000) and some very small ones varied substantially between tadpole extracts. Of greatest value was the region V, in which 4 bands a, b, c and d were always clearly discernible in *B. bufo* whereas b and c were indistinct or absent in all *B. calamita* samples. The presence or absence of strong b and c bands (Mrs 53,000 and 49,000), relative to a and d, was apparently diagnostic; differences in this part of the gel were confirmed by densitometer tracing (Fig. 3B).

Tailfin proteins from larger tadpoles of the two species were different again (Fig. 4A). The most reliable area of comparison, V, indicated that band a (Mr 62,000) was always strong in *B. bufo* but weak in *B. calamita*; and in region b, *B. calamita* showed a doublet (Mrs 57,000 and 58,000) whereas *B. bufo* had just a singlet of 57,000. Region X was often different, with a dense band of estimated Mr around 7,000 in *B. bufo* and little or nothing in *B. calamita*, but comparison of larger numbers of samples indicated that this difference was less reliable than implied by the particular examples shown here. Tailfin samples from *Rana temporaria* larvae (lanes 6 and 7) were once again more different from the bufonids than the bufonids were from each other. Region V differences were totally conserved; these are highlighted by a densitometer trace (Fig. 4B).

DISCUSSION

Bufo bufo and *Bufo calamita* probably diverged from a common ancestor at least 15 million years ago (Blair, 1971; Beebe, 1983). Nevertheless, their early developmental stages remain difficult to distinguish on morphological grounds and this poses considerable problems for ecological and other studies where the two species are sympatric. Similar difficulties arise with other species (e.g. among the amphibia, larvae of the newts *Triturus vulgaris* and *T. helveticus*), and it seems that molecular techniques will be increasingly useful to population studies where identification of large numbers of larvae is essential. It has already been shown that eggs of European newts (genus *Triturus*) can be identified by soluble protein electrophoretograms (Veith, 1987).

The electrophoretic fingerprinting approach described here is reasonably quick, simple, inexpensive and precise. It is easy to collect 1ml spawn jelly samples, or individual small tadpoles, for later analysis; even tailfin sections can be taken in less than a minute. The whole electrophoretic analysis, from the start of lysis (only necessary with spawn,

where protein is too dilute to run directly) to destaining, takes less than 36 hours and large numbers of samples (at least 12 per gel) can be processed simultaneously. Identification can be by inspection; photography or scanning is only required if a permanent record is needed. The chemicals are all cheap and the necessary apparatus present in most reasonably-equipped laboratories. In the multiple samples studied so far, all of known parentage, not a single ambiguity has arisen with respect to identification after examination of tens of specimens and the differences seem well conserved between populations hundreds of kilometres apart. Some bands, however, were more erratic in intensity between individuals than others and these were excluded from use in identification. The reasons for this variability were not clear but I suspect reflect different protein solubilisation efficiencies rather than real differences between individuals; the variation was usually greatest with the high Mr proteins, which may be less soluble or more prone to aggregation (thus not entering the gel properly). As a general rule it would seem wise to include reference samples of known parentage in such analyses when samples from the field are under study. Finally, much of the work can be done non-destructively; taking spawn jelly does not damage embryos, and tailfin clipping leaves viable tadpoles capable of virtually normal swimming. Only small tadpole identification involves mortality, but this is at a stage where abundance is usually so high that small-scale sampling will have negligible effects on population dynamics (both toads lay more than 1,000 eggs, natterjacks up to more than 7,000).

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METHODS FOR THE DETERMINATION OF THE PHYSICAL CHARACTERISTICS OF EGGS OF *ALLIGATOR MISSISSIPPIENSIS*: A COMPARISON WITH OTHER CROCODILIAN AND AVIAN EGGS

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ABSTRACT

The mass, length and breadth of 572 eggs of *Alligator mississippiensis* were measured and described as a complete sample and as subsets of 14 clutches. Egg volume and density were calculated. A multiple regression equation was generated to predict initial egg mass from egg length and breadth. A weight coefficient (K_M) was determined for alligator eggs and its value was compared both to published values for avian eggs and to values for other crocodilian eggs calculated from literature data. The value of K_M in crocodilians was higher than in avian eggs implying that the density of alligator eggs was much higher than the density of avian eggs. Egg volume in alligators was also estimated using the volume coefficient (K_V) for avian eggs but this was found not to be applicable.

INTRODUCTION

Over the past two decades the avian egg has been extensively studied and many different relationships between various egg, and incubation, parameters have been established (see Rahn and Paganelli, 1981 and Rahn, Whittow and Paganelli, 1985). Allometric relationships are observed between egg mass and incubation period (Rahn and Ar, 1974), water vapour conductance of the eggshell (Ar, Paganelli, Reeves, Greene and Rahn, 1974), surface area and density of the egg (Paganelli, Olszowka and Ar, 1974). Such allometric relationships have not been investigated in reptiles. This is surprising considering the similarity between avian eggs and those of many reptiles, particularly crocodilians which are the closest living relatives of the birds. Indeed, egg structure in birds and crocodiles is very similar (Romanoff, 1967; Ferguson, 1985; Manolis, Webb and Dempsey, 1987) but there have been only a few comparative studies. The chemical composition of crocodilian egg yolk and albumen shows both similarities and differences to that of the domestic fowl (Burley, Back, Wellington and Grigg, 1987, 1988). Eggshell conductance, to water and respiratory gases, has been found in crocodilians eggs to be two to five times greater than in avian eggs of comparable size (Packard, Taigen, Packard and Shuman, 1979; Lutz, Bentley, Harrison and Marszalek, 1980). Comparative studies of avian and reptilian eggs may prove to be important in assessing the effects of the eggshell on the physiology of the embryo and evolution of incubation conditions (Packard and Packard, 1980).

Despite such high conductances to water vapour it has been shown that air spaces in crocodilian eggs, although rare in nature and deleterious if large (Ferguson, 1982, 1985), are common in artificially

incubated eggs; the loss of some water from the egg appears to be tolerated by the embryo (Manolis, *et al.*, 1987; Whitehead, 1987; Deeming and Ferguson, 1989). In common with avian eggs, which normally lose water during incubation, crocodilian eggshells are rigid and non-compliant which allows the air cavities to develop, although in contrast to avian eggs crocodilian eggs can swell under some incubation conditions (Manolis, *et al.*, 1987).

In bird eggs air spaces are normal and water loss is essential for normal development (Romanoff, 1967). It is often useful to calculate initial mass of eggs after unknown periods of incubation (Hoyt, 1979). This can be done by filling the air space but this is lethal to the embryo (Grant, Paganelli, Pettit, Whittow and Rahn, 1982). To overcome this problem, several authors have developed techniques for determining the initial mass, volume and density of avian eggs using linear dimensions (Paganelli, *et al.*, 1974; Hoyt, 1979; Rahn, Parisi and Paganelli, 1982). No such methods are available for crocodilian eggs but considering the rapidly developing interest in crocodilian eggs in the field and the laboratory (Webb, Manolis and Whitehead, 1987) such methods to determine whether eggs have lost water during incubation without killing the embryo may be useful. The aims of this study were (1) to describe methods of determining initial mass of *Alligator mississippiensis* eggs from their linear dimensions, (2) to calculate the volume and density of alligator eggs, (3) to examine these characteristics of alligator eggs from different clutches and, (4) to compare the measurements of alligator eggs with other crocodilian eggs and those of birds. It is hoped that these data will give us some indication of the variability in the dimensions of eggs within a species, between species of crocodilians and between crocodilians and birds.

MATERIALS AND METHODS

Eggs of *Alligator mississippiensis* were collected from 14 wild nests at the Rockefeller Wildlife Refuge, Louisiana, USA. All eggs were collected 24 hours after laying (as assessed by the extent of opaque banding of the eggs [Ferguson, 1982, 1985]) and were immediately air-freighted to Manchester, UK. On arrival at the laboratory (day 3 or 4) the eggs were weighed to the nearest to 0.01g. The eggs were placed in incubators (set at 30°C and 33°C) and were used in other studies (Deeming and Ferguson, 1989). The daily rate of water loss of these eggs was less than 0.01g.day⁻¹ under conditions of very high humidity and irrespective of temperature (Deeming and Ferguson, 1989); for the purposes of this study the initial recording of egg mass in the laboratory was considered to be a close approximation of initial egg mass (IEM) at oviposition. During the course of the other study the maximum length (L) and maximum breadth (B) of each egg were measured using Vernier calipers to the nearest 0.01cm. All eggs lost water during incubation but only eggs with intact eggshells were used in this study.

For subsequent calculations the shape of each egg was assumed to be a true ellipsoid; the maximum length and breadth of the egg occurs at the equator of the latitudinal and longitudinal planes. Egg volume (V) was calculated using the relationship:

$$V \text{ (cm}^3\text{)} = \frac{\pi L.B^2}{6} \quad (1)$$

Initial egg density (g.cm⁻³) was calculated from the measured egg mass and calculated volume. The weight coefficient (K_M) has the same units as density but it is simply a coefficient between egg mass and linear dimensions and ignores the effect of egg shape ($\pi/6$ in equation 1). K_M (g.cm⁻³) was determined from eggs measured directly, and from data presented in Ferguson (1985), using the relationship:

$$K_M = \frac{\text{Initial Egg Mass}}{L.B^2} \quad (2 - \text{Hoyt, 1979})$$

Egg volume was also calculated using the volume coefficient, K_V = 0.509, derived from avian eggs:

$$\text{Volume} = 0.509.L.B^2 \quad (2 - \text{Hoyt, 1979})$$

Data were stored on a Prime mainframe computer and calculations were performed using the Minitab statistical package (Ryan, Joiner and Ryan, 1985). Multiple regression techniques were used to produce an equation to predict initial egg mass from linear dimensions (significance levels were assessed using a correlation coefficient [R²] and an F-ratio statistic).

RESULTS

In total 572 eggs of *A. mississippiensis* from 14 clutches were weighed and measured. Mean values for measured physical dimensions, and calculated parameters, of these eggs are shown in Table 1. Both egg length (L) and breadth (B) were individually useful in predicting initial egg mass (IEM), but multiple regression analysis revealed that a better prediction for

egg mass could be achieved using both linear dimensions in conjunction:

$$\text{IEM} = 11.6L + 29.7B - 134, R^2 = 94.8\%, F_{2,571} = 5248. \quad (4)$$

	<i>N</i>	<i>S.D.</i>	<i>Range</i>	
Initial egg mass (g)	72.80	6.55	54.89	— 91.52
Egg length (cm)	7.16	0.32	6.25	— 8.15
Egg breadth (cm)	4.15	0.12	3.83	— 4.44
Egg volume (cm ³)	64.73	5.79	49.00	— 80.88
Egg density (g.cm ⁻³)	1.125	0.024	1.033	— 1.298
K _M (g.cm ⁻³)	0.589	0.013	0.541	— 0.680
Volume — K _V (cm ³)	62.92	5.63	47.64	— 78.61

TABLE 1: Physical dimensions of 572 eggs of *Alligator mississippiensis* from 14 clutches. Initial egg mass, maximum length and maximum breadth at the equator of the egg are direct measurements. Egg volume, density and the value for the observed weight coefficient (K_M) are calculated (Hoyt, 1979). Egg volume calculated from the observed volume coefficient for avian eggs (Volume-K_V, Hoyt, 1979) is included.

There was a wide variation in initial egg mass in the eggs sampled; the range of nearly 37g in the sample (Table 1) was reflected by a range of 20g difference in mean egg mass between clutches (Fig. 1). There was greater variation in egg length within the sample and between individual clutches than was observed for egg breadth (Fig. 1). Generally, both egg length and breadth increased with increasing egg mass although breadth was better correlated with egg mass for each clutch (Fig. 1).

Egg volume was closely correlated with initial egg mass (Fig. 2). There was a range of densities within the sample (Table 1), but there was no correlation with

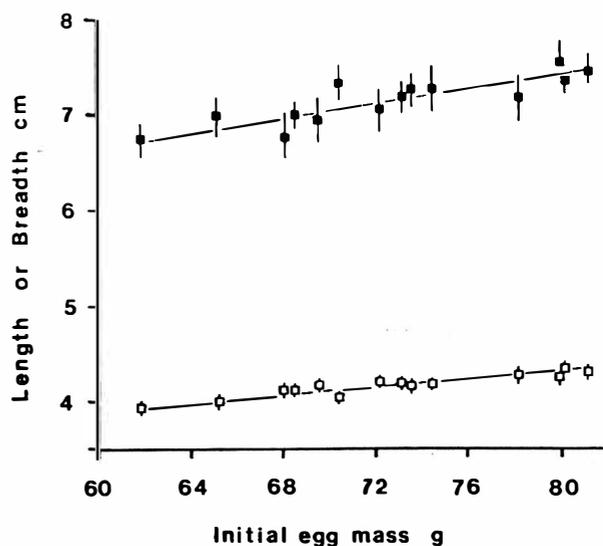


Fig. 1 The relationship between mass and length (closed symbols) and breadth (open symbols) of eggs of *Alligator mississippiensis* from 14 different clutches. Values are means ± S.D. and lines are fitted by eye.

initial egg mass between clutches. The coefficient of variation (Hoyt, 1979) around the mean value for K_M in the sample of eggs was only 2.2%. Egg volume, calculated using the mean K_V for avian eggs underestimated the values for egg volume calculated from egg shape (Table 1).

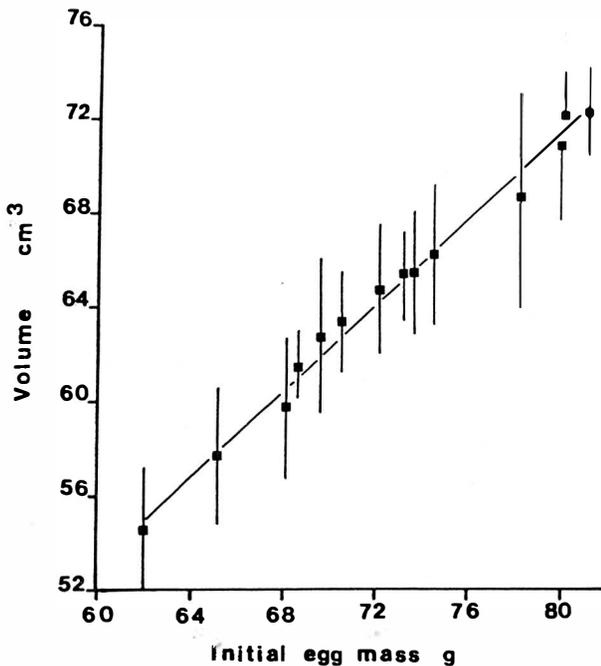


Fig. 2 The relationship between egg mass and volume for alligator eggs from 14 clutches. Values are means \pm S.D. and lines are fitted by eye.

DISCUSSION

Egg size varies between female alligators; each clutch has different characteristics. Some clutches show a large variation in egg dimensions, others do not. Mean egg breadth between clutches is more uniform than mean length which may indicate some

kind of limitation on egg breadth by the oviduct which may not apply to the length of the egg. These differences may be related to clutch size or maternal age but in the present study no clear relationships between clutch size and egg mass could be found. Further study is required to establish the factors which determine the size of eggs in individual clutches.

The initial mass of avian eggs can be calculated (Hoyt, 1979) or can be determined by filling the air space with water (Grant, *et al.*, 1982). It is difficult to repeat such a method in crocodilian eggs because formation of air spaces is not uniform: they can occur within the albumen, between the chorio-allantois and shell membrane, or between the shell membrane and the calcitic shell (Ferguson, 1985; Whitehead, 1987). The methods described in this study allow a value for initial mass to be allocated to alligator eggs from unknown incubation conditions. Such a technique has applications both in the field and in the laboratory in assessing whether the egg has lost water during incubation, though it is not applicable when the egg has swollen and cracked (Manolis, *et al.*, 1987; Grigg, 1987). Knowledge of initial egg mass is useful in assessing the amount of the albumen and yolk in the egg and in converting egg contents into hatchling. Important relationships between egg mass and the metabolic rate of the embryo, incubation period, water vapour conductance and egg surface area in birds (Rahn, *et al.*, 1974; Rahn and Ar, 1974; Ar, *et al.*, 1974; Paganelli, *et al.*, 1974) may also apply in crocodilians and other reptiles but further study is required.

Values for K_M calculated for eggs of various crocodilians (data from Ferguson [1985]) are shown in Table 2. K_M derived from alligator eggs in the present study (Table 1) is lower than that derived from data presented by Ferguson (1985). The reason for this discrepancy may lie with the size and sources of the data. Ferguson (1985) presents a mean value for egg mass and dimensions from several sources collected over many years from different geographic locations both in relation to *Alligator* and other species listed in Table 2. Data for alligator eggs in the present study are

Species	L	B	IEM	K_M
<i>Alligator mississippiensis</i>	7.4	4.3	84	0.614
<i>Alligator sinensis</i>	6.8	3.4	52	0.662
<i>Caiman crocodilus crocodilus</i>	6.5	4.0	59	0.567
<i>Caiman crocodilus yacare</i>	6.8	4.2	75	0.625
<i>Caiman latirostris</i>	6.6	4.6	84	0.601
<i>Paleosuchus palpebrosus</i>	6.6	4.2	69	0.593
<i>Crocodylus johnstoni</i>	6.6	4.2	68	0.584
<i>Crocodylus niloticus</i>	7.5	4.8	110	0.637
<i>Crocodylus novaeguinae</i>	7.6	4.3	85	0.605
<i>Crocodylus palustris</i>	7.5	4.6	84	0.529
<i>Crocodylus porosus</i>	7.7	5.2	113	0.543
<i>Osteolaemus tetraspis tetraspis</i>	6.3	3.7	52	0.603

TABLE 2: Mean values for egg length (L), breadth (B) and initial mass (IEM) from a variety of crocodilians (Ferguson, 1985). Observed weight coefficient is calculated from the relationship: $K_M = IEM/L.B^2$ (Hoyt, 1979).

from a single geographic location, supplied at the same time in the nesting season of one particular year. It is, therefore, likely that these eggs were laid by similar sized females and are more likely to be similar to each other than data from other populations sampled at different times and in different years.

The data from different crocodylians show that, like birds (Hoyt, 1979), K_M varies between species and is not related to egg length, breadth or mass. The values for K_M for 12 species of crocodylian (mean = 0.597, range = 0.529-0.662) are, however, higher than those for 26 species of bird (mean = 0.548, range = 0.527-0.597; Hoyt, 1979) and very much higher than values for eight species of emydid turtles (mean = 0.526, range = 0.304-0.612; calculated from Ewert [1979]). Therefore, for any given set of egg dimensions, crocodylian eggs are heavier, and turtle eggs are lighter, than bird eggs. As K_M ignores egg shape, this suggests that differences between avian and crocodylian eggs are not due to their different shapes (all crocodylian eggs are ellipsoid; Ferguson, 1985) but due to their density. Alligator eggs have a mean density (1.125 g.cm^{-3}) higher than that for many bird eggs (mean = 1.073, range = 1.055-1.104; Rahn, *et al.*, 1982). The density of crocodylian albumen is lower than that for avian eggs but crocodylian yolk has a greater density than avian yolk (Manolis, *et al.*, 1987). Differences in total egg density between birds and crocodylians may lie in the relative densities of the egg contents or the density the eggshell. The extent to which these factors contribute to the observed differences in egg density and K_M is yet to be determined.

The value of K_V for avian eggs underestimated the volume of crocodylian eggs but by a constant amount (2 cm^3). K_V for crocodylian eggs must, therefore, be higher than that for bird eggs. Egg volume is greater for any set of linear dimensions in crocodylians. The volume of alligator eggs was not, however, determined empirically in the present study, and K_V cannot be calculated in this study but may have a value of $0.524 (\pi/6)$.

In conclusion, differences in mass, volume and density occur between avian and crocodylian eggs. The allometric relationships between egg mass, various incubation parameters and shell characteristics (Rahn, *et al.*, 1974; Rahn and Ar, 1974; Ar, *et al.*, 1974; Paganelli, *et al.*, 1974) may well be present in crocodylians, turtles and squamates. However, these three types of reptiles differ greatly in their eggshell structure and incubation requirements (Packard and Packard, 1980, 1988; Ewert, 1985; Ferguson, 1985) and therefore, any attempts to derive allometric relationships for reptiles as a whole (as has been accomplished for birds) may mask important patterns for each type of reptile.

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PALMATE NEWT PREDATION ON COMMON FROG, *RANA TEMPORARIA*, AND COMMON TOAD, *BUFO BUFO*, TADPOLES

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ABSTRACT

In a series of laboratory experiments, male palmate newts that had no previous experience of anuran tadpoles as potential prey were conditioned for five days to small worms, common frog tadpoles, common toad tadpoles or a 50:50 mixture of frog+toad tadpoles. During three experiments, conditioned newts were offered 1) a 50:50 mixture of frog+toad tadpoles 2) only frog tadpoles or 3) only toad tadpoles.

The results showed that palmate newts with no previous experience of either frog or toad tadpoles very quickly learnt to distinguish between them and take only frog tadpoles. This was supported by the results of a fourth experiment using male palmate newts from a pond that contained both tadpole species. Common toad tadpoles were almost totally rejected.

The conclusion is, that common frog tadpoles gain no long term protection against predation from palmate newts through associating with common toad tadpoles.

INTRODUCTION

Three species of newt occur in Great Britain, the warty newt (*Triturus cristatus*), smooth newt (*T. vulgaris*) and palmate newt (*T. helveticus*). All three species are voracious predators and are known to take a wide range of aquatic invertebrates (Avery, 1968; Griffiths, 1986). In addition, smooth newts are also known to take frog tadpoles (Cooke, 1974) but, like palmate newts, reject toad tadpoles (Cooke, 1974; Griffiths, 1986) whilst warty newts will take both frog and toad tadpoles (Cooke, 1974; Heusser, 1971).

Unlike frog eggs and tadpoles, those of toads are generally thought to be unpalatable to many potential predators (Licht, 1968; Wassersug, 1971). The difference in palatability between common frog (*Rana temporaria*) and common toad (*Bufo Bufo*) tadpoles presents an interesting question: In ponds where both tadpole species occur together, do frog tadpoles gain any protection against predation by newts due to the presence of toad tadpoles?

This paper reports the results of a series of laboratory experiments designed to investigate tadpole predation by palmate newts.

METHODS

Four experiments were carried out in the laboratory under natural light conditions and at a temperature of 13.5-15.5°C. to determine whether palmate newts predate common frog and common toad tadpoles. The experiments were also designed to investigate whether mixed tadpole populations affected newt predation rates.

In experiments 1-3, male newts were obtained from a heathland pond that was not used as a breeding site by either common frogs or common toads. These newts therefore had no previous experience of frog or toad tadpoles as potential prey. Forty newts were used in each experiment ($n = 3$) and each newt was only used once. In each experiment, 10 newts were placed in each of four tanks containing 2 litres of pond water ($\text{pH} = 7$) and conditioned (fed) for five days on:

- Tank 1 — 40 frog tadpoles
- Tank 2 — 40 toad tadpoles
- Tank 3 — 20 frog tadpoles + 20 toad tadpoles
- Tank 4 — small earthworms

Twice each day at 10.00hrs and 22.00hrs the number and species of tadpoles remaining in each tank was recorded and any missing tadpoles replaced to maintain a constant prey density of 40. Missing earthworms were also replaced to maintain a constant food supply. After five days, each set of 10 newts were placed in four new tanks containing 1 litre of pond water and deprived of food for 24 hours.

Conditioned newts were then each placed in individual tanks (28 x 16cm) containing 1 litre of pond water ($\text{pH} = 7$) and 10 tadpoles of similar size (frog $\bar{x} = 22.6\text{mm}$; $\text{SD} = 4.01$; $N = 41$; range = 15-29mm; toad $\bar{x} = 18.5\text{mm}$; $\text{SD} = 1.5$; $N = 30$; range = 16-21mm). The number of tadpoles eaten by each newt was recorded each hour for 24 hours and missing tadpoles were replaced to maintain a constant prey density of 10/L. In the three experiments each newt was given:

- Expt. 1 — 5 frog + 5 toad tadpoles
- Expt. 2 — 10 frog tadpoles
- Expt. 3 — 10 toad tadpoles

In experiment 4, 30 male newts were obtained from a pond which was also used extensively by both frogs and toads as a breeding site. Since these newts were already conditioned to a mixture of frog+toad tadpoles no further conditioning was done. All newts were deprived of food for 24 hours before being placed in individual tanks and given 10 tadpoles as in experiments 1-3.

The data were analysed using analysis of variance. Comparisons between the numbers of tadpoles eaten by newts under different conditioning regimes were made using Chi square analysis. Means were compared using Student's *t* test.

RESULTS

Conditioning

At the start of each conditioning period the newts immediately approached and seized the prey provided (worm or tadpole). Worms and frog tadpoles were

subsequently eaten whilst, with the exception of 3 toad tadpoles, the toad tadpoles were released. Although worms and frog tadpoles continued to be taken throughout the conditioning periods, toad tadpoles were ignored after the initial captures.

During the 3 x 5 day conditioning periods, totals of 457 frog tadpoles and 3 toad tadpoles were eaten by the 60 newts presented with either all frog or a 50:50 mixture of frog+toad tadpoles. The 3 toad tadpoles were caught and eaten during the first 12 hours of the conditioning period. No tadpoles were eaten by the newts presented with only toad tadpoles.

The mean number of frog tadpoles eaten by 10 newts given either frog or frog+toad tadpoles during each 12 hour period of conditioning is shown in Fig. 1. During the first 12 hours of the conditioning period newts given only frog tadpoles ate significantly more than those given frog+toad tadpoles ($t = 6.81$; $\text{df} = 4$; $p < 0.01$). After the first 12 hours of conditioning the mean numbers of tadpoles eaten during each subsequent 12 hour period stabilised and were not significantly different (\bar{x} frog = 7.00; $\text{SD} = 3.47$; $N = 27$; range = 1-13; \bar{x} frog+toad = 6.89; $\text{SD} = 2.55$; $N = 27$; range = 2-11; $t = 0.13$; $p > 0.10$).

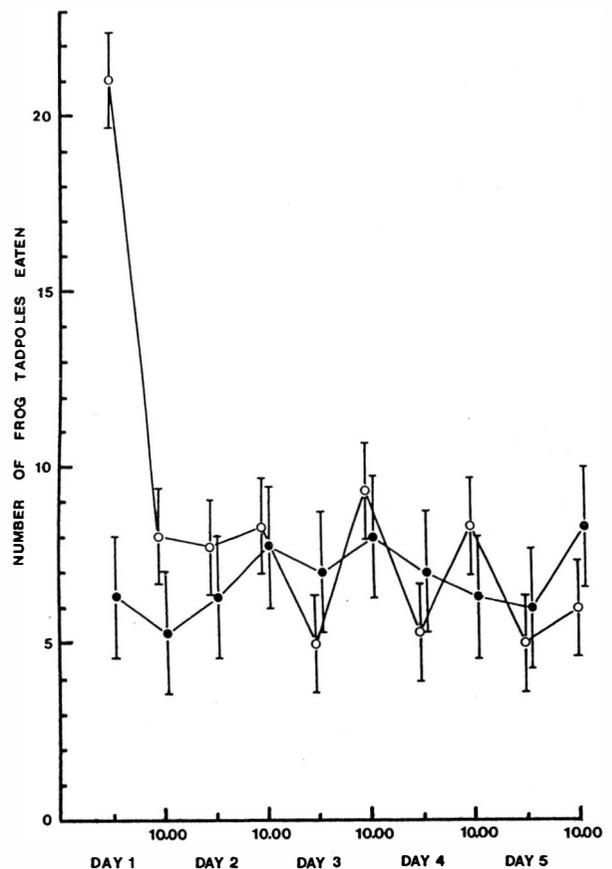


Fig. 1 Mean (\pm SD) number of frog tadpoles eaten every 12 hour by 10 male palmate newts given either frog (o) or frog+toad (●) tadpoles.

Experiments 1-3

In experiment 3 (toad tadpoles) only 1 toad tadpole was eaten and that was caught after 8 hours by a newt conditioned to frog+toad tadpoles.

Although no toad tadpoles were eaten in experiment 1, some frog tadpoles were caught in experiments 1 and 2 and either chewed and released or eaten and regurgitated. Three times as many tadpoles were rejected by the toad conditioned newts given frog tadpoles ($N = 9$) than by any other combination ($N = 2-3$). Rejected tadpoles were always dead and were therefore discounted from the final analysis of numbers consumed.

<i>Conditioned to</i>	<i>Expt. 1 (frog+toad)</i>	<i>Expt. 2 (frog)</i>	<i>Expt. 3 (toad)</i>
Worms	11	19	0
Frog tadpoles	23	27	0
Frog+toad tadpoles	29	31	1
Toad tadpoles	11	32	0

TABLE 1: Number of frog tadpoles eaten in experiments 1 and 2 and toad tadpoles eaten in experiment 3 by Palmate newts conditioned to worms, frog tadpoles, frog+toad tadpoles and toad tadpoles.

The total number of tadpoles eaten by each group of newts in each experiment is shown in Table 1. The null hypothesis in each experiment, tested using Chi square analysis, was that the expected number of tadpoles eaten by each group of newts was equal. Although significant differences were found between newt groups in experiment 1 (overall $\chi^2 = 13.14$, $df = 3$, $p < 0.01$; Table 2), none were detected in experiment 2. Newts conditioned to either worms or toad tadpoles ate significantly fewer tadpoles than newts conditioned to either frog or frog+toad tadpoles.

	<i>Frog</i>	<i>Frog+Toad</i>	<i>Toad</i>
Worms	4.23 *	8.10 **	NS
Frog		NS	4.23 *
Frog+Toad			8.10 **

TABLE 2: Chi square (1df) values for comparisons between the numbers of frog tadpoles eaten by Palmate newts conditioned to worms, frog tadpoles, frog+toad tadpoles and toad tadpoles and given a 50:50 mixture of frog+toad tadpoles (expt. 1). $p < 0.05$ (*); $p < 0.01$ (**); NS = Not significant. Overall $\chi^2 = 13.14$, $df = 3$, $p < 0.01$.

The mean total body lengths (BL = head+body+tail), excluding the tail filament, of newts used in experiments 1 and 2 were compared to determine whether differences in newt feeding rates between experiments might have been the result of differences in newt body size. The two means were not significantly different ($p > 0.05$) and no significant correlation was found between newt body size and the number of tadpoles eaten.

Expt. 1: $\bar{x} = 62.10$ mm; SD = 3.30; N = 40; range = 53-69mm
 Expt. 2: $\bar{x} = 60.72$ mm; SD = 3.66; N = 40; range = 51-68mm

Experiment 4

The results of experiments 1 and 2 show that palmate newts that have never encountered anuran

tadpoles can learn, over a very short period, to distinguish between frog and toad tadpoles. The newts used in this experiment were from a pond which was also a traditional breeding site for both frogs and toads. Since they had been exposed to tadpoles of both species for at least two months before they were caught it was assumed that they were able to distinguish between them. Therefore, the null hypothesis for this experiment was that the numbers of tadpoles eaten by newts offered either frog or frog+toad tadpoles would be equal. The mean numbers of frog tadpoles eaten by newts given frog tadpoles or frog+toad tadpoles were 4.6 (SD = 1.26, N = 10) and 3.2 (SD = 1.75, N = 10) respectively. No significant difference ($\chi^2 = 2.51$; $df = 1$) was found between these two means. As in experiments 1 and 2, no toad tadpoles were taken.

DISCUSSION

Evidence for learning came initially from observing the behaviour of the newts when they were first presented with tadpoles at the start of the conditioning period. Tadpoles, irrespective of species or mix, were immediately seized and then either eaten, in the case of frog tadpoles, or released, in the case of toad tadpoles. After these initial encounters only frog tadpoles continued to be caught. This implied 1) that all tadpoles were initially recognised as potential prey and 2) that frog tadpoles were palatable whilst toad tadpoles were not.

Subsequently, the evidence from experiment 1 showed that newts conditioned to a mixture of frog+toad tadpoles ate more frog tadpoles than expected compared with newts conditioned to either worms or toad tadpoles. Furthermore, toad conditioned newts, that had learnt to avoid tadpoles, and worm conditioned newts, that had no prior experience of tadpoles, both ate fewer tadpoles than expected compared with frog conditioned newts.

The results of comparing the number of tadpoles eaten in experiment 1 by the frog conditioned and toad conditioned newts were interesting. Although the null hypothesis tested was that the number of tadpoles eaten by each group of newts should have been equal it might have been expected that the toad conditioned newts, that had been effectively deprived of food for six days, would have eaten at least as many tadpoles as the frog conditioned newts and perhaps more, rather than fewer, as observed. The difference between the two groups of newts was that the frog conditioned newts recognised all tadpoles as palatable whilst the reverse was true for the toad conditioned newts. Despite the toad conditioned newts being clearly hungry as demonstrated in experiment 2 they nevertheless largely ignored the palatable frog tadpoles. As a result of their conditioning, these newts had to overcome an aversion to tadpoles and learn to recognise frog tadpoles as palatable whilst the frog conditioned newts had no such aversion and only had to learn to recognise toad tadpoles as unpalatable. Furthermore, the toad conditioned newts aversion to tadpoles would also have been reinforced each time a toad tadpole was encountered.

Four clear conclusions can be drawn from the three five day conditioning periods and four one day experiments; 1) palmate newts readily catch and eat frog tadpoles, 2) palmate newts almost totally reject toad tadpoles, 3) recognition of distasteful prey by palmate newts is not innate but learnt and 4) because palmate newts can learn to distinguish between palatable and unpalatable prey, frog tadpoles gain no long term (only short term) protection against newt predation through mixing with toad tadpoles.

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THE POLYMORPHISM OF *PODARCIS PITYUSENSIS* AND ITS ADAPTATIVE EVOLUTION IN MEDITERRANEAN ISLES

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ABSTRACT

The variation in morphological and colouring features shown by the insular lacertid populations of *Podarcis pityusensis* is discussed from the point of view of their adaptive advantages to specific insular ecosystems. Insularity factors, i.e. area and island-age, have been found to be related to average body size, and the average luminosity of each population. Populations tend to show a size increase, a greater morphological homogeneity and darker dorsal colouring on smaller and older islands. The advantages of larger size and melanism are discussed as well as their possible causes in the insular microecosystems of the Pityusic Archipelago. Genetic drift seems to play a secondary role, whereas a positive selection in favour of melanism and giantism is observed. Both features are not linked as cause and effect, but seem to share a common cause: isolation and time enough to allow selection to take place. Predation, though slight in degree, does exist, and seems to be one of the selective pressures favouring melanism, together with the parallel trend towards an increase in body size and the need to an effective thermoregulation during the early hours of the day.

INTRODUCTION

The great morphological variety, number of dorsal scales and body colouring shown by insular lacertids has often been analysed exclusively using taxonomical criteria, without considering the adaptative significance that could lie behind these variations in most of the available reports. It has even been stated that some

body size defining features (giantism and dwarfism in insular populations) or the number of dorsal scales showed a neutral selection (Radovanovic, 1954).

However, most authors nowadays accept that animal features are variable to a greater or lesser degree depending on their adaptative value. The adequate conditions for life in a specific environment must necessarily change if that environment changes.

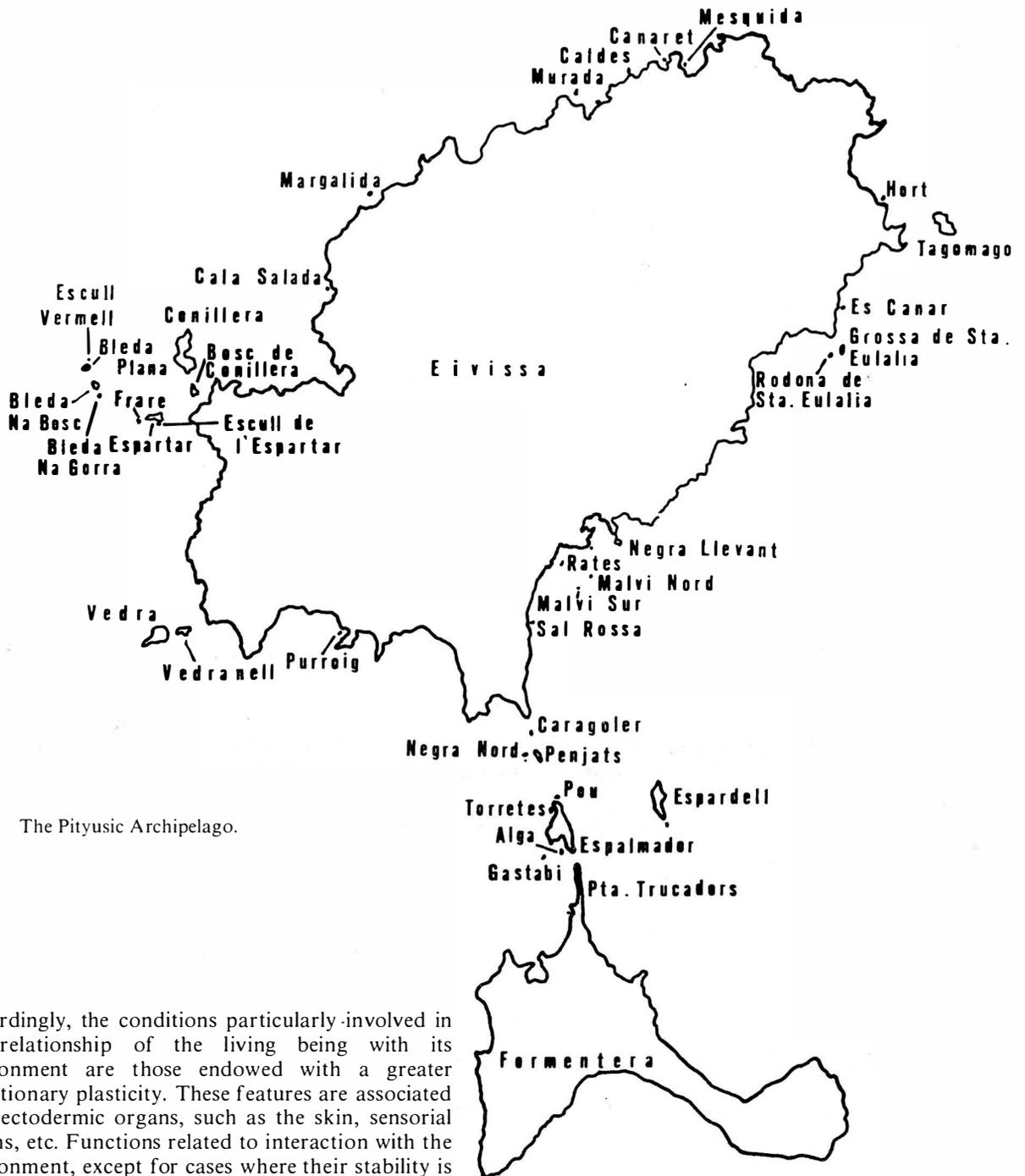


Fig. 1 The Pityusic Archipelago.

Accordingly, the conditions particularly involved in the relationship of the living being with its environment are those endowed with a greater evolutionary plasticity. These features are associated with ectodermic organs, such as the skin, sensorial organs, etc. Functions related to interaction with the environment, except for cases where their stability is essential for the survival of the individual or species, are therefore very plastic. When very similar forms are being studied, i.e. subspecies or close varieties, the most important features are these being shaped at that precise moment by a known environment, whose ecological implications can be studied. These are relevant in terms of population genetics and ecology.

After exhaustive studies for taxonomic purposes (Cirer, 1987), which have provided a deep knowledge of all *Podarcis pityusensis* populations and their intrapopulational variability, this review is presented with the aim of establishing some of the general patterns of morphological variation, between both sexes as well as among the different populations of the species. These patterns are probably due to adaptation to insular environments.

This lacertid appears all over the Pityusic archipelago, south of the Balearic Islands, in the Spanish Mediterranean Sea (Fig. 1), comprising the Island of Ibiza and Formentera southwards (the only islands permanently inhabited by human beings), and a considerable number of islets varying greatly in area, height and distance from the biggest nearby island (Ibiza). All are located on a continental shelf not more than 80 metres deep and, accordingly, when the sea receded in the Quaternary glaciations formed a single piece of emerged land.

Not all biometric and scale number variables used in the foregoing taxonomic studies seem to be relevant to biogeographical studies; therefore, a small number of variables has been selected to avoid the 'background noise' caused by an excess of information. The features taken into account are mainly those related to general body shape and colouring, since they play a more relevant role in interactions with the environment and with other individuals — conspecific or not. The changing of these traits has been studied particularly in insular reptile populations, in which the adaptative significance of features such as gigantism, dwarfism, melanism and other hypertelic trends have been analysed (Sacchi, 1961).

DWARFISM AND GIANTISM AND ISLANDS

Both phenomena are clearly present in all the fauna living in small isles worldwide; among the reptiles, there are such classic examples as the giant turtles from the Indian Ocean Archipelagos, the giant monitors in Komodo, etc. Insular dwarfism has been registered more frequently among mammals and invertebrates, but there are also examples among reptiles.

In the Balearic Islands there are good examples of dwarfism, (terrestrial Gasteropoda) and gigantism (tenebrionid Coleoptera). Balearic lizards, like the ones in all other Mediterranean islands present no remarkable examples of gigantism or dwarfism, but they do show a trend towards increased body size when compared to similar continental populations or, more rarely, towards a decrease in body size. The average snout-vent length in *Podarcis pityusensis* populations is between 62 and 82.6mm for males, and between 54.8 and 72.4mm for the females. Whereas the continental populations of *Podarcis hispanica* measure between 52.0 and 58.2mm for males, and 49.7 and 55.5mm for females. And in *P. muralis* populations males are between 56.9 and 59.4mm and females 57.9 to 61mm. There is no doubt about the fact that *P. pityusensis* is bigger as a species than its continental congeners. The trend towards increased body size in insular lizard populations is clear in other Spanish localities (Columbretes Islands, islets of the Cantabric Coast, etc.).

In the major Balearic islands (the Gimnesians), *P. lilfordi*, the species nearest to *P. pityusensis*, is smaller, at least in some populations. However, its average size is also greater than that of the continental lizards.

Selection leading to large insular forms has been explained through different mechanisms, ranging from polyploidy to the role of islands as reducts. In the case of the Balearic Islands, the most plausible explanation is based on a reduction of predatory pressure, a shortage of food resources and an increase in intraspecific competitiveness. This situation is considered in the Case (1978) model, which seems to fit the data extremely well in our example.

INSULAR MELANISM

The evolution of melanism considers different evolutive models presently included in the field of insular biogeography. These models are based on the following causal hypotheses:

1. *Mimicry*. Evolution would work mainly on epidermic colouring features, which would be affected by a selection favouring cryptic colourings. The disadvantage of this hypothesis is that it cannot easily explain the trend towards melanism shown by many populations. In some other cases, it is not possible to see clearly which selective agent is involved.

2. *Vegetarianism*. Some authors (Eisentraut, 1949) have explained the trend towards melanism shown by many insular populations as a food adaptation to vegetarianism caused by an insect shortage in the islets. In that case the melanism would be a side effect of metabolic processes which would be the real aim of the selection. The main argument against this hypothesis is epidermic tinge diversity in populations with similar diets.

3. *Climate*. Other authors consider melanism to be a consequence of climatic factors and, more specifically, of an adaptation to the high sunshine levels that apparently occur in many islets. This hypothesis does not explain the diversity of tinges observed in populations located near each other and submitted to similar climatic conditions.

4. *Randomness*. This hypothesis is applied not only to melanism but also to all the typical features of insular populations. The evolution of such features would be determined by genetic drift, acting on very reduced populations with its genetic basis being limited due to the founder effect. This hypothesis has many supporters who have formulated it with varying nuances.

Insularity is considered by most authors as being a direct function of the distance from the continent and an inverse function of the logarithm of the area of the island (Soule, 1966; McArthur and Wilson, 1967; Clover, 1975). The area or its logarithm are also good indicators of the ecological diversity of an island. Distance does not appear to be a good indicator of insularity in the case of the Pityusic archipelago because of the features of its continental shelf. There are very close islands but with deep channels between them, and vice versa, remote islands with shallow water between; all islets made part of a single piece of emerged land until the end of the Würm glaciation.

The factor which seems best to define the isolation is the age of separation from the main island (Ibiza) (Cícer, 1982, 1987). Unfortunately this factor cannot be known with precision since we lack the geological studies of the area which would allow us to quantify it, but the separation of the Pityusic massif into the present diverse islets has its origin in the sea level changes occurring during the Würm. Therefore, the level of depth between each isle and the Island of Ibiza is an indirect index quite close to their age.

MATERIALS AND METHODS

Two analyses of *P. pityusensis* individuals were made according to morphometric and colouring variables. The first group of variables was analysed in the 41 current insular populations (Table 1). The available sample for colouring analysis could not be analysed as widely and the test covers only 17 of these populations.

Data of Studied Populations of *Podarcis pityusensis*

Locality	N. Mal	N. Fem	Bl. Mal	Bl. Fem	Dlum. Mal	Dlum. Fem	Area	Age
Eivissa	39	51	64.7	55.1	44.06	42.17	239.2	0.0
Formentera	49	41	73.6	63.3	34.33	35.48	91.1	8.1
Pta. Trucadors	12	13	64.4	56.7	42.07	45.42	3.6	8.1
Rodona Illetes	3	8	71.6	63.8			0.7	8.1
Espalmador	15	12	74.8	64.0		37.75	11.8	8.1
Gastabí	16	6	67.5	61.8		31.87	1.2	8.1
Alga	7	3	72.7	64.3	37.56		1.1	8.1
Torretes	20	17	67.2	56.7	40.14	39.07	2.6	8.1
Pou	33	22	74.9	64.3	38.80	39.38	1.3	8.1
Penjats	30	22	76.5	66.5	39.63	35.16	3.0	8.1
Caragoler	12	5	64.6	60.7			0.8	7.8
Espardell	23	32	77.6	65.9	38.07	40.33	7.5	9.2
Sal Rossa	4	6	71.0	60.7			0.7	7.0
Purroig	26	1	69.0	64.2			0.8	7.0
Negra Llevant	3	3	75.8	58.0			0.7	7.8
Negra Nord	13	17	76.6	66.5	32.57	39.23	1.5	8.1
Rates	13	13	79.6	68.0			1.0	7.0
Malví Nord	12	13	79.4	70.4			0.9	9.0
Malví Sud	11	11	79.4	70.0			0.8	9.0
Rodona Sta. Eulalia	14	14	82.0	72.5			0.7	8.5
Grossa Sta. Eulalia	23	23	76.7	70.0			2.0	8.8
Margalida	2	18	72.0	65.9			1.0	10.8
Es Canar	22	10	78.1	68.5			0.8	8.5
Tagomago	23	35	77.6	65.0			7.7	9.5
Hort	14	16	72.6	66.9			0.8	7.8
Mesquida	10	6	73.9	68.8			0.4	7.8
Canaret	6	5	62.1	58.2			0.4	7.0
Caldés	24	13	68.8	60.8	38.34	40.31	1.5	7.0
Murada	26	36	74.0	65.2		24.89	1.2	9.5
Cala Salada	16	8	73.0	56.7			0.9	7.8
Bleda na Plana	21	34	82.6	69.1	30.16	33.52	1.8	12.6
Escull Vermell	9	7	75.7	69.3			0.3	12.6
Bleda na Bosc	11	14	84.5	73.1			1.9	12.6
Bleda na Gorra	19	15	83.2	72.8			1.4	12.6
Conillera	23	26	75.1	65.5			9.9	7.8
Bosc de Conillera	15	10	68.6	62.9			3.8	7.8
Espartar	36	21	77.6	68.8	33.14	34.76	4.3	9.5
Escull d'Espartar	7	10	79.6	69.5			0.3	9.5
Frare	18	18	75.2	64.7	27.96	30.38	0.9	9.5
Vedrá	29	26	76.4	65.5	32.56	33.62	7.8	10.8
Vedranell	15	13	78.3	66.5			3.4	10.8

TABLE 1: N. Mal. = Sample size of males; N. Fem = Sample size of females; Bl. Mal. = Length snout-vent in males; Bl. Fem. = Same for females; Dlum. Mal. = Back luminosity in males; Dlum. Fem. = The same for females; Area = Square root of island surface in hectares (km² x 100); Log. Age = Logarithm of estimated separation time from the main [10 x (log A - 3)].

For the morphometric analysis the following measurements and counts were considered on each specimen:

— BL. Body length. This variable is a good indicator of size and shape, according to the result of previous factor analysis (Cirer, 1987).

— HW. Head width.

— PL. Pileus length.

— PW. Maximum Pileus width.

— LH. Length of the hindleg.

— W. Weight.

— DTS. The number of dorsal transversal scales.

— DLS. The number of dorsal longitudinal scales.

— L. The number of lamellae of the fourth hindleg toe.

— FP. The total number of femoral pores.

A t-student test for each variable was applied to the original data matrix obtained to determine the degree of sexual dimorphism in this species.

Moreover, the average coefficient of variation (ACV) has been calculated for each population. This coefficient shows us the degree of intrapopulation variability. The coefficient used by Soule (1972) has been chosen, because it seems to be adapted for comparing closely related species or populations.

$$ACV = \frac{\sum_{i=1}^p v_i}{p}$$

Where V_i is the coefficient of variation ($S_i * 100 / x_i$, x_i being the mean of the i th character) and p is the number of variables used, in our case $p = 10$.

Study of the evolutive variation of pigmentation in reptiles is still hindered by the difficulty in quantifying melanism. This problem has been solved by measuring average luminosities on live individuals, using a reflexion colour imeter in accordance with the method described in Cirer and Martínez-Rica (1986). Measurement of only one colour variable (dorsal luminosity) has been taken into account for this study, since it appears to be a good index of melanism. The populations studied, with their respective sample size are listed in Table 1.

A more detailed analysis of the relationship between certain variables and the main defining factors of the insular characteristics of each population was carried out. For this purpose body length and dorsal luminosity were chosen as dependent variables, supposing them to be directly influenced by evolutive trends towards insular gigantism or melanism; the square root of the island area (because of the need to linearise a quadratic variable) and the logarithm of the estimated age of the separation of the islets from the island of Ibiza have been taken as independent variables. Each of the variables has been separately related to every factor, independently for males and females, to eliminate effects of sexual dimorphism. Separate multiple regression analyses have also been carried out, in which each dependent variable has simultaneously been related to both above-mentioned factors, so as to estimate the relative contribution of each of them to the joint regression.

RESULTS

Sexual dimorphism. Sexual dimorphism has been observed in each population and in the species as a whole. The difference between population means of males and females is highly significant in all cases in the variables determining size and shape (BL, HW, PL, PW, LH and W). The population means of scale number variables are not significantly different between males and females in most cases, though the number of dorsal transversal scales (DTS) is significantly different for most of the populations. However, all the scale variables show significant differences for the total of individuals belonging to the species.

Females are considerably smaller and less robust than males although they have a similar number of dorsal scales, which means that there could exist a difference in scale size. To prove this assumption a test with the resultant variables of quotients BL/DLS, W/DLS, BL/DTS and W/DTS was carried out, producing highly significant results in all populations showing that males have bigger dorsal scales than females, though similar in number.

The results allow us to state that *Podarcis pityusensis* shows a high degree of sexual dimorphism in shape and size, a slight or non-existing variation for the number of scales in some populations and very noticeable variation in dorsal scale size.

Intrapopulation variability. The average coefficient of variation allows an estimation of the degree of polymorphism shown by the population. This rate has been related to insularity factors: the area and age of the isle were both found to be significant. Area was found to be positively significant and age negatively significant. The area of the isle is an indirect index of its ecological diversity, therefore small isles should have fewer different microhabitats available to lacertids, which would mean that fewer different lines of adaptation exist and this would result in a homogenisation of the populations. Inversely, in bigger islands, which are usually more diverse, species can respond with different morphologies whose viability depends on the different environments. On the other hand, Hespénhede (1973) points out that living beings having a greater variation in their alimentary habits show a greater polymorphism. Accordingly, in our case it can be expected that polymorphism increases in bigger isles where diet is bound to be more diverse; in contrast, ecologically more homogeneous islands, with a smaller diversity of potential prey will, keep population adapted to the isle's specific conditions, with narrower variability margins, and extreme individuals which have not developed optimal phenetic characteristics for their viability in that specific insular ecosystem will be eliminated.

We should also expect a greater morphological uniformity in those populations where evolution has acted over a longer period of time to adapt phenetic traits to an insular environment. Thus, smaller and/or older islands have more homogeneous populations because evolution, lack of population elements and environmental uniformity cause a decrease in polymorphism.

Trend towards gigantism and melanism. We have tried to classify the relationship linking insular area and isolation time with the average size of all the populations of *Podarcis pityusensis* so as to find out which evolution model best fits our data. These are listed in Table 1. Obviously, the separation and assembly process of the isles has been recurrent, with variations in sea level accompanying glacial periods.

The simple regression analysis in Table 2 shows the existence of a clear relationship between the gigantism index variable (BL) and melanism (dorsal luminosity) with the factors characterising insular environment. Size in males and females shows a strong positive relationship with the isle's separation age, as if the trend towards gigantism could be shown more clearly because selection has been working for a longer time. Dorsal luminosity (naturally inverse to the degree of melanism) also shows a clear negative correlation with the isle's age in male specimens, while the correlation almost reaches a significant level in female specimens (94 per cent). With regard to this point, it should be pointed out that the number of populations whose averages of luminosity we know of is much lower than that which provided size measurements, and the relationship would probably be significant if we had been able to study each population in the same way. It seems evident that both melanism and size are features depending partially on the age of the isle and, in

Y	X	Z	Equation	Corr. Coef.	Signif.
(a) Simple regressions:					
Bl. Mal.	Area		$Y = -0.037X + 74.74$	-0.272	91%
Bl. Fem.	Area		$Y = -0.041X + 65.48$	-0.349	97%
Bl. Mal.	Age		$Y = 1.588X + 60.65$	0.620	>99.9%
Bl. Fem.	Age		$Y = 1.384X + 53.1$	0.629	>99.9%
Dlum. Mal.	Area		$Y = 0.029X + 35.61$	0.412	83%
Dlum. Fem.	Area		$Y = 0.023X + 35.91$	0.282	70%
Dlum. Mal.	Age		$Y = -1.18X + 46.11$	-0.698	99.4%
Dlum. Fem.	Age		$Y = -0.935X + 44.22$	-0.481	94%
(b) Three variable regression:					
Bl. Mal.	Age	Area	$Y = 1.90X + 0.027Z + 57.63$	0.614	73% (Z) >99.9% (X)
Bl. Fem.	Age	Area	$Y = 1.49X + 0.009Z + 52.05$	0.607	37% (Z) >99.9% (X)
Dlum. Mal.	Age	Area	$Y = -1.90X - 0.036Z + 52.94$	0.703	83% (Z) 99.2% (X)
Dlum. Fem.	Age	Area	$Y = -0.029X - 1.51Z + 49.66$	0.399	60% (Z) 93% (X)

TABLE 2: Regression of Size and Pigmentation on the Insularity Indicators.

consequence, evolution seems to work accumulatively in them.

The relationship between the area of the isle and the variables of melanism and size is somewhat less clear than the one for age: it attains a significant level only in females, when size is the variable considered. In the remaining cases, although it is not significant, its sign leads us to assume that smaller isles tend to shelter bigger and darker individuals than larger isles.

Multiple regression analysis has permitted isolation of the relative contribution of each variable to overall regression (Table 2). The age of separation of the islands significantly influences in male and female size (>99.9 per cent), as well as in male dorsal luminosity (99.2 per cent). And for female dorsal luminosity, correlation borders on the critical level (93 per cent). The area shows no significant relationship in any case. The overall result confirms those obtained through simple regression: older isles tend to have bigger and darker animals. And the same is true in smaller isles, although the relationship is not significant in this case.

DISCUSSION

Sexual dimorphism. Only a single lacertid species inhabits the Pityusic archipelago: *Podarcis pityusensis*. Therefore, no interspecific competition with other closely-related species exists, although it is logical to assume some occasional competition with geckonid lizards, and the existence of certain intrapopulation competition for food, reproduction and space. Species occupying similar niches often react by accentuating their morphological differences in sympatric areas, to differentiate themselves from one another, thus

avoiding all possible competition, and making optimal use of the resources offered by the ecosystem. This trend is observed both in mainland species: *Podarcis muralis* and *P. hispanica* (Vives-Balmaña, 1982), and in insular ones: *P. melisellensis* and *P. sicula* (Clover, 1975).

The morphological differentiation between both sexes seems to respond to the same need to mitigate the intrapopulation competition, and exploit optimally the resources of the insular ecosystem. Males and females act as two sympatric closely-related species. Clover (1975) points out that this must be the cause of the growing sexual dimorphism in insular Adriatic Sea populations, where this species does not share a habitat with other species of the same genus. Accordingly, the strong sexual dimorphism of *P. pityusensis* seems to respond to this need to make the most of the scarcity of food and space offered by small islets.

The differences observed in the variables defining size and shape (BL, HW, PL, PW, LH and W) show that males are always bigger, fatter, and have a more robust head and extremities. Smaller and less robust females can be predicted to be relegated to more generalised feeding sources requiring no fighting (the smallest preys and plant buds and flowers). Since body size and robustness are positively related to prey size (Hespenhide, 1973; Seva, 1982), both sexes can carry out more efficient predation against a wider range of prey sizes.

Dorsal scaling, as well as scale morphology appears to be related to thermoregulation. Martínez-Rica (1977) observes that more thermophile species have a greater number of dorsal scales and that those scales are smaller. Soule (1966) has observed in *Uta stansburiana* that populations with problems of

Continental			Insular		
Species and Locality	Males	Females	Species and Locality	Males	Females
<i>P. muralis</i>			<i>P. muralis</i>		
France	58.8	60.3	France (Atlant.)	64.5	60.9
France (mountain)	59.7	62.5	France (Medit.)	61	—
Belgium	56.6	55	Spain	70	—
Germany	58	57.7	Italy	65.5	60.2
Switzerland	59.3	65	All populations	65.5	60.3
Austria	53.8	56	<i>P. tiliguerta</i>	69.8	62.4
Spain	58.4	58	<i>P. erhardi</i>	62.5	59.5
Spain (mountain)	57.7	60.2	<i>P. lilfordi</i>	64.8	61
All populations	58.2	59.1	<i>P. pityusensis</i>	69.4	61.2
<i>P. hispanica</i>			<i>P. bocagei</i>	61	59
Spain	55	53.1	<i>P. melisellensis</i>	62.2	53.9
Spain (mountain)	54.4	52.1	<i>P. sicula</i>	68.3	63.1
North Africa (mountain)	50	49	<i>P. taurica</i>	66	60.9
North Africa	51.2	52.4	All insular forms	65.5	60.9
Portugal	53	49.1			
All populations	53	52.1			
<i>P. bocagei</i>					
Spain	57.6	56.3			
Spain (mountain)	49.4	50.2			
All populations	57.7	56.4			
<i>P. melisellensis</i>	56.4	54.8			
<i>P. peloponnesiaca</i>	73.3	65.6			
<i>P. sicula</i>	69.5	61.7			
<i>P. taurica</i>	59.4	56.4			
All continental forms	57.7	56.4			

TABLE 3: Body Size (mm) in different European populations of Genus *Podarcis* (Data from Boulenger, 1920 and from Perez Mellado and Galindo, 1986).

overheating tend to show a decrease in their number of dorsal scales, which become bigger and more overlapping. The fact that males have bigger dorsal scales seems to indicate that they have different thermoregulatory requirements from females, with more pronounced overheating problems, possibly due to their greater robustness, or to their different reproductive role.

Trend towards giantism. Median body length in different European lizard populations of *Podarcis* genus, both continental and insular, is shown in Table 3. It is evident that insular species or populations have a greater average size than continental ones, and also that, in the same species, insular populations contain bigger individuals than their continental homologues. This difference shows a trend towards an increase in body size, not easily accounted for by such evolutive models as the one outlined by Thaler (1973) which involves a stable and balanced biocenosis. The Heaney (1978) model appears to be more plausible, even though it assumes an isochronal colonisation which seems not to have existed in the Pityusic Islands.

Anyway, the factors believed to guide size evolution in insular populations are island area and time of isolation of the specific population, and these would act mainly through predative pressure, shortage of resources and competitiveness. These three factors change when island area decreases, in which circumstance we can expect some sort of relationship between the average population size and the average area of the isle inhabited or the time of isolation.

This relationship has in fact been found in the above-mentioned evolutive models and, in some cases (Heaney, 1978), the type of relationship has even been specified. It would be a parabolic one: body size would grow with the logarithm of the isle's area, attaining a maximal value and then decreasing in larger islands, where biocenosis would already be of continental type.

Consequently, the following conclusions can be drawn:

(a) Models linking the trend to giantism in insular environments with isle area are not totally applicable to the case of *P. pityusensis* or at least the differentiation between populations has not existed long enough to make those models seem appropriate.

(b) The fact that the age of insular separation has an effect on the average size of both males and females suggests that this type of evolution is accumulative and is more dependent on a systematic trend than on an arbitrary cause; the role of genetic drift seems then, to be secondary in relation to this feature.

This general trend towards gigantism does not seem to be present in the populations inhabiting Punta de Trucadors (the most northerly point in Formentera) and the Isle of Caragoler, which show a certain trend towards a decrease in size. To a lesser extent this trend is also observed in the Isle of Alga and in Punta de Tramuntana (the most northerly point in the Isle of Espardell). These areas have a light brown-yellow coloured sand rock, which is flat and devoid of vegetation. Lizards are small and slender, with highly luminous, ochre dorsal colouring, nearly free of reticular patches and thus cryptic in relation to their environment. It seems evident, in these cases, that the dominant selective pressure is predation and, accordingly, cryptic (light ochre) forms, which must have less thermoregulating capacity, have been selected so that this colouring goes together with lesser sizes, as thermoregulation would be more difficult in larger but not dark lizards.

Trend towards melanism. If, as seems to be the case, the degree of pigmentation changes under the influence of the population size and of the time of its separation, it is necessary to recall evolutive patterns in which these factors work. Genetic drift is one of these evolutive mechanisms, which would adequately explain a quicker evolutive process in smaller populations. But what is the reason for this general trend towards darkening? If genetic drift acts arbitrarily there should not be any preferential evolutive trends. Why then, does this trend towards melanism exist not only in this species, but also in most insular species of Mediterranean lacertids?

The relationship to population age suggests that a weak, but permanent, selective pressure exists, overlapping genetic drift and favouring an increase in pigmentation. Thus, an accentuated melanism must carry with it some sort of ecological advantage for lizards which, some time later, will allow a uniformation of populations after an initial heterogeneity caused by genetic drift.

What advantages might melanism hold for insular mediterranean lacertids? These advantages can obviously only affect the animal's relationship with its environment, with its congeners or with animals belonging to other species.

In relation to the environment, a darker colour can be an advantage to a lizard, only if it affects some exchange process in which the skin plays a role. The only plausible one is the energetic exchange between the animal and its environment. It would not be surprising that a greater or less pigmentation would influence the lizards' ability to absorb heat. Other small saurians, also abundant in the Mediterranean isles, are capable of darkening or lightening their skin according to thermoregulating processes (Martínez-Rica, 1974). Lizards can adapt themselves permanently (and not only physiologically) to a situation of thermal

deficit. It is difficult to imagine a thermal deficit existing in the Mediterranean isles, but lizards' activity patterns suggest the existence of such a deficit at least during the early hours of day. Rapid heating can mean an important ecological advantage for the animal because it allows it to initiate activity sooner, swallow its quarry, take advantage of the dew drops which have not yet evaporated and move swiftly to escape predators.

While studying other lacertids, Crisp *et al.* (1979) established a relationship between average size and degree of melanism, considering both traits as cause and effect, when, probably, they were both dependent on a common cause. The interpretation given by these authors is that size increase favours melanism, because melanism would make up for reduced heating speed of big animals, owing to a smaller area/volume ratio. According to these authors, the trend towards a darker pigmentation would not be selected of itself, but would occur as a consequence of a previous selection, favouring great size. This explanation cannot be considered totally accurate in regard to *P. pityusensis* (there are melanic populations of small lizards and non-melanic, large size populations) since it is excessively simplified, even though a certain relationship between average size and degree of melanism is registered. The explanation that both characteristics depend on common factors seems more plausible.

The second group of factors bound to play a role in favour of an increase in the degree of melanism is related to intraspecific social interactions. Even though a lot is unknown about behaviour patterns and the visual perception of lacertids, it can be stated that design and colouring features affecting social interactions are not located on their backs (the visibility of this part being very problematic in lizards) but on their neck and sides. Apart from that, judging from what happens in other lacertids and other saurians, the designs intervening in intraspecific interactions show a bright colouring and not only melanism. Consequently, hypotheses trying to explain the trend towards melanism by causes linked to intraspecific interactions are not very credible. Giving arguments which are different from the ones here stated, Stamps (1983) also discards the possibility that in most territorial saurians females choose males for mating on the basis of the males' colour or aspect.

The third group of hypotheses related to this topic includes interspecific relationships as agents causing melanism. Among these relationships, there are, logically, the trophic ones, and especially the most often mentioned interactions of lizards with their predators.

Melanism could be favoured by selection if this were to help lizards to be undetected by their predators, which are mainly birds who identify lizards primarily by looking at them from above. If a melanic back can be cryptic in its specific environment, predation will decrease while a trend to melanism grows. In the species studied, this trend is only observed in stony and strongly-fissured isles. The Pityusic Archipelago has a very mild climate, free of mist and with long periods of sunshine during most of the year; especially during the spring, summer and autumn, the period of lacertids

maximum activity (Perez Mellado and Salvador, 1981). Since a very bright sunlight strikes on stone edges and cracks, long and very clear-cut shadows are projected, with little blurring of their profiles. Such an environment makes it easy for birds to confuse a lizard's long black profile with the predominating shadows, especially if we take into account that many birds preying on *P. pityusensis* do not have binocular vision (*Larus*, *Lanius*, *Turdus* and *Upupa*). Subsequently, it seems that melanism would cause a decrease in predation in stony, fissured environments. However, this selective pressure is not completely eliminated since some species of *Falco* (with stereometric vision) also play a role in this predation (Araujo, *et al.*, 1977); accordingly, selective pressure owing to predation would be noticeably reduced with melanism but not completely eliminated.

Summarizing, melanism is a consequence of a balance among the different pressures undergone by the population: there is a trend towards an increase in size and the subsequent need of a more effective thermoregulation, allowing the possibility of being active in the early hours of the morning, suffering less predation. This balance is broken in populations living in sandy and clear areas since dorsal darkening would cause an increase in visibility and, subsequently, in predation. In the last mentioned areas light brown cryptic forms are selected which, in these species, seem to go together with small size.

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**THE FOOD OF *CYRTODACTYLUS KOTSCHYI* (STEINDACHNER, 1870)
(SAURIA-GEKKONIDAE) DURING THE WET SEASON IN THE MEDITERRANEAN
INSULAR ECOSYSTEMS OF THE AEGEAN**

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ABSTRACT

This report gives data on the feeding ecology of *Cyrtodactylus kotschyi* (Sauria-Gekkonidae), during the wet season in the mediterranean ecosystems of the Aegean. *C. kotschyi* feeds mainly on the larvae of insects. There are no significant differences in the food of this gecko among the different populations in the Aegean ecosystems.

INTRODUCTION

Cyrtodactylus kotschyi (Steindachner, 1870) (Sauria-Gekkonidae) is the most widely spread lizard in all the ecosystems of the Aegean archipelago. In quite a large number of them, it co-dominates with lizards of the family Lacertidae, while in others, it is the unique dominant species. In the above ecosystems, *C. kotschyi* is active during the whole year, belongs to the sit-and-wait predators and feeds mainly on arthropods. It has to be reported however that most of the data about the food of *C. kotschyi* has come from specimens collected during the warm period of the year, while data from the wet period are rather limited (Valakos and Vlachopoulos, 1987).

This study reports data on the food of *C. kotschyi*, collected during February 1988, from ecosystems of the island of Antikythera (S.W. Aegean), together with a comparison of the data with that already published on the wet period in an ecosystem of Naxos island (central Aegean).

The climate of the central and north Aegean islands belongs to the thermomediterranean type (hot, semi-arid). The average annual precipitation is about 400-500mm, while the mean temperature of the year is 19°C, the hottest being 25°C and the coldest 12°C. The dry season is restricted to the April-October period while the wet is from October to April. The vegetation is characterised by evergreen shrublands and phrygana.

LOCALITIES AND METHODS

The insular ecosystems of the central and south Aegean Sea, as well as the climate, belong to the Mediterranean type.

During the month of February 68 specimens were collected from the island of Antikythera, where *C. kotschyi* is the commonest among the reptile species.

The main characteristics of the area are the rocky terrain and the vegetation, which is mainly degraded maquis. The most predominant plant species are *Juniperus phoenicea*, *Pistacia lentiscus*, *Thymus capitatus* and *Genista acanthoclada*.

The geckoes were collected by hand during the daily period of 9 a.m. to 4 p.m. and were put in aqueous solution of methanesulfonate (MS222) (Polymeni, 1988), in order to get them anaesthetised.

Finally, the animals were put and kept in 75 per cent alcohol with 5 per cent glycerine. Both the whole length and the body length (snout-vent) for each specimen were recorded. The same procedure was followed for the animals collected on Naxos island during November 1986 and March 1987. During the next step, the animals were examined under an ocular micrometer, fitted to a dissecting microscope, where their sex was determined and the content of the stomach was recorded.

The food items were distributed into length categories of 5mm. The volume of each food item was calculated as if it were the volume of a prolate spheroid according to the type:

$$V = \frac{4}{3} \pi \left(\frac{a}{2}\right) \left(\frac{b}{a}\right)^2 \quad (\text{Dunham, 1983})$$

where: V = the volume of each food item.

a = the maximum length of the food item.

b = the maximum width.

The food niche breadth (B) was calculated according to the type:

$$B = \frac{1}{\sum p_i^2} \quad (\text{Simpson, 1949})$$

where p_i = the percentage of each prey of the i^{th} category.

The food overlap between allopatric species or allopatric populations (Q_{kj}) was calculated using Pianka's formula:

$$Q_{kj} = \frac{\sum_1^n (p_{ik} \times p_{ij})}{\left(\sum_1^n p_{ik}^2 \times \sum_1^n p_{ij}^2\right)^{1/2}}$$

where Q = overlap

p_i = the percentages of the i^{th} category of prey for the species k and j.

Food category	n	%n	V	%V	f
Gasteropoda	6	3.13	50.30	1.71	0.04
Araneida	19	9.90	201.00	6.83	0.20
Pseudoscorpions	9	4.69	13.80	0.47	0.10
Opiliones	3	1.70	2.00	0.07	0.04
Thysanura	24	12.50	104.50	3.54	0.27
Coleoptera	24	12.50	99.60	3.38	0.33
Embioptera	2	1.00	4.30	0.14	0.03
Heteroptera	2	1.00	48.20	1.63	0.03
Hymenoptera	1	0.50	9.15	0.31	0.01
Mantidae	1	0.50	10.90	0.37	0.01
Blattidae	1	0.50	5.50	0.19	0.01
Diptera	4	2.10	3.16	0.10	0.03
Insects larvae	72	37.60	1833.00	62.17	0.66
Neuroptera larvae	2	1.00	9.14	0.31	0.03
Isopoda	18	9.40	552.10	18.72	0.21
Diplopoda	2	1.00	0.24	0.03	0.01
Total	190		2948.00		
B	5.26		2.32		

TABLE 1: Food items found in stomachs of 68 *C. kotschy* specimens. The symbols represent: n = number of food items, %n = percentage of the number of food items, V = volume of food items in mm³, %V = percentage of the total volume, f = number of specimens containing one food category/total number of specimens (frequency), B = niche breadth.

The niche overlap between males, females and juveniles was found using the method of Petraitis (1985), calculated with the help of computer program (Lundwing and Reynolds, 1988). The correlation between the body length of each animal and the mean length of food items was determined by means of Spearman coefficient (Zahr, 1984).

The percentage of lizards containing each prey category is mentioned as frequency (f = number) of specimens containing one food category/total number of specimens.

RESULTS

From the 68 geckoes examined, only two had empty stomachs. The categories, the number, the volume of the prey, as well as the corresponding percentages and frequency are presented in Table 1.

It is obvious that larvae were the main constituents of the prey of *C. kotschy* followed by Coleoptera, Thysanura, spiders and Isopoda. The percentage and the frequency of the remaining groups was very low.

According to the volumes, larvae represented the highest percentage, 62.17 per cent, followed by Isopoda (18.72 per cent) and spiders (6.83 per cent).

The food niche breadth was found to be larger when it was determined as a function of the number of specimens of each group of the prey, while it was smaller when determined as a function of the volume.

According to Table 2, where the prey of males, females and juveniles is shown, larvae made the largest contribution among the different categories of food.

High overlap occurred between males and females (general overlap GO = 0.966, statistic V = 10.42

p<0.05), as well as between adults and juveniles (GO = 0.92, V = 32.23 p<0.005).

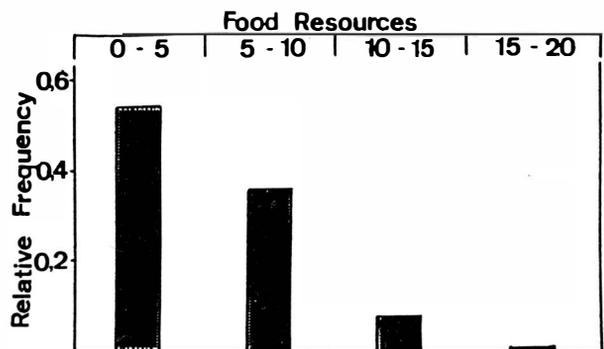


Fig. 1 Relative frequency in use of food categories (in mm) by *C. kotschy*.

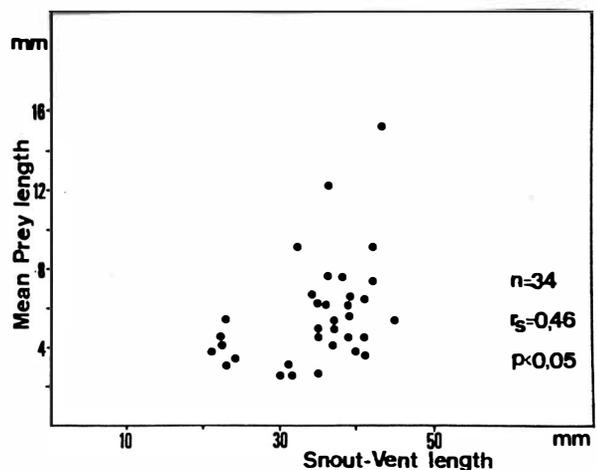


Fig. 2 The correlation between mean prey length and snout-vent length (in mm).

Food category	Males		Females		Juveniles	
	n	%n	n	%n	n	%n
Gasteropoda	2	2.68	4	5.26	—	—
Araneida	7	9.21	11	14.20	1	2.77
Opiliones	—	—	—	—	3	8.33
Pseudoscorpions	4	5.26	4	5.26	1	2.77
Thysanura	10	13.15	6	7.89	8	22.20
Coleoptera	12	15.78	10	13.15	2	5.26
Embioptera	1	1.31	1	1.31	—	—
Mantidae	—	—	1	1.31	—	—
Blattidae	1	1.31	—	—	—	—
Heteroptera	1	1.31	1	1.31	—	—
Hymenoptera	—	—	1	1.31	—	—
Diptera	2	—	2	2.68	—	—
Insects larvae	28	36.84	23	30.26	21	58.33
Neuroptera larvae	1	1.31	1	1.31	—	—
Isopoda	7	9.24	9	11.34	2	5.55
Diplopoda	—	—	2	2.68	—	—
Total	76		76		38	
B	5.29		6.84		2.85	
GO			0.96		—	
					0.92	

TABLE 2: Food items found in the stomachs of 28 males, 23 females and 15 juveniles *C. kotschyi*, GO = general niche overlap. Other symbols as in Table 1.

Food category	n	%n	November (10)			n	%n	March (10)		
			V	%V	£			V	%V	£
Araneida	8	30.8	6.07	1.83	0.7	1	2.6	3.02	0.98	0.1
Chilopoda	1	3.8	3.88	1.19	0.1	—	—	—	—	—
Coleoptera	3	11.5	24.80	7.39	0.3	5	13.6	22.3	7.24	0.3
Ants	8	30.8	7.21	2.18	0.2	—	—	—	—	—
Hymenoptera	1	3.8	9.58	2.89	0.1	1	2.6	0.13	0.04	0.1
Diptera	2	7.7	3.65	1.10	0.1	—	—	—	—	—
Collembola	2	7.7	—	—	0.1	—	—	—	—	—
Larvae of Holometabola	1	3.8	276.1	83.42	0.1	5	13.6	143.42	46.36	0.1
Larvae of Hemiptera	—	—	—	—	—	26	68.4	140.47	45.41	0.3
Total	26		330.90			38		309.34		
B	5.88		1.42			1.49		1.19		

TABLE 3: Food items found in stomachs of *C. kotschyi* from the island of Naxos during November and March. Number in parenthesis: number of the geckoes. Other symbols as in Table 1.

Fig. 1 shows the different size groups of the prey. It was noticed that *C. kotschyi* fed mainly on prey items belonging to two big groups. One group contained food items of length less than 5mm, while the second contained food items with lengths between 5 and 10mm. The relative frequency of the other groups was low (less than 10 per cent).

A positive correlation was found between the average food length and the length of the animals themselves with full stomachs ($r_s = 0.46p < 0.05$ Fig. 2).

Table 3 shows the categories, the number and the volume of prey for the months of November and

March from the ecosystem of Naxos. In November *C. kotschyi* fed mainly on spiders and ants (30.8 per cent) followed by Coleoptera (11.5 per cent), while in March it fed mostly on larvae of Hemiptera (68.4 per cent), followed by larvae of Holometabola (13.6 per cent) and Coleoptera (13.6 per cent). According to volume, insect larvae represented comparatively high percentages both in November and March 42 per cent and 92 per cent respectively. It can be gathered that there was no significant difference between geckoes' prey in the two ecosystems. Also larvae represented the biggest percentage in the volume of the prey of

C. kotschyi. In this case too, the food niche breadth was the widest when measured by the number of the specimens of each group, instead by the volume. The volumes of the prey in the two ecosystems, during the three months, were similar. (February-November $Q_{jk} = 0.85$, February-March $Q_{jk} = 0.86$, November-March $Q_{jk} = 1$).

DISCUSSION

During summer, in the Aegean ecosystems, *C. kotschyi*, like most Gekkonidae, feeds mainly on insects. Larvae participate in the prey, with a percentage of 78 per cent and 98 per cent in volume. (Valakos and Vlachopoulos, 1987). According to the results, the above findings are valid for the wet season. In Naxos ecosystems, during March, *C. kotschyi* feeds mainly on larvae (81 per cent in taxon and 92 per cent in volume). On the contrary, during November it feeds mainly on spiders and ants. During this period the percentage of larvae in the soil fauna is low. Differences concerning the prey categories between March and November are due to the different conditions existing on the soil fauna during the two periods (Paraschi, 1988).

It is already known that most Gekkonidae are sit-and-wait predators. (Ananjeva and Tsellarius, 1986). *C. kotschyi*, in Naxos ecosystem, behaves similarly. (Valakos and Vlachopoulos, 1987). The results from the Antikythera ecosystem are in agreement with the above ones. The arguments which follow, support the above conclusion:

1. The prey is composed of many kinds of mobile animals, like spiders, Thysanura, Coleoptera, Diptera (Pianka, 1981).
2. Some groups are present in the prey in particularly high percentages. (Huey and Pianka, 1981). In our case the insect larvae contributed to the prey by more than 60 per cent. Yet, similar results were reported for the summer. (Valakos and Vlachopoulos, 1987).
3. For the sit-and-wait predators, there is a positive correlation between predator's body size and average prey length. (Roze, 1976). In fact, the results concerning the wet season support this point of view along with those for the summer (Valakos and Vlachopoulos, 1987).

According to Fuentes (1976), similar species of lizards that live in the Mediterranean type biotopes, even when living in two different continents, use similar food resources. The food resources for allopatric Lacertidae species and subspecies in the Aegean ecosystems are very similar. (Valakos, 1987). In fact a great similarity is observed in the food of the populations of *C. kotschyi* of Antikythera and Naxos islands. On the contrary, sympatric species, *C. kotschyi* and *Podarcis erhardii* (Sauria-Lacertidae), of the island of Naxos, show a big difference between the groups of their prey. In accordance with previous works (Valakos, 1986), the degree of similarity between the two species is $Q_{jk} = 0.3$.

Lizards select their prey more by size than by taxon, (Schoener, 1968). Comparing the different groups of

the prey size of *C. kotschyi* on the island of Antikythera, to the prey size of *Tarentola mauritanica* (Sauria-Gekkonidae), from Mediterranean Spanish ecosystems (Mellado, *et al.*, 1975), we are led to the conclusion that there is a high degree of similarity: $Q_{jk} = 0.86$. Similar is the case of sit-and-wait predators of the Mediterranean ecosystems of Chile and California (Fuentes, 1976).

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BOOK REVIEWS:

(1) *Phylogenetic relationships among gerrhonotine lizards. An analysis of external morphology.* D. A. Good. University of California Publications, Zoology, Vol. 121, pp. x + 139 (1989). 15.00 US dollars.

To the European herpetologist the name Anguidae is likely to suggest a limbless lizard such as the familiar slow-worm. However, many members of the family possess well developed legs, and perhaps the most notable of these are the alligator lizards of the subfamily Gerrhonotinae. They are characteristically long-bodied lizards with rather short legs and a heavy armour of scales to which they owe their vernacular name; they are found in North and Central America. The present study is a phylogenetic analysis, based on the cladistic method; of the 38 species in the group, the features considered include details of scalation, colour patterns, degree of development of the lateral fold (a characteristic feature of the best known genus, *Gerrhonotus*), and the form and size of the body and limbs. The biogeographical implications of the suggested relationships between the various genera and species are discussed. There is a useful systematic account of the different species, and an extensive bibliography. A general summary of the findings would have been welcome.

Studies of this kind make somewhat austere reading, at least for the non-systematist. However, the author has undoubtedly made a significant contribution to our knowledge of this interesting group of lizards.

A. d'A. Bellairs

(2) *Crocodiles.* Rodney Steel. 198pp. Christopher Helm Publishers Ltd. (1989). £14.95.

It is difficult to exaggerate the public interest in crocodylians of all types, which in a sense is unfortunate leading as it has to publications more properly related to folk-lore than to science. How much credence should be given to the oft repeated account of the annihilation of an entire battalion of armed Japanese by hordes of salt-water crocodiles? Either the soldiers were too dim-witted to use their weapons, or they were promoting conservation at a strange time and at considerable personal sacrifice. As no one person can be an authority on more than a few of the crocodylian species, the value of a book on crocodiles depends on the author's ability to distinguish reasonable from unreasonable reports. Steel has succeeded in this regard admirably. It is true that some of the statements concerning species in remote areas of the tropics will prove wrong but this cannot be avoided. How reliable are accounts on size, population density, range, sex ratios, breeding habits, rates of growth, longevity, etc.? Serious research on even the most plentiful and accessible species was not begun until well after the Second World War.

The author has taken a dispassionate view of the problems concerning conservation, which is refreshing. With the possible exception of those living on the bank of a waterway filled with large crocodiles, most of us

hope to see these reptiles prosper to the point where they regain much of their old habitat. In contrast to those believing in not killing them for almost any purpose, the author favours domestic propagation and game management. The rate of increase in successful crocodylian farming is greater than Steel predicted, in fact, within a few years the market for hides and meat may be saturated. For example, in Louisiana (USA) alone, the collection of 250,000 alligator eggs was authorised in 1989. Incubation followed by feeding the hatchlings in a controlled environment should yield over 150,000 alligators (each over one meter long) in 1990. We have the knowledge now to save all crocodylian species from extinction, even if we don't put it to use.

Some will criticise the book for its absence of a comprehensive bibliography, and others for the fact that you don't have to be a herpetologist to make sense out of it. Evidently the author sought a balance to encourage the widest readership. Who is to say he is wrong?

The section on the prehistoric forbears of modern crocodylians is detailed and fascinating, listing 165 extinct members of the order. At the risk of seeming uncaring, we may be better off without the 15 meter species weighing as much as three elephants.

In sum, a fine book.

Roland A. Coulson

(3) *Fauna of Saudi Arabia.* Vol. 9, 1988. Editors: W. Büttiker and F. Krupp. 480pp. Pro Entomologia. (1988). SFr. 153.

The Fauna of Saudi Arabia series was first published in 1979 and has now become well-known for its very high quality of both editing and production. Volume 9 is no exception, and is of particular interest to herpetologists since 282 pages are devoted to 'The Snakes of Arabia', an impressive piece of work by John Gasperetti, who has been working for over 40 years in Arabia.

This treatment of the Arabian snakes is a delight to read, and achieves the most ideal objective of bringing different strands of information from all sources into one comprehensive publication. All relevant subjects are treated. The introduction gives a detailed illustrated guide to snake scalation and skeletal features. There is a section giving a chronological historical summary and the conservation of snakes is also considered. A physiographic sketch is outlined for the Arabian Peninsula and the zoogeographing of the snakes is discussed in some detail.

However the majority of the text is devoted to the systematic list of the snakes. Identification keys are provided including all species and there is an introduction for each family and genus. All synonyms are listed for each.

C. J. Raxworthy

(4) *Amphibians and Roads*. Edited by Thomas E. S. Langton. Published by Aco Polymer Products Ltd. (1989).

This book is a summary of the proceedings of the Toad Tunnel Conference held at Rendsburg on 7-10th January 1989. It consists of various contributions from European and American authors. These deal with the problems of toad tunnel and fencing construction, and the effectiveness of the various systems so far employed. The use of substitute ponds as a means of reducing road mortality is also considered. A section is devoted to aspects of orientation and migration, including the possible problem of opportunistic predation of amphibians artificially concentrated by drift fencing.

The round table discussions which expand on the themes raised by each paper are also included. However, despite its title the book doesn't deal with other aspects of amphibians and roads such as the actual effectiveness of toad crossing signs and 'toad lifting'.

Nevertheless it is a useful survey of the state of the art in a growing conservation area.

J. Denton

(5) *Conservation of European Reptiles and Amphibians*. Edited by Keith Corbett. 274pp. Helm, London (1989). £11.95.

By editing this book Corbett places the often neglected groups of reptiles and amphibians clearly within the scope of European nature conservation. How difficult and huge this task was will be understood properly only by those who have inside information. As chairman of the Conservation Committee of the Societas Europaea Herpetologica he led and encouraged a hard working team of herpetologists from all over Europe, who in this book compile their work together with him. The book surely forms the highly needed starting point for national and real European conservation programmes for reptiles and amphibians.

The book contains three different parts. The first gives a European checklist and describes the need for protection and conservation of a substantial portion of this species list. In the second part a number of key species and some key areas are treated. Part three gives national accounts for all European countries.

In spite of its importance the book shows clear signs of haste with typing errors and tedious mistakes and anomalies in the main text and in some non-English literature references. As I feel deep regard for the whole of this work I will deal with most of these hiccups here:

The check-list in part one deviates markedly from earlier published ones but is lacking references; it also double lists the Madeiran lizard as *Lacerta dugesii* and *Podarcis dugesii*.

Bombina variegata is abbreviated to *B. variegata* but listed between the *Bufo* species (Czechoslovakia); *Scolopendra cingulata* (a large centipede) appears as a plant and *Citellus citellus* (the suslik) is with the invertebrates (The Meadow Viper); an '*Emys mauremys*'

occurs (Spain): *Psammodromus hispanicus* appears wrongly as *Podarcis hispanicus* (Portugal); *Ophiomorus punctatissimus* is wrongly stated for open oak forest, perhaps in stead of *Ophisaurus apodus* (Evros); similarly *Elaphe scalaris* in place of the declining *Elaphe situla* (Italy); text reference to Plates 8 and 9 is mistaken; and lastly the species totals for Denmark, Portugal, Romania, Greece, and Turkey do not quite tally.

Multi-authorship produces difficulties of cross reference, these have not always been resolved, thus: the suslik is given as *Citellus citellus* and *Spermophilus citellus* (The Meadow Viper, and Evros.); *Natrix natrix cetti* and *N.n.corsa* are check listed but appear only as one taxon in the text (Italy and France); *Lacerta perspicillata* and *Podarcis perspicillata* can similarly be found; the Balkan frog *Rana shquiperica* is check-listed but is not to be found in the national Balkan texts; the range extension of *Bombina bombina* and the occurrence of *Lacerta praticola* (Evros) are not reflected elsewhere (Greece, and Fire-bellied Toad).

Concerning the texts of the key species in part two the following remarks can be made; — *Rana latastei*: Too much emphasis can be placed on individual observation of habits with an implication that this is always typical; thus if taken to the extreme by a reserve manager it could lead to the encouragement of *Plantago major*! Exact literature references have been omitted.

Vipera ursinii: based on repeated personal visits to some of its habitats I really doubt whether the estimation of only 200 to 300 adult specimens in France is a real estimate.

A part of eastern Sardinia and a part of the Greek province of Evros are shown as already known key areas. This information is based on special studies carried out for the Council of Europe through SEH. When dealing with the Sardinian study again some mistakes sneaked in, e.g. the Sardinian treefrogs have different names in different habitat types and in the habitat 'Agricultural Areas' there is no mention of *Algyroides fitzingeri*, which species appeared to be really abundant there during the study.

When reading the results of the Evros study it strikes the eye, that a certain species combination is nearly ubiquitous there, i.e. *Testudo graeca*, *T. hermanni*, *Emys orbicularis*, *Mauremys caspica*, *Ophisops elegans* and *Lacerta trilineata*. This combination is called 'notably present' for five of the seven very different habitat types. It must be said that they indeed occur on many places in that area, but starting the species list of nearly all the various habitats with these six reptiles uncovers a certain degree of prejudiced thinking. I got the same idea when reading the short paragraph on 'persecution' in the same part; neither poaching of tortoises nor deliberate killing of animals should be mentioned here, because they do not constitute real threats in the area. The reference to Plate 15 is wrong when dealing with the open oak forest habitat; Plate 15 shows an example of the old pine forest habitat. Furthermore, it should be said that the tall deciduous forest described there only occurs in deep valleys and on north-facing slopes, and not on south-facing slopes.

Finally something about the very detailed country accounts in part 3:

— why were *Hyla arborea* and *Podarcis muralis* called 'possibly native' in the UK?

— France: there is a discussion about the specific status of the *Discoglossus* species of Port Cros (*D. sardus* or *D. montalentii*), while the national species list solely mentions *Discoglossus pictus*.

— Italy: it is very strange to learn without comments that islands like Sicily and even the pelagic ones like

Linosa and Pantelleria belong to mainland Italy, while Sardinia and its neighbouring islets do not.

Apart from all these more scientifically orientated remarks I want to state that the book merits great attention from all those who are concerned with the European herpetofauna. And I surely think that its political significance is far greater and stronger than my comments.

H. Srijbosch

THE HERPETOLOGICAL JOURNAL

INSTRUCTIONS TO AUTHORS

1. The *Herpetological Journal* publishes a range of features concerned with scientific herpetology. These include: full papers (no length limit); reviews and mini-reviews (generally solicited by the editor); short notes (with a single data set); controversies, under 'Forum' (details available from editor); and book reviews. Faunistic lists and letters are not published.
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 - Bellairs, A. d'A. (1957). *Reptiles*. London: Hutchinson.
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9. Final acceptance of a paper will depend upon the production by the author of a typescript and illustrations ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.
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