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GROWTH, MOVEMENT AND POPULATION DYNAMICS OF NATRIX MAURA IN A DRYING RIVER

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ABSTRACT

Viperine water snakes were studied by mark-recapture in a small river in Eastern Spain from 1981 to 1983, a period of drought. Observed growth rates between captures were low and highly variable. Growth rings were counted in skull bones; narrow rings could not be found, and the observed rings were probably from periods of faster growth or normal growth before the drought. The rings predict that males and females reached maturity in their third and fifth years, respectively. The effect of drought was greater on growth than on reproduction. Movements of snakes captured several times at long intervals suggest that the home ranges of mature males and females were 170m and 250m of river, respectively, although some individuals moved 1km between years. A review of published data showed that widely foraging grass and garter snakes have greater displacements between captures than the more sedentary water snakes.

There were estimated to be 1060 and 390 adult males and fem ales in the main study area, which was a 2km length of river which included most of the permanent unpolluted water in the river system. Annual survival of adult snakes remaining within the study area was estimated as 0.53 ± 0.16 and 0.71 ± 0.25 in males and females, respectively. A simple model of the dynamics of this population was developed from results on survival, recruitment, growth and fecundity, as a hypothesis for further study. The model suggested that: 1) There was dispersal of adult males but not adult females — this was supported by the population size structure in peripheral areas where mature females were scarce and which were probably stocked by dispersal. 2) The number of adult males and females was stable or increasing, and juvenile survival of about 0.65 year⁻¹ would be necessary for total population stability.

INTRODUCTION

The dynamics of snake populations have proved difficult to study, as these animals are difficult to find or catch (especially juveniles), they have slow growth without external indicators of age, and often show long seasonal movements. After surveying the available data (which suggested that those populations which had been studied were unable to maintain themselves), Turner (1977) concluded 'one is left with distinct reservations as to the suitability of snake populations for this sort of ecological endeavour'. After the extensive studies of the 1950s and 1960s (Carpenter, 1952; Tinkle, 1957; Fitch, 1960, 1963, 1965, 1975; Viitanen, 1967; Prestt, 1971) the popularity of large scale marking efforts has declined. Since then, population studies have concentrated on snakes which gather at hibernacula (Parker, 1976; Gregory, 1977) where large numbers can be captured in a short time.

During a study of the physiological ecology of the viperine water snake *Natrix maura*, a large number of individuals were marked and released. This paper presents information on their growth, movements and numbers, and a model of the dynamics of the population as a hypothesis for further study. This work is continuing in cooperation with Spanish herpetologists and in parallel with further physiological studies. In this way long-term data on one snake population can accumulate as a by-product of other work; we agree with Turner that pure snake population studies are uneconomical in terms of the data obtained per unit research time.

SITE DESCRIPTION

Natrix maura were studied in the river Jalon, eastern Spain (39°N, 0°E) between August 1981 and August 1983. A map of the river bed is shown in Fig. 1; Hailey (1984) gives a more detailed map including topography, neighbouring river systems, and the estimated catchment area. The river is 40km long in total, with a catchment area above Jalon village of 135km². Most parts of the river were investigated, and the only permanent fresh water was found near the villages of Alcalali and Jalon; elsewhere the river was a dry rocky barranco. There was a treated sewage outlet and an area of polluted water below each village along the river.



The study area was a 2km length of river at Jalon, from C-F in Fig. 2. A detailed map of this area (Hailey, 1984) was produced with compass and measuring line, enabling captures to be located to the nearest 10m. This area was permanently wet, but the river was reduced to a series of pools when the connecting stream dried up in summer. There was no water for several km above Alcalali or below Lliber.

The stream meandered across the river bed, which was an area 5-50m (in most places 10-20m) wide and about 3m below the level of the surrounding terraced



Fig. 2 The study area between Alcalali and Jalon — the edges of these villages are shown as shaded areas. The outline of the river bed is shown, together with the course of the stream and positions of pools. ■ House, --- Road, ▲ Sewage outlet, •Rock pile where juveniles were common. Thin bars across the river are weirs, thick bars are bridges. The inset shows the sections of river in situ.

farmland (mostly citrus groves and vegetable plots). Some parts of the river bed were damp and muddy with *Juncus* reeds and grass, and other parts were dry and stony with oleander bushes. Most of the river bed was was flanked with dense bands of bamboo. Two herds of about 100 sheep and goats used the area in dry weather, passing up and down the river on the way to other pasture, feeding on the way.

The study took place during a period of drought, which lasted from 1979 to 1983 in Alicante and Valencia provinces. The river flowed three times during the study; water levels rose in a few hours due to the large catchment area of bare hills, and fell in a few days. The estimated area of water in the region C-F varied during the study between about 0.2 to 0.8 ha, mean 0.3 ha; flow rates measured with markers in the current were between 0 and 0.1 m³.s⁻¹. Area and flow increased to about 4 ha and 15m³.s⁻¹ when the river flowed.

The stream bed was stony, with few water weeds apart from algal mats. There were a few large beds of bulrushes, otherwise cover was provided by the marginal bamboo and rocks and stone walls. The availability of prey has already been described (Hailey and Davies, 1986a), particularly the drying pools with trapped fish which were a feature of the drought.

METHODS

Snakes were captured by hand after searching systematically along the stream and over the river bed. At night they were located with a torch, retained overnight in cloth bags for handling, and released the next day at the place of capture. Each snake was weighed with a Pesola scale and measured against steel tape rule. All lengths are snout-vent lengths, SVL.

In most cases sex was determined from the appearance of the tail, which is long and has a swelling at the base in males. This was often unclear in small snakes and those in poor condition, and these were probed with a grass stem or a round-ended nylon bristle to determine the presence of hemipenes (Schaefer, 1934). An attempt to use plastic mesh tunnel traps failed; although snakes were captured in this way, the traps and fences were soon disturbed by sheep and moved or destroyed.

Snakes were marked by clipping the ventral scales, and they were also recognised by natural markings (Hailey and Davies, 1985). Some snakes were removed for studies of metabolism and reproduction (Hailey and Davies, 1986b, 1987a respectively). These were mostly from outside the study area; small snakes from Alcalali (Fig. 2, A-B) and adult females from pools 1-3 (Fig. 2, B-C). The heads of these snakes were analysed for growth rings.

1460 individuals were marked in the area C-F from August 1981 to August 1983, 1413 of these during the main sampling sessions. About 400 more were captured in the area B-C from June to August 1983, only one of which (an adult male) was originally marked in the area C-F; most of these snakes were marked and released, but are not included in the population analysis. Similarly, about 300 have been captured at Alcalali (A-B) at various times, but no marked snakes have been found or released there. In total the 1860 snakes marked in the area B-F were captured 2410 times, many of the recaptures being at short intervals.

GROWTH RINGS

Heads were boiled in water (sometimes in the field) for several hours to soften the flesh, then the ectopterygoid bones were removed, cleaned of muscle, and air-dried. These were cleared in glycerol for 0 to 16 hours, in proportion to the size of the bone, and examined under 40 x magnification (Bryuzgin, 1939; Petter-Rousseaux, 1953). Mandible bones were treated similarly, but proved to have less clear rings and were not used.

RESULTS

Growth

Observed growth

Only data from captures separated by at least 100 days of active season (allowing for a 120 day hibernation period for recaptures in different years) have been used. Errors in measurement of SVL make short term growth difficult to study in snakes which grow slowly. Observed growth rates were highly



Fig. 3 Observed growth rates of *Natrix maura* between captures at intervals of >100 days. a) females, b) males. Equations (1 and 2) in the text.

variable (Fig. 3), reflecting the high variability in feeding opportunities in time and space in the drying river (Hailey and Davies, 1986a). Only about 5 per cent of this variability could be explained by the size of the snake, although the regressions of growth rate (mm SVL. day⁻¹) on initial SVL (cm) were significant, and are used as summaries of size-specific growth:

Females: Growth rate =
$$0.104 - 0.00172$$
 SVL (1)
(n = 109, r = -0.23 , P<0.05)

Males: Growth rate =
$$0.057 - 00134$$
 SVL (2)
(n = 87, r = -0.21 , P< 0.05)

As the observed growth rates were so variable, no attempt has been made to fit the data to more complex growth formulae (Fukada, 1961; Andrews, 1982).



Fig. 4 Number of growth rings in the ectopterygoid of *N. maura* a) females, b) males. Source of specimens: • Alcalali (Fig. 2, A-B); o pools 1-3, area B-C. Equations (3 and 4) in the text.

Growth rings

Narrow rings which would be expected to accompany slow growth were seldom seen. It is

therefore thought that most rings were produced during periods of faster growth, or remained from normal growth preceding the drought. The relationship between the number of growth rings and SVL (cm) is shown in Fig. 4, described by the equations:

Females: Growth rings =
$$0.291$$
 SVL — 3.3 (3)
(n = 119, r = 0.81 , P< 0.01)

Males: Growth rings =
$$0.342 \text{ SVL} - 5.0$$
 (4)
(n = 105, r = 0.73 , P< 0.01)

If it is assumed that the number of growth rings equals the age in years, then equations 3 and 4 can be rearranged to show size vs age:

Females:
$$SVL = 3.44 \text{ Age} + 11.3$$
 (5)

Males:
$$SVL = 2.92 \text{ Age} + 14.0$$
 (6)

These equations predict growth rates of 3.4 and 2.9cm. year⁻¹ and hatchling SVL of about 11.5 and 14.5cm in females and males, respectively.



Fig. 5 Seasonal abundance of *N. maura* of different sizes (including recaptures), with inferred growth curve for the first full year fitted by eye. a) Males, truncated at 30cm, b) females, truncated at 40cm.

Growth of juveniles

No data are available on observed growth of juveniles as none were recaptured, and few heads were available to study growth rings of small snakes. Growth of juvenile snakes may also be estimated from the seasonal abundance of individual size (Fitch, 1961; Saint Girons, 1965). The smallest snakes found, of both sexes, had SVL of 12-14cm (Fig. 5), similar to the size of hatchlings (Davies, unpublished). Fig. 5 shows suggested growth during the first full year from 13 to 20cm.

Snakes of 12-14cm were commonly found under piles of rocks in early spring at two locations (Fig. 2), from where they dispersed, and slightly larger snakes were found in many places later in the year. No juveniles were found under these rocks, or anywhere else, in autumn, and the activities between hatching (probably in September, from eggs laid in July — Hailey and Davies, 1987a) and the first hibernation are unknown. The lack of growth until the following spring suggests that they do not feed much, and they may remain near the nest.

MOVEMENT

Movements of marked snakes between captures are of interest in two respects, considered over different time scales. 1) Short term movements (<30 days between captures) show the scale of exploration and foraging during routine daily activity. 2) Long term displacements (captures in different years) show the overall extent of the area used, or home range. Only mature snakes are considered, as others were seldom recaptured. G-tests have been used to compare frequency histograms of displacements of males and females in different seasons (Fig. 6).

Short term movements of both sexes were greater in spring (March to May, Fig. 6b), when the stream connected the pools, than in the dry period (June to October, Fig. 6a) when the pools were isolated and movements would have to be over dry land (P<0.01 for each sex). It is therefore not possible to separate ease of movement from searching for mates as causes of increased movement in spring. There was no difference between the sexes in short term movements in either period (P>0.1).

Long term displacements (Fig. 6c) were greater in females (mode 80-320m) than males (mode 20-80m),



Fig. 6 Distance between captures of adult *N. maura*, males above, females below. a) Short term movements in summer, b) short term, spring, c) long term. Note the logarithmic distance scales; means and sample sizes in Table 1.

| | Males | Females | |
|-----------------------------------|---------------|---------------|--|
| Short term, summer | 23 (132) | 9 (18) | |
| Short term, spring | 68 (32) | 76 (27) | |
| Long term | 113 (54) | 204 (48) | |
| Between successive captures* | 66 (800, 66) | 110 (950, 40) | |
| Between first and last captures** | 100 (300, 14) | 180 (620, 10) | |
| Minimum home range length** | 170 (800, 14) | 250 (950, 10) | |

TABLE 1: Movements of adult *N. maura*; mean displacements along the river, in m. Upper: total data, the variation of which is shown in Fig. 6 (with number of movements). Lower: snakes with four or more captures at intervals of >30 days (with maximum, number of movements* or individuals**).

P<0.001. These movements were all in one dimension, up or down the river, giving a linear home range. Few snakes were found in the river bed away from water, and these were usually between pools where there was no conneting stream. The length of the home range is estimated from snakes with four or more captures at intervals of >30 days. This was on average 170m in males and 250m in females (Table 1). The greater long-term movements and home ranges in females reflect the female> male size dimorphism in *N. maura* (Hailey and Davies, 1987a).

POPULATION STRUCTURE

The sex ratio and size distribution of males and females varied between different parts of the river (Fig. 7 and Table 2). In the area C-E slightly more males than females were captured. The sex ratio of adults was more heavily male-biased as they reach maturity at a smaller size (about 24 and 37cm in males and females, respectively; Hailey and Davies, 1987a). This area held the highest density of snakes and their prey, but snakes were also found in other places thought to be peripheral areas.

In the polluted area at Jalon (E-F) there were fewer small or large snakes (Fig. 7b), most being in the range 25-35cm, i.e. adult males and subadult females. The overall sex ratio was even, but the adult sex ratio was heavily male-biased (Table 2). A similar pattern was found at Alcalali (A-B), though there were more adult females (Fig. 7c).



Fig. 7 Size frequency histograms of *N. maura*, females above, males below; recaptures excluded. a) Central study area, Fig. 2 part C-E, b) polluted area at Jalon, E-F, c) Alcalali, A-B. Sample sizes in Table 2. ---- Size at maturity.

POPULATION SIZE AND TURNOVER

The number of snakes in the area C-F was estimated using Bailey's triple catch method (Begon, 1979) on three main sampling sessions: August-September 1981, April-May and September-October 1982, June-August 1983. Although the September-October 1982 sample was large, it was from a restricted area due to an extremely low water level at that time and lack of snakes elsewhere. It was therefore unsuitable for use separately, and was pooled with the spring 1982 sample.

The results for mature males and females are shown in Table 3. A large proportion of the estimated

| Area | All individuals | | | A dults | | | | |
|------|-----------------|---------|------------------|---------|-------|---------|------------------|---------|
| | Males | Females | Males Females | Р | Males | Females | Males Females | Р |
| C-E | 672 | 593 | 1.1 | < 0.05 | 567 | 250 | 2.3 | < 0.001 |
| E-F | 72 | 76 | 0.95 | >0.05 | 64 | 9 | 7.1 | < 0.001 |
| A-B | 85 | 119 | 0.71 | < 0.025 | 72 | 23 | 3.1 | < 0.001 |

TABLE 2: Sex ratios of individuals found in different parts of the river. The number of different males and females, the ratio of males per female, and the probability (X^2 test) that the true ratio is 1.0, are shown for all snakes and for adults only.

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| | Males | Females | |
|-----------------------|----------------------------|-------------|--|
| Sample | numbers captured: released | | |
| 1981 | 129:128 | 53: 53 | |
| 1982 | 327:309 | 173 : 166 | |
| 1983 | 240 : 238 | 74 : 65 | |
| Last previous capture | number | | |
| 1981-1982 | 20 | 16 | |
| 1981-1983 | 6 | 3 | |
| 1982-1983 | 38 | 22 | |
| Estimate (with SE) | | | |
| Population size 1982 | 1060 (360) | 390 (140) | |
| Survival 1981-1982 | 0.53 (0.16) | 0.71 (0.25) | |
| Recruitment 1982-1983 | 0.52 | 0.42 | |

TABLE 3: Mark-recapture data and population estimates for adult *N. maura* in the area C-F. Sample numbers in 1982 and 1983 include those recaptured from previous years.

population were handled, 60 per cent of 1060 males and 66 per cent of 390 females. The sex ratio of adults is 2.7 males per female from the population estimates. The data also allow estimates of survival and recruitment of adults between samples (Table 3).

POPULATION DENSITY

The density of animals which are found along rivers is not a simple concept (Turner, 1977), and cannot be reduced to a single value. Two densitites are considered, of value in different contexts, depending on the definition of the area occupied.

Ecological density

This is concerned with the number of animals in the area where they are active (Odum, 1959), and should be used when considering rates of contact with prey, predators and conspecifics. In *N. maura*, all foraging occurred in or close to the water, and mating and basking snakes were almost always within 2m of the water, often overhanging it (Hailey and Davies, 1986a, 1987a,b). The ecological density is therefore based on the area of surface water, 0.3 ha, i.e. about 4800 adults ha⁻¹.

Crude density

This covers the area used at all times of the year, and any pockets of unused habitat (Odum, 1959), i.e. the area which would have to be protected to conserve the population undamaged. In *N. maura* this includes daily refuges in the river bed and rock piles and walls above the river bed used for nesting and hibernation (Hailey and Davies, 1987a,b). It is based on the area of the river bed plus a band 5m wide on each side including stone walls of the lowest terrace of farmland, a total of 6 ha, i.e. about 240 adults ha⁻¹. *N. maura* were not found in the surrounding farmland, either by us or by the farmers, who readily distinguished them from the commonly seen 'culebra bastarda' (*Mal polon mons pessulanus*).

DISCUSSION

GROWTH AND AGE AT MATURITY

The results from Jalon are compared with those for *N. maura* in central France, based on the seasonal distribution of length, gonad histology and growth in enclosures (Duguy and Saint Girons, 1966). Their results have been converted from total length to SVL using the equations of Hailey and Davies (1987a), and are summarised in Fig. 8. Histology revealed that males underwent the first, abortive, spermatogenesis at two years old, and were mature at three. Duguy and Saint Girons had less data for females, but suggested that they were mature at four.



Fig. 8 Growth curves of *N. maura*, a) females, b) males. OBS) Observed growth above 20cm, equations 1 and 2, MAX) maximum observed, rates of 0.2 and 01.mm.day⁻¹ in females and males, respectively, R1NGS) from growth rings, equations 5 and 6, FRANCE) from Duguy and Saint Girons (1966) study of *N. maura* in France. ---- size and age at maturity.

The size of hatchlings in France, 13cm, is similar to that of the smallest snakes found at Jalon, where they were first seen in spring. Growth to 20cm after the first full year is suggested by the seasonal distribution of SVL (Fig. 5). Observed growth above 20cm in 1981-1983 was slow (Figs. 3 and 8), presumably the result of

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drought and low food supply. Snakes with two growth rings had SVL of about 25cm (Fig. 4), and it is thought that both sexes normally grow to 25cm after two years. These snakes were from Alcalali, where worms were abundant near the polluted area even during the drought — these are a common food of small snakes (Hailey and Davies, 1986a).

The growth ring data (equations 5 and 6) suggest constant growth of SVL above 25cm, at rates of 2.9 and 3.4cm.year⁻¹ in males and females, respectively. The maximum observed growth rates' were about 0.1 and 0.2mm.day⁻¹ in males and females (Fig. 3), or 2.5 and 5.0cm.year⁻¹ over an active season of 245 days. These rates are shown as growth curves in Fig. 8 — they are slightly lower than those found in France. It is concluded that: 1) The drought severely reduced growth, particularly above 20cm, and that in normal years; 2) Males reach adult size at two years old (in the autumn) and breed the following spring in their third year as in France; 3) Females reach adult size and first breed in their fifth year.

POPULATION DYNAMICS

The dynamics of the population are now explored to calculate the juvenile survival rate needed for stability and make predictions for further study. The results suggest that the adult female population was increasing at the proportional rate $e^r = 1.13$ per year (survival 0.71 + recruitment 0.42, Table 3). This seemed unlikely during a drought and so, as it is not apparent which is an overestimate, both survival and recruitment have been divided by 1.13, to give 0.63 and 0.37 respectively and a stable population (i.e. $e^r = 1.0$). This gives an annual turnover of 0.37 x 390 = 145 adult females. A similar adjustment for males ($e^r = 1.05$) gives both survival and recruitment values of 0.50.

Mean fecundity was 7.1 viable eggs per adult female per year (Hailey and Davies, 1987a), or 2770 eggs for the whole population, half of the eggs are assumed to be female. In the five years to maturity this number must be reduced by a factor of 0.105 for recruitment of 145 adults. This is equivalent to constant survival at the rate $0.105^{1/5} = 0.64$ year⁻¹ over this period, i.e. similar to that of adult females.

Survival of immature males and females should be similar; what is the effect of a survival rate of immature males of 0.65 year⁻¹ on the male population dynamics? This would give annual recruitment of 380 three year olds, 0.36 of the adult population. The difference between this value and recruitment calculated by mark-recapture, 0.50-0.36 = 0.14, could be due to immigration. In that case there should be a similar loss in emigration, and the survival rate within the study area from mark — recapture (0.50) plus this emigration would give a total survival rate of adult males of 0.64 year⁻¹.

Three conclusions can be drawn from this discussion:

1) The adult male and adult female populations were stable or increasingly slightly.

2) There was dispersal of adult males but not of adult females.

3) Total survival (including emigrants) of adults was about 0.65 year⁻¹ for both sexes, and immature snakes would have to survive at the same rate for the population as a whole to be stable.

The second conclusion is a prediction from the model, and is supported by the population structure data. Dispersal of adult males (and of subadult males and females, immigration balancing emigration), but not of adult females or juveniles, would produce the population structure found in peripheral areas (Fig. 7b,c). In the near absence of adult females, these areas must be stocked by dispersal.

COMPARISONS WITH OTHER SNAKES

Comparison with previous population studies of snakes suggests two areas for particular study at Jalon. 1) Growth and age at maturity of females in normal conditions. The five years suggested here seems rather long for a small colubrid — females of most small snakes are mature at 2-4 years (Turner, 1977). 2) Survival of juveniles. Most studies have suggested that survival of juvenile snakes is very low (Turner, 1977), although numerical values have rarely been obtained, and low probability of recapture may also reflect the difficulty of finding them.



Fig. 9 Frequency distribution of reported crude population densities of a) snakes and b) lizards. Data from Table IX and Fig. 1 of Turner (1977). Note the logarithmic density scale. The position of the *N. maura* crude density of adults is shown in (a).

Densit y

The crude density can be compared to those reviewed by Turner (1977), which had a geometric mean of about 3 Ha⁻¹, an order of magnitude lower than for lizards — Fig. 9. The high value in *N. maura* is not surprising in view of the rich food supply normally associated with water.

The very high ecological density shows a high potential for contacts with conspecifics around the water. *Natrix maura* did not seem to have complex social or reproductive behaviour; courtship, aggression or territoriality were never seen, and mating accounted for only about 0.3 per cent of all sightings. Snakes usually seemed to ignore each other, though on two occasions they were seen competing for food, by simultaneous ingestion. Hailey and Davies (1987a) calculated that females mated several times per year by observing sperm in cloacal fluid — this would be interesting to compare in a less dense population.

Survival

There are not sufficient data on snake survival to allow firm conclusions to be drawn, but the 14 populations reviewed by Turner (1977) are suggestive. Survival of these ranged from 0.25 to 0.86 year⁻¹, mean 0.61. Small colubrids (*Carphophis, Diadophis, Heterodon, Rhabdophis, Thamnophis*) had relatively low survival (0.25-0.63, mean 0.43), large colubrids (*Coluber, Elaphe, Masticophis*) were intermediate (0.40-0.86, mean 0.67) and viperids had highest values (0.70-0.82, mean 0.75). The survival of adult *N. maura* is thus greater than that of other small colubrids. This, together with the high population density, is probably due to the scarcity of predators (see Conservation below).

EFFECTS OF DROUGHT

The adult population as a unit was resistant to drought, possibly even increasing. Female reproduction was also little affected, assuming that females have a fixed number of follicles developing each year according to body size; on average only 18 per cent of these follicles were atretic (Hailey and Davies, 1987a). In contrast growth was very slow (Fig. 8), and most adults did not grow at all. Annual differences in reproduction within populations, correlated to food supply, have been shown in a number of reptiles (Ballinger, 1977; Swingland, 1977; Andren and Nilsson, 1983; Seigel and Fitch, 1985). Annual variation in growth has been shown in longlived reptiles (Peabody, 1958; Stubbs and Swingland, 1985). Among female reptiles, only snakes and crocodiles show substantial growth after maturity (Hailey and Davies, 1987a), suitable to show clear trade-offs between growth and reproduction with different food supply. This study shows that growth is reduced before reproduction in adult female *N. maura*; it is suggested that they grow only after their reproductive capacity for the year has been completed.

MOVEMENT

Table 4 summarises data on the movements of nonmigratory natricine snakes; those which migrate to hibernacula may move much further, for example 11km in *Thamnophis sirtalis* in Canada (Gregory and Stewart, 1975).

The widely foraging grass and garter snakes move further than the more sedentary water snakes, both between successive daily radio fixes and between captures at longer intervals. This correlates with the activity metabolism of these ecological types, active natricines having a greater capacity for sustained aerobic activity (Hailey and Davies, 1986 c).

Home ranges show no pattern, as expected as these should be related to the amount of food available within an area (Mace, Harvey and Clutton-Brock, 1983) rather than to the distance moved during foraging within that area. All of these natricines are found in productive marsh or riparian habitats.

| | Widely foraging | | Sit-and-wait | | |
|---------------------|---------------------|----------|--------------------------|-----|-----|
| | (a) Distar | nce betw | een captures (m) | | |
| Thamnophis sirtalis | 300 | (1) | Natrix maura* | 44 | (4) |
| Thamnophis butleri | 115 | (2) | | | |
| Thamnophis butleri | 72 | (3) | 24 | | |
| Thamnophis sirtalis | 62 | (3) | | | |
| Thamnophis sirtalis | 58 | (2) | | | |
| | (b) Daily displacer | nents of | radio-tracked snakes (m) | | |
| Natrix natrix | 30 | (5) | Nerodia sipedon | 4 | (6) |
| Thamnophis sirtalis | 10 | (6) | | | |
| | (c) | Home ra | ange (ha) | | |
| Natrix natrix | 12 | (5) | Nerodia spp | 5.7 | (5) |
| Thamnophis sirtalis | 11 | (1) | Natrix maura** | 0.6 | (4) |
| Thamnophis sirtalis | 0.8 | (2) | Nerodia sipedon | 0.5 | (7) |
| Thamnophis buileri | 0.3 | (2) | | | |

TABLE 4: Studies of movement in natricine snakes according to foraging mode. A simple (unweighted) mean is used where data were originally divided by sex or season. References: 1) Fitch (1965); 2) Carpenter (1952); 3) Freeman and Catling (1978); 4) this study; 5) Madsen (1984); 6) Fitch and Shirer (1971); 7) Fraker (1970).

* Short term, as other data are for successive captures.

** Assumed to be 30m wide, corresponding to the area used for the crude population density.

CONSERVATION

The study population is clearly large, dense, and of ecological interest — is it likely to survive? Many snakes were killed by people, particularly large females which were though to be poisonous — 32 of these were found decapitated or battered on paths close to the stream or in the water. However, this is probably not a new occurrence, and the population seems able to withstand it. The high density is indeed likely to be due to human interference, on predators of snakes. There were very few predatory birds or mammals in the river, and no terrapins (one *Pseudemys* (!) was found at Jalon, but several stuffed *Mauremys* were seen on sale at nearby coastal resorts).

The main threat is further urbanisation of the Jalon valley and increasing pollution, eventually killing the fish in the river. These are probably necessary prey for large *N. maura*, although small snakes commonly take worms which are common in polluted areas (Hailey and Davies, 1986 a). This has probably already happened at Gata (Fig. 1) and other places in Alicante and Valencia provinces, which are vulnerable because of low normal rainfall.

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A REVIEW OF GEOGRAPHICAL VARIATION IN *GERRHOSAURUS MAJOR* DUMÉRIL (SAURIA : CORDYLIDAE)

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ABSTRACT

Examination of most of the available material of *Gerrhosaurus major* indicates that only two geographical races should be recognised, the typical form (with *grandis* Boulenger as a synonym) in eastern Africa and *G.m. bottegoi* Del Prato (with *zechi* Tornier as a synonym) ranging from northern Somalia west to Ghana.

In the last revision of the genus, Loveridge (1942) recognised four races, but did not realise that the name *bottegoi* was applicable to the dark form which he called *zechi*. The range of variation in the typical form includes all the material that Loveridge assigned to *bottegoi* and *grandis*.

INTRODUCTION

When the genus *Gerrhosaurus* was last reviewed by Loveridge (1942) most of the available material of G. *major* was from East Africa, and he assigned it to three races based on colour pattern, using the following key:

'7. Head above, buff, each scale spotted with black . . 8

Head above, uniform buff or fulvous brown ... 9

8. Above head, body and tail almost black, each scale with a small buff spot or streak arranged to form interrupted lines on back and sides; belly streaked with dusky; range Belgian Congo and Togom. zechi

Above, head and body buff, each scale (except those forming an ill-defined, buff, dorsolateral line) heavily streaked with black or dark brown in regular lines on back and sides with a tendency to