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DIET AND FORAGING BEHAVIOUR OF *NATRIX MAURA*

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ABSTRACT

There was an ontogenetic change in the diet of the water snake *Natrix maura*, from earthworms and tadpoles in juvenile snakes to fish in adults. This was related to the absolute sizes of these prey types and to the scaling of encounter rates with snake size. Within each prey type relative prey weight RPW was independent of snake size, except for fish taken from drying pools (RPW inversely related to snake size). Overall, RPW increased with snake size (prey taken during normal foraging) or was independent of snake size (including fish from drying pools). Snakes handled fish too large for them to ingest. Multiple captures were common from drying pools, the fish being smaller than when a single fish was taken.

Foraging behaviour of wild *N. maura* could be described as exploratory activity and cruising (finding slow-moving or trapped prey during slow movement); sentinel predation (an extreme sit-and-wait strategy for catching fish); active pursuit and undirected 'fishing' (less commonly observed). Sentinel *N. maura* took up different positions in the water according to their size. Breathing took up 20 per cent of their time; those at the surface spent shorter intervals foraging and breathing than those with deeper perches. Strike rate was once per 7.4 minutes, capture success was low, 2 out of 124 strikes, neither ingested. The relationship between the different types of foraging used by *N. maura* and other natricine snakes, and their stimulus control, are discussed.

INTRODUCTION

The feeding ecology of natricine snakes is well studied, especially the role of chemoreception in the detection (e.g. Arnold, 1981; Burghardt, 1975; Dix, 1968; Dunbar, 1979; Mushinsky and Lotz, 1980) and location (Kubie and Halpern, 1979) of prey. Czaplicki and Porter (1974), Porter and Czaplicki (1977) and Drummond (1979) investigated the stimuli controlling foraging in small laboratory pools in *Nerodia*, and Drummond (1983) described this behaviour in wild *Thamnophis*. There are few studies of feeding behaviour in wild snakes, due to the difficulty of following them (Reinert, Cundall and Bushar, 1984 studied foraging in rattlesnakes with the aid of radio tracking). This paper describes the foraging behaviour and diet of wild viperine water snakes, *Natrix maura*.

METHODS

N. maura were studied in the river Jalon, Spain, from April 1981 to August 1983. During this period the river was a series of pools up to 2m deep, linked by a small stream which dried up in summer. Snakes were captured by hand, forced to regurgitate any food, and weighed with a Pesola scale. Unless stated otherwise, the expression 'with food' includes snakes handling or forced to regurgitate prey. Prey was measured or weighed, using the length — weight regression from Hailey and Davies (1986) to estimate weights of partly digested fish. At night a powerful torch was used to find snakes, which were held in cloth bags until the following day. For data analysis snakes were grouped into four size classes: tiny (T; <4g), small (S; 4-15g), medium (M; 15-40g) and large (L; >40g). Snakes seen but not captured were assigned to one of these classes by visual estimation. The location and behaviour of each snake were noted, and some undisturbed foraging snakes were observed with 8x binoculars.

RESULTS

DESCRIPTION OF FORAGING BEHAVIOUR
Sentinel Foraging (SF)

This was the most commonly observed foraging behaviour of larger *N. maura*, but was not seen in tiny snakes. The snake was stationary in the water, on the bottom or in debris or vegetation, and made strikes at passing fish with the front part of its body which was held in a concertina position. Most strikes involved an extension of about 20 per cent of the snake's body, though occasionally the whole body was extended; in this case the snake usually then left its perch.

Location. Fig. 1a shows the positions of S, M and L SF snakes in the water during the day and at night. G tests (Sokal and Rohlf, 1981) are used to assess significance of these data, pooling classes where necessary to give >5 observations per cell. Snake size and water depth

were significantly associated during the day (P<0.05) and at night (P<0.001); smaller SF snakes frequented shallower water. This may be related to the ease of reaching the surface to breathe and/or to the

occurrence of different sizes of fish in different depths of water. Small fish were often seen at the margins of pools in shallow water, large fish favoured deeper water.
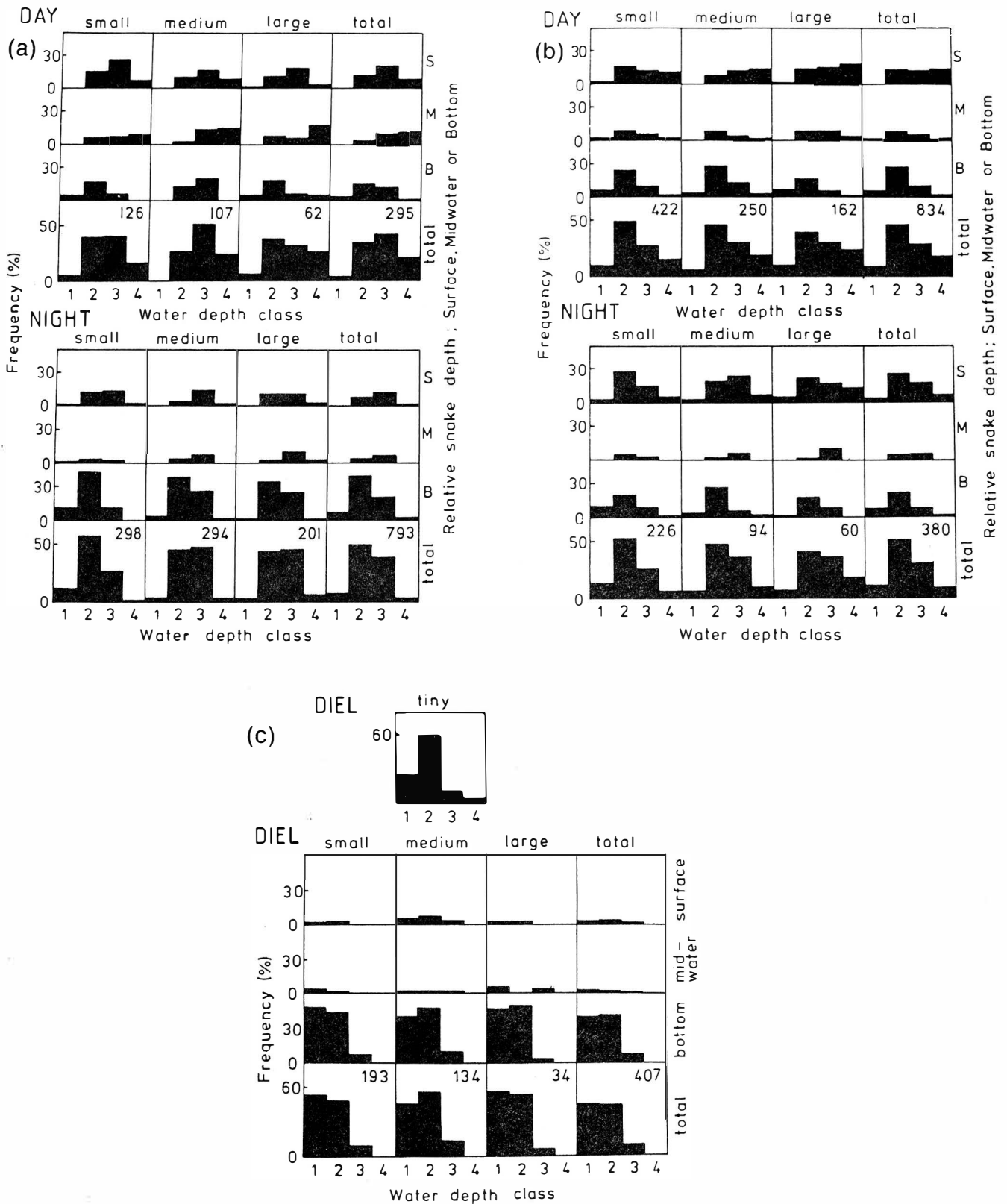

Fig. 1. Positions in the water of (a) sentinel, (b) active and (c) cruising *n. maura* of different sizes, day and night. Water depth classes are 1 = 0-5cm, 2 = 5-15cm, 3 = 15-50cm, 4 = >50cm.

All sizes of SF snakes were seen more often in shallow water at night than in the day; this association between day/night and water depth is significant (P<0.05) for all size classes. Snakes were common in exposed shallow water at night, in situations where they would have been very vulnerable to predation in the day. Water depth and relative snake depth were associated in all sizes of SF snakes during the day; in deeper water snakes were often found in midwater or at the surface, in shallow water they were relatively more frequent on the bottom (Fig. 1a: P<0.001 for S, M and L combined). This may be related to the distribution of fish or to the need for movement to the surface to breathe. Snakes were seen relatively more frequently on the bottom at night than during the day (Fig. 1a; P<0.001 for S, M and L combined). This may be related to the difficulty of seeing fish at night; they would be much more visible when viewed from below, seen in silhouette against the sky.

These distributions may be compared with those of snakes active in the water (Fig. 1b). During the day there was no association between snake size and water depth (0.5>P>0.1), and there was a significant association between activity type (activity and SF) and water depth for all size classes (P<0.001 for each class). This suggests that most activity during the daytime was not the breathing excurions of SF snakes, but was a different behaviour, probably exploration. In contrast, at night snake size and water depth were associated in active snakes (P<0.05) and the water depth distribution of S and M snakes did not differ significantly between activity and SF (P<0.05). This suggests that much of the activity observed at night was the breathing excurions or small positional changes of SF snakes. If SF snakes at night spent 20 per cent of their time in breathing excurions (as during the day, below), this would account for over half of the snakes seen active at night. Water depth was associated with activity type in L snakes (P<0.05), these being relatively more abundant in deep water when active than when sentinel foraging.

Capture Success. Snakes achieved a low rate of food intake while SF. 48 SF S and M snakes were watched carefully for a total of 921 minutes, excluding breathing, in the day at water temperatures between 25°C and 29°C during July and August 1983. They made 124 strikes at fish (one per 74 minutes), of which only two made contact. One fish was obviously too large to be ingested and leapt from the water, dragging the snake from its perch and escaping immediately. The other was also large (~50% of the snake's weight); it was taken to some floating reeds but escaped after two minutes.

Breathing. SF snakes periodically had to interrupt foraging to breathe, accounting for 175 minutes additional to the 921 minutes actually foraging (19 per cent of the total time). Those near the surface could breathe without leaving their perches, and spent significantly shorter intervals foraging and breathing than those with deeper perches which had to leave them to breathe (Fig. 2). Surface SF snakes used 20 per cent of their time for breathing, deep SF snakes used 17 per cent for breathing and moving to the surface

and back. Most SF snakes were found already foraging; those not noticeably scared away remained for 5-65 ($\bar{x}$ 22.8) minutes before moving away.
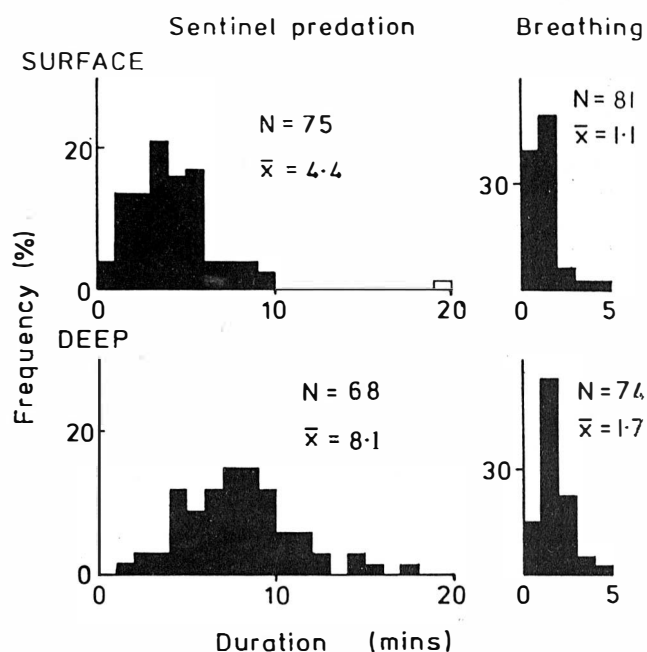

Fig. 2. Duration of periods of SF and breathing. Upper histograms refer to snakes near the surface, lower are for snakes in midwater or on the bottom. These differ significantly in both breathing and foraging intervals (G tests, P<0.01 and P<0.001, respectively).

Sensory control. Four snakes were seen to change from exploratory activity in water to SF after locating fish schools. They crept stealthily towards the fish, and occasional tongue flicks were seen during approach. Two other snakes moving on floating reeds saw fish below them and started SF. During daytime SF the snakes aimed strikes at fish mostly by sight. Contact stimuli were also used; SF snakes also struck at objects which touched them, including non-prey such as beetles and other snakes. At night SF snakes would approach a light, tongue flicking; they could be induced to strike if brushed lightly with fingers.

In laboratory pools (Hailey and Davies, 1986) snakes responded to introduction of fish, or other disturbance, by tongue flicking. Strikes were mostly aimed by sight, but also by contact. Snakes would strike at each other if they made contact when foraging: this was never seen in the absence of fish.

Fishing

This rare but characteristic foraging behaviour was seen five times; three at night and two in the early morning. The snakes swam round in an exaggerated manner, following a figure 8 course, with their jaws open. Fish were present nearby, but the snakes were not pursuing particular individuals or groups.

Cruising foraging (CF)

Tiny snakes did not have any special foraging behaviour, but were found moving about slowly in damp areas and shallow water, and seem to fit Regal's (1978) 'cruising forager' category. Larger snakes were also commonly found moving about slowly, but those which found fish normally reverted to SF, creeping nearer and then waiting for the fish to approach. The exception was where fish were confined in shallow drying pools. Snakes approached these pools flicking their tongues rapidly, and probably detected them by chemoreception; the fishy smell was obvious even to the human nose.

Once in the water snakes moved around after fish, lunging at them and swimming rapidly after them as far as the extent of the water allowed. Following fish about is described as CF; swimming after them is termed 'pursuit'. CF normally took place in shallow pools (Fig. 1c), but was also seen in some larger pools which became anoxic with fish gasping at the surface. Strikes were aimed as in SF, by sight and contact. CF also involved taking dead fish, earthworms and tadpoles, though such foraging was not clearly distinct from feeding during exploratory activity. Worms and tadpoles were the sole prey available to snakes in a polluted part of the river (Hailey, 1984) and no SF was seen there.

Feeding success in drying pools was much greater than that in other pools; 3.19 per cent of 439 snakes from drying pools were handling ingestible prey, compared to 0.66 per cent of 2720 snakes from other pools (G test P<0.001). There was no significant difference between the feeding success of small, medium and large snakes (Table 1); overall 1 per cent of snakes in water (i.e. potentially foraging) were handling useful prey. The act of handling prey had little effect on the susceptibility of snakes to capture by man. 64 per cent of 45 snakes handling prey were captured, compared to 53 per cent of 4863 snakes not handling prey ($X^2 = 1.73$, P>0.1).
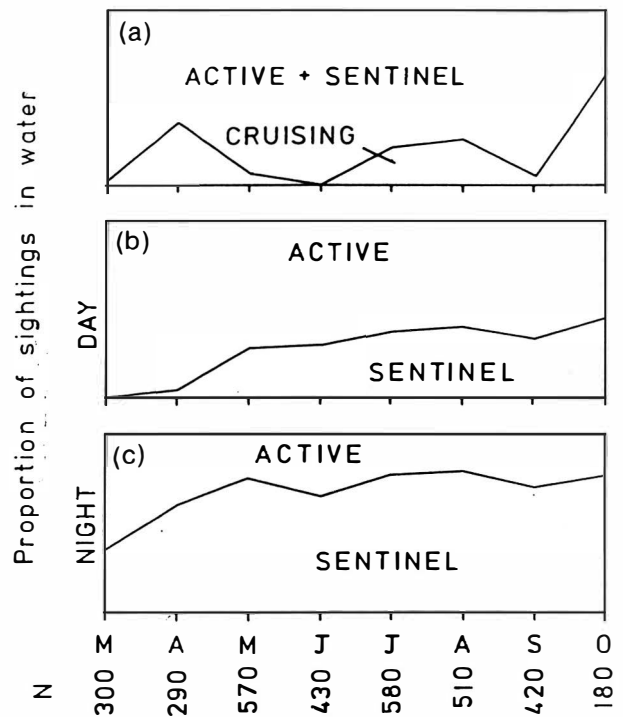

Fig. 3. Variation of activity type of snakes in water with season. (a) shows the number of cruising snakes relative to others in water, (b) and (c) show the relative numbers of active and sentinel snakes, day and night. N shown is for the total sample in the water.

| | % with prey (n) | | | |
	Small	Medium	Large	P
Drying pools	1.3 (235)	4.3 (163)	9.8 (41)	>0.1
Other pools	0.71 (1266)	0.57 (880)	0.70 (574)	>0.9
Total	0.80 (1501)	1.15 (1043)	1.14 (615)	0.5

TABLE 1: Proportion of snakes in water (potentially foraging) which were handling ingestible prey. P is for G test comparing the three sizes of snakes.

Prey type	n (n	measured)	RPW (%) mean (range)	intensity* mean (range)
Earthworms	37	(16)	5.7 (0.5-28)	1.32 (1-3)
R. ridibunda tadpole	9	(6)	7.2 (2.1-13)	1.28 (1-2)
R. ridibunda frog	11	(6)	37 (18-54)	1 (1)
Fish (CF, regurgitated)	129	(95)	9.2 (1.1-55)	1.52 (1-6)
Fish (CF, handled)	15	(10)	33 (6.3-75)	
Fish (SF, regurgitated)	39	(26)	13 (1.0-51)	1.07 (1-2)
Fish (SF, handled)	24	(9)	44 (10-104)	

TABLE 2: Relative prey weight (RPW) of different prey types

* intensity = no of prey in snakes with that prey type.

In addition one leach and two B. bufo tadpoles were regurgitated, and five dead fish were seen being handled.

Direction of ingestion	RPW (%)			
	0-5	5-10*	10-15*	>15*
			number of fish	
Head first	35	26	20	24
Tail first	12	2	2	0

TABLE 3: RPW and direction of ingestion of roach

* Combined for G test. P<0.005.

Fig. 3 shows the daily and seasonal pattern of foraging activity. As noted by Hailey, Davies and Pulford (1982), SF is most common at night, activity during the daytime. The seasonal distribution of CF reflects the opportunities for this type of foraging.
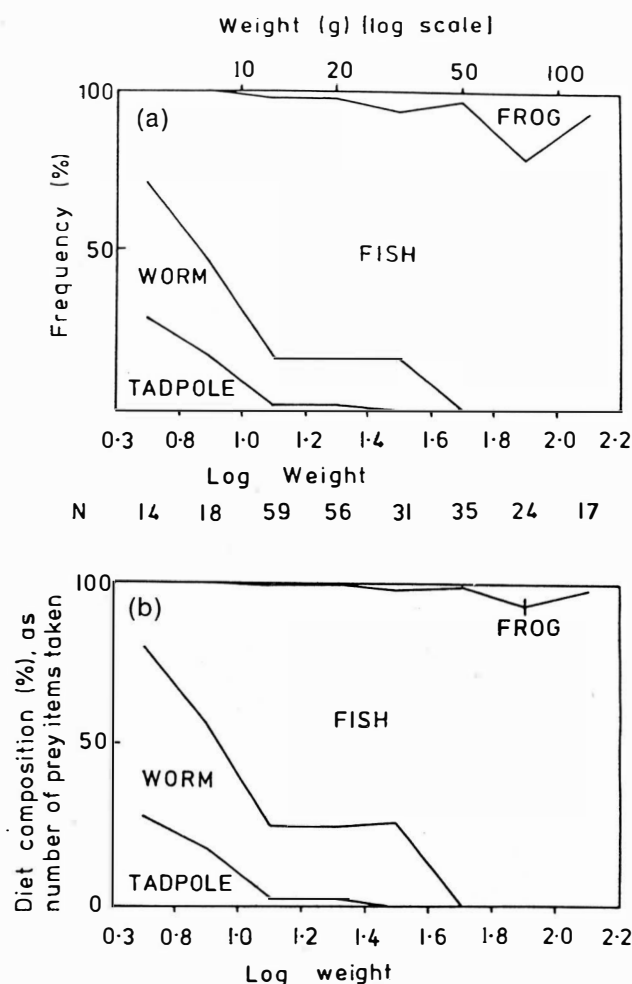

Fig. 4. Variation of diet with snake size. (a) Frequency of prey items, proportional to their energetic contribution, (b) Divided by the mean weight of each prey type, proportional to the number of prey items taken.

DIET

Taxonomic composition

Tiny snakes were found with earthworms and tadpoles (*Rana ridibunda*, the only amphibian in the river Jalon apart from *Bufo bufo*), larger snakes with fish (roach *Rutilus rutilus*, the only fish in the river Jalon) and some frogs (Fig. 4a). The importance of frogs in the diet is overestimated, as seven of the 11 found were discovered by following the characteristic calls they made while being eaten, and were thus much more obvious than the other prey types. Table 2 shows the relative sizes of the different prey types. 87 per cent of all fish were ingested head-first; large fish were more likely to be ingested head first than small fish (Table 3).

Size composition

Within each prey type relative prey weight (RPW = prey weight/snake weight, as a percentage) was independent of snake size (Fig. 5), except for fish captured while cruising in shallow pools, for which RPW was inversely related to snake size (Fig. 5b). There are two possibilities here, either selection of fish by snakes, or a change in the size frequency distribution of fish when pools dried. Large fish died first in the later stages of drying of a pool, so that larger snakes then had to take fish of low RPW. When all types of prey (excluding fish from drying pools) are pooled, RPW increased with snake size (Fig. 6). When these fish are considered as well, there was no significant effect of snake size on RPW (Fig. 6 legend).

Two snakes were found dead with fish lodged in the throat (Fig. 7a), RPW 66 and 69 per cent. About 60 per cent RPW is the largest safe size for roach ingestion (Hailey and Davies, 1986); four snakes were captured handling fish of RPW >60 per cent (Figs. 5c, 7b), and five others were seen with fish clearly well over this size, but were not captured. Eight of these observations were made in daylight, one at night. Oversize fish are not merely suboptimal, they are valueless at best, and at worst involve the snake in direct (choking) or indirect (predation) risks of death. It is therefore interesting that 9/36 fish seen being handled were oversized (though the relative frequency of such large fish will be exaggerated if snakes handle them for a long time before giving up). This has been investigated by Hailey and Davies (1986).
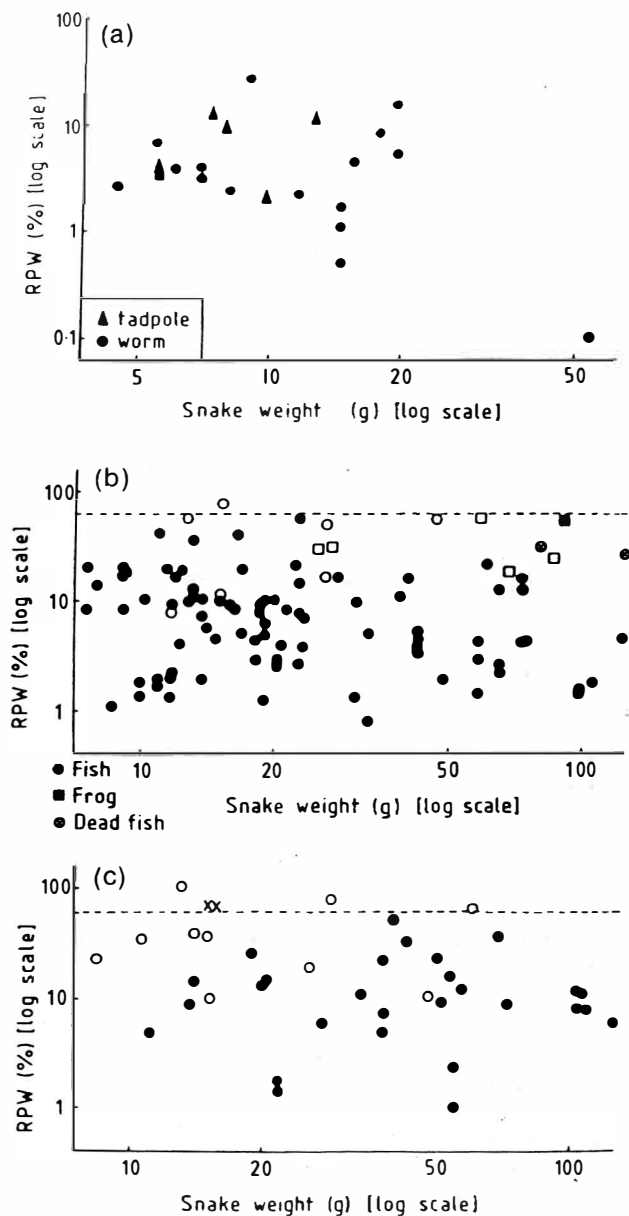
Fig. 5. Variation of relative prey weight with snake size for (a) worms and tadpoles, (b) fish from drying pools, and frogs, (c) fish from other pools. Solid symbols = regurgitated, open = handled. Dashed line shows RPW = 60 per cent. Crosses in (c) are snakes found choked on fish. Slopes of regressions of log RPW on log W do not differ significantly from 0 (t tests) except for regurgitated fish in (b), for which the equation is log RPW (%) = -0.22 log W + 1.1 (t test P<0.05).

Fig. 6. Variation of prey weight with snake size, prey types combined (except fish from drying pools). The regression fit (solid line) is log prey weight = 1.39 log snake weight — 1.7 (slope differs significantly from 1, t test P<0.05). The dashed line is for fish from drying pools.
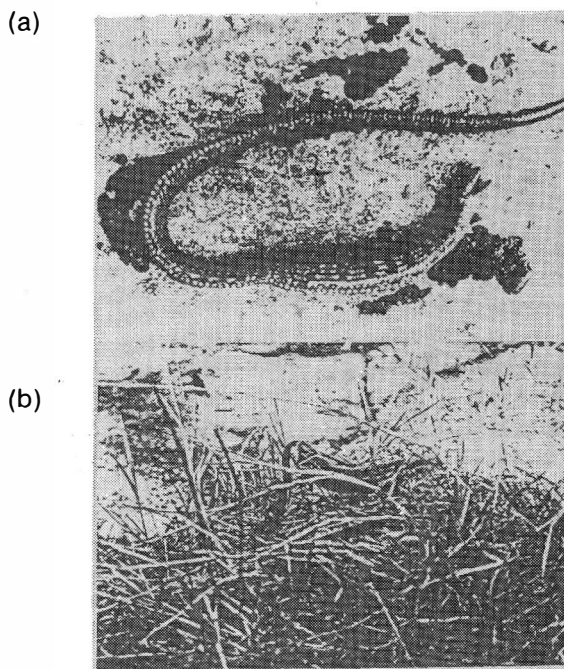
Fig. 7. (a) Snake found choked on fish, RPW = 66%, (b) Snake handling fish too large for it to ingest, RPW = 74%.

Multiple captures

Snakes not found near drying pools had one or two prey items (Table 2). Those from drying pools had up to six fish (Fig. 8a). Such multiple captures gave RPW up to 45 per cent, but mostly below 30 per cent (Fig. 8b). Fish from snakes with only one fish were larger than fish from snakes with more than one fish (Fig. 8c). This suggests that if a snake catches a small fish it is more likely to stay to catch more than if it catches a large one.
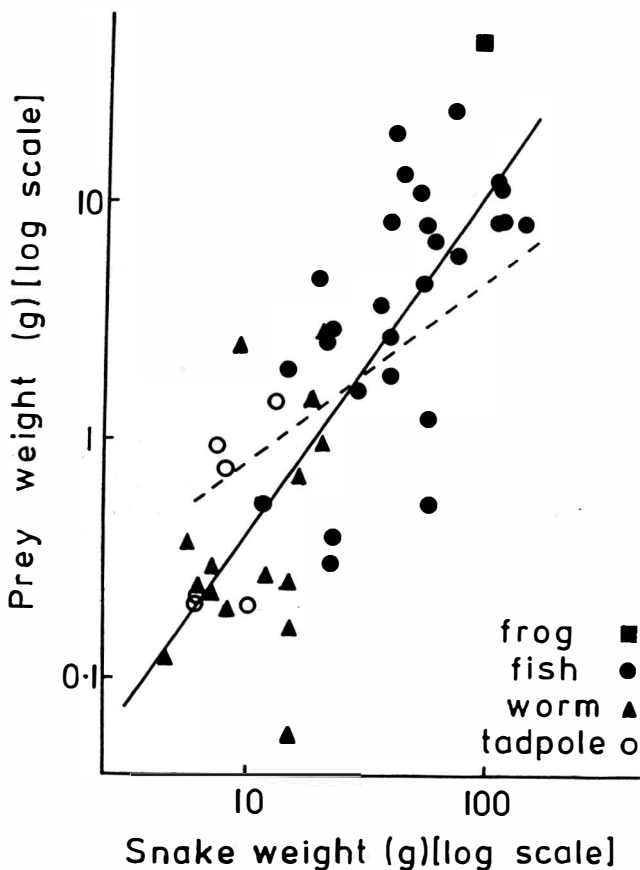
DISCUSSION

CHANGE OF DIET WITH SIZE

Changes of diet with size are known in several species of snakes (e.g. Paniagua, 1976, Saint Girons, 1980, Godley, 1981, Mushinsky, Hebrard and Vodopich, 1982). Two factors can explain this pattern in *N. maura*.

1. Very small fish were rarely seen, and were active in midwater (though often at the edge where it was shallow), and thus more difficult to catch than worms and tadpoles. T snakes foraging for worms and tadpoles in shallow puddles and on land would then be less likely to encounter fish by chance, reinforcing the diet change. The fish taken by T snakes were from drying pools, in which all sizes of snakes were found.

2. Earthworms do not grow very large, and are relatively small prey for larger snakes, which would thus have to catch more of them. As an estimate of this effect, encounter rate will be α to speed, and thus to length, whereas energy requirements will be α to metabolic rate, and thus to weight $_{0.75}$ (Hailey and Davies, submitted). A 100g, 80cm snake would thus encounter 5x as many worms as a 29g 16cm snake, but would require 20x the energy.

Frogs were more commonly taken by the largest snakes, a pattern found in *Nerodia erythrogaster* and *N. fasciata* by Mushinsky et al (1982).

DIET COMPOSITION: ENERGY AND NUMBERS

Diet composition may be considered in terms of both the number of individuals eaten and the energetic contribution of different prey types. Where the time which a prey item remains detectable (either seen being handled or found in the stomach) is proportional to its size (Hailey and Davies, 1986) diet composition by frequency of occurrence will be equivalent to composition in terms of the energy composition. To show the diet composition by numbers, frequency of occurrence has to be adjusted by dividing by the relative size of the prey (Fig. 4b). Worms and tadpoles are more, and frogs less, important in terms of numbers compared to energy.

THE PATTERN OF FORAGING

Several aspects and types of foraging behaviour have been described in this paper and in other works on foraging in natricine snakes. This section attempts to integrate them to show the overall pattern of foraging in *N. maura* and other natricines.

Exploratory cruising

Many snakes were seen moving about in water and on land between pools, apparently exploring. This is taken as the starting point of foraging activity, and is termed exploratory cruising. Cruising is here used in the sense of Regal (1978) as a foraging method of slow movement, rather than the restricted sense of Drummond (1979). Different types of foraging behaviour may follow exploratory cruising to suit the prey situation encountered (Fig. 8).
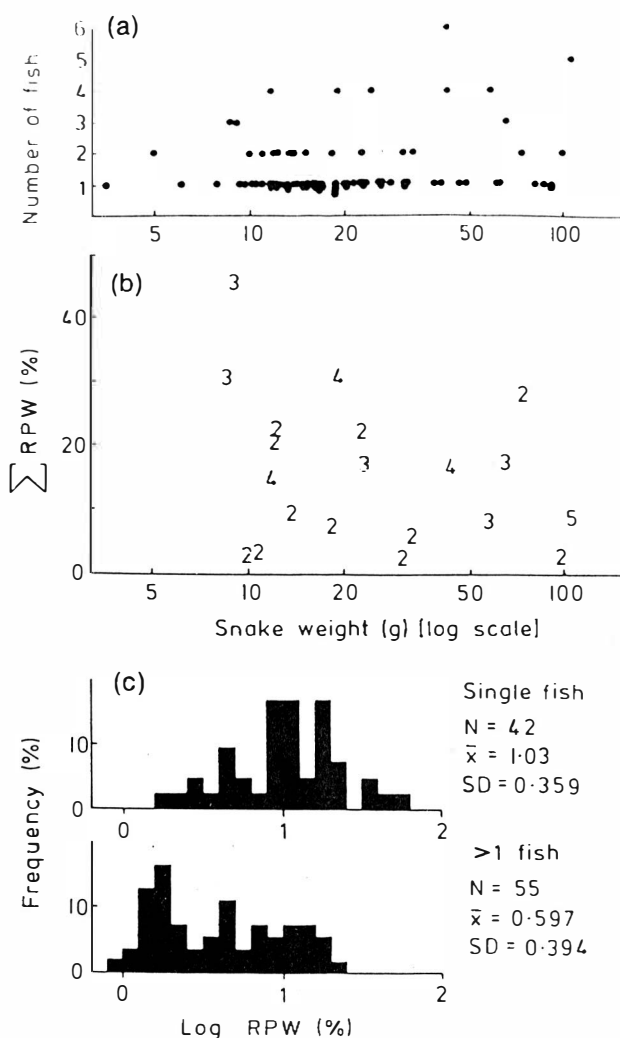

Fig. 8. Multiple fish captures from drying pools. Variation of (a) number of fish per snake with fish, (b) RPW for snakes with >1 fish (number of fish shown), with snake size, (c) Distribution of RPW of fish from snakes with 1 and with >1 fish. The means are significantly different (t test P<0.001).

Slow moving terrestrial prey

Worms are discovered while cruising in moist areas; they were present in soil and under rocks near the river. Chemoreception is used to locate them and other slow moving or cryptic prey. There have been many studies showing the use of aerial chemoreception in the detection of prey, and in the discrimination between different types of prey (Arnold, 1977, 1981, Burghardt, 1968, 1970, 1971, 1975, Czaplicki, 1975, Dix, 1968, Dunbar, 1979, Fuchs and Burghardt, 1971, Gove and Burghardt, 1975, Mushinsky and Lotz, 1980). A differential tongue-flicking response to several prey types was found in T and S *N. maura* (Hailey et al, 1982); worm and tadpole surface extracts produced the greatest response. Sight is not necessary when orienting to ingest prey (Drummond, 1979), but chemoreception is (Halpern and Frumin, 1979).

Active terrestrial prey

Mobile or distant prey on land are detected (refs above) and located (trailing — Kubie and Halpern, 1979) by chemoreception. Once found, the pursuit of active prey is visual (Naulleau, 1964). This activity was not found in *N. maura* in the present study, but may occur in other areas where amphibians are common prey (Arnold and Burton, 1978). Naulleau (1964) describes this behaviour both in *N. maura*, and in *N. natrix* in which it is the usual foraging behaviour (Hailey, 1984). Prey movement may be important in eliciting attack (Brown, 1958, Drummond, 1979).

High density aquatic prey

Exploring snakes may find pools containing trapped fish. These are identified as such by chemoreception. Drummond (1979) found that *Nerodia sipedon* entered small laboratory pools with 'fishy' water but ignored those with clean water, and noted that in the field these snakes by-pass shallow pools without fish but enter those with fish.

Czaplicki and Porter (1974), Porter and Czaplicki (1977) and Drummond (1979) found that sight was important to *Nerodia* catching fish in small pools. *N. maura* crawl after fish schools, striking at fish as they pass close. This is termed cruising, and is similar to exploratory cruising. Contact may initiate striking; this is presumably important at night. After a missed strike the snake may pursue a fish or school. This was only seen where fish movement was restricted by shallow water; in open water fish can outswim snakes (Brown, 1958). Vision is important in pursuit because snakes may swim rapidly and directly after fish for several metres. Drummond (1983) and Drummond and Burghardt (1983) describe the activities of *Thamnophis* engaged in this type of foraging.

Undirected attacks

This category (Drummond, 1979) includes strikes made in the vicinity of prey rather than at one individual or small group. Fishing (Evans, 1942) was observed to be initiated by an unsuccessful strike — fish still in the vicinity are presumably located by contact. In pools with many fish *N. maura* was sometimes seen to make a lunging open-mouthed sweep through the water when in the midst of a fish school. This was interpreted as a strike at the school rather than at a particular fish. There is probably a continuum between this type of strike and fishing.

Diurnal open-mouthed searching has been described in *Nerodia* by Drummond (1979) and Mushinsky and Hebrard (1977). The latter describe the snakes swimming slowly, open-mouthed, in circles in shallow pools shovelling prey with the lower jaw and using the body to trap groups of prey. This appears to be a development of fishing ('combing' — Stoner, 1941) for the purpose of capturing small fish and tadpoles. It was not seen in *N. maura*.

Low density fish

Most pools in the study area contained fish at low density. Exploring snakes probably discover fish by sight and move closer following visual cues. Sentinel foraging (Davies *et al*, 1980, Hailey *et al*, 1982) is then

initiated. This is an extreme sit-and-wait (SW) strategy; the snake strikes from its perch rather than leaving it to rush the prey, the alternative tactic. While this distinction is not important for time and energy budgeting, it may be so for activity physiology. A sentinel predator need have no capacity for rapid locomotion (e.g. boid snakes, chamaeleons) whereas a rush SW predator would (e.g. *Agama* — Loumbourdis and Hailey, submitted). *N. maura* has retained its capacity for short term activity (which is similar to that of the widely foraging *N. natrix* — Hailey, 1984), probably for other foraging activities and for escape. Strikes are initiated as a result of visual and tactile cues. At night SF snakes on the bottom would be able to see fish silhouetted against the sky as they swam overhead.
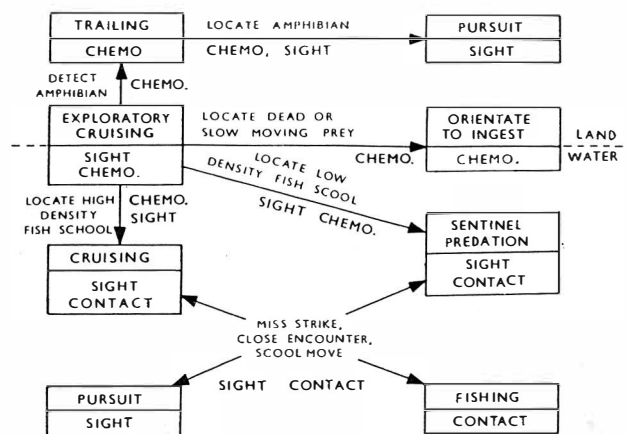

Fig. 9. Diagram of relationships between the different types of foraging behaviour in *N. maura* and other natricine snakes. Boxes are types of foraging and the senses used. Arrows show the course of activity resulting from encounters with different prey, and the senses used.

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