SELECTION OF PREY FROM GROUPS: WATER SNAKES AND FISH

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ABSTRACT

This paper investigates the selection, ingestion and digestion of different sized goldfish by viperine water snakes *Natrix maura*. A previous study had suggested that sentinel foraging *N. maura* preferentially select medium sized fish to give the maximum rate of energy intake during ingestion. It was however found that snakes preferentially struck at the largest fish available in the range 1-20 per cent relative prey weight, even though these fish gave no advantage in ease of capture or rate of energy intake during ingestion or digestion. The advantage of this selection is shown to result from the schooling behaviour of fish and the low rates of capture during sentinel foraging. It was confirmed that snakes capture and attempt to ingest fish too large for them. A large fish provides an energy supply large in relation to the snake's requirements (covering about 60 days maintenance) compared to the small cost of handling before rejection. It would thus be better to handle all fish unless much too large, rather than rejecting those closer to the maximum and possibly making a mistake.

INTRODUCTION

Prey in groups may be difficult to catch for several reasons (Bertrum, 1978). Their vigilance and ability to defend themselves or confuse the predator may be greater, and if only one of them can be captured at a time then the rest can escape while this is being handled. This paper discusses how viperine water snakes, *Natrix maura*, can maximise their energy intake while catching fish from groups. The snakes were studied during sentinel sit-and-wait foraging, their usual method of catching fish: the repertoire of feeding behaviour used by this species is described by Hailey and Davies (1986). In the area where the snakes were collected there was only one species of fish (roach, *Rutilus rutilus*), avoiding the complication of choice between prey species (Voris, 1972; Voris, Voris and Liat, 1978).

There were two specific problems to investigate. Firstly, wild *N. maura* capture and handle fish too large for them to ingest (Hailey and Davies, 1986). As snakes must swallow prey whole, these fish are not only suboptimal, they are at best useless and at worst involve risks of choking or predation. This was investigated by offering snakes fish of different sizes to find the largest they could ingest, and whether they would strike at and attempt to handle even larger fish in conditions of good visibility.

Davies, Patterson and Bennett (1980) investigated selection and ingestion of different sizes of goldfish by *N. maura*. They found that medium sized fish gave the highest rate of energy intake during ingestion, and suggested that such fish were preferentially taken from mixtures with 'suboptimal' smaller or larger fish. Their data show, however, that the larger fish in each mixture were preferentially taken, even when they were 'suboptimal' (Fig. 6b in their paper: 17 per cent of encounters were with large fish and 83 per cent were with 'optimal' medium fish; 36 per cent of ingestions were of large fish). There are several possible explanations for this apparent paradox:

1. Medium fish are preferentially selected, but the opposite result was obtained by chance. The selection experiment was therefore repeated with much larger samples.

2. Medium fish are preferentially struck at, but larger fish are easier to catch or ingest, and so more of them were eaten. Prey selection was therefore recorded both in terms of the number eaten and the number of strikes made.

3. There is a difference between the size — energy relations of roach (to which the snakes are presumably adapted) and goldfish. Goldfish energy content is independent of size, and the rule 'choose large fish' gives a lower rate of intake when applied to them. If large roach have higher energy content (per g) than small roach, the same rule applied to roach may give the maximum rate of energy intake. The energy content of roach of different sizes was therefore measured.

4. The efficiency of digestion is related to fish size. If large fish are digested more efficiently than small fish, then the rate of intake of usable energy during ingestion may be greater from large fish, even though smaller fish give a greater rate of gross energy intake. Absorption efficiency was therefore measured for different sizes of fish.

5. Ingestion time may be an inappropriate measure of handling time. If the time needed to digest a fish is much longer than that needed to ingest it then the rate of digestion will limit food consumption. A large fish may give a greater rate of food intake per unit time if digested faster than several small fish. The speed of digestion of fish of different sizes was therefore measured.

6. The model where foraging animals choose prey on the basis of maximising the rate of energy intake per unit handling time may be inappropriate to the problem of selecting prey from groups.

METHODS

All experiments used 25°C acclimated snakes and were at 25°C unless stated otherwise. Statistical tests follow Sokal and Rohlf (1981).

PREY CHARACTERISTICS

100 roach (2-13cm) were netted, blotted dry, weighed, and the following were measured with vernier calipers: standard (excluding tail fin) length, maximum height, maximum width. They were then killed and dried separately in foil envelopes in a field oven at 50-70°C, and stored in a desiccator. Additional fish of 2-5cm were dried in groups as extra material for calorimetry. In the UK they were re-dried to constant weight at 70°C, then grouped into 1cm length classes, powdered, pelleted, and the energy content found using a Parr semi-micro bomb calorimeter, two determinations per sample. Morphometric and energy data were obtained in the same way for goldfish, which were purchased in fortnightly batches from a local supplier and remained unfed at 10-15°C until used. Fish size relative to snake size was expressed as relative prey weight, RPW (prey weight/snake weight x 100).

HANDLING AND INGESTION

Snakes were kept overnight in 42cm x 22cm x 25cm plastic cages with 0.5-1 litre water dishes, and single live goldfish were introduced the following day. Ingestion time was taken as the time from capture until the snake's jaws closed behind the fleshy part of the fish (i.e. excluding the tail fin). There was an additional, shorter, time for the fish to reach the stomach, but this was hard to measure precisely. Two groups of snakes, small (10-30g) and large (50-110g), were given a range of relative fish sizes within the limitations of fish supply (usually 1-8g). For comparison, handling times were also measured at 15°C and 35°C.

In a second series of trials 20-30g snakes in cages with 2-3 litre water dishes were offered live fish of 10-70 per cent RPW to see if they would capture, and could ingest, them. Fish were introduced singly in the morning and the cages were observed hourly throughout the day. A capture attempt was recorded if the fish was seen being handled, or was removed from the water, or showed signs of a struggle (torn fins, loose scales in the water). Fish did not leap spontaneously from these large water dishes.

DIGESTION AND ABSORPTION

The term digestion is used for gastric digestion, the term absorption for the whole digestive process to the voiding of faeces. 20-30g snakes housed singly in cages with 0.5 litre water dishes were fasted for 10 days, then fed *ad lib* until more than 10g of 1-2g or 2-3g fish, or three 6-9g fish, had been eaten. The time interval between the first fish eaten and the first production of faeces was noted (Greenwald and Kanter, 1979). Afterwards, the snakes were fasted until faeces production ended.

On several occasions during each experiment, and at the end, the faeces (excluding urates) were collected and dried at 70°C. Ten snakes were used for each fish size; their faeces were pooled, and the energy content determined from two samples with the bomb calorimeter. Absorption efficiency

$$\frac{\text{Consumption} - \text{Faeces}}{\text{Consumption}} \times 100$$

of energy was calculated for each snake in each group using the mean energy content of faeces from that group.

After some of the observations on ingestion time the snakes were checked every four hours during the day until the fish could no longer be detected by palpating the stomach gently. Ingestions were staggered (after trial and error) so that this end point of digestion would occur during the day.

SELECTION AND CAPTURE

Ten large snakes were kept in a 2m x 1m arena with a 1m x 1m x 0.35m pool. Air temperature was 15°C, with two 250 W reflector lamps provided for thermoregulation for 12 h a day. Low intensity room lighting was provided at night (just bright enough to read newsprint). Aquarium heaters maintained the water at 22-25°C. Small branches in the water were used as perches.

20 large (5-8, $\bar{x}$ 6g) and 40 small (2-3, $\bar{x}$ 2.5g) live goldfish were kept in the pool, those eaten being replaced twice daily until 50 had been eaten. The fish were then removed and the snakes were fasted for a week. The same mixture of fish were then introduced and the experiment continued until a further 50 had been eaten. The number of strikes made at small and large fish was observed in this second period, mostly on the day following fish introduction, when most of the snakes were foraging. The first half of this experiment was repeated using 20 large and 20 small fish, then 20 large and 80 small fish.

The whole experiment was repeated with 10 small snakes in a 1m x 0.6m x 0.3m pool, containing 10 large (4-5, $\bar{x}$ 4.5g) and 20 small (2-3, $\bar{x}$ 2.5g) fish. As the starting number of fish was rather small there was the possibility that if the snakes began foraging simultaneously they could substantially alter the relative abundance of large and small fish before these could be replaced. This was avoided by feeding the snakes before the first trial so that they did not all begin foraging together.

RESULTS

PREY CHARACTERISTICS

The weight-length relationship of 2-13cm roach was weight (g) = 0.0113 length (cm)$^{3.18}$ r^2 = 0.99 n = 100. Energy content of the tissue did not vary with roach size (Hailey, 1984, Fig. 5.10), the mean value being 5.1 KJg live weight.$^{-1}$

The factor limiting the size of fish which a *N. maura* could ingest is assumed to be the stretched circumference of its neck at the narrowest point, as the jaws can open wider than this (pers. obs.), and the cross-sectional shape of the body is highly plastic. The dimension of a fish limiting its ingestibility would then be its maximum circumference, estimated as the circumference of an ellipse with diameters width x height. For roach

Circumference (cm) = 2.75 weight$^{0.314}$ r^2 = 0.99 n = 100.

Small goldfish were stouter than roach:

weight = 0.0459 length$^{2.75}$ r^2 = 0.97 n = 134

and, for the same weight, had a greater maximum circumference:

circumference = 2.82 weight$^{0.364}$ r^2 = 0.97 n = 68.

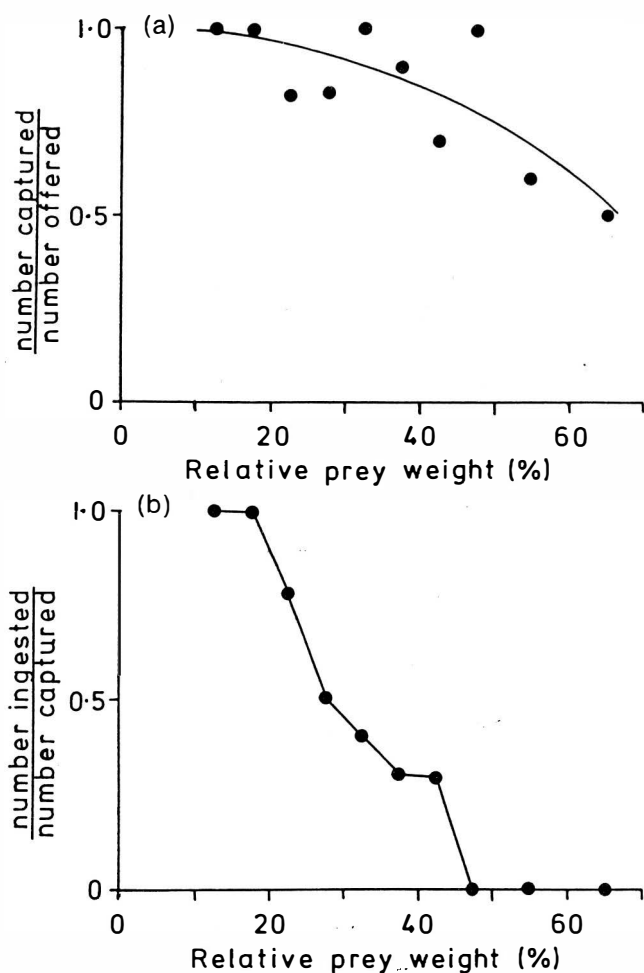Energy content of goldfish was 4.0KJg live weight^{-1}, independent of size (Hailey, 1984).

Fig. 1 Frequency of (a) capture and (b) ingestion of fish of different RPW by 20-30g snakes. Curve fitted by eye. Each point is for 10-15 fish.

HANDLING AND INGESTION

Snakes captured and attempted to ingest fish of all sizes offered (RPW 10-70 per cent), but could only ingest those of RPW less than 45 per cent (Fig. 1). Capture position (the part of the fish caught by the snake; head, middle or tail) was independent of RPW (Table 1a). Large fish were more likely to escape after capture (Table 1b) and to be ingested head-first (Table 1c, see also Loop and Bailey, 1972), but equally likely to be removed from the water for ingestion (Table 1d). Fish caught by the tail were more likely to escape after capture than those caught by the head (Table 1e), but this was not significant. Ingestion direction was associated with capture position; fish caught by the head were always ingested head-first, some of those caught by the middle or tail were ingested tail-first (Table 1f). 'Difficult' ingestions (involving fish caught by the tail which had to be turned right round, or tail-first ingestions) usually took place on land (Table 1g).
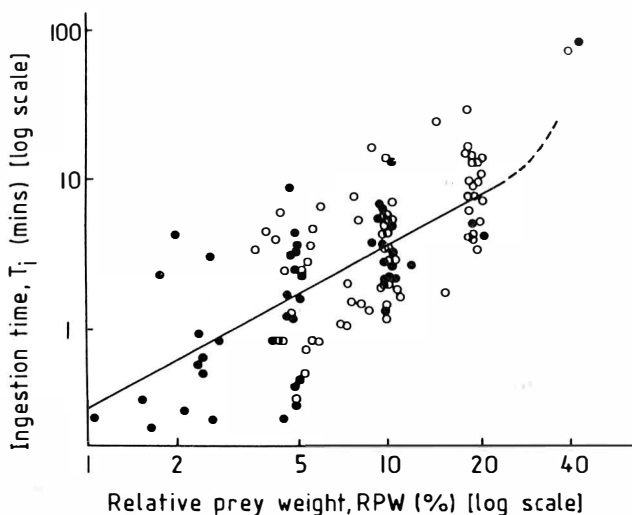

Fig. 2 Ingestion time vs RPW for small (o) and large (•) snakes. Regression slopes (excluding the two largest fish) for both groups and for the pooled data differ significantly from 0 but not from 1 (t tests). The equation for the pooled data is:
$$\log Ti = 1.08 \log RPW - 0.52 \quad (r^2 = 0.47).$$

Ingestion time was linearly related to RPW for fish of RPW 1-25 per cent, and did not differ between the two sizes of snakes (Fig. 2). Values of ingestion time are similar to those of Davies *et al* (1980) for prey of 1-10 per cent RPW. Fish of RPW above 40 per cent took much longer to ingest. Since the energy content of fish tissue was independent of size, RPW/ingestion time is a measure of the rate of energy intake during ingestion. This was highly variable and not significantly affected by RPW, although apparently greatest for fish of RPW about 5 per cent (Fig. 3). This pattern is similar to that found by Davies *et al* (1980, Fig. 5d in that paper). Some of the variability in ingestion time is attributable to capture position; fish caught in the middle or at the tail but ingested head-first had to be turned round, increasing ingestion time (Table 2a). There was, however, no effect of the direction of ingestion itself on ingestion time of small fish (Table 2b).
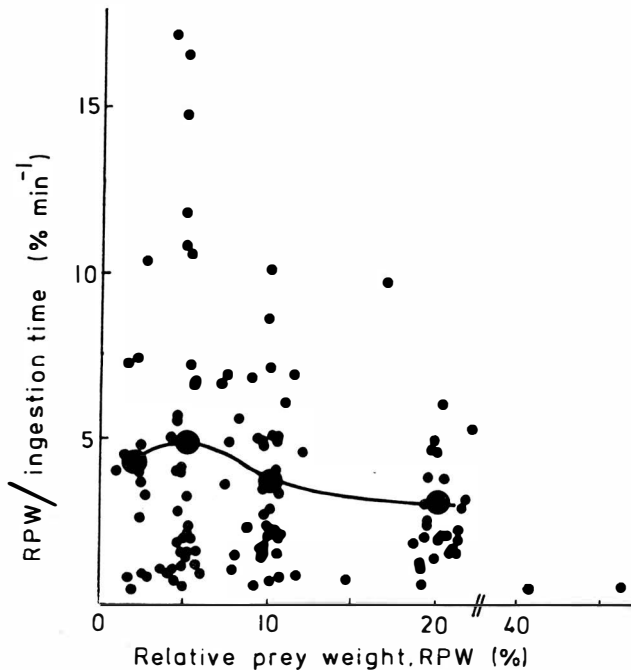
Fig. 3   The rate of energy intake during ingestion (RPW/Ti) vs RPW, data for small and large snakes combined. Large points are means for the RPW classes 1.5-3.5, 4-6, 8-12 and 18-22 per cent, curve fitted by eye. There is no significant variation of RPW/Ti between these classes (Kruskal-Wallis test P>0.1).

(a) Capture position and relative prey weight.

RPW (%) (parts a-d)	1-4	4-8	8-15	15-25
Capture position	Number of captures			
Head	8	17	20	24
Middle	5	11	15	16
Tail	4	16	10	19

G test 0.9>P>0.5.

(b) Fish escape after capture and relative prey weight.

	Number of captures			
Escaped	2	6	3	31
Ingested	15	38	42	28

G test P<0.001.

(c) Direction of ingestion and relative prey weight.

Direction of ingestion	Number of ingestions			
Head first	10	35	40	28
Tail first	5	3	2	0

8-15 and 15-25 per cent RPW classes combined for g test, P<0.01.

(d) Place of ingestion and relative prey weight.

Place of ingestion	Number of ingestions			
In water	8	15	19	10
On land	7	23	23	18

G test 0.9>P>0.5.

(e) Fish escape after capture and capture position.

Capture position	Head	Middle	Tail
Small fish (RPW <15 per cent)			
Escaped	3	2	6
Ingested	42	29	24
Large fish (RPW >15 per cent)			
Escaped	10	9	12
Ingested	14	7	7

G tests: small fish and large fish separately, both 0.5>P>0.1; combined 0.1>P>0.05.

(f) Capture position and direction of ingestion (fish of RPW <15 per cent)

Capture position	Head	Middle*	Tail*
Direction of ingestion	Number of ingestions		
Head first	42	24	19
Tail first	0	5	5

* Combined for testing, Fisher's exact test P<0.001. X^2 test for no preferred direction of ingestion of fish captured by the middle (against expected equal probability of head or tail first ingestion) P<0.001.

(g) Capture position, direction and place of ingestion (fish of RPW<15 per cent)

Capture Position Direction of ingestion	Tail, or Tail first	Head or Middle, and Head first
Place of ingestion	Number of ingestions	
In water	3	39
On land	26	27

G test P<0.05.

TABLE 1: Qualitative aspects of fish capture and ingestion, with tests of the null hypothesis: there is no association between row and column categories.

There was no effect of temperature on RPW/ingestion time between 15-25°C, but this was higher at 35°C (Table 2c). The capacity of *N. maura* for activity certainly increases between 15°C and 25°C (Hailey and Davies, *in press*), so there is presumably an effect of goldfish performance which cancels this out. Goldfish were noticeably less vigorous at 35°C, and often survived for only an hour or two.

DIGESTION AND ABSORPTION

Fish size had no effect on the initial rate of absorption (time to first faeces), on the rate at which food could be processed (*ad lib* feeding rate), or the absorption efficiency (Table 3). Values of *ad lib* feeding rate and absorption efficiency are similar to those for other natricine snakes feeding on fish (Brown, 1958; Goodwin, 1971). Fish of higher RPW remained palpable in the stomach for longer (Fig. 4). The relationship is best shown by the 7-20g snakes, for which the widest range of RPW was used; it appears to be linear, passing through the origin. Data for larger snakes fall above this line, as expected since their prey are absolutely larger. Comparison of Table 3 and Fig. 4 suggests that the *ad lib* feeding rate (6 per cent day^{-1}) is lower than the rate of gastric digestion (14% day^{-1}).

(a) Effect of capture position (head first ingestion only).

Capture position		
Head	6.4	(39)
Middle	2.8	(25)
Tail	1.6	(19)

These are all significantly different (P<0.05).

(b) Effect of direction of ingestion.

Capture position	Direction of ingestion	
	Head first	Tail first
Middle	2.8 (25)	3.0 (5)
Tail	1.6 (19)	1.9 (5)

There are no significant differences between head first and tail first ingestions of fish captured in the middle or by the tail (P<0.05).

(c) Effect of temperature.

15°C	4.4	(36)
25°C	4.2	(83)
35°C	9.8	(15)

35°C data differ significantly from combined 15° and 25°C data (P<0.01).

TABLE 2: The effect of capture position, direction of ingestion, and temperature on the rate of energy intake during ingestion for fish of RPW <15 per cent. Values are mean RPW/ingestion time (% min^{-1}) (with n). P values are for Wilcoxon two sample tests.
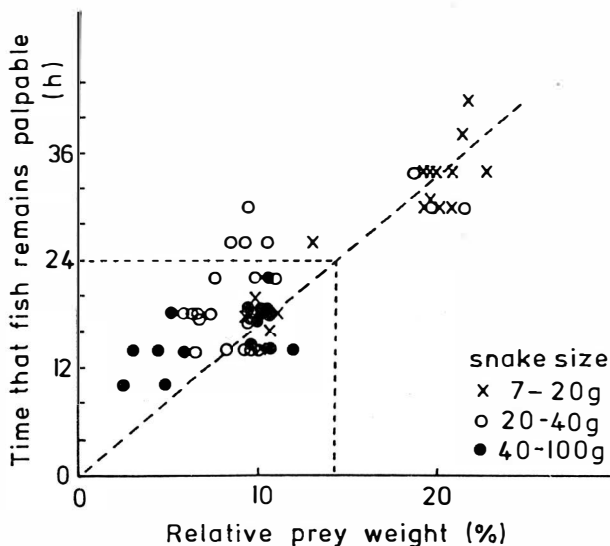

Fig. 4 The effect of RPW on the length of time that a goldfish remained detectable by palpating the snake's stomach. Dashed line fitted by eye to the 7-20g snake data. Dotted lines show estimation of the rate of gastric digestion as 14 per cent day^{-1}.

Fish Weight (g)	Absorption efficiency (%)	Time to first faeces (h)	Ad lib feeding rate (% day^{-1})
1-2	89.1 (3.5)	32 (16-36)	6.6 (1.5)
2-3	91.9 (1.5)	32 (20-36)	5.8 (1.2)
6-9	90.8 (0.7)	32 (16-40)	7.4 (1.3)

TABLE 3: The effect of fish size on the rate and efficiency of digestion. Each value is the mean for 10 20-30g snakes, each fed >10g of fish (with SD); time to first faeces is shown as the mode and range, in four hour intervals.

SELECTION AND CAPTURE

Both sizes of snakes struck at the larger fish about twice as often as expected from their relative abundance (Table 4). For the large snakes, capture success (CS = captures/strikes) and ingestion success (IS = ingestions/captures) were similar for the two fish sizes, and so the large fish were ingested about twice as frequently as expected from their relative abundance. For the small snakes (Table 4b) capture success of the large fish was greater but ingestion success was much lower, so that the frequency of ingestion of large fish did not differ significantly from their relative abundance.

DISCUSSION

HANDLING USELESS FISH

Hailey and Davies (1986) found wild *N. maura* apparently choked on roach of RPW 66-69 per cent, and suggested that the maximum RPW for safe ingestion of roach would be slightly below this. This is confirmed by feeding on goldfish, the largest of which to be successfully ingested had an RPW of 43 per cent. For a 20g snake this is an 8.6g goldfish, maximum circumference 6.2cm; a roach of this circumference would weigh 13.2g, i.e. 66 per cent RPW for the 20g snake. Thus both in captivity and in the wild, *N. maura* captured and attempted to ingest fish too large for them. This apparently maladaptive behaviour probably results from:

1. The large amount of energy which a large fish represents in relation to the snake's energy requirements, and thus the large disadvantage of mistakenly leaving a fish as too large which could have been ingested. Energy requirements of *N. maura* are about $65Jg^{0.75} day^{-1}$ for maintenance and low activity (Hailey, 1984), 0.6kJ day^{-1} for a 20g snake. A 12g roach (RPW 60 per cent) would yield 36kJ after losses in absorption and specific dynamic action (respectively 10 per cent and 30 per cent of the total 60kJ content of the fish — Hailey, 1984), equivalent to 60 days maintenance.

2. The difficulty of making an accurate judgement of fish size. It would thus be better to attack fish unless definitely too large; this costs only a few minutes handling before rejection.

(a) Large snakes: 80 (50-110)g.

Fish weight (g)	6 (5-8)	2.5 (2-3)	P
RPW (%)	7.5	3	
Number present	20	40	
Number eaten	55	52	X^2 P<0.001
Selectivity	2.1	0.47	
Number of strikes	101	93	X^2 P<0.001
Selectivity	2.2	0.46	
Number of captures	13	13	G 0.9>P>0.5
Capture success	0.13	0.14	
Number of ingestions	9	9	G P>0.999
Ingestion success	0.7	0.7	
Number present	20	20	
Number eaten	33	18	X^2 P<0.05
Selectivity	1.8	0.54	
Number present	20	80	
Number eaten	20	36	X^2 P<0.005
Selectivity	2.2	0.45	

(b) Small snakes: 25 (20-30)g.

Fish weight (g)	4.5 (4-5)	2.5 (2-3)	P
RPW (%)	18	10	
Number present	10	20	
Number eaten	39	66	X^2 0.5>P>0.1
Selectivity	1.2	0.85	
Number of strikes	114	102	X^2 P<0.001
Selectivity	2.2	0.45	
Number of captures	30	15	G P<0.05
Capture success	0.26	0.15	
Number of ingestions	10	14	X^2 P<0.001
Ingestion success	0.3	0.9	

TABLE 4: Selection and capture of fish from groups in large pools, with X^2 or G tests of the null hypothesis; columns and rows are independent. Snake and fish weights shown as mean and range. The number of fish eaten exceeds the number present in the pool as fish were replaced as they were eaten. Selectivity of fish eaten (or of strikes) for large fish was calculated as:

$$\frac{\text{Number large eaten}}{\text{Number small eaten}} \times \frac{\text{Number small present}}{\text{Number large present}}$$

PREFERENCE FOR LARGE FISH

Of the six possible explanations for snakes preferring large fish listed in the introduction, the first five can now be rejected. Preference for large fish is thus not due to chance in a small sample (1), or to differences between energy content (3), efficiency of digestion (4) or rate of digestion (5) of different sizes of fish. The capture success with large goldfish was significantly greater than with small fish (Fig. 5a; G test P<0.01), but ingestion success was significantly lower (Fig. 5b; G test on data pooled so that no frequency is <5, P<0.001). When capture and

ingestion success are combined, the possibility of a strike leading to a successful ingestion is independent of RPW (Fig. 5c), and explanation 2) can be rejected. This leaves the possibility that snakes selecting fish from groups are doing so on some other basis than their energy intake per unit handling time.
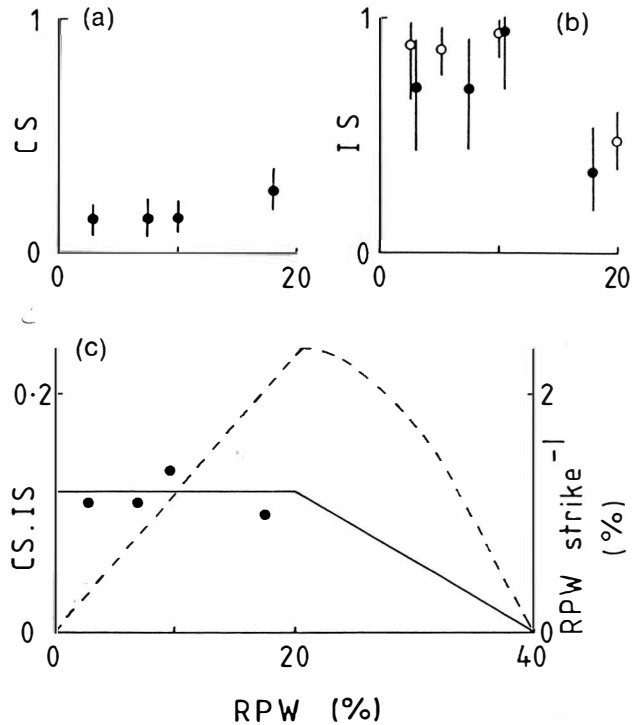

Fig. 5 (a) capture success (captures/strikes) and (b) ingestion success (ingestion/captures) for snakes feeding on goldfish of different RPW. Bars are 95 per cent CL of the proportions. Data from large pools (●, Table 4) and small dishes (o, Table 1). (c) Strike success (ingestions/strikes = CS.IS) (solid line) and the resulting energy intake per strike (dashed line).

Schooling fish such as roach and goldfish are encountered in groups from which the snake can select an individual at which to strike. The maximum energy intake *per strike* will be given by selecting from the group the fish giving the greatest value of CS.IS.RPW. The group is likely to move away or be more wary after a strike at one of its members (pers. obs.), so that only one strike may be possible on each group, or subsequent strikes may be much less successful.

Now consider instead the energy intake *during a period of foraging.* If a snake forages for a length of time T and selects fish of a given energy content (measured as RPW) and ingestion time Ti, its energy intake E will be:

$$E = (T-H).R.CS.IS.RPW \qquad (1)$$

where R is the strike rate (time^{-1}) and H is the time spent handling fish:

$$H = (T-H).R.CS.((IS.Ti)+((1-IS).Te)) \qquad (2)$$

where Te is the handling time of fish which escape after capture.

R will be the same for all fish in a group, and so provides no basis for preferring one fish to another. The same applies to (T-H), since H is very small in

relation to T: field data in Hailey and Davies (1986) show that H is about 0.002 T. The important part of equation 1 is thus:

$$E \propto CS.IS.RPW$$

i.e. the maximum energy intake would be from the fish giving the maximum intake per strike. Depending on the values of CS and IS, this is likely to be achieved by selecting fairly large fish (Fig. 5c).

In the long term there will be an additional advantage of selecting large fish: insurance against reduced availability in the future. Even if there is no advantage in selecting a particular size of fish when the rate of intake during a period of foraging is considered, if the quality of foraging opportunities is unpredictable it would be better to ingest a large fish when available.
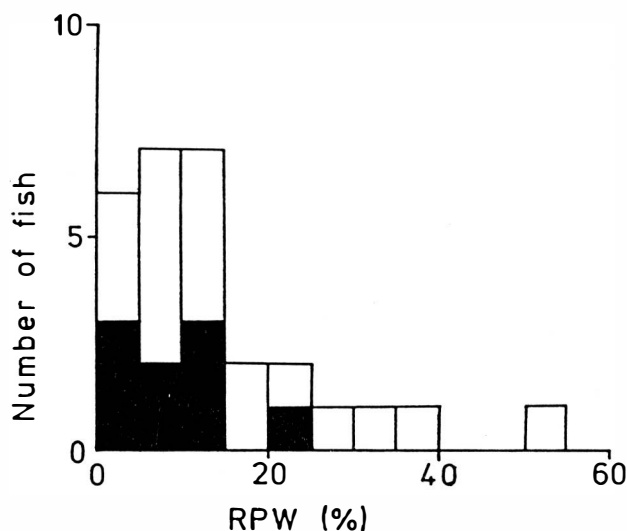

Fig. 6 Frequency distribution of RPW of regurgitated roach from wild snakes. Data for snakes >30g are shaded.

There is some evidence from prey regurgitated (Fig. 6) that fish above 20 per cent RPW were not preferentially selected in the wild. The size distribution of fish available is not known, and therefore selection cannot be shown directly. It can be inferred, however, as the distributions of RPW for small and large snakes are similar. In the absence of selection, or as a result of selection for the largest fish available, small snakes would catch fish of similar absolute size, and therefore higher RPW, to those taken by large snakes.

This sample model will be modified according to the behaviour of the local fish. If they are highly mobile, as are roach, they are likely to move away while the snake is waiting for a larger one to come nearer. It would then be better to strike at the best fish within striking distance. The potential for selection will be reduced if fish schools are made up of fish of similar size. If such schools are found in characteristic positions (e.g. water depth), the position a snake chooses will be more important than the selection of individual fish in determining the sizes of fish taken (Hailey and Davies, 1986). The mechanism of selection is not known; the snakes may use some simple rule such as strike at the fish within striking distance which appears largest. Water snakes are known to form search images for prey colour (Czaplicki and Porter, 1974; Porter and Czaplicki, 1977).

Capture success with goldfish (17 per cent of 410 strikes) was significantly higher than that with wild roach (Hailey and Davies, 1986: 1.6 per cent of 124 strikes, X^2 P<0.001). The field observations were made in the few pools left with fish during a drought, and so snakes were common and the fish were frequently attacked. The capture success with goldfish may be a better estimate of that with unsuspecting roach in the wild, but would be compensated for by lower strike opportunity at low fish density.

REFERENCES

Bertram, B. C. R. (1978). Living in groups: predators and prey. 64-96 In *Behavioural ecology: an evolutionary approach.* Krebs, J. R. and Davies, N. B. (Eds). Oxford: Blackwell.

Brown, E. E. (1958). Feeding habits of the northern water snake, *Natrix sipedon* L. *Zoologica, N.Y.* **43**, 55-71.

Czaplicki, J. A. and Porter, R. H. (1974). Visual cues mediating the selection of goldfish (*Carassius auratus*) by two species of *Natrix. Journal of Herpetology* **8**, 129-134.

Davies, P. M. C., Patterson, J. W. and Bennett, E. L. (1980). The thermal ecology, physiology and behaviour of the viperine snake *Natrix maura*: some preliminary observations. *Proceedings of the European Herpetological Symposium, Oxford 1980.* 107-116. Cotswold Wild Life Park.

Goodman, D. E. (1971). *Thermoregulation in the brown water snake, Natrix taxispilota.* Ph.D. thesis, University of Florida, Gainesville.

Greenwald, O. E. and Kanter, M. E. (1979). The effects of temperature and behavioural thermoregulation on digestive efficiency and rate in corn snakes (*Elaphe g. guttata*). *Physiological Zoology* **52**, 398-408.

Hailey, A. (1984). *Ecology of the viperine snake, Natrix maura.* Ph.D. thesis, University of Nottingham.

Hailey, A. and Davies, P. M. C. (1986). Diet and foraging behaviour of *Natrix maura. Herpetological Journal* 1,

Hailey, A. and Davies, P. M. C. Effects of size, sex, temperature and condition on activity metabolism and defence behaviour of the viperine snake *Natrix maura. Journal of Zoology* in press.

Loop, M. S. and Bailey, L. G. (1972). The effect of relative prey size on the ingestion behaviour of rodent-eating snakes. *Psychomonic Science* **28**, 167-169.

Porter, R. H. and Czaplicki, J. A. (1977). Evidence for a specific searching image in hunting water snakes *N. sipedon. Journal of Herpetology* **11**, 213-216.

Sokal, R. R. and Rohlf, F. J. (1981). *Biometry.* (2nd Ed). San Francisco: W. H. Freeman & Co.

Voris, H. K. (1972). The role of sea snakes (Hydrophiidae) in the trophic structure of coastal ocean communities. *Journal of the Marine Biological Association of India* **14**, 429-442.

Voris, H. K., Voris, H. H. and Liat, L. B. (1978). The food and feeding behaviour of a marine snake, *Enhydrina schistosa* (Hydrophiidae). *Copeia* **1978**, 134-146.