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FOOD, FEEDING RATES AND PREY-SIZE SELECTION IN JUVENILE AND ADULT FROGS, *RANA ARVALIS* NILSS. AND *R. TEMPORARIA* L.

ABSTRACT: The food of frogs, *Rana arvalis* and *R. temporaria*, was found to be almost identical. There was an approximately linear relationship between frog and prey sizes. Large frogs took fewer small prey items per day than did small frogs. Within one size-class of frogs, prey-size distribution was log-normal. The feeding rate (weight of food per unit weight of frog per day) of large individuals was slower than that of small ones. The feeding rate of adult *R. arvalis* was slower than that of equally-sized sub-adult and adult *R. temporaria*. The feeding rate of *R. arvalis* in meadow was higher than in forest while the opposite took place in *R. temporaria*. No difference in feeding rate at different times of the diel rhythm could be detected for either species.

KEY WORDS: Forest and meadow habitats, *Rana arvalis*, *R. temporaria*, food (prey) composition, feeding rates, prey-size selection, age dependence.

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1. INTRODUCTION

In south Sweden the two brown frog species, *Rana arvalis* and *R. temporaria*, have a similar natural history. Since two sympatric species must have certain differences in critical niche dimensions, it seems interesting to examine what these are in this case, not primarily to illustrate the competitive exclusion principle, but because the nature of the differences should indicate what factors are important in limiting the population numbers.

In an earlier paper (L o m a n 1978a) I have shown that adult frogs utilize partly different habitats and thus prey populations, *R. temporaria* being relatively more common than *R. arvalis* in forest habitat. The cause of this difference may, however, be competition for food as well as different species susceptibilities to predation in the two habitats (forest and meadows). If food is limiting we may expect certain differences in the three sub-niches of the food niche, viz. hunting habitat, hunting time and hunting mode. Since most potential prey species are specialized with respect to activity period as well as to macro- and microhabitat distribution, all three modes of frog segregation would lead to the exploitation of different prey populations (reduced exploitation competition) and to a reduction of the probability that frog individuals will compete for the same prey individuals (a kind of reduced interference competition).

A frog population contains, at any moment, individuals from a large size range. If they consume prey in sizes proportional to their own sizes, this pattern would reduce intraspecific competition. It may also, even in the absence of competition, be energetically favourable.

There are several estimations of the food of these two species. Thus *R. arvalis* has been studied by Zimka (1966) and Karg and Mazur (1969) and *R. temporaria* by Itämies and Koskela (1970), Houston (1973) and Blackith and Speight (1974). Inozemtsev (1969) calculated the two frog species' combined utilization of their prey populations.

In this study I investigate if any differences exist with respect to the prey utilized by the two frog species and by their different size classes. I also study one sub-niche of the food-niche: diel variation in feeding rate. Finally, an attempt is made to calculate the feeding rate of the frogs.

2. STUDY AREA AND METHODS

The study was conducted at Stensoffa ecological research station in south Sweden (55°40' N, 13°30' E). The area is rich in good breeding and post-breeding habitats for frogs and supports relatively high densities of the two species. Other anurans present in the study area are *Bufo bufo* (L.), *B. calamita* Laur., and *Pelobates fuscus* Laur. They were, however, scarce or absent within the study plots. Two meadow and three forest plots were sampled. All five plots were within an area of 800 × 500 m. The meadow plots had a dense cover of grass and herbs on peat soil while the forest plots had a tree layer of birch and a sparse undergrowth, mainly of grass, on peat soil.

For the stomach analyses frogs were captured by hand during four 24-hour periods: August 20–21, August 25–26, September 1–2, 1975, and September 5–6, 1977. Collections were made during 30 minutes every second hour in each of the forest and meadow habitats. Even if more were seen, only ten frogs of the smallest size class were collected as the number of these was already considered sufficient. The frogs were killed immediately and stored in alcohol, with their body cavity cut open. Subsequently, they were weighed and measured (snout to urostyle). The stomach content was weighed after draining on filter paper. The portion of the food that did not show any obvious signs of being digested was also weighed separately. All

prey specimens that could be identified at least to order were recorded and their length and the greatest width measured.

The prey specimens were determined to order. Imagines and larvae were considered separately. Every time one or several specimens of one of the categories thus formed were found in a stomach, this category scored one point. This procedure was adopted because different prey specimens were not taken independently of each other; a stomach often contained several specimens of one category. In all 518 frog stomachs were analysed (257 of *R. arvalis* and 261 of *R. temporaria*). Juvenile frogs, metamorphosed during the same summer (less than 26 mm for *R. arvalis* and less than 30 mm for *R. temporaria*) constituted 49% (*R. arvalis*) and 43% (*R. temporaria*) of the total samples. Those frogs that could possibly take part in the breeding during the following spring were called adults.

In the subsequent analysis of the taxonomic composition of the prey, two-tailed χ^2 -tests have been used. Taxonomic categories that show overall morphological similarities have been combined. Thus Araneae, Hemiptera and Coleoptera; Hymenoptera and Diptera; larvae of Lepidoptera and Hymenoptera were combined and the least common categories were lumped, so that in the χ^2 -tests, no more than 20% of the expected values were less than 5.

To study the speed of digestion I fed adult frogs (9 *R. temporaria* and 2 *R. arvalis*) with known prey and killed them after different periods of time.

The time it took for the frogs' stomachs to become empty was studied by catching samples of frogs and killing fractions of these after regular intervals. Two samples of adult *R. temporaria* (16 animals in each) and one sample of juveniles of both species (43 *R. temporaria* and 23 *R. arvalis*) were used for this purpose.

3. RESULTS

3.1. PREY COMPOSITION

3.1.1. Species and sex of frogs

No difference between the food consumed by males and females were found (Tables I, II). They are, therefore, pooled in further analysis. The distribution of prey taxa consumed by the two species was also remarkably similar (Fig. 1, Tables I, II).

3.1.2. Habitats

Only minor differences in food consumed by frogs between the two habitats were detected. Mites (Acari) were taken proportionally more frequently in forest than in meadow by juveniles of both species. Snails (Gastropoda) were taken proportionally more frequently in meadow than forest by all four species-size categories. Worms (Lumbricidae) were taken proportionally more frequently in forest than meadow by adults of both species. In juvenile *R. arvalis*, adult *R. arvalis* and adult *R. temporaria* the proportion of different prey categories differed significantly between the habitats ($\chi^2 = 18.3$, *d.f.* = 4, $p < 0.01$; $\chi^2 = 16.5$, *d.f.* = 5, $p < 0.01$; $\chi^2 = 15.8$, *d.f.* = 5, $p < 0.01$, respectively).

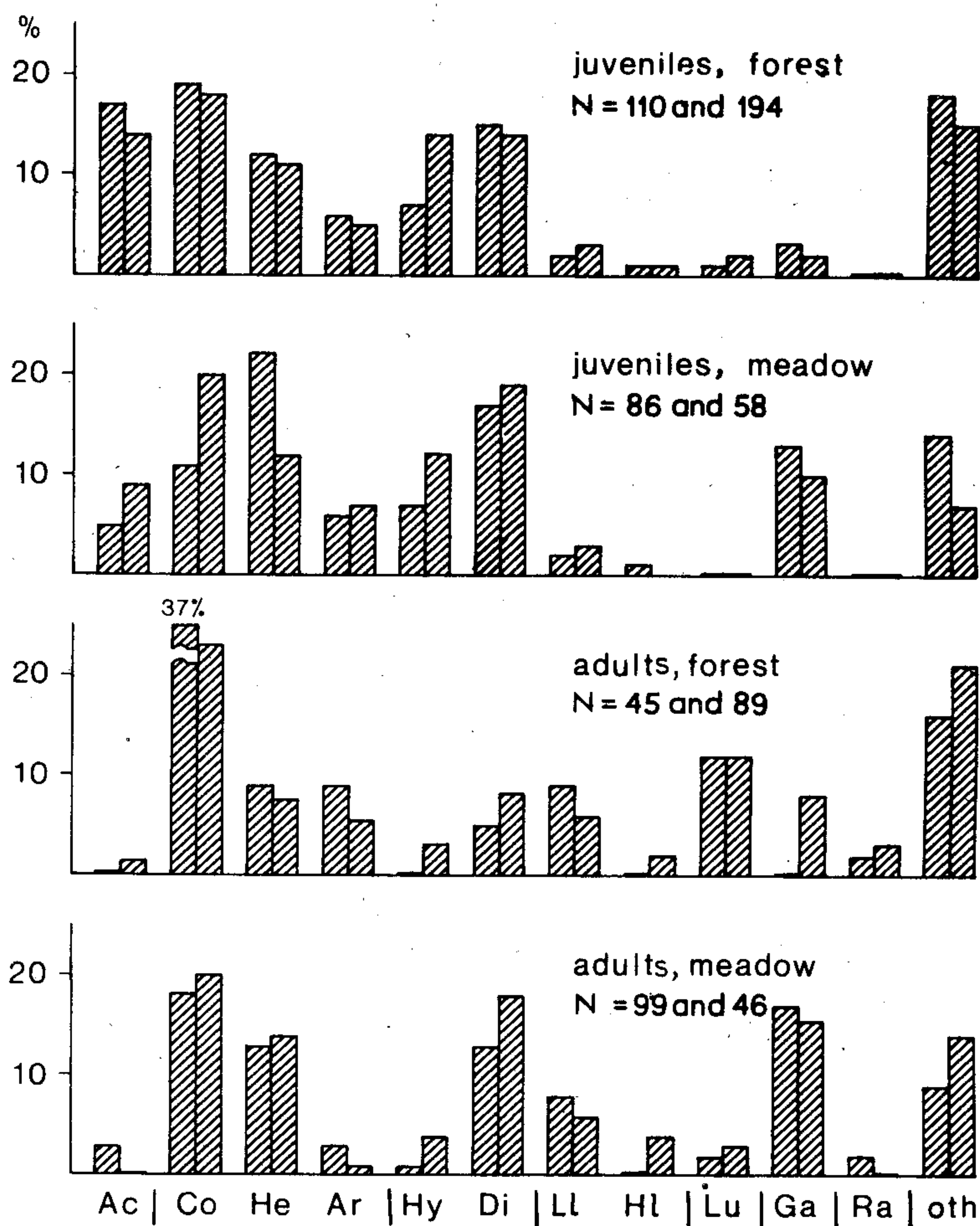


Fig. 1. The relative occurrence of different types of food in different categories of frogs. The left hand columns in each pair and the left hand *N*-values refer to *R. arvalis*, the right hand ones to *R. temporaria*. Ac – Acari, Co – Coleoptera, He – Hemiptera, Ar – Araneae, Hy – Hymenoptera, Di – Diptera, Ll – larval Lepidoptera, Hl – larval Hymenoptera, Lu – Lumbricidae, Ga – Gastropoda, Ra – juvenile *Rana*, oth – other taxa. A test for difference between the species gave for the four categories (in order from top to bottom) the following χ^2 -values (*d.f.* and *p*-value is given in parenthesis): 3.19 (5, 0.7–0.5), 1.30 (4, 0.9–0.8), 5.48 (0.3–0.2) and 4.01 (5, 0.5–0.3). Groups of taxa considered as one class in this test, if sufficiently large, are separated by bars. Small taxa are lumped with the class “other”

3.1.3. Frog size

Differences found were due to smaller frogs taking smaller prey (mites, springtails) and larger frogs taking larger prey (worms, small frogs) irrespective of frog species. The difference between

Table I. Composition of the prey of *Rana arvalis*

The first figure gives the number of times one or several specimens of the taxon were found in a stomach (occurrences) and the second the total number of prey specimens found. The third line in the head gives the frog length (mm)

Taxon	Forest						Meadow					
	females			males			females			males		
	≤ 26	27-36	≥ 37	≤ 26	27-36	≥ 37	≤ 26	27-36	≥ 37	≤ 26	27-36	≥ 37
Gastropoda	2, 3			2, 2	1, 1		4, 5		8, 12	7, 9	1, 1	9, 16
Slugs	1, 1			1, 1					1, 1			
Oligochaeta			4, 7	3, 3	1, 1	1, 2			2, 2			
Isopoda	1, 1			1, 1				1, 1				
Araneae	6, 6		4, 4	7, 10	1, 1		2, 3		8, 9	3, 4		6, 6
Opiliones		1, 2	1, 1	2, 3	1, 1				4, 13		1, 1	2, 3
Acarina	14, 73	2, 4		23, 135	2, 2		1, 1		3, 3			
Diplopoda			1, 1	2, 2								1, 1
Chilopoda												
Collembola	7, 8		1, 1	7, 11	1, 1	2, 2				1, 1		
Orthoptera								1, 2		1, 1		
Dermaptera									1, 2			
Thysanoptera	2, 2			6, 7			1, 1					
Hemiptera	12, 15	1, 1	2, 3	15, 18	3, 3	2, 3	7, 10		8, 13	12, 16	1, 1	5, 9
Neuroptera					1, 1	1, 1					1, 1	
Coleoptera												
imagines	19, 27	7, 11	13, 14	22, 31	4, 4	3, 4	5, 6	1, 1	9, 10	5, 7		10, 14
larvae		1, 1	1, 1	2, 2			1, 1					
Lepidoptera												
imagines	1, 1			1, 1								
larvae	3, 3	2, 2	3, 4	2, 2	2, 3	1, 1	1, 1		5, 6	1, 1	1, 2	3, 4
Diptera												
imagines	14, 23		1, 1	18, 31	2, 2	1, 1	8, 11	2, 3	3, 4	7, 9	1, 1	10, 11
larvae				3, 3					1, 1	1, 1		
Hymenoptera												
imagines	7, 14			9, 13			3, 6			3, 3		1, 3
larvae				1, 1			1, 1					
Formicidae	2, 4			2, 2			3, 4			5, 6		
<i>Rana</i> (small frogs)						1, 1			1, 1			1, 1
Occurrences	91	14	33	129	19	12	37	4	51	49	6	48
Number of prey specimens	181	19	39	279	20	15	50	6	73	61	7	68
Number of stomachs	41	13	25	41	8	10	16	3	41	28	1	30
Number of prey per stomach	4.4	1.5	1.6	6.8	2.5	1.5	3.1	2.0	1.8	2.2	7.0	2.3

Table II. Composition of the prey of *Rana temporaria*
 Explanations as for Table I

Taxon	Forest						Meadow					
	females			males			females			males		
	≤ 30	31-46	≥ 47	≤ 30	31-46	≥ 47	≤ 30	31-46	≥ 47	≤ 30	31-46	≥ 47
Gastropoda	3, 7	2, 2	3, 4			3, 4	2, 3		1, 3	3, 3	6, 11	6, 8
Slugs			2, 5			1, 1						1, 1
Oligochaeta	2, 2	5, 6	7, 11	1, 1	3, 3	4, 7			1, 1		2, 3	
Isopoda											1, 1	
Araneae	5, 5	1, 1	2, 2	5, 5	1, 1	1, 1	2, 2	1, 1		2, 2	1, 1	1, 3
Opiliones	1, 1	1, 2	3, 4	2, 2	5, 8	6, 7					3, 4	3, 10
Acarina	12, 80	1, 2		16, 69			3, 7			2, 3		
Diplopoda	1, 2	1, 2	1, 1	2, 2	2, 2	2, 3						1, 1
Chilopoda	1, 1				1, 1							1, 1
Collembola	4, 4	2, 2		6, 9			1, 2					
Thysanoptera	1, 1											
Hemiptera	9, 10	4, 4	2, 2	13, 16	3, 4	4, 5	4, 4	2, 6		3, 8	5, 7	5, 7
Neuroptera					1, 1							
Coleoptera												
imagines	16, 22	8, 13	13, 21	18, 23	9, 17	10, 12	8, 10	2, 3	3, 4	3, 4	2, 2	7, 11
larvae	5, 5		4, 6	1, 1	2, 2		1, 1				1, 1	
Trichoptera						1, 1						
Lepidoptera												
imagines						1, 5	1, 1				2, 2	
larvae	4, 4	4, 5	3, 3	2, 2	1, 1	1, 1			2, 2	2, 2	1, 1	2, 2
Diptera												
imagines	12, 25	4, 4	4, 5	16, 35	6, 7		6, 8	2, 3	6, 7	4, 7	3, 3	4, 7
larvae	3, 3			1, 2	1, 1	1, 1				2, 9		
Hymenoptera												
imagines	18, 28	3, 4	1, 1	9, 13	1, 1	1, 1	5, 9			2, 5	2, 2	1, 2
larvae	1, 1		2, 2	1, 1		1, 1					2, 2	1, 1
Formicidae	2, 2		1, 1	1, 1		1, 1				1, 1	3, 4	
<i>Rana</i> (small frogs)			2, 2		2, 2	1, 1						
Occurrences	100	36	48	94	38	39	33	7	13	25	32	33
Number of prey specimens	203	47	69	182	51	52	47	13	16	44	44	48
Number of stomachs	45	24	25	38	20	23	15	6	9	14	22	20
Number of prey per stomach	4.5	2.0	2.8	4.8	2.6	2.3	3.1	2.2	1.8	3.1	2.0	2.4

small and large frogs was significant only in the forest samples, mainly because mites, springtails and worms were very scarce in frogs from meadow habitat ($\chi^2 = 19.5$, *d.f.* = 5, $p < 0.01$; $\chi^2 = 54.6$, *d.f.* = 6, $p < 0.001$ for *R. arvalis* and *R. temporaria*, respectively).

3.2. GASTRIC EVACUATION TIME

After 24 hours without opportunity to feed, 50% of the adult frogs tested had no food left in their stomachs (Fig. 2). The corresponding figure was 75% for juvenile frogs (Fig. 3) but the

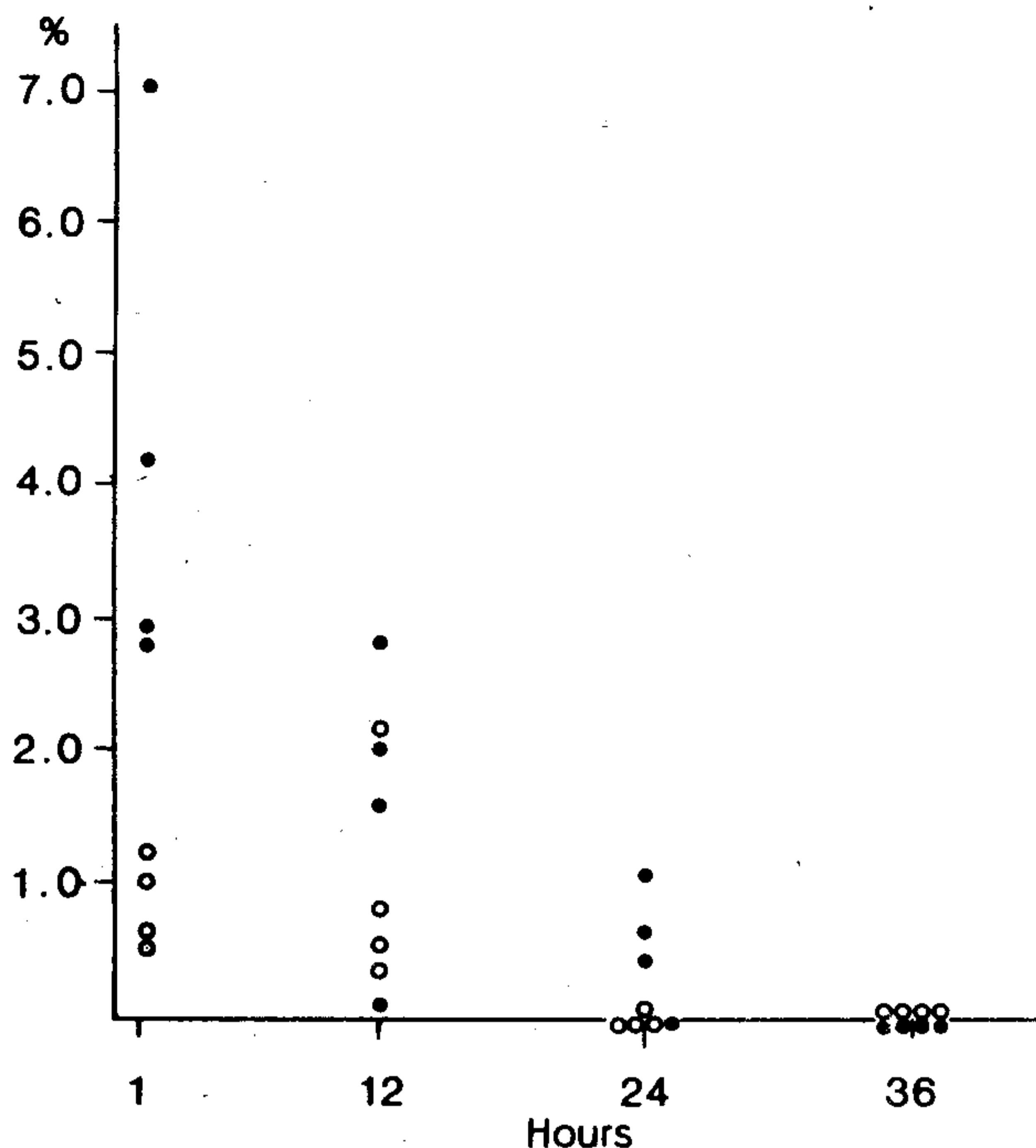


Fig. 2. Amount of food (expressed as percentage of body weight) in adult *R. temporaria* that have been starving for different periods of time

Filled circles refer to a sample caught at 6 to 7 p.m. and open circles to a sample caught at 2 to 3 a.m.

difference between adults and juveniles was insignificant (Fisher exact, $p > 0.10$). After 36 hours all stomachs (juveniles and adults) were empty. In the juvenile samples there was no indication of a species difference. In the feeding tests more fragile prey was completely digested (or at least passed from the stomach) in less than 12 hours while tougher prey remained for up to 36 hours. A gastric evacuation time for prey items of 24 hours in adult frogs and of 18 hours in juveniles seems to be a reasonable approximation which will be used when estimating the feeding rate. As only 10% to 20% of the stomach content in the frogs captured was indigested (Table III), this part had probably been in the stomach for less than 6 hours, regardless of taxon. This was confirmed by the feeding tests as all prey was visibly altered by digestion even in the frogs starving during 6 hours.

3.3. DIEL FEEDING ACTIVITY

To study the diel feeding periodicity I divided the day into four six-hour periods and recorded the proportion of stomachs from frogs captured and killed in these periods that contained food items on which the digestive process had not yet started to a noticeable extent. All four frog categories (size-species) studied distributed their feeding activity evenly over the diel period. Throughout, about 50% of the frogs contained food that had been taken less than 6 hours before (Table IV). A tendency for juvenile frogs to feed more during day than at night is, however, present ($p < 0.10$ for both species).

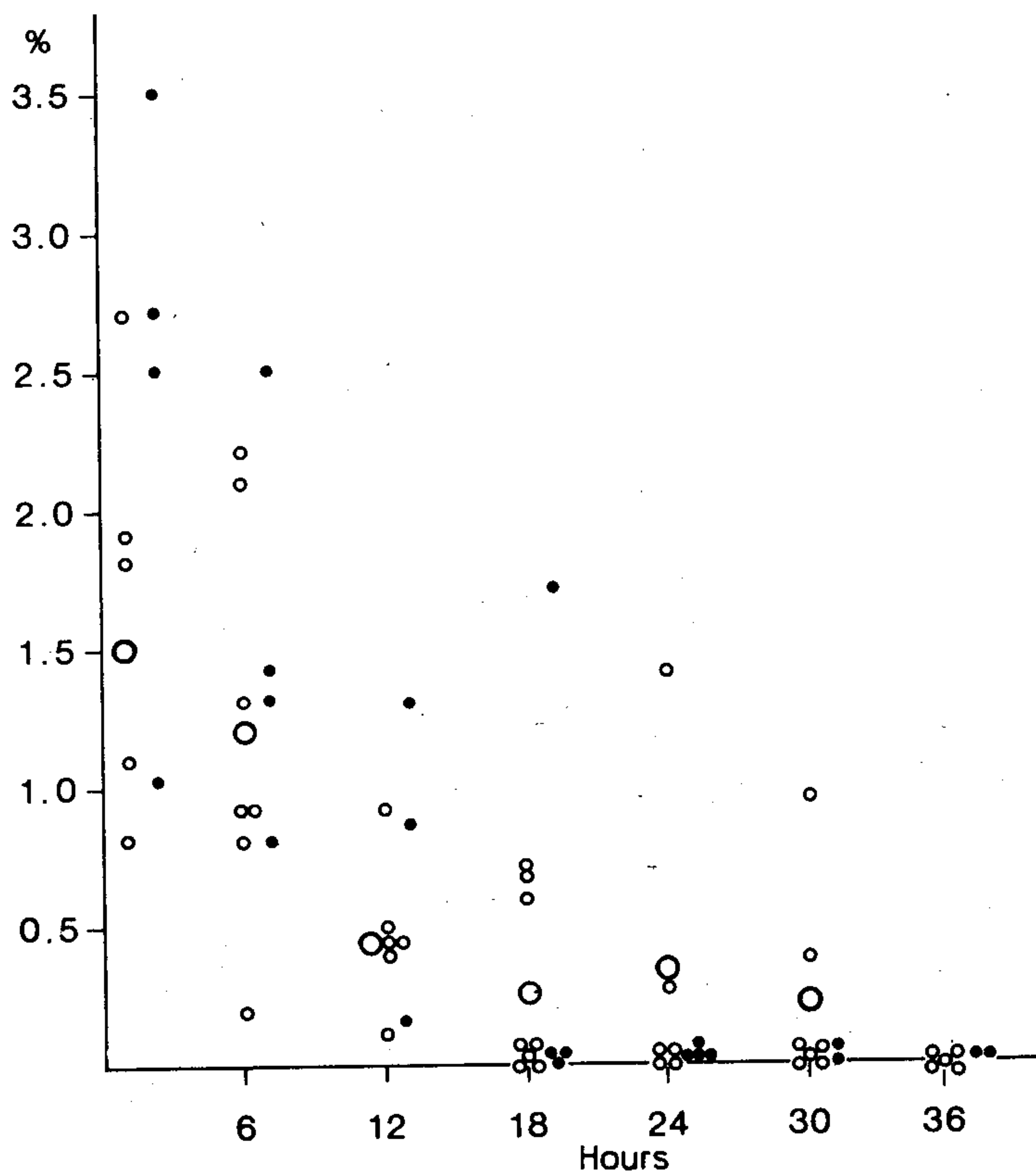


Fig. 3. Amount of food (expressed as percentage of body weight) in juvenile frogs that have been starving for different periods of time
All frogs were caught at 2 to 4 a.m. Filled circles refer to *R. arvalis* and open circles to *R. temporaria*. Large open circles are mean values for *R. temporaria*

Table III. Comparison between the total stomach content and that part that did not show any clear signs of digestion (data for 1975)

Species and age	<i>N</i>	Mean weight of stomach content (mg)	Mean weight of indigested content (mg)	Latter as percentage of former
<i>R. arvalis juveniles</i>	135	28	2.8	10
<i>R. temporaria juveniles</i>	115	24	4.9	20
<i>R. arvalis adults</i>	37	140	13.2	9
<i>R. temporaria adults</i>	46	380	54.0	14

Table IV. Temporal distribution of stomach samples containing indigested food
No deviations from random distribution are significant at the 0.05 level

Species and age	Variables	Time when the frog was caught and killed				χ^2	d.f.
		02-06	08-12	14-18	20-24		
<i>R. arvalis</i> juveniles	sample size	27	52	50	25	3.80	3
	proportion with indigested food (%)	52	58	72	60		
<i>R. temporaria</i> juveniles	sample size	19	35	51	13	2.95	3
	proportion with indigested food (%)	32	46	47	62		
<i>R. arvalis</i> adults	sample size	17	10	6	21	0.08	1
	proportion with indigested food (%)	24	30	50	29		
<i>R. temporaria</i> adults	sample size	22	16	29	36	1.18	3
	proportion with indigested food (%)	50	38	48	39		

3.4. TOTAL FOOD CONSUMPTION

Comparing frogs from forest with those from meadow, adult *R. temporaria* seemed to feed at a higher rate in forest than in meadow while the opposite applied to adult *R. arvalis*. The differences, however, were insignificant (two-tailed median tests; $\chi^2 = 1.40$, $p = 0.30-0.20$; $\chi^2 = 2.85$, $p = 0.10-0.05$ for *R. temporaria* and *R. arvalis*, respectively) (Table V). The data

Table V. Weight of stomach content

Species and age-size categories (mm)	Habitat	N	\bar{x} (mg)	Weight of frogs (g)
<i>R. arvalis</i> juveniles ≤ 26	forest	88	28	0.83
	meadow	47	28	0.95
mixed category 31-46	forest	52	91	8.5
	meadow	47	167	9.7
adults ≥ 37	forest	34	123	10.3
	meadow	78	168	12.9
<i>R. temporaria</i> juveniles ≤ 30	forest	89	25	0.79
	meadow	26	22	0.88
subadults 31-46	forest	39	212	7.7
	meadow	21	250	6.9
adults ≥ 47	forest	54	432	15.3
	meadow	29	265	16.2

also suggest that, regardless of habitat, *R. temporaria* feeds at a higher rate than *R. arvalis*. This can be tested for the size category 26–46 mm. Although the specimens of *R. arvalis* were heavier than those of *R. temporaria* in both habitats, the latter contained more food. The difference was significant for the forest habitat (two-tailed median test, $\chi^2 = 4.49$, $p < 0.05$).

An exact calculation of the total consumption per 24-hour period requires knowledge on the digestion rate for all prey items. Because of lack of these data, a rough value is calculated by another method.

The mean weight of the stomach content is divided by the gastric evacuation time (18 hours for juvenile frogs and 24 hours for adults). The feeding rate was similar for juveniles of the two species and decreased in adults. This decrease was greater in *R. arvalis* than in *R. temporaria* although the latter is larger in size (Table VI).

Table VI. Feeding rate of different categories of frogs

Age and species	Mean weight of frogs (g)	Mean weight of stomach content (mg)	Feeding rate (mg per 24 hours)	Feeding rate (percentage of body weight per 24 hours)	N
Juveniles					
<i>R. arvalis</i>	0.88	27.8	37	4.2	135
<i>R. temporaria</i>	0.82	24.0	32	3.9	115
Subadults					
<i>R. temporaria</i>	7.4	225	225	3.0	60
Adults					
<i>R. arvalis</i>	12.1	154	154	1.3	112
<i>R. temporaria</i>	15.6	375	375	2.4	83

Table VII. Important prey taxa for frogs (data for both habitats are lumped)

It is assumed that categories with digestion rate index 2 are digested twice as fast as those with index 1. The volume index is approximately proportional to the size of individual prey specimens of the categories

Age of frogs and prey taxon	Digestion rate index	Volume index	<i>R. arvalis</i>		<i>R. temporaria</i>	
			per cent of prey specimens	per cent of prey volume	per cent of prey specimens	per cent of prey volume
Juveniles						
Oligochaeta	2	250	1	23	1	23
Hemiptera	2	25	10	23	6	14
Coleoptera	1	12	12	14	9	10
Diptera	2	8	8	19	8	18
Adults						
Oligochaeta	2	1200	4	26	10	45
Hemiptera	2	100	14	8	8	3
Coleoptera	1	300	22	18	26	15
Lepidoptera (larvae)	2	500	8	22	4	8
Diptera	2	200	9	10	10	8
<i>Rana</i> (small frogs)	1	1500	2	8	2	6

To compare the relative importance of the different prey categories, I classified the various taxa as fast or slow digested. I used data from the feeding tests and extrapolated them to untested taxa from similar tested ones. The mean volume of a prey taxon was assumed to be proportional to: maximum length \times maximum breadth². This was measured on prey specimens. The most important prey taxa for juvenile frogs were worms, bugs, beetles and flies and for adult ones: worms, bugs, beetles, butterfly and moth larvae, flies and juvenile frogs (Table VII), Mites, although numerically important for juvenile frogs, did not contribute much to the total volume.

3.5. SIZE OF THE PREY

3.5.1. Size distribution of the prey

The size distribution of the prey was approximately log-normal, i.e., a plot of frequency against \ln [prey size] is approximately normal (Figs. 4, 5). The distribution of the prey caught by juveniles in forest is slightly skewed to the left, what is a result of the large number of mites taken.

3.5.2. Relation to frog size

A positive correlation was found between frog size and prey size for all species-habitat-size categories. With respect to prey breadth, in both habitats, and prey length in meadow, the relation is linear (Figs. 6, 7) and the y-intercept of the linear regression is nearly zero. However, with respect to prey length in forest (Fig. 7 A), the y-intercept is negative. This is because short and stout-bodied mites form a large part of the small frogs' diet but are altogether absent in the diet of larger frogs. The relation is thus realistically modelled by a concave graph.

3.5.3. Relation to frog species

There was no significant difference of prey breadth between the two frog species (Table VIII). The mean length of juvenile frogs' prey differed; in forest habitat the prey of *R. temporaria* was longer than that of *R. arvalis* (Mann-Whitney *U*-test, $p < 0.01$) while the opposite applied in meadow habitat (Mann-Whitney *U*-test, $p < 0.01$). The prey of adult frogs did not differ in length.

4. DISCUSSION

4.2. FEEDING RATE

Chłodny and Mazur (1969) studied the energy requirements of *R. arvalis* by offering frogs surplus food under laboratory conditions and measuring its intake. The intake decreased from a maximum in June and July to 55% of that value in October and November. From their figures a daily intake of 1.3% measured as g fresh weight of food per g frog weight, can be calculated for the end of August. This is the same value as I found for this species (Table VI).

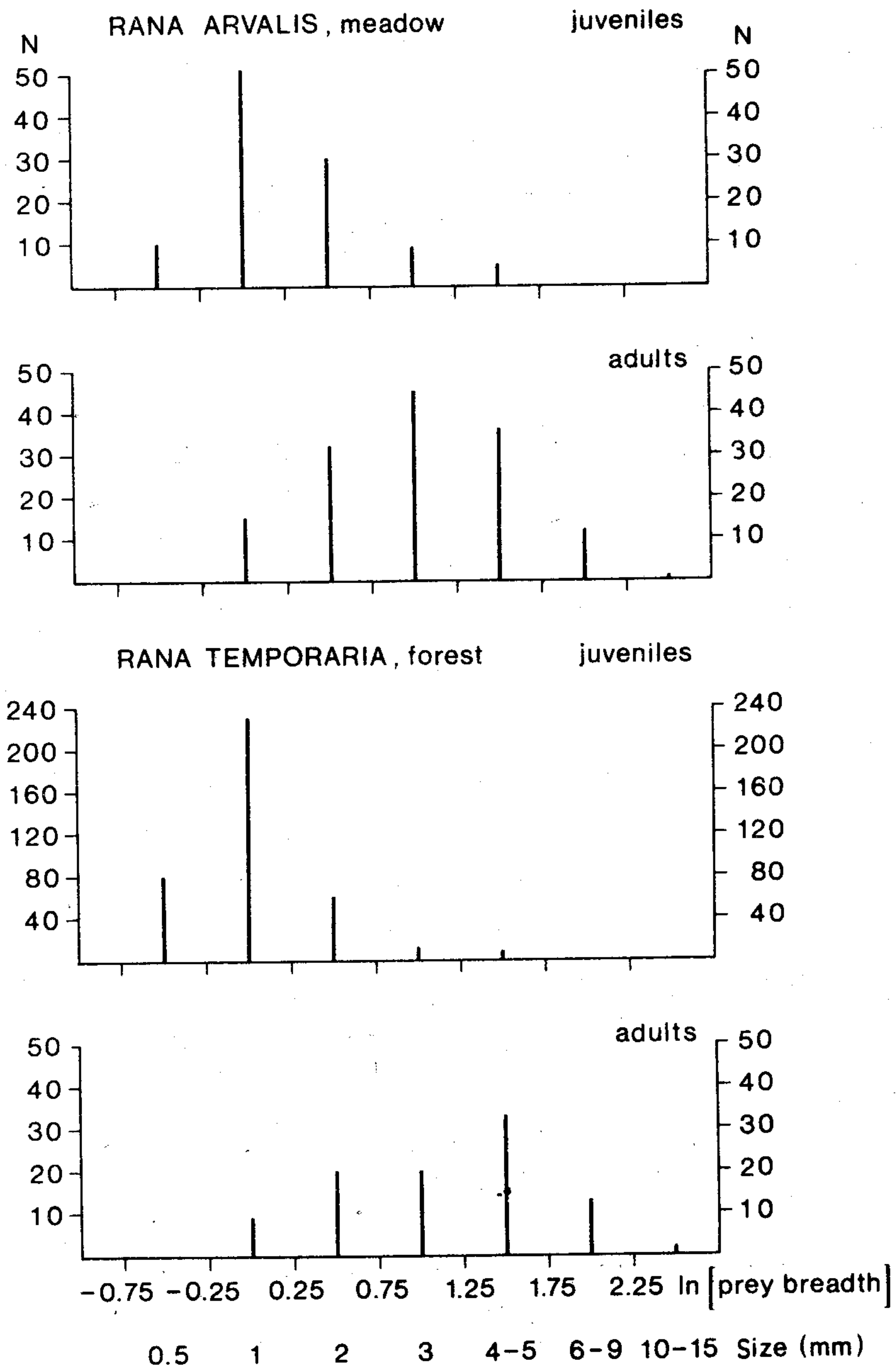


Fig. 4. Distribution of breadth of prey caught by frogs
The y-axis gives the number of prey specimens

The most important sources of error in the laboratory study are that frogs under confined conditions possibly may not feed unrestrictedly and in my field study the exact information on digestion times is lacking. My finding regarding the gastric evacuation time, however, is

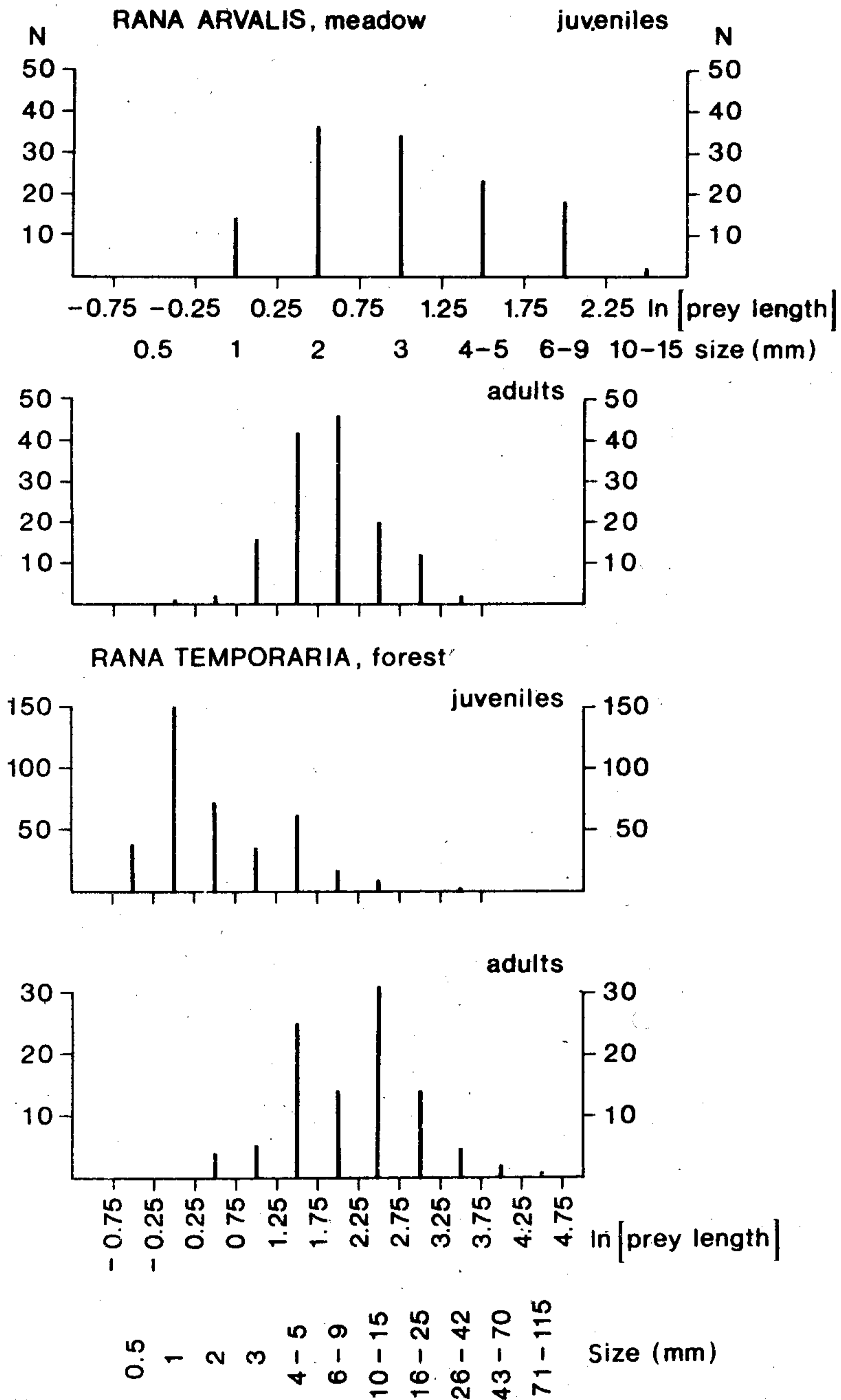
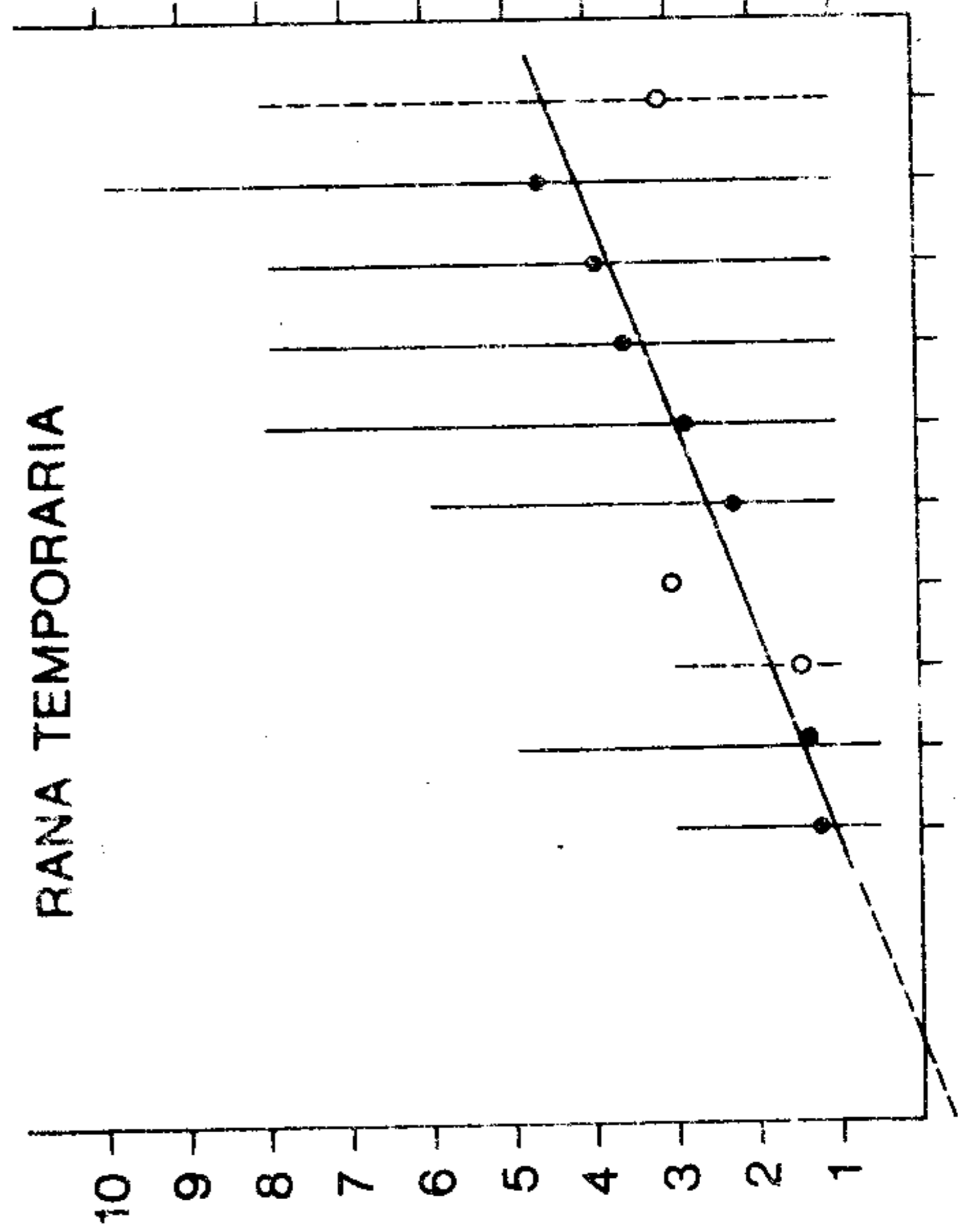
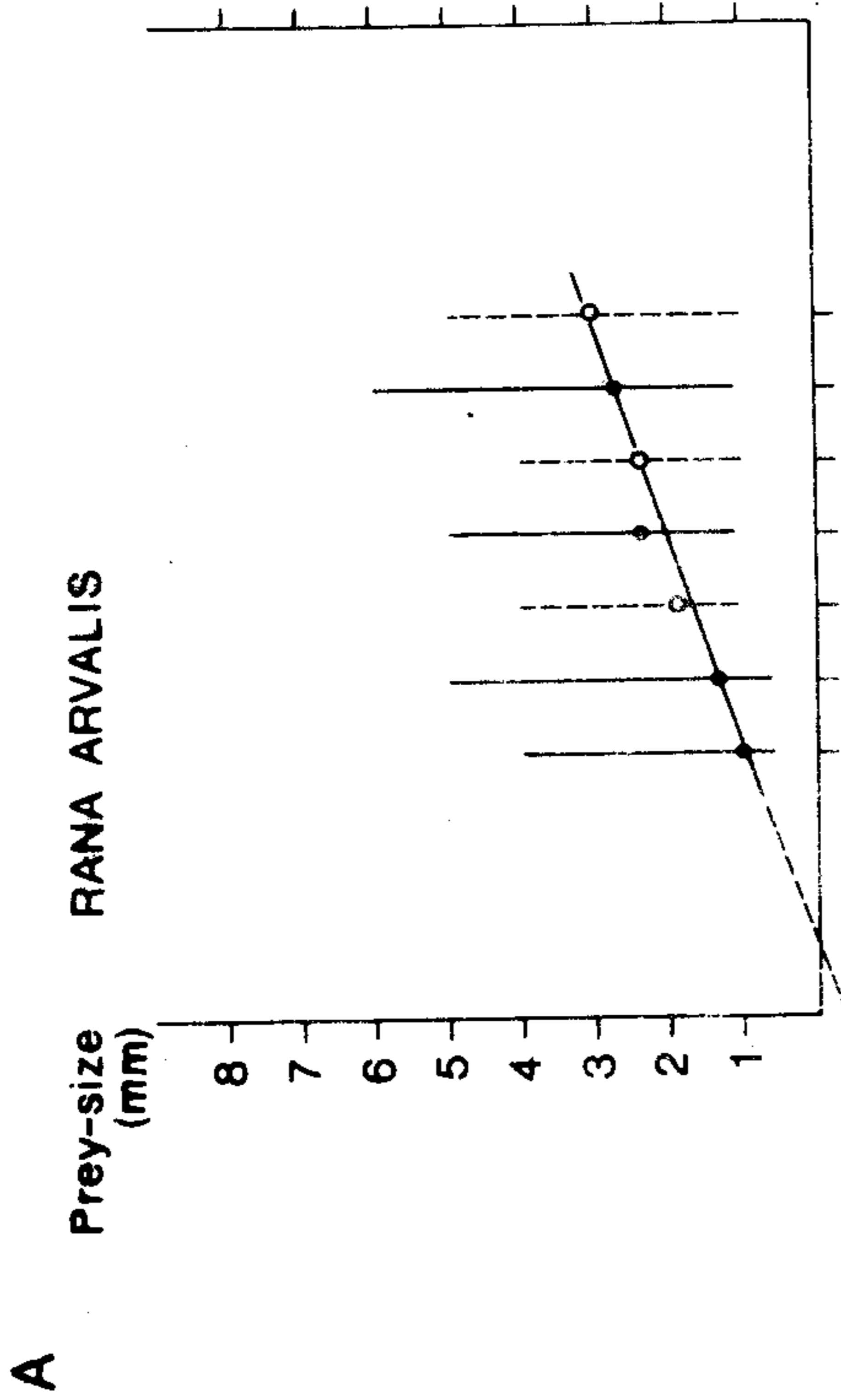
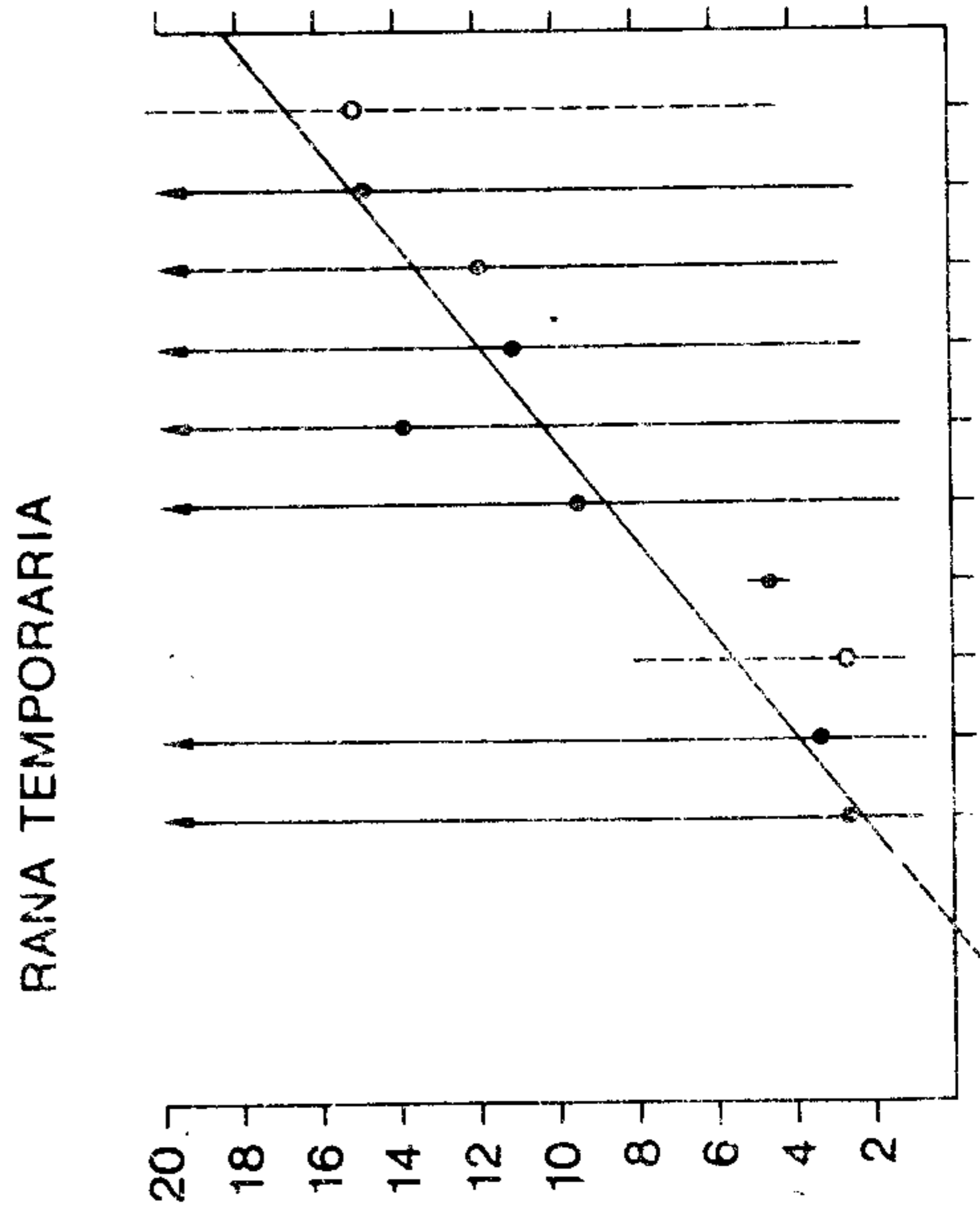
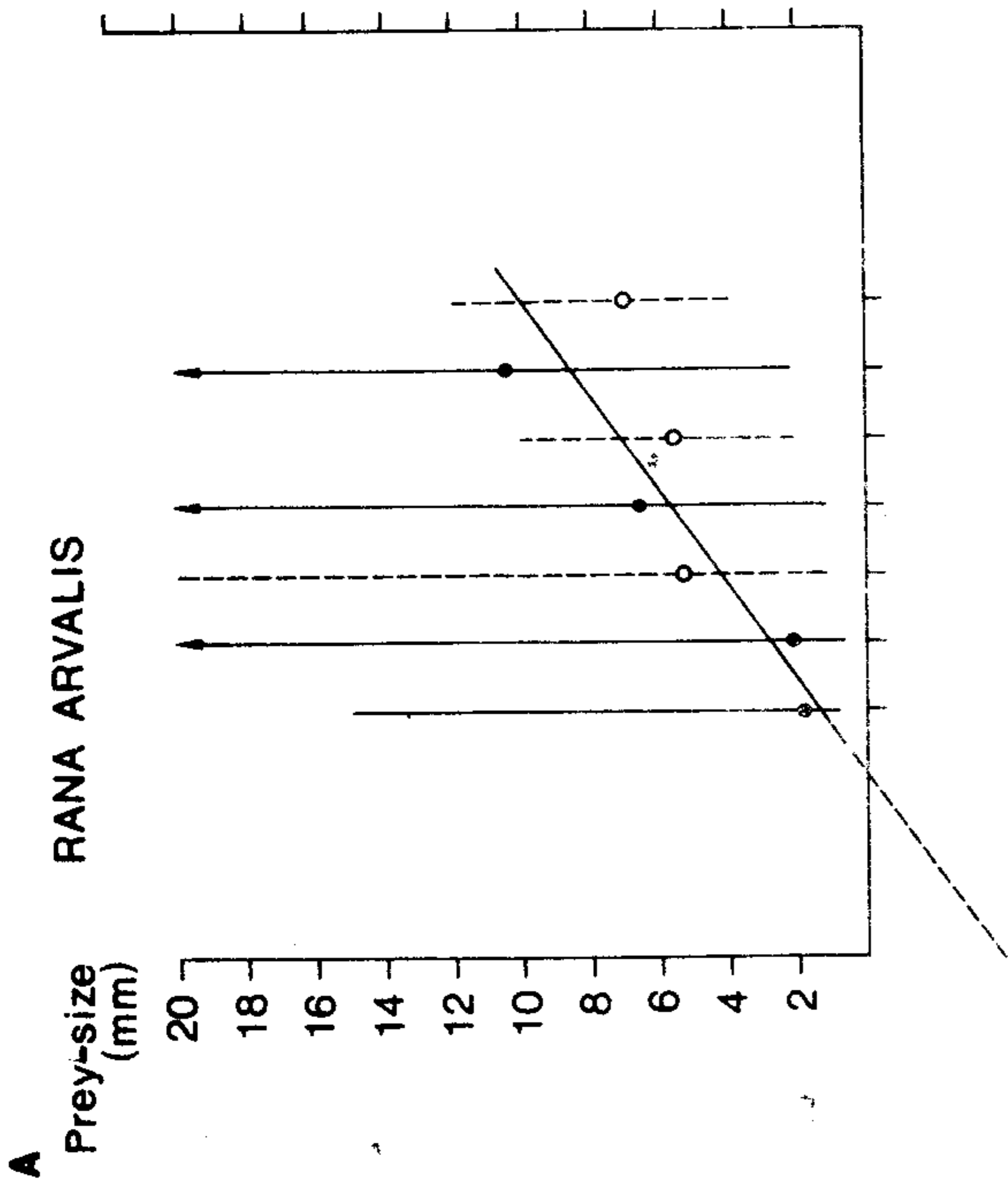
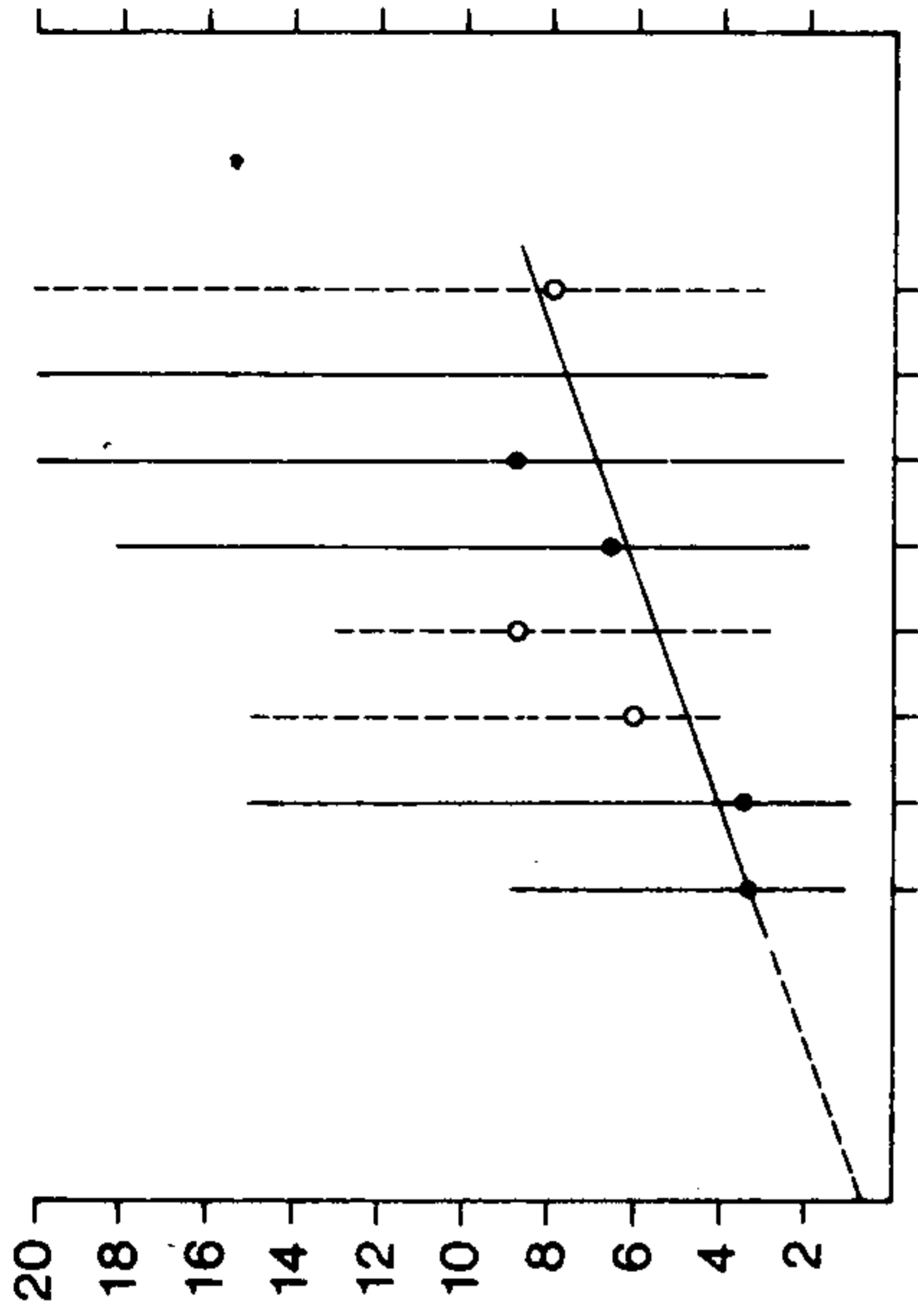


Fig. 5. Distribution of length of prey caught by frogs
The y-axis gives the number of prey specimens

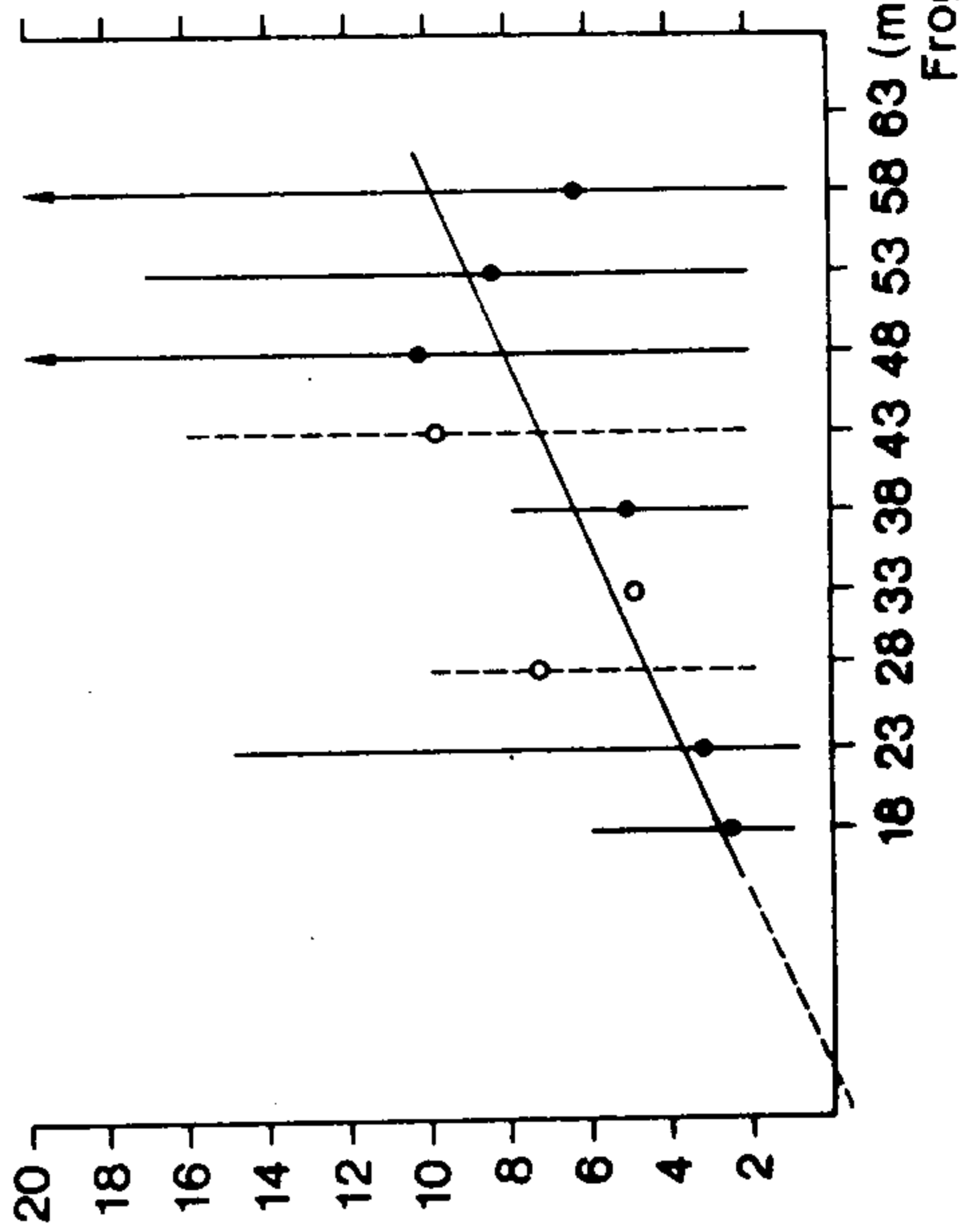


RANA ARVALIS

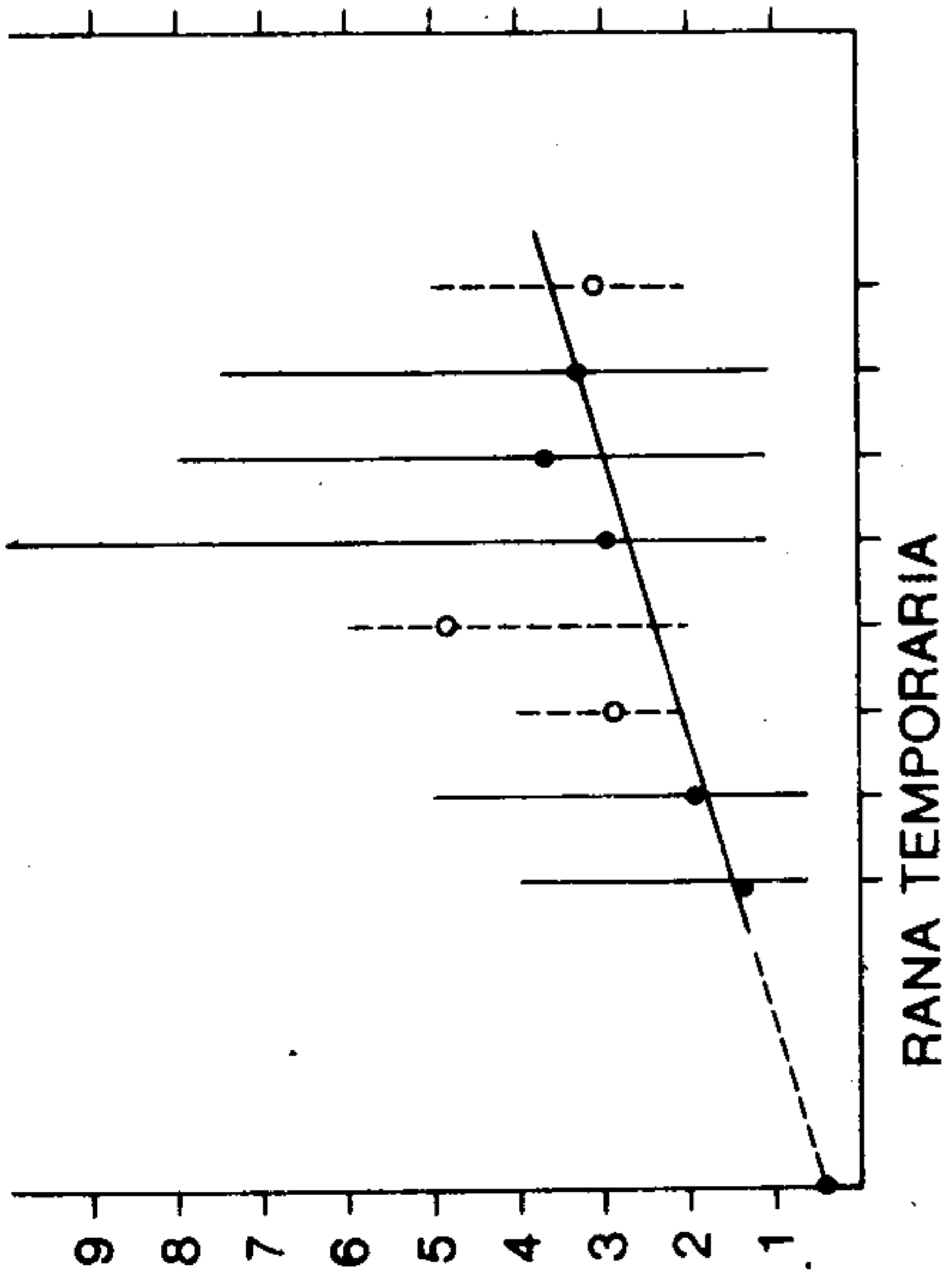


B

RANA TEMPORARIA



RANA ARVALIS



B

RANA TEMPORARIA

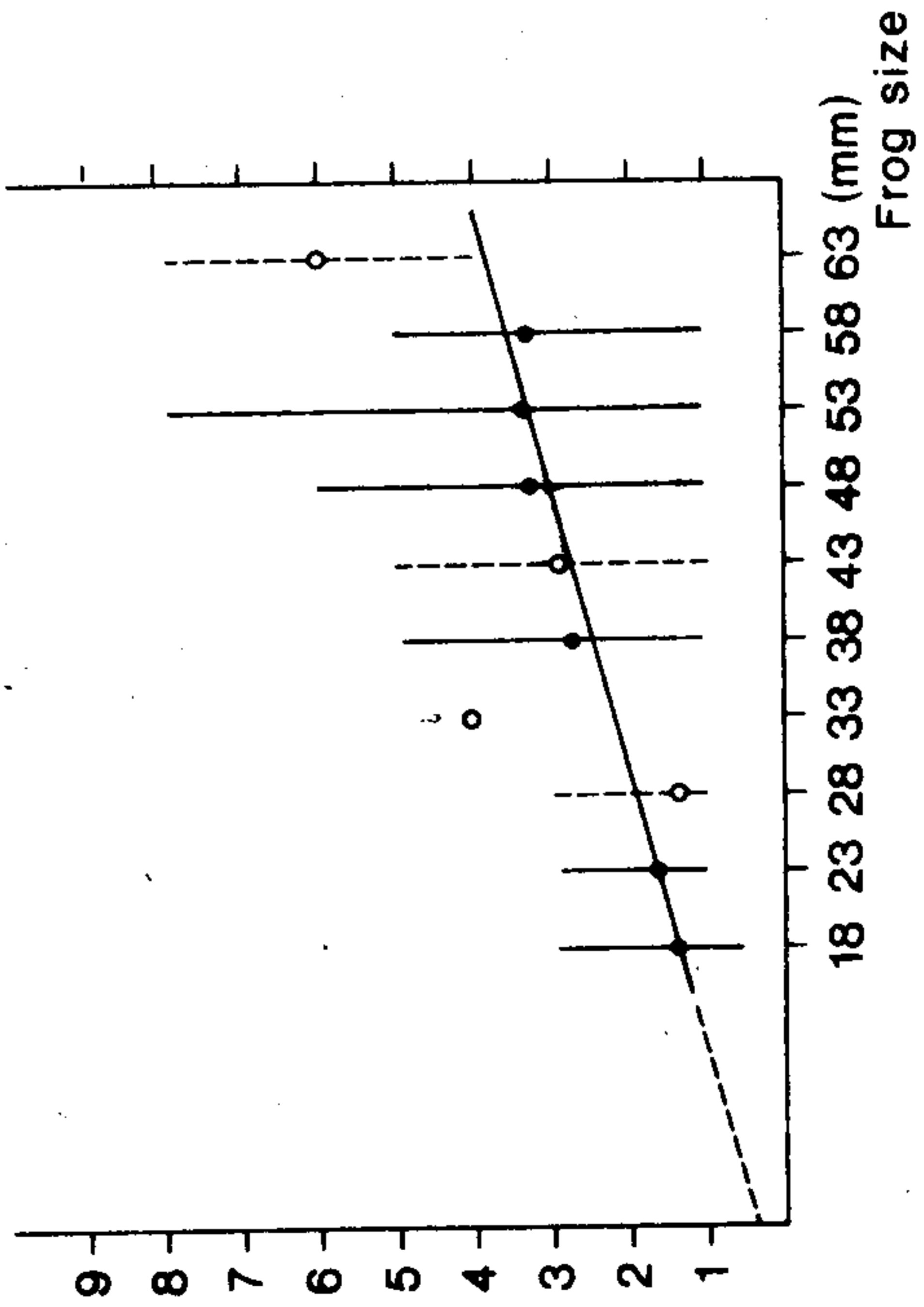


Fig. 6. The relation between frog size and prey breadth. Mean values and total span for different size classes of frogs are given. Open circles and dashed lines refer to samples of up to 20 prey items. The regression line is included. A - forest samples, B - meadow samples

Fig. 7. The relation between frog size and prey length. All symbols as in Figure 6

Table VIII. Size of prey taken by different categories of frogs

Habitat and frog size and species	Mean length of frogs (mm)	Mean breadth of prey (mm)	Mean length of prey (mm)	N (prey specimens)
Forest				
Small frogs (16–25 mm)				
<i>R. arvalis</i>	21.0	1.2	2.1	507
<i>R. temporaria</i>	20.5	1.1	2.9	368
Large frogs (36–50 mm)				
<i>R. arvalis</i>	41.9	2.6	8.9	65
<i>R. temporaria</i>	43.9	3.0	11.5	127
Meadow				
Small frogs (16–25 mm)				
<i>R. arvalis</i>	20.8	1.6	3.5	127
<i>R. temporaria</i>	20.4	1.5	2.9	87
Large frogs (36–50 mm)				
<i>R. arvalis</i>	44.7	3.3	7.8	128
<i>R. temporaria</i>	44.1	3.1	8.5	84

supported by Inozemcev (1969) who determined a gastric evacuation time to be 24 hours, the same value as I found for adult frogs. The results suggest that the survival and growth of the frogs in my study plots were not limited by lack of food.

Food may still be an evolutionary important factor, lack of which could have been the cause of segregation, e.g., in different habitats, if this lack occurs sufficiently often at other places and at other times, but the case is weakened.

The decrease in feeding rate in larger frogs (Table VI) was also found by Chłodny and Mazur (1969). As these frogs had access to surplus food, some physiological mechanism seems to be responsible for the trend rather than differences in the availability of food from different size classes.

The lower feeding rate of *R. arvalis* in both habitats (Tables V, VI) is probably the cause of the lower growth rate of this species (Loman 1978b). Why the feeding rate of *R. arvalis* is lower is unclear. If these frogs hunt by a sit-and-wait strategy, as Dole (1965) has shown for *Rana pipiens* Schreber, the movements necessary to capture a prey could involve a hazard and *R. arvalis* might "choose" to take this risk only when the expected benefit-cost ratio was higher than does *R. temporaria*, e.g., only when spotting larger prey individuals. There was, however, no indication of a difference in prey size (Table VIII).

4.2. INTERSPECIFIC SEGREGATION

Previous studies have shown that both species are unselective predators. Blackith and Speight (1974) even compared *R. temporaria* to "holes in the ground"! Zimka (1966) found that *R. arvalis* selected predaceous forms over others as prey. This was because these were the more mobile ones. Inozemcev (1969) found the diet of the two species to be almost identical.

In the present study only two differences could be found: (a) Juvenile *R. arvalis* took longer prey specimens than equally large *R. temporaria* in meadow while the situation was reversed in forest. (b) Judging from the amount of stomach content, *R. arvalis* was a more successful forager in meadow than in forest while the opposite applied to *R. temporaria*.

Though direct evidence is lacking, (a) could be due to different microhabitats being utilized by the two species. In this context I regard microhabitat utilization and hunting mode as synonyms. Such a difference would be a way of reducing exploitation competition. A difference in hunting mode has been demonstrated for adult frogs in the meadow plots of the study area. *R. arvalis* was found somewhat higher up in the grass than *R. temporaria* (L o m a n 1978a). This difference was apparently not sufficiently marked to cause any significant differences in the prey taxa utilized. It appears that within-habitat food segregation between the two species is weak and probably does not reduce possible competition between the two species to a significant extent.

On the other hand, a partial habitat segregation does exist (L o m a n 1978a), adult *R. temporaria* being relatively more abundant in forest and adult *R. arvalis* in meadow habitat. This difference in the present study was found to be accompanied by a corresponding difference in foraging efficiency, judging from the amount of food in the stomachs of specimens from the two habitats. This division of habitats may be due to latent competition for food, although this cannot be proven on the present evidence.

The lack of periodicity in feeding activity over the diel rhythm could be due to a sampling error; it is possible that feeding and, therefore, possibly more active frogs were more easily captured. However, most frogs were caught after flushing, and if this is a defence against predation it should be equally common at all times unless the frogs are actually hard asleep at some times. I n o z e m c e v (1969) states that the feeding activity is concentrated at dusk. He does not, however, state how this was found.

4.3. PREY-SIZE SELECTION

The fact that large frogs tend to take larger prey than do small frogs may be due to either of the following mechanisms:

1. All frogs take all prey organisms up to a certain size limit that is proportional to the predator size (Fig. 8 A).

2. For each frog size there is an optimum prey size, and the sizes of prey actually taken are more or less normally distributed around this optimum size. Possible skewness may be due to differences in availability of different prey sizes (Fig. 8 B). In the latter case three explanations may apply:

- a. The cost-benefit relation after the potential prey is sighted is such that only prey within a limited size range are attacked. Other "considerations" by the frog than mere size of prey may be responsible for the dome-shape of the size-distribution.

- b. Because of the mentioned cost-benefit relation, frogs may select to hunt in places where the probability of encountering prey within the optimal size range is maximal.

- c. Small frogs may perceive smaller prey than do larger frogs although they are searching in the same places. Small frogs may, for example, more easily see prey specimens that are sitting under the edge of leaves, etc.

A definite choice between these mechanisms, especially between a-c, is impossible, but some considerations may be offered.

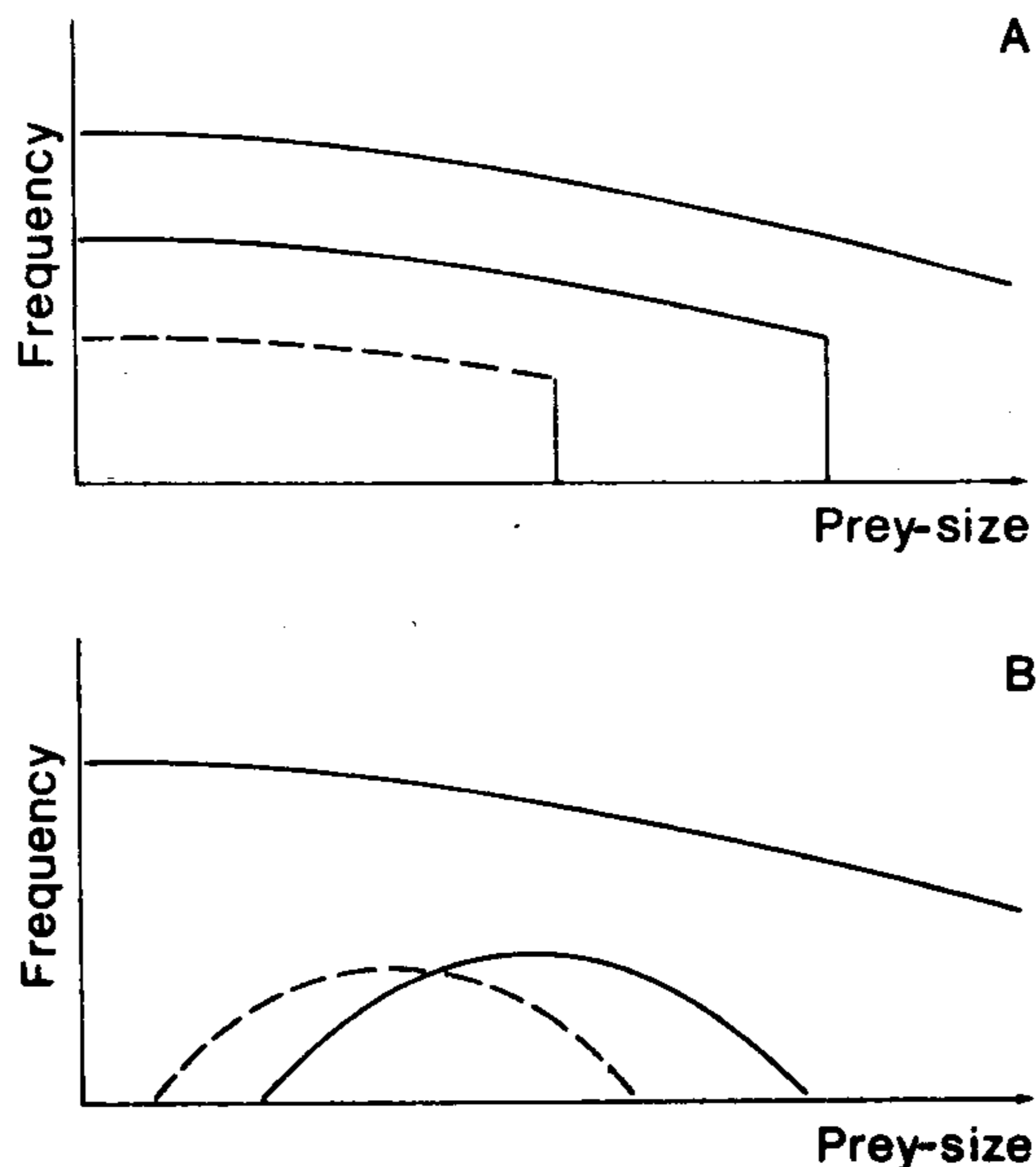


Fig. 8. Expected size distribution of prey according to two models of prey-size selection. Dashed lines refer to prey taken by small frogs and solid lines to that taken by large frogs. The uppermost lines refer to the size distribution of available prey.

If there is a definite upper size limit for prey taken, the prey size distribution should be similar to distribution illustrated in Figure 7 A. This is not the case. The distribution is roughly log-normal. This distribution seems to be the rule for predators with varied diet such as insectivorous birds (Hespenheide 1975), lizards (Schoener and Gorman 1968, Sexton, Bauman and Ortleb 1972) and *R. temporaria* (Houston 1973).

The pattern could also be rejected for another reason. The relative importance of small (1 mm wide) and medium-sized (2–3 mm wide) prey to small and large frogs is compared. In order to make the comparison conservative, it is assumed that small frogs digest prey of both size classes at the same speed (18 hours). This may be reasonable as the smaller prey items largely are hard-bodied mites. For large frogs it is assumed that smaller prey items are digested with four times the speed of the larger (6 hours as opposed to 24 hours). Tests with small and large meal worms indicate that this is more than the real difference (Table IX). Both classes of frogs clearly take both kinds of prey. However, per day, small frogs take more specimens of small than of medium-sized prey while the opposite is true for large frogs (Table IX). This supports the pattern shown in Figure 8 B as opposed to 8 A. Although, to judge from the observed size distribution seldom reached, there is probably a definite upper size limit to prey accepted by a frog of a particular size. If this limit differs for different prey taxa, this may, at least in part, explain the pattern observed. I would include this pattern in mechanisms 2a and 2b above.

If pattern a or b applies, there should be a definite cost associated with the capture of small prey as there otherwise is no individual benefit in specializing to the extent that available food is rejected (MacArthur and Pianka 1966). The cost could be time, but this is unlikely as only 2–7 food items are taken per day and the capture and handling of an insect, especially a small one, by a frog is a quick affair. More likely the cost is represented by the risk of alerting a

Table IX. Feeding rate of small and large frogs on prey of different size classes
The values give the estimated number of prey items taken per day. Prey size is measured as the greatest body breadth and frog size as snout-urostyle length (mm)

Prey size (mm)	<i>R. temporaria</i>				<i>R. arvalis</i>			
	forest		meadow		forest		meadow	
	≤ 30	≥ 47	≤ 30	≥ 47	≤ 26	≥ 37	≤ 26	≥ 37
1	3.7	0.75	2.8	1.2	5.5	1.0	1.5	0.66
2-3	1.1	1.0	1.7	1.5	1.2	1.2	1.2	1.1
Number of stomachs	83	48	29	29	82	35	44	71

predator that may be associated with the move to snap an insect or other prey. The weight of a small mite, $1 \times 1 \times 0.5$ mm, is about 0.1% of the total daily food intake and even a small risk should be sufficient to reject it.

4.4. RESOURCE PARTITIONING BETWEEN THE TWO SPECIES

Both species are still growing when maturity is reached at an age of about 2 (*R. temporaria*) or 3 (*R. arvalis*) years. This causes an extensive overlap in size distribution although *R. temporaria* grows to a larger size. However, as *R. temporaria* is relatively fast-growing and reaches a size of 50 mm (a mean value with much variation) at the end of the second summer, while *R. arvalis* only reaches this size at the end of the fifth summer, when most individuals are dead (L o m a n 1978b), the overlap is far from being complete. Since juveniles, i.e., young of this year, are less than 26 mm (*R. arvalis*) or 30 mm (*R. temporaria*), they do not overlap with older individuals of either species except for some slow-growing *R. arvalis*. They will not be considered in the following discussion. Mature *R. arvalis* are seldom found in forest, as mentioned above.

The forest plots sampled in this study were thus unusual for this area as they supported both species. The mean size of second-year frogs and older ones in forest was in the sample of the present study 40 mm, $N = 51$, for *R. arvalis* and 47 mm, $N = 47$, for *R. temporaria*. The mean breadth of prey utilized by these sizes was 2.5 mm and 3.3 mm, respectively (Fig. 6 A). The situation in the meadow habitat was more complex one. With plots of the size utilized in this study, approximately 1 ha, there is much variation between mean size of frogs from different plots. This applies especially to *R. temporaria* (L o m a n 1978a). The fact that those second-year and older frogs in meadow that were analyzed in the present paper did not differ much in size (45 mm, $N = 78$, and 49 mm, $N = 55$, with a mean prey breadth of 3.1 and 3.1 mm for *R. arvalis* and *R. temporaria*, respectively; Fig. 6 B) is not typical of the study area. *R. temporaria* is the larger species when adult. The sample used in the analysis of habitat distribution is drawn from 12 meadow plots and the mean size of second-year and older frogs is 42 mm, $N = 67$, and 49 mm, $N = 115$, respectively, with a mean expected prey breadth of 2.9 and 3.1 mm, respectively. Despite the size difference, the overlap is thus extensive, and the existence of such a large overlap seems to support the proposal that adult frogs of both species

do not compete severely for food as their co-existence in the study area is probably permanent.

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5. SUMMARY

The food composition and food (prey) size distribution was determined for the two frog species, *Rana arvalis* and *R. temporaria*, in meadow and forest habitats in south Sweden. Experiments were also carried out to determine the speed of food digestion, permitting an estimation of the total food consumption.

The taxonomic composition of food of the two species was almost identical (Fig. 1). This suggests that they are not competing for food and, in turn, that food for metamorphosed frogs is not in short supply.

The experiments have shown that most food was visibly affected by digestion within 6 hours and this information was used to study daily variation in feeding rate. No clear variation could, however, be established by this method and the present sample size (Table IV).

The feeding rate (fresh weight of prey per fresh weight of frog and 24 hours) was less for older than for younger frogs (Table VI). For adult frogs the rate was 1.3% (*R. arvalis*) and 2.4% (*R. temporaria*).

The size distribution of prey was approximately log-normal (Figs. 4, 5) and there was a positive correlation between the size of frogs and the mean size of their prey (Figs. 6, 7).

6. POLISH SUMMARY

Określono skład i rozkład wielkości pokarmu (ofiary) u 2 gatunków żab (*Rana arvalis* i *R. temporaria*) w siedlisku łąkowym i leśnym południowej Szwecji. Przeprowadzono również eksperymenty w celu określenia tempa trawienia pokarmu, co pozwoliło oszacować całkowitą jego konsumpcję.

Skład taksonomiczny pokarmu omawianych gatunków żab był prawie identyczny (rys. 1). Na tej podstawie można sądzić, że nie konkurują one o pokarm, oraz że baza pokarmowa żab, które przeszły metamorfozę, jest wystarczająco obfita.

Eksperymenty pokazały, że większość pokarmu była w widocznym stopniu zmieniona wskutek trawienia w ciągu 6 h i fakt ten znalazł zastosowanie w badaniu dobowej zmienności racji pokarmowej. Nie można było jednak ustalić wyraźnej zmienności dobowej racji pokarmowej na podstawie zastosowanej metody i obecnej wielkości próby (tab. IV).

Racja pokarmowa (świeża masa ofiary w stosunku do świeżej masy żab w ciągu 24 h) była mniejsza u starszych żab w porównaniu z młodszymi (tab. VI). Wynosiła ona u dorosłych żab 1,3% (*R. arvalis*) i 2,4% (*R. temporaria*).

Rozkład wielkości ofiary był w przybliżeniu log-normalny (rys. 4, 5). Stwierdzono istnienie dodatniej korelacji między wielkością żab i średnią wielkością ich ofiary (rys. 6, 7).

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