

## Prey size selection and food habits of Water Frogs and Moor Frogs from Kis-Balaton, Hungary (Anura: Ranidae)

Selektion der Beutegröße und Nahrungsgewohnheiten  
von Wasserfröschen und Moorfröschen des Kis-Balaton, Ungarn  
(Anura: Ranidae)

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### KURZFASSUNG

Die Untersuchung der Mageninhalte bei semiaquatischen Fröschen des *Rana esculenta* - Komplexes und von *R. arvalis* zeigte, daß beide ähnliche Beutegröße bevorzugten. Innerhalb einer Population konsumierten größere Individuen größere Beute, während kleinere Tiere gewöhnlich kleinere Beutetiere fraßen. Eine deutliche Bevorzugung bestimmter Beutetiergrößen ließ sich bezüglich der Hauptbeutegruppen Coleoptera, Hymenoptera und Diptera feststellen. Unsere Daten unterstützen die Hypothese, daß die taxonomische Zusammensetzung der Beute eher durch deren Verfügbarkeit bestimmt ist, während hinsichtlich der Beutegröße eine gewisse Selektion erfolgt.

### ABSTRACT

Analysis of the stomach contents in the semiaquatic frogs of the *Rana esculenta* complex and *R. arvalis* showed that they preferred similar prey size. Within populations, larger individuals consumed larger prey while smaller ones usually ate smaller prey. A clear size preference was found concerning the main prey groups (Coleoptera, Hymenoptera, Diptera). Our data support the hypothesis that the taxonomic composition of the prey items is rather determined by their availability, while there is some selection for prey size.

### KEY WORDS

*Rana esculenta* complex, *Rana arvalis wolterstorffi*, feeding ecology, predator-prey size relationship, diet overlap, feeding flexibility; Hungary

### INTRODUCTION

From the 1960's, an intensive eutrophization process has continued in the largest shallow lake of Europe, Lake Balaton. Its pollution by nitrogenous and phosphorous substances increasingly took effect because of the destruction of marsh lands which served as a filter area in the west of the lake. Some small patches of this area survived and now form the Kis-Balaton Nature Reserve. To re-establish the filter function of the previous marsh lands, an artificial water reservoir was set running there in 1985. At the same time a monitoring project started to record the long term changes in this newly formed wetland ecosystem. Part of this study has been to investigate the role of amphibians in both areas, the artificial pond and the nature reserve (LŐW & al. 1989; SZALAY-MARZSÓ

& al. 1990; TÖRÖK & CSÖRGŐ 1992).

Three main problems were incorporated in this project: i) hybridisation among the members of the *Rana esculenta* complex which was studied by the analysis of blood samples (LŐW & al. 1990), ii) growth and sexual maturation in different frog species estimated from annual growth rings in finger bones and relative developmental stage of the reproductive organs, iii) feeding ecology of amphibians studied by analysis of stomach contents. The present paper is dedicated to the latter question, concentrating on prey size preference of two common frog species.

From ten species of amphibians occurring in the Kis-Balaton Nature Reserve, the Water Frogs of the *R. esculenta* complex (*R. lessonae* CAMERANO, 1882, *R. ridi-*

*bunda* PALLAS, 1771, and their hybrid *R. kl. esculenta* LINNAEUS, 1758) and the Moor Frog (*R. arvalis wolterstorffi* FEJÉR-VÁRY, 1919), are dominant in number. Both are generalist feeders and their diets overlap greatly (TÖRÖK & CSÖRGŐ 1992). Frogs of the *Rana esculenta* complex feed on Hemiptera, Hymenoptera, Diptera, Coleoptera, Homoptera (Aphididae) (TYLER 1958; KÜHLHORN 1960; GUTOWSKI 1988). The nominate race of the Moor Frog eats mainly Coleoptera, Hemiptera, Diptera, Homoptera (Aphididae), Gastropoda (ZIMKA 1966, 1974; LOMAN 1979). There is very little data on other aspects of the feeding ecology of these frogs. It was observed in other species, that amphibian size is correlated with prey size (MITCHELL & WOOLCOTT 1985; MITCHELL & TAYLOR 1986; NUUTINEN & RANTA 1986; WHEATER 1986; MARSHALL & CAMP 1995) which may be purposeful to maximize net energy gain

and/or to reduce potential competition for food.

The basic assumption of the "optimal foraging theory" is that maximum efficiency in energy intake is favoured by natural selection (PYKE 1984). Accepting this, we should expect prey size to play an important role in the foraging strategies of most amphibians. From the energetic point of view, energy net gain in larger ectotherm predators might be enhanced by the consumption of larger prey. To examine this notion the goal of our study was to test for the existence of predator-prey size relationship within the populations of the *R. esculenta* complex and *R. arvalis* in the Kis-Balaton Nature Reserve. We also compared the size distributions of flying insects available in the environment with those in the stomach contents of frogs. In addition, we report on diet composition of these frogs and seasonal changes in their food composition.

## MATERIAL AND METHODS

This study was conducted in the Kis-Balaton Nature Reserve situated at 17°10' E., 47°20' N., in Western Hungary. The slow-moving River Zala flows through the middle of this extent marsh. There are only small remains of open water surfaces. The vegetation consists mainly of *Phragmites communis* and *Glyceria maxima* with small patches of *Salix*, *Populus* and *Alnus* trees and bushes. Frogs were collected along the river side and the edges of the marsh in the afternoon (from 2:00 to 4:00 p.m.).

We collected a total of 284 Water Frogs and 270 Moor Frogs in 1985 (autumn) and 1986 (whole activity period) within the scope of a wide monitoring project recording long-term changes in Kis-Balaton Nature Reserve. These frogs were used in different studies among which the present paper is dealing with the feeding ecological observations. Most of the specimens were juvenile; and juveniles of the *R. esculenta* complex were not identified down to lower taxonomic units due to unreliability of determination. We will therefore use the collective term water frogs in this paper. For each specimen snout-vent length (SVL) was measured with a ruler to the nearest 1.0 mm. Frogs were anaesthe-

tised; blood samples were taken, and the stomachs and reproductive organs (ovaries or testes), and two fingers were preserved in 70% methanol for analysis.

All recognisable stomach contents were analysed under a binocular microscope and intact prey items were measured with a ruler to the nearest 1.0 mm. Although the degree of digestion of prey varied depending on chitin content of the cuticle, the observed stomach contents can be regarded as random samples of the diet selected by an individual over some unspecified time period.

We calculated the mean prey size for three size categories of frogs: small (SVL ≤ 30 mm), medium (SVL 31-50 mm), large (SVL > 50 mm). The same size categories of frogs were used in comparing the insects available in the environment and those found in the stomachs. Linear regression analysis was applied to test for predator size related prey size preference. Normal distribution of prey sizes was achieved by log transformation of data during the computation of Pearson's correlations. Predator-prey size relationship was analyzed for five main prey groups (Aphididae, Coleoptera, Diptera Hymenoptera, others).

In terms of the number of prey items, three groups of flying insects (Diptera, Hymenoptera, and Aphididae) were dominant (20-60%) in the diet. To get information on the prey size distribution in the environment we collected these groups of potential prey species with window traps and yellow bowls (SOUTHWOOD 1978). Nine window traps collecting flying insects operated for 24 hours on those days when frogs were collected. Yellow bowls were also placed out at the same time for aphids. Renkonen's proportional similarity index

(RENKONEN 1938) was used to compare available supply and diet of frogs:

$$S_{1,2} = \sum \min(p_{1,i}; p_{2,i})$$

where  $p_{1,i}$  and  $p_{2,i}$  are the proportions of prey type or size category  $i$  in species 1 and 2, respectively.

Renkonen's similarities were calculated by NICHE® program of SCHLUTER (1988) which was freely available from the author on request. All other computations were done by STATISTICA® for Windows® program package (StatSoft Inc., Tulsa, 1994).

## RESULTS

Water frogs and *R. arvalis* consume a great variety of prey from the soil surface and low vegetation. Aphids, dipterans, hymenopterans, beetles and spiders were the most numerous in our samples studied, although heteropterans and snails were also eaten in large numbers. Almost every prey item was terrestrial except amphipods and some isopods and coleopterans, which were swallowed probably in or near the water.

Combining data from 1985 and 1986, the mean SVL of sexes in *R. arvalis* (males  $\bar{x}$  = 36.8 mm,  $n$  = 100; females  $\bar{x}$  = 35.3 mm,  $n$  = 124) did not differ ( $F$  = 1.16,  $p$  = 0.284) while female water frogs ( $\bar{x}$  = 42.5 mm,  $n$  = 125) were significantly larger than males ( $\bar{x}$  = 33.7 mm,  $n$  = 119,  $F$  = 28.94,  $p$  < 0.0001). There was a great difference in average prey size within each species between the two years (water frogs: 1985  $\bar{x}$  = 4.6 mm; 1986  $\bar{x}$  = 6.1;  $t$  = -2.43,  $p$  = 0.016; *R. arvalis*: 1985  $\bar{x}$  = 3.5 mm; 1986  $\bar{x}$  = 7.2 mm;  $F$  = 21.93,  $p$  = 0.0001). The average prey size of the two frog species differed in both years. In 1985, water frogs ate larger prey ( $F$  = 7.70,  $p$  = 0.006), while, in 1986, *R. arvalis* did ( $t$  = 2.21,  $p$  = 0.028).

For either species mean total prey size increased with predator size in both years (fig. 1). Minimum, maximum, and range of prey size increased with increasing SVL (fig. 2). Prey size range widened more in water frogs than in *R. arvalis*.

We further examined the relationship of log prey size versus log body size in five main food type categories (table 1). Positive and significant size correlations were found in all cases but two (water frogs - Aphididae; *R. arvalis* - Diptera). The prey

size for Aphididae did not differ among different sized water frogs. The range of aphids size was between 1 mm and 5 mm; possibly frogs were unable to discern along this small size spectrum.

We separately analysed spring, summer and autumn food samples of frogs collected in 1986 (table 2). Different prey groups dominated at different times of the year. However, the average prey size varied only slightly with season (water frogs:  $F$  = 1.84,  $n$  = 133,  $p$  = 0.162; *R. arvalis*:  $F$  = 0.93,  $n$  = 148,  $p$  = 0.398). Aphididae were very frequent in the diet of both frog species in autumn. Interestingly, in all seasons *R. arvalis* ate much more Coleopterans than the water frogs. Dipterans (mostly chironomids) were abundant in the spring diet of both species; water frogs consumed them in particularly large quantities.

Using data from window traps and yellow bowls we estimated the size distribution of available flying insects: aphids, dipterans and hymenopterans. These insects formed 48.2% of the diet of *R. arvalis* and 62.9% of that of water frogs. In the small frogs of either species, the size of aphids and dipterans eaten resembled the available supply most closely (table 3), although, in 1986, the small *R. arvalis* were more selective. The correspondence between sizes of insects available and those eaten was less good for medium sized frogs in most cases. Large frogs usually preferred much larger size categories than those represented in the traps so that the similarity statistics were poor. Furthermore, these large frogs did not eat hymenopterans at all and ate only a few aphids and dipterans.

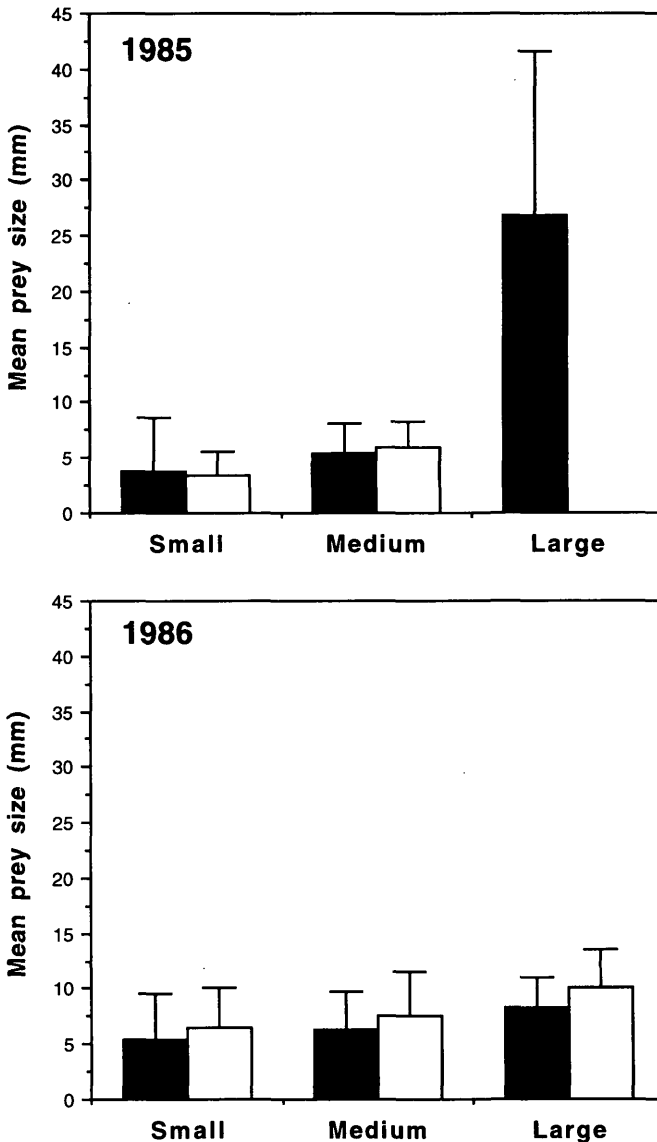


Fig. 1: Mean prey size of 554 small (SVL  $\leq 30$  mm), medium (SVL 31-50 mm), and large (SVL  $> 50$  mm) frogs from Kis-Balaton Nature Reserve (Hungary) in 1985 and 1986.

Filled columns - Water frogs (1985: small  $n=132$ , medium  $n=14$ , large  $n=5$ ; 1986: small  $n=74$ , medium  $n=44$ , large  $n=15$ ), open columns - *R. arvalis* (1985: small  $n=118$ , medium  $n=4$ ; 1986: small  $n=78$ , medium  $n=63$ , large  $n=7$ ). Vertical bars indicate standard deviation. Note that in 1985 there were no large *R. arvalis*.

Abb. 1: Mittlere Beutegröße von 554 kleinen (SVL  $\leq 30$  mm), mittelgroßen (SVL 31-50 mm) und großen (SVL  $> 50$  mm) Fröschen des Kis-Balaton Naturschutzgebietes (Ungarn) in den Jahren 1985 und 1986.

Gefüllte Säulen - Wasserfrösche (1985: klein  $n=132$ , mittelgroß  $n=14$ , groß  $n=5$ ; 1986: klein  $n=74$ , mittelgroß  $n=44$ , groß  $n=15$ ), leere Säulen - *R. arvalis* (1985: klein  $n=118$ , mittelgroß  $n=4$ ; 1986: klein  $n=78$ , mittelgroß  $n=63$ , groß  $n=7$ ). Vertikale Säulen zeigen die Standardabweichung. 1985 gab es keine großen *R. arvalis*.

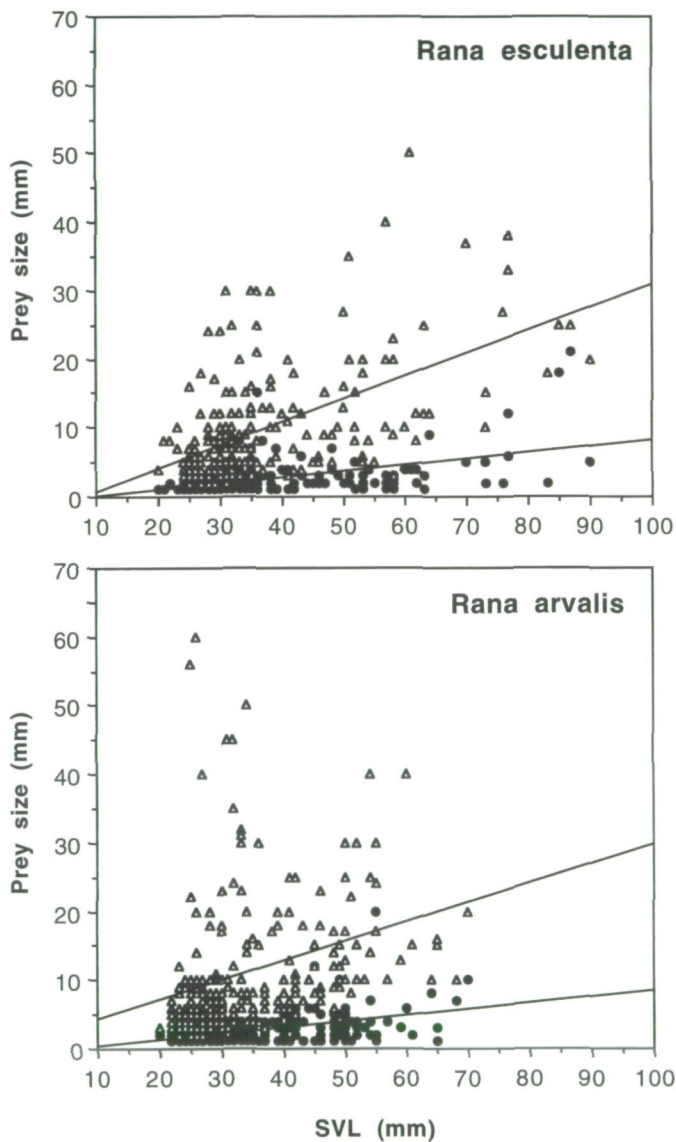


Fig. 2: Minimum (●) and maximum (Δ) prey size as a function of frog size (SVL) in water frogs and *R. arvalis* from Kis-Balaton Nature Reserve (Hungary). Combined data of 1985 and 1986. (water frogs, min:  $y=0.09x-0.83$ , max:  $y=0.34x-2.81$ ; *R. arvalis*, min:  $y=0.09x-0.57$ , max:  $y=0.28x-1.48$ )

Abb. 2: Minimale (●) und maximale (Δ) Beutegröße als Funktion der Froschgröße (SVL=Kopf-Rumpflänge) bei Wasserfröschen und *R. arvalis* des Kis-Balaton Naturschutzgebietes (Ungarn). Daten von 1985 und 1986 zusammengefaßt.

(Wasserfrösche, min:  $y=0,09x-0,83$ , max:  $y=0,34x-2,81$ ; *R. arvalis*, min:  $y=0,09x-0,57$ , max:  $y=0,28x-1,48$ )

Table 1: Correlations between log snout-vent length and log prey size in water frogs and *R. arvalis* from Kis-Balaton Nature Reserve (Hungary) in five prey type categories (two tailed test; \* -  $p=0.02$ ; \*\* -  $p=0.0001$ ).

Tab. 1: Korrelation von log Kopf-Rumpfl nge und log Beutegr  e bei Wasserfr schen und *R. arvalis* im Kis-Balaton Naturschutzgebiet (Ungarn) in f nf Beutekategorien (zweiseitige Signifikanz \* -  $p=0.02$ ; \*\* -  $p=0.0001$ ).

	Aphididae	Coleoptera	Diptera	Hymenoptera	Others / Andere	Total / Insgesamt
Water frogs	0.02	0.42**	0.41**	0.58**	0.44**	0.52**
<i>R. arvalis</i>	0.26*	0.48**	0.07	0.51**	0.42**	0.52**

Table 2: Seasonal variation in taxonomic composition (%; top) and size (mm; bottom) of prey in water frogs and *R. arvalis* from Kis-Balaton Nature Reserve (Hungary) in 1986. mean - mean value; SD - standard deviation; n - sample size.

Tab. 2: Saisonale Ver nderungen in der taxonomischen Zusammensetzung (%; oben) und Gr  e (mm; unten) der Beute bei Wasserfr schen und *R. arvalis* des Kis-Balaton Naturschutzgebietes (Ungarn) im Jahr 1986. mean - Mittelwert; SD - Standardabweichung; n - Stichprobenumfang.

	Spring / Fr�hjahr		Summer / Sommer		Autumn / Herbst	
	Water frogs	<i>R. arvalis</i>	Water frogs	<i>R. arvalis</i>	Water frogs	<i>R. arvalis</i>
Prey type / Futtermiertyp						
Mollusca	9.7	14.8	19.8	16.6	2.6	4.1
Aphididae	5.8	1.0	3.5	2.4	44.2	30.8
Heteroptera	-	5.1	3.3	3.2	0.3	-
Coleoptera	10.2	18.1	6.8	27.6	4.5	15.9
Diptera	34.4	13.3	16.8	7.6	15.6	13.7
Hymenoptera	5.2	-	12.6	2.6	13.1	8.2
Arachnoidea	14.2	11.1	21.6	10.4	4.5	2.7
Acarinea	-	1.2	-	0.4	2.2	6.7
Others / Andere	20.5	35.0	15.6	29.2	13.0	17.9
Prey size / Futtermiergr��e						
mean / Mittelwert	7.69	6.90	5.79	7.75	5.86	6.80
SD / Standardabweichung	2.27	3.63	3.41	3.68	4.71	4.19
n / Stichprobenumfang	17	60	73	52	43	36

Table 3: Renkonen's proportional similarity index as a measure of similarity between available supply and stomach contents of water frogs and *R. arvalis*. The size distributions of three important flying insect groups are compared.

Tab. 3: Renkonens proportionaler  hnlichkeitsindex als Ma  der  hnlichkeiten zwischen vorhandenem Nahrungsangebot und Mageninhalt von Wasserfr schen und *R. arvalis*. Verglichen werden die Gr  enverteilungen in drei der wichtigsten Gruppen von Fluginsekten.

Taxon	Year / Jahr	Water frogs - SVL			<i>R. arvalis</i> - SVL		
		�30 mm	30-50 mm	�50 mm	�30 mm	30-50 mm	�50 mm
Aphididae	1985	0.95	0.60	-	0.94	0.60	-
	1986	0.71	0.56	-	0.80	0.80	0.05
Diptera	1985	0.57	0.43	0.04	0.74	0.42	-
	1986	0.63	0.37	-	0.37	0.37	0.45
Hymenoptera	1985	0.63	0.63	-	0.51	0.27	-
	1986	0.40	0.48	-	0.22	0.36	-

DISCUSSION

Our results show a clear predator size related prey size preference within populations of the *R. esculenta* complex and Moor Frogs in the Kis-Balaton Nature Reserve. Several studies have shown that larger Amphibian (mainly Urodela) species consume larger prey than do smaller congeneric species (ALTIG & BRODIE 1971; POWDERS & TIETJEN 1974; FRASER 1976; LUNCH 1985). A similar pattern was found among different size categories of populations (FRASER 1976; LUNCH 1985; WHEATER 1986).

When congeneric species were similar in size there was no considerable difference in prey size preferences (GRIFFITHS 1986), as we found in our two species.

We showed here that there is a positive correlation between prey and predator body sizes in both species (fig. 2). As both frog species grow throughout their lives, this means that their food changes during ontogeny. The (seasonal) changes in the size structure of populations must account partly for the seasonal changes in their diet

(table 2). For a South American treefrog, a strong relationship was observed between electivity for prey types and frog size, independent of prey size (LIMA & MOREIRA 1993). This makes niche partitioning even more fine and efficient. Predator size related differences in the electivity for prey size might reduce competition for food in the frog populations of Kis-Balaton as well.

Although we did not monitor the dynamics of potential prey types in the study area it was clear that frogs took these particular prey groups in large quantities when they were most abundant in supply. This interpretation is supported by the existence of similar seasonal shifts in the food preferences of the two frog species, i.e. in the diet of both species, nematoceran dipterans were dominant in spring while aphids were more numerous in autumn.

If frogs select prey, they do so not on the basis of type but rather of size and/or other features. Important factors might include shape (FREED 1988), colour, conspicuousness, hairiness etc. of the food. Large individuals preferred large prey (worms, coleopterans, snails) but also ate small aphids and sometimes mites as well. Small frogs were largely restricted to small prey and only occasionally consumed large prey like a long worm.

In general, COHEN & al. (1993) found that large predators in food webs eat prey of wider range in body size than do smaller predators. We observed a similar relationship between prey size range and body size (SVL) in both frog species (fig. 2). COHEN & al. (1993) showed that correlation between prey and predator body sizes is rarely strong when it is positive and in some cases even negative. A different trend was found in our example of water frog and *R. arvalis* populations. There is a relatively strong positive correlation between prey and predator sizes (table 1).

The selection of prey according to its size could also be interpreted in the light of the optimal foraging theory: As frogs grow, they should not simply eat increasing numbers of small prey items but gradually

change to larger and larger prey items for reasons of energy maximization. However, there could be a trade-off between the benefits of eating larger prey and the costs of capturing and handling this prey. In addition, the lower encounter rate could make larger prey less favourable. Yet we found that bigger frogs appeared to be very consistent in preferring larger prey (fig. 2). In case of flying insects where the exact size distribution of the supply has been surveyed, larger frogs showed a clear selection for larger prey sizes (table 3). According to our understanding, opportunistic foraging in terms of taxonomic prey types becomes possible when food is abundant, since food competition is little then, and there is no need to specialise in certain food types. Although we could not estimate the encounter rate of different prey types in a complex environment like this, opportunistic food selection implies that supply is not a limiting factor. So lower encounter rate does not contribute to the cost side of prey selectivity.

The question still remains unresolved how syntopic water frogs and *R. arvalis* tolerate such a high degree of diet (both type and size) overlap (fig. 1, table 2)? The first, most likely hypothesis is that food resources are not limiting for these species, so that there is little or no competition for food between them, allowing a high overlap in their diet (AVERY 1968; GRIFFITHS 1986; PARKER 1994). On the other hand, in a variable environment, competition is not a steady process as predicted by the "ecological crunch" hypothesis (WIENS 1977). However, variation in environmental conditions (change in availability of food and/or foraging conditions) could cause competition for food in certain periods of the year (DODD 1994). The third assumption is that other resources (e.g. spawning sites) may be limiting in different periods of the life span of frogs, and may be the subject of competition. Moreover, the present study has not addressed the issue of larval feeding; shared enemies such as predators and pathogens; or differential vulnerabilities to environmental stress.

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