



Feeding Habits of the Japanese Tree Frog, *Hyla japonica*, in the Reproductive Season

Authors: Hirai, Toshiaki, and Matsui, Masafumi

Source: Zoological Science, 17(7) : 977-982

Published By: Zoological Society of Japan

URL: <https://doi.org/10.2108/zsj.17.977>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Feeding Habits of the Japanese Tree Frog, *Hyla japonica*, in the Reproductive Season

Toshiaki Hirai and Masafumi Matsui*

Graduate School of Human and Environmental Studies,
Kyoto University, Sakyo, Kyoto 606-8501, Japan

ABSTRACT—We examined the diet of *Hyla japonica*, a prolonged breeder, in the reproductive season (early May to late July). This species breeds in rice fields. Females attended the breeding site only at the time of spawning, but males remained and foraged in rice fields for their continuous advertising during the prolonged season. A high frequency of empty stomachs and fewer and less stomach contents observed at the beginning of the breeding season, may result from energetic constraints associated with reproduction in males. Diverse ground-dwelling invertebrates predominated in the diet, but aquatic organisms were quite few. We estimated the prey availability in the environment by sweeps. The most easily available prey such as ants, beetles, dipterans, caterpillars, and spiders were numerously consumed by frogs. Significant correlations between the diet compositions and prey availability suggest that *H. japonica* is an opportunistic predator.

INTRODUCTION

Hylidae is a huge family (>700 species) and distributed world-wide except for Africa and Southeast Asia. The genus *Hyla* is a representative of this family, and includes 281 species (Matsui, 1996). However, feeding habits on this genus have been studied only for species occurring in North America such as *H. cinerea*, *H. regilla*, and *H. crucifer* (e.g., Kilby, 1945; Johnson and Bury, 1965; Oplinger, 1967). Only fragmentary knowledge is available on diet for species distributed in Europe and East Asia such as *H. chinensis* and *H. arborea* (Do and Lue, 1982; Kuzmin, 1995; Nečas *et al.*, 1997), although a detailed report has been made for *H. arborea japonica* (= *H. japonica*) by Nishikawa (1932).

Frogs of the North American *Hyla* are regarded as opportunistic predators, consuming various prey in response to its availability in the environment (e.g., Johnson and Bury, 1965; Oplinger, 1967). However, the above studies lack actual comparisons of frog diet composition with prey availability, and only one species of *Acris*, another hylid genus, has been demonstrated to be truly an opportunistic predator among hylids (Labanick, 1976). Therefore, further studies of the genus *Hyla* are indispensable to generalize hylid prey selection.

Anurans are divided into explosive or prolonged breeders from their breeding habits (Wells, 1977a). The explosive breeders such as *Bufo japonicus* (Hirai and Matsui, unpubl. data) or *Rana nigromaculata* (Hirai and Matsui, 1999) do not forage in their breeding seasons. On the contrary, *Hyla*

japonica, with prolonged breeding periods from April to July in mainland of Japan (Maeda and Matsui, 1999), forages even in its breeding season. However, prolonged breeders probably experience a considerable loss of energy intake during breeding seasons due to constraints by their reproductive behavior. For example, males of *Rana clamitans* were reported to have empty stomachs in higher percentages, and to take less food than females when its breeding activity peaked (Jenssen and Klimstra, 1966). Kilby (1945) observed a similar trend in *Hyla cinerea*, whose males took less food than females during their breeding season over four months.

Nishikawa (1932) presented a detailed list of prey consumed by *H. japonica* in mulberry fields, but did not investigate sexual differences or reproductive constraints. Also, mulberry fields usually do not include breeding sites of this species.

In this study, we conducted a detailed diet study of breeding *H. japonica* in rice fields, which are used as breeding sites in this species. Specifically, we examined sexual differences during the breeding season, and relationships between diet and prey availability, to determine whether *H. japonica* is an opportunistic predator.

MATERIALS AND METHODS

Field work

The study was conducted in rice fields surrounded by coniferous forests in a montane region at Momoi in Kyoto, Japan (35°11'N, 135°53'E, 650 m above sea level). The rice fields were of traditional, terraced type, bounded on the lower side by a stream and the higher side by banks continuing to the forest and covered with bushes and grasses.

* Corresponding author: FAX. 075-753-2891.

E-mail: fumi@zoo.zool.kyoto-u.ac.jp

In order to determine the utilization pattern of rice fields by *H. japonica*, we collected frogs weekly from 27 April to 24 October in 1995, and bi-weekly from 29 April to 22 October in 1996. Each collection was conducted at night between 1800 hr and 0300 hr because frogs were more frequently observed at night than during the daytime. We defined the breeding season of this species as a period when male advertisement calls (Wells, 1977b) were heard.

Within two hours of capture, we anesthetized frogs in a 1% solution of MS-222 (methane tricaine sulfonate), extracted their stomach contents with forceps, and preserved the contents in 10% buffered formalin for later analysis. Next, we recorded snout-vent length (SVL; to nearest 0.1 mm) and body mass (BM; to nearest 0.1 g) of frogs and marked them by toe-clipping for individual identification. After these procedures, we released frogs where they were captured.

We estimated prey availability by a sweeping method on footpaths and banks over 120 x 1 m where frogs were abundant. Sweeps were made through the air and vegetation, 0–0.5 m above the ground with an insect sweep net, before sunset (1800 hr–1900 hr) on three dates (25 May, 29 June, and 28 July in 1995). The organisms sampled were killed with ethyl acetate and stored in ethylene glycol for later analysis.

Diet analysis

The reproductive season of this species in our study site extended from early May to late July (see results). At other times we found few individuals in rice fields. Metamorphosis began in early July, and metamorphs soon dispersed to adjacent forests. Thus, we could collect only four young individuals in our study periods. Because it is difficult to generalize feeding habits of adult frogs during non-reproductive seasons and of young frogs with such a small sample size, we analyzed only adult frog samples collected in the reproductive season.

We identified stomach contents to the lowest practical taxonomic level, which was usually to class or order except Hymenoptera, which was classified into Formicidae and others. For holometabolous insects, larvae and adults were separated. We measured maximum length and width of each item to the nearest 0.1 mm using either a caliper or a calibrated ocular micrometer fitted to a dissecting microscope. For partially digested prey items, we estimated lengths (L) by measuring widths (W) and then using predetermined length-width regressions from intact prey. Volumes of prey items were calculated using the formula for an ellipsoid (Dunham, 1983):

$$V = 4/3\pi(L/2)(W/2)^2$$

To determine whether frogs are opportunistic or selective predators, we examined the relationship between the relative abundance of prey taxa in frog diet and its abundance in the habitat by calculating Kendall's rank correlation coefficients (tau). Only monthly diet in 1995 was used in this calculation because sweeps were made only for that year. In this analysis, we included only prey taxa occurred in both sweep samples and the stomachs, because some prey items such as aquatic or terrestrial ones were difficult to sample by sweeps,

and other prey (e.g., orthopterans) were presumed to be unavailable for frogs since they are too large to be ingested even though they were abundant in the habitat.

In addition, to examine seasonal changes in the feeding intensity of frogs, we compared the frequency of empty stomachs between months and the number of prey items in a stomach by χ^2 test and Dunn's multiple comparisons test, respectively.

To quantify dietary overlap between males and females, we calculated a simple similarity index (Schoener, 1968):

$$C_{xy} = 1 - 0.5 \sum |P_{ix} - P_{iy}|$$

based on proportion of prey taxa (i) in diets of each sex (x and y). We also compared the frequency of occurrence of prey taxa between the sexes with Fisher's exact probability tests. In addition to these analyses, the frequency of empty stomachs was compared by Fisher's exact probability tests, and the number of prey occurring in a stomach and the volume of contents were compared by Mann-Whitney U-tests.

RESULTS

Breeding season

We collected breeding males emitting advertisement calls from early May to late July. In 1995, calling males were collected on all 11 censuses from 9 May to 21 July, except for 27 April. Only 11 of 235 individuals collected during this period were females. Similarly in the second year, no individuals or calls were observed on 29 April, but calling males were collected on every six census dates from 9 May to 20 July. Only 11 females were found among a total of 119 individuals collected. After the reproductive season, only three females and six males were collected and advertisement calls were rarely heard in rice fields. Because breeding periods did not differ in 1995 and 1996, we combined the data for both years.

Feeding intensity

Feeding intensity changed seasonally from May to July for both males and females (Table 1). Out of a total 332 males collected in the reproductive season, 126 with empty stomachs (38.0%) were found. In females, eight (36.4%) of 22 had empty stomachs. Males with empty stomachs were especially frequently found in May (58.3–84.2%), but the frequency drastically decreased thereafter (Fig. 1). Males collected in May had empty stomachs in significantly higher proportions than in June and July ($\chi^2=110.50$, $df=2$, $p<0.01$). Both the number and the volume of stomach contents in males were signifi-

Table 1. Seasonal change of number and volume of prey items found in a stomach and the frequency of empty stomachs. Number of frogs sampled in each month is shown in parentheses.

	Male			Female		
	May (144)	June (103)	July (85)	May (11)	June (7)	July (4)
Number						
Mean \pm SD	3.1 \pm 2.4	4.4 \pm 3.4	5.5 \pm 3.3	2.3 \pm 0.5	6.0 \pm 3.7	5.3 \pm 3.8
Range	1 – 11	1 – 15	1 – 15	2 – 3	1 – 10	1 – 10
Volume						
Mean \pm SD	33.2 \pm 44.7	64.0 \pm 61.7	125.8 \pm 117.5	56.7 \pm 43.4	62.7 \pm 33.9	94.0 \pm 78.7
Range	0.3 – 208.2	0.9 – 252.6	2.0 – 621.8	6.3 – 119.4	16.4 – 97.2	3.8 – 181.5
Empty (%)	69.4	16.5	10.6	45.5	42.9	0

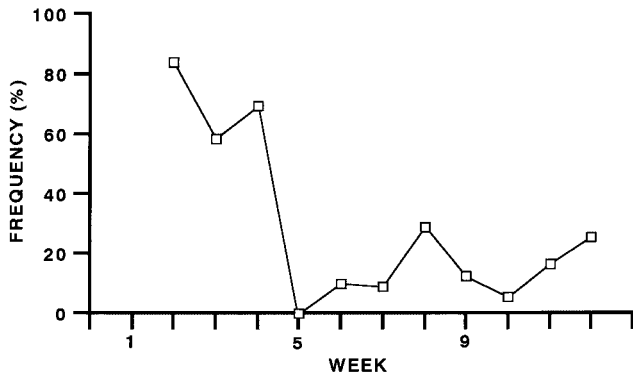


Fig. 1. Percent frequency of male *Hyla japonica* with empty stomachs during the reproductive season from May to July. Values are expressed by an average of 1995 and 1996. 1, 5, and 9, respectively, corresponds to the first week of May, June, and July.

cantly smaller in May than in June and July (Dunn's multiple comparisons test, $p < 0.05$ for both). Furthermore, the food volume in June was significantly smaller than in July ($p < 0.05$), but the number was not significantly different between the two months ($p > 0.05$). On the contrary, all these variables did not differ significantly between the months in females.

Diet composition

We extracted 989 prey items from 220 stomachs in the

two reproductive seasons. Arthropoda included three classes (Crustacea, Arachnida, and Insecta) which occupied more than 99.9% both in number and volume of the total stomach contents. Insecta included 11 orders and occupied 88.8% in number and 93.7% in volume (Table 2). Among the arthropodian prey taxa, ants (Formicidae), beetles (Coleoptera), dipterans, caterpillars (Lepidoptera larvae), bugs (Hemiptera), and spiders (Araneae) were more frequently found in stomachs (Frequency of occurrence $> 20\%$). No particular prey taxa predominated in diet. Ants occupied the largest proportion numerically, followed by beetles, dipterans, caterpillars (all $> 10\%$). Volumetrically, caterpillars and beetles occupied the largest proportions ($> 20\%$), and the other taxa contributed much less ($< 6.0\%$).

Beetles included various taxonomic groups; click (elaterid; 4.4% of the total prey items), snout (curculionid; 3.2%), slider (cantharid; 2.4%), and leaf (chrysomelid; 2.3%) beetles were prominent, and scarab, ground (carabid), ladybug (coccinellid), and rove (staphylinid) beetles also occurred but in lower frequencies ($< 0.5\%$). The only other invertebrate prey ingested was an earthworm. Shed skins, plant materials, and minerals occurred in 0.9%, 10.5%, 1.8%, respectively, of the stomachs examined.

Sexual differences in diet

Females (mean \pm SD = 34.8 \pm 1.63 mm, range = 31.1–37.5 mm) were significantly larger in SVL than males (31.0 \pm 2.29

Table 2. Diet composition of *Hyla japonica* in reproductive season, sampled from males (930 prey from 206 frogs, total volume 16501.3 mm³), females (59 prey from 14 frogs, total volume 967.6 mm³), and their total (989 prey from 220 frogs, total volume 17468.9 mm³).

Prey taxa	Frequency of occurrence (%)			Numeric proportion (%)			Volumetric proportion (%)		
	Total	Male	Female	Total	Male	Female	Total	Male	Female
Insecta									
Hymenoptera									
Formicidae	39.1	38.8	42.9	17.9	17.4	20.3	2.1	2.1	2.5
other Hymenoptera	17.7	18.5	7.1	5.1	5.1	3.4	3.3	3.4	1.3
larvae	16.8	16.5	21.4	5.0	4.8	5.1	9.3	9.3	7.9
Coleoptera	40.5	40.3	42.9	16.5	15.8	22.0	22.5	21.3	39.2
larvae	11.4	10.7	21.4	4.4	4.1	6.8	5.5	5.0	12.8
Diptera	35.5	35.9	28.6	15.7	15.5	13.6	3.7	3.7	3.8
larvae	9.6	9.7	7.1	3.4	3.5	1.7	1.9	1.9	1.9
Lepidoptera	6.4	6.8	–	1.6	1.7	–	1.8	1.9	–
larvae	26.4	27.2	14.3	11.0	11.3	3.4	36.7	38.0	10.5
Trichoptera	0.9	0.5	7.1	0.2	0.1	1.7	0.3	0.1	3.0
larvae	1.8	1.9	–	0.4	0.4	–	0.1	0.1	–
Neuroptera	0.5	0.5	–	0.1	0.1	–	<0.1	<0.1	–
Mecoptera	1.8	1.9	–	0.5	0.5	–	0.6	0.6	–
Hemiptera	20.5	20.9	14.3	6.3	6.3	3.4	5.4	5.5	2.8
Orthoptera	0.5	0.5	–	0.1	0.1	–	0.1	0.1	–
Plecoptera	1.4	1.5	–	0.3	0.3	–	0.2	0.2	–
Collembola	1.4	1.0	7.1	0.3	0.2	1.7	<0.1	<0.1	<0.1
Arachnida									
Araneae	25.9	25.7	28.6	8.0	7.6	11.9	3.6	3.4	7.2
Acarina	2.3	1.9	7.1	0.8	0.6	3.4	<0.1	<0.1	<0.1
Crustacea									
Isopoda	6.4	6.3	7.1	2.3	2.3	1.7	2.9	2.7	7.3
Amphipoda	0.5	0.5	–	0.1	0.1	–	<0.1	<0.1	–
Oligochaeta	0.5	0.5	–	0.1	0.1	–	<0.1	0.1	–

Table 3. Monthly and yearly variations in diet of breeding *H. japonica*, and its relationships with the relative abundance in sweep samples. Number of prey items examined in each year is shown in parentheses.

Prey taxa	May (142 / 7)			June (217 / 185)			July (248 / 190)		
	Sweep n	Diet (%)		Sweep n	Diet (%)		Sweep n	Diet (%)	
		1995	1996		1995	1996		1995	1996
Formicidae	28	25.4	28.6	39	20.7	9.7	147	20.2	13.7
other Hymenoptera	5	7.0	–	13	5.5	5.4	8	4.4	4.2
larvae	11	–	–	7	10.1	5.4	7	6.5	0.5
Coleoptera	8	19.0	–	30	10.6	21.1	52	19.8	13.2
larvae	7	4.2	14.3	12	3.7	9.7	–	2.0	2.6
Diptera	114	21.1	–	132	17.1	18.4	237	14.1	10.0
larvae	–	2.8	14.3	–	1.8	2.2	–	4.4	5.3
Lepidoptera	–	0.7	–	1	0.9	0.5	1	2.8	2.6
larvae	2	2.8	–	5	2.8	7.0	11	9.7	32.6
Trichoptera	1	–	–	–	0.5	–	–	–	0.5
larvae	–	1.4	–	–	0.9	–	–	–	–
Neuroptera	–	–	–	–	–	–	–	–	0.5
Mecoptera	–	–	–	–	–	2.7	–	–	–
Hemiptera	5	3.5	14.3	11	7.8	8.1	63	6.5	4.2
Orthoptera	10	–	14.3	133	–	–	557	–	–
Plecoptera	2	–	–	–	–	0.5	–	–	1.1
Collembola	–	–	14.3	–	–	–	–	0.8	–
Araneae	14	9.9	–	5	10.1	8.7	5	7.3	4.7
Acarina	–	0.7	–	–	1.8	0.5	–	0.8	–
Isopoda	–	0.7	–	–	5.5	–	–	0.8	4.2
Amphipoda	–	–	–	–	–	–	–	0.4	–
Chilopoda	–	–	–	–	–	–	1	–	–
Oligochaeta	–	0.7	–	–	–	–	–	–	–

mm, 25.4–39.8 mm) (*U*-test, $p < 0.01$). However, mean length of prey items in a stomach did not differ significantly between the sexes (males = 7.1 ± 3.37 mm, 2.4–23.8 mm; Female = 6.8 ± 2.51 mm, 3.7–12.4 mm). The frequency of empty stomachs (males = 38.0%; females = 36.4%; Fisher's exact probability test, $p > 0.05$), mean number of prey items (males = 4.5 ± 3.30 , 1–15; females = 4.2 ± 3.09 , 1–10; *U*-test, $p > 0.05$), and the mean volume (males = 80.2 ± 91.91 mm³, 0.3–621.8 mm³; females = 69.1 ± 51.88 mm³, 3.84–181.47 mm³; *U*-test, $p > 0.05$) were not significantly different between the sexes.

Diet compositions were quite similar between males and females, as indicated by a high dietary overlap (0.82). The frequency of all prey taxa occurring in the stomachs was also not significantly different between sexes (Table 2: Fisher's exact probability test, $P > 0.05$ for all prey taxa). Only volumetric proportions of caterpillars, beetles and beetle larvae slightly differed between them (Table 2).

Relationships between diet and prey availability

Fourteen out of 22 prey taxa shown in Table 2 were sampled by sweeps (Table 3). Seven of eight prey taxa not sampled included either aquatic organisms such as maggots (dipteran larvae), caddisfly (trichopteran) larvae and amphipods, or soil invertebrates such as springtails (collembolans), mites (acarina), woodlice (isopods), and earthworms (oligochaeta). All these taxa were minor components among the diets.

Orthopterans ($n=700$) that occurred most abundantly in sweep samples, were not found in any stomachs of frogs col-

lected simultaneously in 1995. Dipterans, ants, and beetles that were the next most abundant prey, were numerous consumed by *H. japonica* (numeric proportion > 10%). Consequently, the diet compositions significantly correlated with the relative abundances of swept potential prey in all the three months ($\tau=0.815$, $p < 0.01$, May; $\tau=0.568$, $p < 0.05$, June; $\tau=0.535$, $p < 0.05$, July).

Yearly variation in diet was conspicuous only in a few prey taxa. Caterpillars found in July varied from 9.7% to 32.6%, ants in June from 20.7% to 9.7%, and beetles in June from 10.6% to 21.1%.

DISCUSSION

In the rice fields studied, *H. japonica* was collected exclusively from early May to late July. The majority of collected individuals was calling males. After the breeding season, however, we could find only nine individuals in the rice fields. This result indicates that *H. japonica* uses rice fields principally for breeding purposes.

At the beginning of reproduction (early May), empty stomachs were conspicuously found in males. Even when they had some prey items, both the number and volume were smaller than in the later seasons. Since the stomach contents were recovered from juveniles of syntopic *R. nigromaculata* collected in early May (Hirai and Matsui, 1999) together with *H. japonica*, seasonal change in feeding intensity of *H. japonica* is thought to have resulted from energetic constraints associated with male reproductive behavior rather than the scarcity

of foods available.

Sexual size dimorphism, with larger females than males, is generally seen in anurans (Shine, 1979). In the case of the prolonged breeders, smaller body size in males is partially explained by the energetic costs associated with male reproduction, because males are deprived of their foraging time by reproductive activities such as advertisement, agonistic behavior, and territorial defense, and by the energy expenditure on such activities (Woolbright, 1983).

Females of *H. japonica* were larger than males in our study site, but the occurrence of empty stomachs, and the number and volume of stomach contents did not differ significantly between the sexes. This result suggests that foraging activities of females are also restricted at the time of spawning. Das (1996) similarly observed a cessation of feeding by both sexes of *R. hexadactyla* prior to egg-laying. Our collection of frogs during the breeding season was male biased in the rice fields. Females may have been foraging elsewhere and attended rice fields only to spawn. Therefore, to compare energy intake during the reproductive season between the sexes we need to examine the diet of females collected outside of the breeding place.

Both the mean and maximum numbers of stomach contents we detected (4.5 and 15 respectively for males; 4.3 and 10 for females) were much smaller than those found by Nishikawa (1932) in the population of *H. japonica* from mulberry fields (10 and 150). Because mulberry fields are not considered to include breeding sites, these differences might result from the differences in energy constraints related to reproduction, but as Nishikawa (1932) pooled data for both sexes and age classes, and did not mention reproduction, we cannot make direct comparisons.

In this study, we estimated prey availability in the environment by sweeps, and found significant correlations between the relative abundance of available prey taxa and the diet composition. This result strongly suggests that *H. japonica* is an opportunistic predator at the breeding site we studied. In general, most anurans including hylids are presumed to be opportunistic predators and consume prey in response to the environmental availability (Johnson and Bury, 1965; Oplinger, 1967). Only two other species, *A. crepitans* (Labanick, 1976) and *R. nigromaculata* (Hirai and Matsui, 1999) have been shown to be true opportunistic predators by comparing the diet with prey availability in the environment. Thus, this is the first report that has demonstrated opportunistic feeding habits of *Hyla*. A generalization that anurans are opportunistic predators, must be re-examined by additional rigorous testing of other species.

Opportunistic predators exhibit different patterns of feeding in different habitats (e.g., Elliott and Karunakaran, 1974). This seems to apply to *H. japonica* at mulberry fields and rice fields. For example, ants were most numerous consumed in both sites, but the proportions differed between the mulberry fields (57.9%: Nishikawa, 1932) and rice fields (17.9%: this study). In addition, beetles were the next numerous prey for both populations (21.7% and 16.5%, respectively), but the

composition differed. Leaf beetles, and ladybugs were prominent in the mulberry fields, but click, and snout beetles predominated in the rice fields. These variations seem to have resulted from different availability of prey between the two sites and are consistent with our conclusion that *H. japonica* is an opportunistic predator.

Although most adult frogs are carnivorous, a neotropical hylid, *H. truncata*, is frugivorous and is reported to have subsisted for four months in captivity by feeding exclusively on fruits (Da Silva *et al.*, 1989). Nishikawa (1932) also reported that *H. japonica* frequently ingested minerals, fruits, and seeds in nature, and could survive more than two months in captivity by taking only minerals. In our analysis, however, vegetables and minerals were not found frequently in *H. japonica*. Because diet value of these materials is unknown for frogs, it is unlikely that *H. japonica* depends on these materials as the staple diet in nature.

Diverse food items found in the stomachs would illustrate the ability to utilize a wide variety of prey taxa. This ability seems to enable this species to breed for a long period by foraging in the breeding site. *Hyla japonica* occurs extensively in East Asia, and occurs in many habitats from urban areas to high mountain regions (Maeda and Matsui, 1999). This wide distribution might be associated with its wide range of feeding habits, and the habits might also partially account for the worldwide success of the family Hylidae.

ACKNOWLEDGMENTS

We thank S. J. Hecnar for his invaluable comments on the earlier version of the manuscript, and S. Chen for providing literature. We also thank Kinji Fukuyama and an anonymous reviewer for their critical comments.

REFERENCES

- Da Silva HR, De Britto-Pereira MC, Caramaschi U (1989) Frugivory and seed dispersal by *Hyla truncata*, a neotropical tree-frog. *Copeia* 1989: 781–783
- Das I (1996) Folivory and seasonal changes in diet in *Rana hexadactyla* (Anura: Ranidae). *J Zool Lond* 238: 785–794
- Do M, Lue K (1982) Comparative stomach contents analysis on the eleven species of amphibians in Taiwan, including endemic species of *Hynobius formosanus*. *Annual of Taiwan Museum* 25: 225–234 (in Chinese with English abstract)
- Dunham AE (1983) Realized niche overlap, resource abundance, and intensity of interspecific competition. In "Lizard Ecology" Ed by RB Huey, ER Pianka, TW Schoener, Harvard Univ Press, Cambridge, pp 261–280
- Elliott AB, Karunakaran L (1974) Diet of *Rana cancrivora* in fresh water and brackish water environments. *J Zool Lond* 174: 203–215
- Hirai T, Matsui M (1999) Feeding habits of the pond frog, *Rana nigromaculata*, inhabiting rice fields in Kyoto, Japan. *Copeia* 1999: 940–947
- Jenssen TA, Klimstra WD (1966) Food habits of the green frog *Rana clamitans* in southern Illinois. *Amer Midl Nat* 76: 169–182
- Johnson CR, Bury RB (1965) Food of the pacific treefrog, *Hyla regilla* Baird and Girard, in northern California. *Herpetologica* 21: 56–58
- Kilby JD (1945) A biological analysis of the food and feeding habits of

- two frogs, *Hyla cinerea* and *Rana pipiens sphenoccephala*. Quart J Florida Acad Sci 8: 71–104
- Kuzmin SL (1995) Die Amphibien Rußlands und angrenzender Gebiete. Westarp Wissenschaften, Magdeburg
- Labanick GM (1976) Prey availability, consumption and selection in the cricket frog, *Acris crepitans* (Amphibia, Anura, Hylidae). J Herpetol 10: 293–298
- Maeda N, Matsui M (1999) Frogs and Toads of Japan. Rev Ed Bun-ichi Sogo Shuppan, Tokyo (in Japanese with English abstract)
- Matsui M (1996) Natural History of the Amphibia. University of Tokyo Press, Tokyo (in Japanese)
- Nečas P, Modrý D, Zavadil V (1997) Czech Recent and Fossil Amphibians and Reptiles. Edition Chimaira, Frankfurt am Main
- Nishikawa S (1932) The food habits of *Hyla arborea japonica* collected in Mulberry-field. Tech Bull Sericult Exp Stat 43: 1–41 (in Japanese)
- Oplinger CS (1967) Food habits and feeding activity of recently transformed and adult *Hyla crucifer crucifer* Wied. Herpetologica 23: 209–217
- Schoener TW (1968) The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. Ecology 49: 704–726
- Shine R (1979) Sexual selection and sexual dimorphism in the Amphibia. Copeia 1979: 297–306
- Wells KD (1977a) The social behavior of anuran amphibians. Anim Behav 25: 666–693
- Wells KD (1977b) Territoriality and male mating success in the green frog (*Rana clamitans*). Ecology 58: 750–762
- Woolbright LL (1983) Sexual selection and size dimorphism in anuran Amphibia. Amer Nat 121: 110–119

(Received February 7, 2000 / Accepted April 6, 2000)