# FOOD PARTITIONING BETWEEN TWO SYNTOPIC RANID FROGS, *RANA NIGROMACULATA* AND *R. RUGOSA*

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*Rana nigromaculata* and *R. rugosa* consumed different food resources when they coexisted in Japanese rice fields. *Rana nigromaculata* consumed prey from many taxa including a small proportion of ants (16% in number of the total prey items), while *R. rugosa* ate mainly ants (56%). However, presence of the same terrestrial prey types in the bulk of their diets suggests that the frogs forage on the ground syntopically, and do not partition their feeding sites. Moreover, the comparatively wider mouth of *R. rugosa* (relative to similiar sized *R. nigromaculata*), suggests that *R. rugosa* does not eat more ants because of morphological constraints. This dissimilar pattern of food resource utilization seems to have resulted from selection of different prey, as indicated by the stronger avoidance of ants by *R. nigromaculata* compared to *R. rugosa*. This food partitioning may be facilitating their coexistence in rice fields.

*Key words*: Rana nigromaculata, R. rugosa, food partitioning, prey selection, syntopic foraging

## INTRODUCTION

*Rana* is a representative genus of the cosmopolitan family Ranidae (Duellman & Trueb, 1986). According to dietary studies from various regions of the world, *Rana* are regarded as generalist predators and are not specialized for eating particular prey taxa (e.g. Houston, 1973; Premo & Atmowidjojo, 1987). Food partitioning of congeneric species of *Rana* has been observed solely between species with larger size differences, such as *R. catesbeiana* and *R. clamitans* (e.g. Werner, Wellborn & McPeek, 1995). In cases of species with similar body sizes, habitats are usually partitioned (e.g. Marshall & Buell, 1955; Loman, 1978). When they are sympatric, they take prey at different sites (e.g. Licht, 1986).

*Rana nigromaculata* and *R. rugosa* occur sympatrically in some parts of East Asia (Maeda & Matsui, 1999). Fully mature *R. nigromaculata* (SVL > 50 mm) are larger than adult *R. rugosa* (35 $\leq$ SVL < 60 mm), but the ranges of their body sizes largely overlap when immature individuals are included. The diets of both species have been well studied. *Rana nigromaculata* takes a wide variety of prey taxa, like many other ranids (Hirai & Matsui, 1999), but *R. rugosa* consumes mainly ants (Hirai & Matsui, 2000*a*). However, the pattern of food partitioning between these species when in sympatry has never been investigated. We therefore examined their food resource utilization in rice fields where they coexist, and further tried to detect factors that caused them to partition food items.

## MATERIALS AND METHODS

The study site is located in Iwakura, Kyoto, central Japan, at approximately 35°06'N, 135°52'E and 130 m elevation. *Rana nigromaculata* and *R. rugosa* coexist in rice fields in this area. Forty censuses were made, these occurring each week from 16 April to 22 October in 1995 and biweekly from 27 April to 24 October in 1996, yielding a total of 34 sampling dates. Besides the two species studied, three other anuran species (*Hyla japonica*, *Rhacophorus arboreus*, and *Rh. schlegelii*) were found at the study site. In contrast to the two ranids, these three species utilized rice fields principally for reproduction and were found only during their breeding periods.

We captured frogs at night between 1800 hr and 0200 hr. Within two hours of capture we anaesthetized frogs in 1% solution of MS-222 and extracted their stomach contents by using forceps. For each frog, we recorded snout-vent length (SVL) and mouth width (MW), and used a toe-clip code for individual identification. After these procedures, we released frogs where they were captured. In the laboratory, we identified stomach contents to the lowest practical taxonomic level, and measured maximum length and width of each prey item. For partially digested prey items, we estimated lengths by measuring width and then using predetermined length-width regressions from intact prey (see Hirai & Matsui, 1999; 2001 for more details).

We classified each prey item as either terrestrial or aquatic on the basis of the habitat in which it typically occurs. Although some prey items were difficult to classify, we regarded maggots (Diptera larvae), adult and larval water beetles (e.g., Dytiscidae), larval caddisflies (Trichoptera), pond-skaters (Gerridae), nymphal dragonflies (Odonata), freshwater shrimps (Amphipoda), and pond snails (e.g. Lymnaeidae) as aquatic prey.

To estimate prey availability, we sampled potential prey invertebrates on the *aze* (slightly elevated narrow trail between adjoining rice fields) by sweep-netting and ground plot techniques on six days (spring: 28 May and 27 June; summer: 25 July and 26 August; autumn: 27 September and 22 October in 1995) (details in method in Hirai & Matsui 1999, 2000*a*).

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Concurrently with frog collections for diet analyses, we estimated the relative abundance of frogs at the study site. Relative abundance is here defined as the number of individuals collected in one hour by walking along footpaths (the *aze*) between adjoining rice fields. The abundance values were compared by the Wilcoxon signed-rank test.

In order to detect interspecific differences in the use of food resources, we compared frequencies of occurrence of all prey taxa by Fisher's exact probability test, and quantified diet similarity by calculating the simple overlap index, $C$ (Schoener, 1968), where $C_{xy}=1-0.5\Sigma|P_{ix}-P_{iy}|$, and $P_{ix}$ and $P_{iy}$ are the proportions of prey taxon $i$ in diets of the two different species, $x$ and $y$. The values of $C$ range from 0 (no overlap) to 1 (complete overlap). The index was calculated for every two month period (spring: May and June; summer: July and August; autumn: September and October) to evaluate the seasonal change in the feeding relationships of the frogs. The difference in feeding site was tested by comparing frequency of occurrence of aquatic forms using Fisher's exact probability test. The specific difference of prey selection was also examined with Ivlev's electivity index $E$, (Ivlev, 1961), $E=(P_c-P_a)/(P_c+P_a)$, where $P_c$ and $P_a$ are the proportions of prey items in question in the diet and environment respectively. This index is vulnerable to small proportions in the diet or in the environment (Lechowicz, 1982). We calculated $E$ only for ants, because the proportions of prey taxa other than ants were not large enough for this analysis. The index values vary symmetrically between $-1.0$ to $+1.0$ as a prey taxon is avoided or preferred respectively. For this analysis, we approximated prey availability within an area of 120 m² in each season by combining the total abundances of sweep and ground plot samples.

In addition, we examined relationships between snout-vent length (SVL) and mouth width (MW), between MW and mean prey length, and between MW and maximum prey length. ANCOVA was performed on common logarithms of all these four variables to detect differences between the species. In order to eliminate sampling bias, we included only such frogs that contained at least three prey items in their stomachs to calculate mean and maximum length of prey for each frog. In all diet analyses, stomach contents from recaptured individuals were treated as independent samples because diet composition seems not to differ individually within species.

## RESULTS

### LIFE HISTORY AND RELATIVE ABUNDANCE

We encountered *Rana nigromaculata* and *R. rugosa* in and around the rice fields throughout the study period. Forty-five out of 389 individuals of *R. nigromaculata*, and 27 of 64 individuals of *R. rugosa* were recaptured more than once (maximum of three times for *R. nigromaculata*, and nine times for *R. rugosa*).

In addition to these two species, we observed reproduction of *Hyla japonica* from early May to mid July ($n=128$), *Rhacophorus arboreus* in mid June ($n=4$), and *Rh. schlegelii* from early May to mid June ($n=33$). Neither rhacophorids had animal prey in their stomachs, but plant pieces or minerals – or both – were found in 21.2% of *Rh. schlegelii* stomachs. From 87.5% of stomachs of *H. japonica*, animal foods were recovered, but this species was collected only in the limited breeding season (Hirai & Matsui, 2000c). Because only the two ranid species utilized rice fields throughout the activity periods, we include only these species in subsequent analyses.

The two species became active at the beginning of May, and were consistently captured until mid-October. During the hibernation periods, from November to April, we could not find any frogs at the study site (Fig. 1). The reproductive season of *R. nigromaculata* was short at the study site, and breeding males were found only in early May. Whilst males were calling from the water fields, other individuals were mostly captured on the ground (*aze*), usually near the water. *Rana rugosa* was found syntopically with *R. nigromaculata*, but breeding males of this species were calling at the water's edge during a prolonged season from late May to late August. We observed that larval *R. nigromaculata* metamorphosed simultaneously at the beginning of July, but larval *R. rugosa* remained in the ditch that does not dry out in summer, and metamorphosed sporadically from September to October.
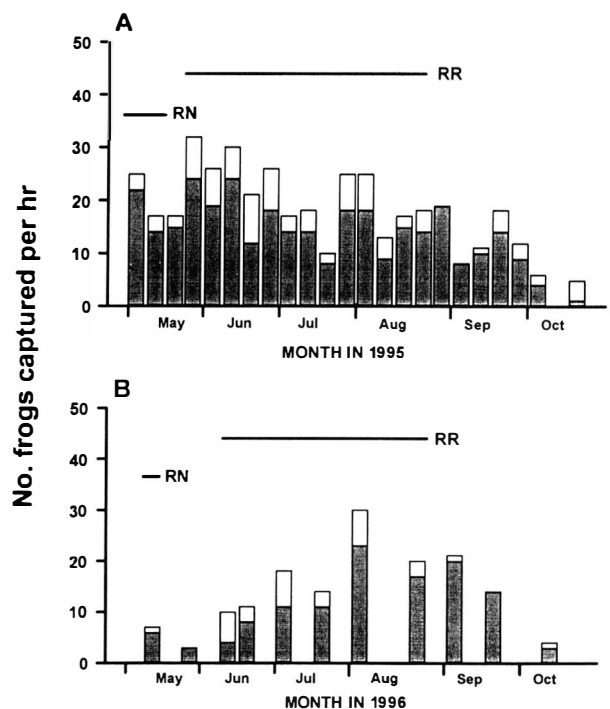


FIG. 1. Seasonal fluctuation in relative abundance of *R. nigromaculata* (RN, hatched rectangle) and *R. rugosa* (RR, open rectangle) in 1995 (A) and 1996 (B). Solid lines indicate periods when males emitting advertisement calls, were captured. No frogs were found in surveys between November and April.

TABLE 1. Diet composition (%) of *Rana nigromaculata* (RN: 2589 prey from 400 frogs, total volume 106145.0 mm³) and *R. rugosa* (RR: 1470 prey from 118 frogs, total volume 13696.6 mm³).

| Prey taxon | Frequency of occurrence | | Numerical proportion | | Volumetric proportion | |
|---|---|---|---|---|---|---|
| | RN | RR | RN | RR | RN | RR |
| Insecta | | | | | | |
| Hymenoptera | | | | | | |
| Formicidae | 39.5 | 84.8 | 16.0 | 56.3 | 2.1 | 9.1 |
| non-Formicid | 9.3 | 12.7 | 1.9 | 1.2 | 1.6 | 0.9 |
| larvae | 5.0 | 0.9 | 1.5 | 0.1 | 1.1 | 0.5 |
| Coleoptera | 45.3 | 61.0 | 11.1 | 12.7 | 24.8 | 30.0 |
| larvae | 9.5 | 8.5 | 2.9 | 1.0 | 3.5 | 3.8 |
| Diptera | 40.0 | 40.7 | 12.2 | 5.0 | 2.9 | 3.3 |
| larvae | 10.5 | 11.0 | 3.6 | 5.7 | 1.8 | 2.3 |
| Lepidoptera | 13.8 | 4.2 | 2.6 | 0.4 | 2.6 | 0.4 |
| larvae | 25.3 | 14.4 | 5.7 | 1.4 | 14.6 | 6.8 |
| Trichoptera | 0.5 | 0.9 | 0.1 | 0.1 | <0.1 | <0.1 |
| larvae | 0.5 | - | 0.1 | - | <0.1 | - |
| Neuroptera | 1.8 | - | 0.3 | - | 0.1 | - |
| larvae | 0.3 | - | <0.1 | - | <0.1 | - |
| Hemiptera | 31.8 | 26.3 | 8.3 | 3.2 | 10.7 | 5.8 |
| Dermaptera | 6.5 | 6.8 | 1.2 | 0.6 | 1.0 | 1.9 |
| Orthoptera | 19.0 | 5.9 | 3.6 | 0.5 | 9.0 | 5.4 |
| Odonata larvae | 1.0 | 1.7 | 0.2 | 0.1 | 0.6 | 1.7 |
| Ephemeroptera | 0.3 | - | 0.1 | - | <0.1 | - |
| Thysanoptera | 0.3 | - | <0.1 | - | <0.1 | - |
| Collembola | 2.8 | 3.4 | 0.5 | 1.4 | <0.1 | <0.1 |
| Arachnida | | | | | | |
| Araneae | 46.5 | 41.5 | 17.2 | 6.0 | 2.9 | 4.3 |
| Opiliones | 0.5 | 0.9 | 0.1 | 0.1 | <0.1 | <0.1 |
| Acarina | 2.0 | 7.6 | 0.3 | 1.0 | <0.1 | 0.1 |
| Crustacea | | | | | | |
| Isopoda | 9.0 | 7.6 | 2.3 | 1.4 | 1.8 | 4.5 |
| Decapoda | 0.5 | 0.9 | 0.1 | 0.1 | 0.5 | 4.3 |
| Amphipoda | 0.3 | - | <0.1 | - | <0.1 | - |
| Chilopoda | 3.8 | 2.5 | 0.6 | 0.2 | 0.5 | <0.1 |
| Diplopoda | 5.3 | 5.1 | 1.0 | 0.4 | 0.3 | 0.7 |
| Gastropoda | 16.3 | 3.4 | 5.1 | 0.7 | 2.8 | 0.5 |
| Oligochaeta | 8.0 | 4.2 | 1.5 | 0.3 | 14.0 | 13.5 |
| Amphibia | | | | | | |
| Anura | 0.3 | - | <0.1 | - | 0.9 | - |

*Rana nigromaculata* was consistently more abundant than *R. rugosa* in 32 out of 34 censuses (94.1%). Wilcoxon signed-rank test revealed that the relative abundance differed significantly ($P<0.01$) in both 1995 (mean±SD, 14.0±5.9 for 323 *R. nigromaculata*; 4.0±2.6 for 93 *R. rugosa*) and 1996 (10.9±6.9 for 120 *R. nigromaculata*; 2.9±2.7 for 32 *R. rugosa*).

FOOD PARTITIONING

*Diet composition.* Stomach contents were found in 400 out of a total 443 stomachs of *R. nigromaculata* (90.3%), and in 118 out of a total 125 stomachs of *R. rugosa* (94.4%). The two species had a wide variety of prey taxa in common (Table 1), but were markedly different in their utilization of some prey taxa. *Rana rugosa* consumed small prey such as ants, mites and small beetles more frequently than did *R. nigromaculata*, and the frequencies of occurrence significantly differed between the two species ($P<0.01$). In particular, ants were ingested by 84.8% of *R. rugosa*, as compared with only 39.3% of *R. nigromaculata*. Numerical proportions of ants also differed markedly

TABLE 2. Comparison of mean number (±SD) of prey items found in a stomach of the two species in three seasons. Range and sample size of stomachs are shown in parenthesis.

|  | Spring | Summer | Autumn |
|---|---|---|---|
| R. nigromaculata | 5.0±3.2 | 8.0±7.4 | 5.4±4.4 |
|  | (1-16, 136) | (1-59, 184) | (1-19, 80) |
| R. rugosa | 12.2±14.3 | 11.9±9.1 | 15.1±14.4 |
|  | (1-65, 52) | (2-47, 50) | (2-50, 16) |
| U-test | P<0.01 | P<0.01 | P<0.01 |



FIG. 4. Relationships between SVL and mouth width of *R. nigromaculata* (open circle) and *R. rugosa* (dark circle).

between *R. rugosa* (56.3%) and *R. nigromaculata* (16.0%). Instead, *R. nigromaculata* more frequently consumed large prey such as moths (lepidopterans), caterpillars (larval lepidopterans), grasshoppers (orthopterans), and gastropods (*P*<0.05 for caterpillars, *P*<0.01 for the others). By volume, beetles made up the largest proportions in both species, followed by caterpillars, earthworms, and bugs in *R. nigromaculata*, and earthworms in *R. rugosa*.
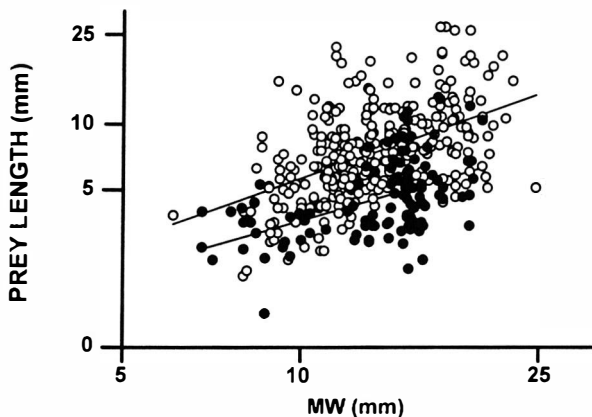


FIG. 2. Relationships between mouth width and mean prey size of *R. nigromaculata* (open circle) and *R. rugosa* (dark circle).
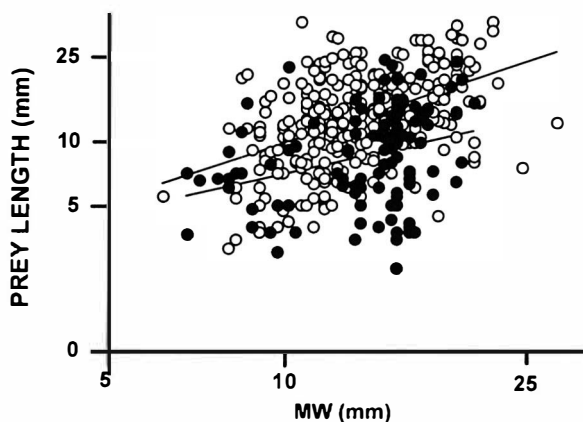


FIG. 3. Relationships between mouth width and maximum prey size of *R. nigromaculata* (open circle) and *R. rugosa* (dark circle).
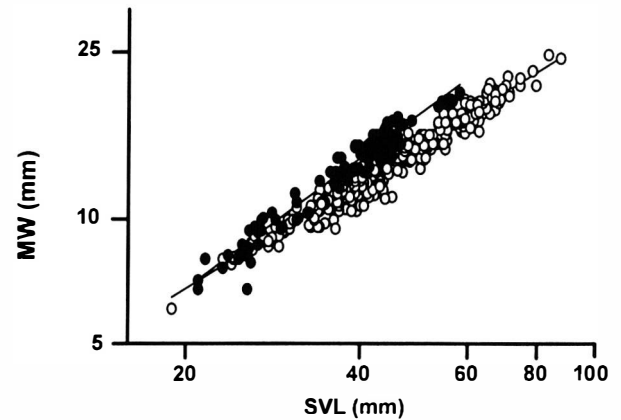
*Seasonal changes and prey selection.* *Rana nigromaculata* took significantly fewer prey than did *R. rugosa*, consistently from spring to autumn (Table 2). No particular prey taxon predominated in the diet of *R. nigromaculata*, and various prey such as ants, beetles, dipterans, bugs, spiders were taken in similar proportions. Ants represented only 7.9-21.1% of total prey items in this species. On the contrary, ants were dominant in all seasons in the diet of *R. rugosa* (37.8%-62.9%; Table 3).

Diet similarities showed little seasonal variation, with low values from 0.49 to 0.55. Aquatic forms made smaller contributions numerically than terrestrial ones in the diets of both species (numerical proportions in spring, summer and autumn were 8.5%, 13.6% and 8.0% in *R. nigromaculata*, and 6.8%, 3.9% and 17.0% in *R. rugosa*, respectively). *Rana nigromaculata* took aquatic forms more often in the summer (frequencies of occurrence in spring, summer and autumn were 21.3%, 45.7% and 18.8%, respectively), but *R. rugosa* took them consistently in all seasons (21.2%, 20.0%, and 25.0%, respectively). A significant difference between the species in this frequency was detected only in summer (*P* < 0.01).

In the habitat studied, ants were the most easily available prey throughout the seasons (spring, 82.6%; summer, 73.0%; autumn, 69.0%) (Table 4). The electivity indices indicated that both frog species avoided ants, but *R. nigromaculata* avoided them more strongly (*E*=-0.82, -0.55, -0.70 in spring, summer, and autumn, respectively) than *R. rugosa* (-0.19, -0.07, -0.29).

*Frog and prey sizes.* *Rana nigromaculata* (mean±SD, 46.7±12.9 mm; range, 18.9-86.9 mm) was significantly larger in SVL than *R. rugosa* (39.9±8.4 mm, 20.9-59.7 mm). However, the ranges overlapped considerably. Prey size was significantly correlated with frog size in both species (*R. nigromaculata*: $r_{mean}$=0.48, $r_{max}$=0.46, *R. rugosa*: $r_{mean}$=0.48, $r_{max}$=0.30; *P*<0.01 for all; Figs. 2, 3). Mouth width relative to the body size was narrower in *R. nigromaculata* than *R. rugosa* (Fig. 4), and the relationship between SVL and mouth width differed significantly between the species

TABLE 3. Feeding relationships between *Rana nigromaculata* (RN) and *R. rugosa* (RR). Values are numerical proportions (%) of total prey items. See text for dietary overlap, *C*.

| Prey taxon | Spring | | Summer | | Autumn | |
|---|---|---|---|---|---|---|
| | RN | RR | RN | RR | RN | RR |
| Insecta | | | | | | |
| Hymenoptera | | | | | | |
| Formicidae | 7.9 | 57.1 | 21.1 | 62.9 | 11.5 | 37.8 |
| non-formicid | 2.3 | 0.5 | 1.0 | 1.9 | 4.1 | 1.7 |
| larvae | 3.1 | 0.2 | 1.1 | - | 0.5 | - |
| Coleoptera | 16.1 | 16.2 | 9.7 | 11.5 | 8.0 | 6.6 |
| larvae | 1.2 | 1.3 | 3.7 | 0.8 | 2.8 | 0.4 |
| Diptera | 24.8 | 6.5 | 7.4 | 4.2 | 8.9 | 3.3 |
| larvae | 1.9 | 4.1 | 4.1 | 2.7 | 4.4 | 17.0 |
| Lepidoptera | 1.6 | 0.2 | 2.9 | 0.5 | 3.0 | 0.8 |
| larvae | 2.6 | 0.8 | 6.2 | 1.7 | 8.7 | 2.1 |
| Trichoptera | - | - | 0.1 | - | - | 0.8 |
| larvae | - | - | 0.1 | - | 0.2 | - |
| Neuroptera | 0.6 | - | 0.2 | - | 0.2 | - |
| larvae | - | - | - | - | 0.2 | - |
| Hemiptera | 5.0 | 3.5 | 7.2 | 2.5 | 17.0 | 4.1 |
| Dermaptera | 1.2 | 0.8 | 1.2 | 0.5 | 1.4 | 0.4 |
| Orthoptera | 3.2 | 0.2 | 3.8 | 0.5 | 3.9 | 1.2 |
| Plecoptera | - | 0.2 | - | - | - | 0.4 |
| Odonata larvae | 0.2 | - | 0.3 | 0.3 | - | - |
| Ephemeroptera | - | - | 0.1 | - | - | - |
| Thysanoptera | 0.2 | - | - | - | - | - |
| Collembola | 0.3 | 0.3 | 0.3 | - | 1.6 | 7.9 |
| Arachnida | | | | | | |
| Araneae | 14.2 | 4.6 | 19.4 | 6.2 | 14.7 | 9.1 |
| Opiliones | 0.3 | - | - | 0.2 | - | - |
| Acarina | 0.3 | 0.3 | 0.1 | - | 0.9 | 5.4 |
| Crustacea | | | | | | |
| Isopoda | 3.8 | 1.1 | 0.9 | 2.2 | 4.8 | 0.4 |
| Decapoda | - | - | 0.1 | 0.2 | - | - |
| Amphipoda | - | - | 0.1 | - | - | - |
| Chilopoda | 1.2 | 0.2 | 0.4 | 0.3 | 0.2 | - |
| Diplopoda | 2.0 | 0.5 | 0.5 | 0.3 | 0.1 | 0.4 |
| Gastropoda | 4.5 | 1.4 | 6.5 | 0.2 | 1.4 | - |
| Oligochaeta | 1.8 | 0.5 | 1.6 | 0.3 | 0.5 | - |
| Amphibia | | | | | | |
| Anura | - | - | - | - | 0.2 | - |
| Dietary overlap, *C* | 0.49 | | 0.55 | | 0.51 | |

(ANCOVA; slopes: $F$=55.82, elevations: $F$=415.91, $P$<0.01 for both). However, *R. nigromaculata* took significantly larger prey than the relatively wider-mouthed *R. rugosa* (slopes: $F_{mean}$=1.09, $F_{max}$=2.35, $P$>0.05 for both; elevations: $F_{mean}$=119.18, $F_{max}$=68.55, $P$<0.01 for both; Figs. 2, 3).

## DISCUSSION

*Rana nigromaculata* and *R. rugosa* had a wide variety of prey taxa in common, but markedly differed in ant utilization. Dissimilarities in their diets, as also indicated by low overlap values (0.49-0.55), were recognized consistently from spring to autumn. The

TABLE 4. Prey availability estimated from the number of potential prey animals collected by sweep (S) and ground plot sampling (G). See text for the details about availability (Avail.).

| Prey taxon | May | | Jun | | Spring | | Jul | | Aug | | Summer | | Sep | | Oct | | Autumn | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | S | G | S | G | Avail. | % | S | G | S | G | Avail. | % | S | G | S | G | Avail. | % |
| Formicidae | 20 | 49 | 3 | 83 | 15863 | 82.6 | 3 | 43 | 36 | 13 | 6759 | 73.0 | 39 | 33 | 14 | 18 | 6173 | 69.0 |
| non-formicid | 5 | - | 4 | - | 9 | <0.1 | 1 | - | 28 | - | 29 | 0.3 | 19 | - | 23 | - | 42 | 0.5 |
| larvae | 2 | - | - | - | 2 | 0.1 | - | - | - | - | - | - | 3 | - | - | - | 3 | <0.1 |
| Coleoptera | 17 | - | 8 | 3 | 385 | 2.0 | 7 | - | 66 | - | 73 | 0.8 | 14 | - | 8 | - | 22 | 0.3 |
| larvae | - | - | - | - | - | - | - | - | - | - | - | - | 1 | 1 | - | - | 121 | 1.4 |
| Diptera | 66 | - | 13 | - | 79 | 0.4 | 7 | - | 164 | - | 171 | 1.9 | 126 | - | 64 | - | 190 | 2.1 |
| Lepidoptera | 1 | - | - | - | 1 | <0.1 | - | - | 6 | - | 6 | <0.1 | 5 | - | 3 | - | 8 | <0.1 |
| larvae | - | - | - | - | - | - | - | - | 5 | 1 | 125 | 1.4 | 8 | - | 3 | 2 | 251 | 2.8 |
| Hemiptera | 5 | - | 2 | - | 7 | <0.1 | 2 | 2 | 108 | - | 350 | 3.8 | 81 | - | 18 | - | 99 | 1.1 |
| Dermaptera | - | - | - | 1 | 120 | 0.6 | - | 2 | - | 6 | 960 | 10.4 | - | 1 | - | - | 120 | 1.3 |
| Orthoptera | 20 | - | 45 | 3 | 425 | 2.2 | 36 | 1 | 98 | - | 254 | 2.7 | 68 | - | 20 | - | 88 | 1.0 |
| Thysanoptera | - | - | - | - | - | - | - | - | - | - | - | - | 3 | - | - | - | 3 | <0.1 |
| Araneae | 31 | 10 | - | 3 | 1593 | 8.3 | - | - | 47 | 3 | 527 | 5.7 | 106 | 6 | 35 | 6 | 1581 | 17.7 |
| Isopoda | - | - | - | 3 | 360 | 1.9 | - | - | - | - | - | - | - | - | - | - | - | - |
| Diplopoda | 2 | 2 | - | 1 | 362 | 1.9 | - | - | - | - | - | - | - | - | - | 1 | 120 | 1.3 |
| Oligochaeta | - | - | - | - | - | - | - | - | - | - | - | - | - | 1 | - | - | 120 | 1.3 |

overall dissimilarities result from the difference in the consumption of ants.

Diets of other populations of these two species have been studied in detail (Hirai & Matsui, 1999, 2000a). In these studies, R. nigromaculata ate a broad range of prey taxa in similar proportions, and ants represented only 20.3% of total prey items (Hirai & Matsui, 1999). In contrast, R. rugosa took numerous ants regardless of differences in body size or habitats, and ants represented 56.8-59.4% of the diet (Hirai & Matsui, 2000a). Thus, the results obtained in this study (16.0% in R. nigromaculata and 56.3% in R. rugosa) were similar to those of previous studies, and the consistency in the values for R. rugosa is clear.

In resource partitioning studies, it is more important to attempt to reveal factors regulating the patterns of resource partitioning than to merely document differences in resource use (Toft, 1985). According to resource partitioning studies in Rana (e.g., Marshall & Buell, 1955; Loman, 1978, 1979; Licht, 1986), habitats were partitioned most frequently between congeneric species pairs. Even when congeneric species are in sympatry, they generally take prey from different sites. For instance, R. pretiosa forages principally in the water, but R. aurora takes prey on the ground (Licht, 1986).

In this study, the terrestrial areas available for foraging were limited to the levee banks between the rice paddies, and there was no significant difference between the species in the proportions of aquatic prey in the diet. Both species eat mainly terrestrial prey. These findings suggest that they take prey on the ground syntopically, and dissimilarities in the diets are not attributable to differences in feeding sites.

Frogs are often gape-limited predators, and the consumable size of prey is determined by the size of gape or body (Kramek, 1972; Toft, 1980). Narrow-mouthed anurans like dendrobatids and microhylids are specialized for eating small prey such as ants (Toft, 1980; Hirai & Matsui, 2000b). However, in our study, the relatively wider-mouthed R. rugosa consumed more ants than the narrower-mouthed R. nigromaculata. This result suggests that ant eating by R. rugosa is not due to gape-limitaion.

These lines of evidence indicate that food partitioning between R. nigromaculata and R. rugosa is not caused by differences in either feeding site or feeding apparatus, but by different prey selection. In fact, the electivity index suggested that both frogs avoided ants – notwithstanding their abundance in the habitat – but the degree of avoidance was much stronger in Rana nigromaculata (E ranging from -0.82 to -0.55) than in R. rugosa (E ranging from -0.29 to -0.07). From these results, we consider that different prey selection is responsible for food partitioning between R. nigromaculata and R. rugosa, that are congeneric and syntopic.

Food partitioning among coexisting ranids has been explained previously as a result of differences in body size or feeding site (e.g., Stewart & Sandison, 1972; Licht, 1986; Werner et al., 1995). To our knowledge, this study is the first to report food partitioning by differences in prey selection in Rana. Such partitioning might be one of the important factors regulating the structure of anuran assemblages in rice fields.

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