

アカネズミとヒメネズミの餌資源に対する機能的反応

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論 文

Functional Responses to Food Resources of Wood Mice, *Apodemus speciosus* TEMMINCK and *Apodemus argenteus* TEMMINCK

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SONÉ, Koichi: Functional responses to food resources of wood mice, *Apodemus speciosus* TEMMINCK and *Apodemus argenteus* TEMMINCK. J. Jpn. For. Soc. 72: 321~328, 1990. The feeding of two species of wood mice, *Apodemus speciosus* TEMMINCK and *A. argenteus* TEMMINCK, on adults of the *cryptomeria* bark borer and the train millipede and peanuts was studied in a laboratory from 1987 to 1989. Four out of five individuals of *A. speciosus* and three out of five *A. argenteus* attacked and ate the borers. Both species of mice did not discriminate against the sex and the size of the borers in their attacks. Functional responses of *A. speciosus* and *A. argenteus* to the borer density were HOLLING's Type II and III, respectively. When the borer density was at a low level, *A. speciosus* showed a greater preference for the borer. When the level of borer density was high, however, the preference of the mice for the borer differed significantly among individuals depending on their innate characters. *A. argenteus* showed an equal preference for the borer when the borer density was not high. When the borer density level was high, the preference of *A. argenteus* differed among individuals as in the case of *A. speciosus*. Four out of ten individuals of *A. speciosus* ate the millipede. The preference for the millipede increased with its increasing density, whereas *A. argenteus* did not eat them at all.

曾根晃一：アカネズミとヒメネズミの餌資源に対する機能的反応 日林誌 72:321~328, 1990. ピーナッツとともにスギカミキリとキシヤヤスデを異なった割合で与えたアカネズミとヒメネズミの採餌様式を観察した。カミキリとピーナッツを与えた場合、2種のネズミはカミキリの供試数にかかわらず、ほぼ一定量のピーナッツを摂食した。カミキリのサイズと性はカミキリに対するこれら2種のネズミの攻撃および捕食と無関係であった。カミキリの密度に対するアカネズミとヒメネズミの機能的反応は、それぞれ HOLLINGのII型およびIII型に相当した。餌中に占めるカミキリの割合の変化に対するこれら2種のネズミの反応として、アカネズミではカミキリの割合が低いときにカミキリに対する高い嗜好性が認められた。他方、ヒメネズミではその割合が低~中程度のときにはカミキリに対する嗜好性は変化しなかったが、高いときには低下した。ただし、ネズミの個体によりその反応差は大きかった。ヤスデとピーナッツを与えた場合、ヒメネズミはまったくヤスデを食べなかった。アカネズミでは10個体中4個体がヤスデを食べ、うち2個体が餌中に占めるヤスデの割合の増加に伴うピーナッツからヤスデへのスイッチングが認められた。これらの結果をもとに、2種のネズミの採餌決定要因および餌個体群の制御能力について論議した。

I. Introduction

Granivorous wood mice, *Apodemus* spp., can change their diets from seeds to arthropod prey when the former are not abundant (WATTS, 1968; ZEMANECK, 1972; DON, 1979). Thus, forest entomologists stressed the importance of these small mammals in the control of sawflies and other insect pests (GRAHAM, 1929; HAMILTON, JR. and COOK, 1940; SATO, 1978). MAKIHARA (pers. comm.) thought that the greater adult mortality of the *cryptomeria* bark borer, *Semanotus japonicus* (LACORDAIRE) (Coleoptera: Cerambycidae), in a mountainous area was partly due to heavy predation by wood mice, *Apodemus speciosus* TEMMINCK and *A. argenteus* TEMMINCK. MORRIS *et al.* (1958) stated that small mammals were not important as a regulatory factor of pest insect populations in outbreak.

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To evaluate a predator's ability to regulate a prey population, we should examine the predator's response to changes in the prey density. SOLOMON (1949) divided the predator's response into a numerical response and a functional response. HOLLING (1959) sophisticated SOLOMON's dichotomy by subdividing numerical and functional responses into three and four classes, and stated that his Type III functional response could regulate the prey population irrespective of the numerical response. MURDOCH (1969, 1973) stressed the importance of "switching" of the predator's diet in regulation of prey populations. Thus, the changes in a predator's diet with the prey density should be more important than those in the number of predators.

Foods and stomach contents of *Apodemus* spp. were studied by some workers (WATTS, 1968; HANSSON, 1971; DON, 1979), but only a few studies were conducted to examine the relationships between food and diet in the field (SONÉ *et al.*, 1986). In this study, I focused on the feeding of two species of wood mice, *A. speciosus* and *A. argenteus*, on peanuts and arthropod prey (the *cryptomeria* borer and the train millipede, *Parafontaria laminata armigera* VERHOEFF (Diplopoda: Xystodesmidae)) under laboratory conditions, and in this paper discuss the factors which determined their diet and the ability of these mice to regulate the populations of these arthropod prey.

II. Materials and Methods

1. Materials

The two species of wood mice, *A. speciosus* (*A.s.*) and *A. argenteus* (*A.a.*), were collected in Ibaraki, Tochigi, and Yamanashi Prefectures of central Japan in 1986~1988. Before being subjected to the experiments, they were reared individually with artificial foods in a laboratory under 12 h of light for more than two months to reduce as much as possible the effects of previous experiences in the field on their feeding habits. The mean body weights of *A.s.* and *A.a.* were 36.2 ± 5.8 (S.D.) g ($n=15$) and 20.7 ± 4.0 (S.D.) g ($n=15$), respectively.

The adults of the *cryptomeria* bark borer were collected in spring of 1987 in Ibaraki Prefecture (central Japan) and in Okayama, and Toyama Prefectures (western Japan). The mean fresh body weights of male and female borers were 146.2 ± 52.1 (S.D.) mg ($n=178$) and 203.7 ± 69.1 (S.D.) mg ($n=72$), respectively, and their calorific values were calculated at 468.2 ± 166.9 (S.D.) cal and 652.4 ± 221.3 (S.D.) cal, respectively.

The train millipedes were collected in October, 1988 in Yamanashi Prefecture where there was an outbreak of this millipede. Body weights of male and female millipedes were 179~472 mg and about 250 mg on the average, respectively.

2. Methods

1) Feeding experiments with the *cryptomeria* bark borer

I conducted the experiments using five *A.s.* and five *A.a.* in April and May, 1987. I examined the

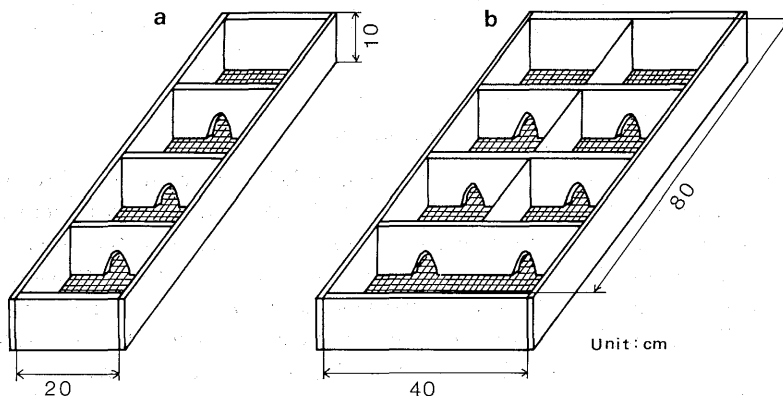


Fig. 1. Arenas used in the feeding experiments of the borers (a) and the millipedes (b) by wood mice

feeding of the mice in an arena (20×80×10 cm with a 3 mm wire mesh floor and a transparent acrylic-ceiling) divided into four compartments (Fig. 1a). Mice could move freely from one compartment to another through a small hole, but the intercompartment movements of the borers were restricted to some extent. Before starting the experiments, I marked individual borers with paint, checked their sexes, and measured their body weights. I also measured the total weights of peanuts supplied. I put eight peanuts, that is two in each compartment, and various numbers (1, 2, 4, 8, 16, and 32) of the borers in the arena. In the experiments with one and two borers, I put a borer in one and two, respectively, of the four compartments. The compartments where I placed a borer were chosen at random. In the experiments with 4, 8, 16, and 32 borers, I put equal number of the borers in each compartment, that is, 1, 2, 4, and 8 borers, respectively. After starving a mouse for three hours, I released it into the arena and allowed it to eat peanuts and borers for two hours under red light. Red light did not disturb the behavior of the mice. I observed feeding and other behaviors for an initial 30 min. After two hours of feeding, I collected all of the remaining peanuts, live borers, and carcasses or pieces of borers. After examining the evidences of the attack (biting or clawing) and feeding of the mice on each borer, I measured the weights of the carcasses or pieces of the attacked and eaten borers. I also measured the weights of the remaining peanuts.

I repeated the experiments twice with one borer, and once with two or more borers for each mouse of both species. I conducted the experiment with 32 borers for only one *A.s.*

2) Experiments with the train millipede

I conducted feeding experiments with the train millipedes from October, 1988 to February, 1989. I observed feeding behaviors of ten *A.s.* and ten *A.a.* in the arena shown in Fig. 1b. I started a series of experiments for each mouse with ten millipedes and two or four peanuts for *A.a.* or *A.s.*, respectively. When the mice ate millipedes, I continued the experiment with various combinations of numbers of peanuts and millipedes. When the mice did not eat millipedes at all for the first successive two nights, I gave them only millipedes on the third night. If the mice did not eat millipedes on the third night too, I stopped the experiment.

III. Results

1. Feeding on peanuts

It was estimated that mice could get about 2 kcal of energy by eating a peanut (about 0.4 g). *A.s.* and *A.a.* ate 1~2 and 0.5~0.7 peanuts, respectively, during the two hours of the experiments with borers. The weights of peanuts eaten by each species of mice did not differ significantly among the experiments with different numbers of borers ($F=2.64$ and 0.21 for *A.s.* and *A.a.*, $p>0.05$, respectively). But individuals of *A.a.* which ate the borers took more peanuts than those which did not eat the borers ($F=9.81$, $p<0.01$).

In the experiments with millipedes, all of the mice ate all of the peanuts supplied (less than seven peanuts) in all cases. When more than ten peanuts were supplied, *A.s.* ate six to eight peanuts.

2. Attack and feeding on borers

Mice ate only the abdomens of the borers and did not eat the legs, antennae, upper wings, and other parts of cuticle. They obtained about 0.2 kcal of energy by eating an adult borer.

Four out of the five *A.s.* and three out of the five *A.a.* attacked the borers and ate them. I could obtain enough data for four *A.s.* and two *A.a.* to examine whether or not they discriminated against the sex and the size of the borer in their attacks. One individual *A.a.* ate only one borer throughout the experiments. Table 1 shows the results of the MANN-WHITNEY *U* test (SIEGEL, 1959) for the differences in body weights between eaten and uneaten borers. In all five cases of *A.s.*, the body weights of eaten borers did not differ significantly from those of uneaten ones. In the case of *A.a.*, *Aa-4* ate larger borers in the experiment with 16 borers, but did not show such a trend in that with 8 borers. The body weights did not differ between the eaten and uneaten borers in *Aa-5*. No mice showed a significant difference in feeding ratios according to the sex of the borers (Table 2). These results suggest that both mice species discriminated against neither the sex nor the size of the borer when they attacked. The mice which did not eat the borers seemed to show no interest in the borers or to be in fear of them.

Table 1. Results of the MANN-WHITNEY U test for the differences in body weights between the eaten and uneaten borers by the wood mice

Individual no. of mice	No. of borers released in the experiment	U -values	
A_s -2	8	6	N.S.
A_s -2	16	19	N.S.
A_s -4	16	17.5	N.S.
A_s -4	32	112.5	N.S.
A_s -5	16	13	N.S.
A_a -4	8	3	N.S.
A_a -4	16	16	*
A_a -5	16	11	N.S.

A_s , *A. speciosus*; A_a , *A. argenteus*.

* Body weights differed significantly between eaten and uneaten borers at the $p=0.05$ level. N.S., Body weights were not significantly different at the $p=0.05$ level.

Table 2. Results of chi-square tests for the effects of the sex of borers on feeding of the wood mice

Individual no. of mice	Chi-square values	
A_s -1	0.11	N.S.
A_s -2	0.60	N.S.
A_s -4	0.15	N.S.
A_s -5	0.04	N.S.
A_a -4	0.71	N.S.
A_a -5	0.61	N.S.

A_s , *A. speciosus*; A_a , *A. argenteus*.

N.S., Percentages of eaten borers by the wood mice did not differ significantly between the sexes at the $p=0.05$ level.

3. Feeding ratios and borers' densities

Figure 2 shows the relationships between feeding ratios and borer densities in the two species of mice which ate borers. The feeding ratio of *A. s.* decreased as the borer density increased, whereas *A. a.* showed an unimodal change with a peak at the borer density of four. These results suggest that the functional responses of *A. s.* and *A. a.* to the borer density coincided with HOLLING's Type II and III, respectively.

4. Response to two species of prey

Figure 3 shows the relationships between the proportions of borers in the available food (F_1) and those in the diets (P_1) for all mice of the two species which ate the borers. The null case and switching curves also are given based on the relationship between the preference for the borers and their relative abundance in the food.

The null-case curve presents the relationships between F_1 and P_1 in the null case where the preference (c) is a constant at all values of the relative density of some prey. In the null case,

$$N_1/N_2 = c \times (H_1/H_2)$$

where N_1 and N_2 are the numbers eaten of prey species 1 and 2, respectively, and H_1 and H_2 are the densities of prey species 1 and 2, respectively.

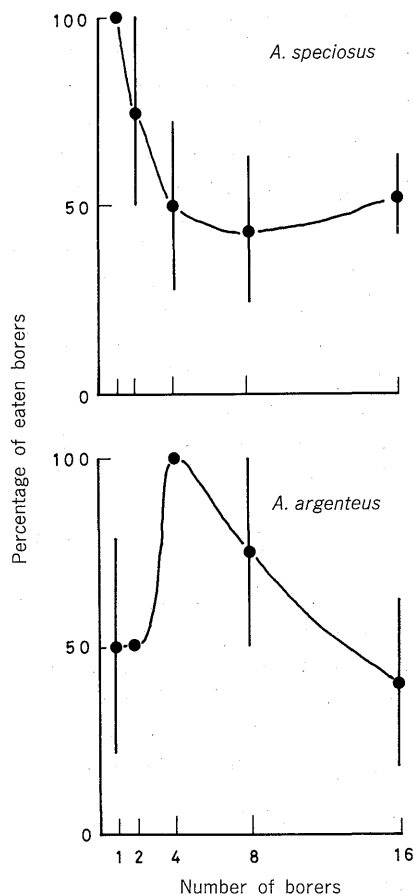


Fig. 2. The relationships between feeding ratios and densities of the borers for all mice which ate borers. Vertical lines show standard deviations.

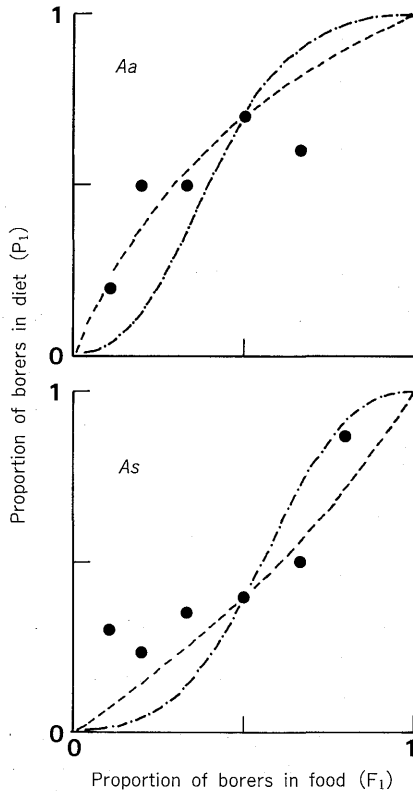


Fig. 3. The relationships between the proportions of borers in the available food (F_1) and those in the diet (P_1) for all mice of *A. speciosus* (As) and *A. argentatus* (Aa) which ate the borers

Dashed lines show the expectations in the null case. Dash-dot lines are the simple switching curves. See details in the text.

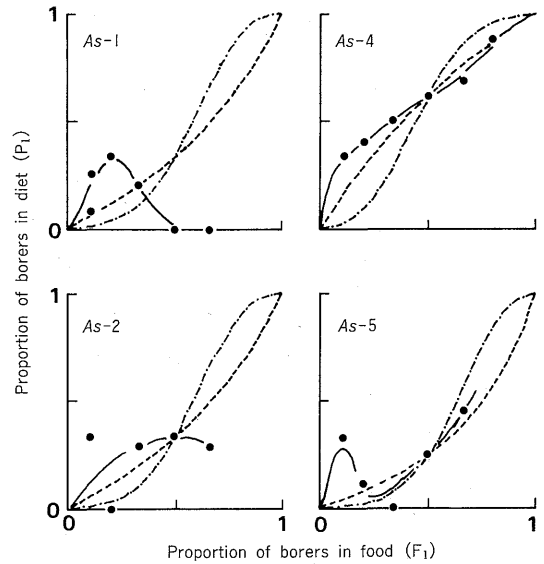


Fig. 4. The relationships between the proportions of borers in the available food (F_1) and those in the diet (P_1) for *A. speciosus* (As) individuals which ate the borers

Dashed lines show the expectations in the null case. Dash-dot lines are the simple switching curves. See details in the text.

And

$$P_1 = cF_1 / (1 - F_1 + cF_1)$$

The simple switching-curves present the relationship between F_1 and P_1 in the case where the preference for the borer is related linearly to its relative abundance in the food and are given by following equation:

$$P_1 = c' \times F_1^2 / \{(1 - F_1)^2 + c' F_1^2\}$$

where if c' is the preference at equality, $N_1/N_2 = c'(H_1/H_2)^2$. And $c' = c$ when $F_1 = 0.5$ (MURDOCH and OATEN, 1975).

A.s. showed greater values of P_1 when F_1 was less than 0.5, indicating a greater preference for the borers at their low density level. In the case of *A.a.*, the values of P_1 changed with F_1 along the null-case curve when F_1 was less than 0.5, but it was less than the expected value in the null case when F_1 was more than 0.5. These results suggest that the preference for the borers was relatively constant when the borer density was not high, and decreased at higher densities of the borer. In both cases, the simple switching-curves did not represent well the relationship between F_1 and P_1 .

Responses to the two prey species differed among individuals of both species of mice. Figures 4 and 5 show the relationships between F_1 and P_1 of four *A.s.* and two *A.a.*, respectively. In *A.s.*, when F_1 was greater than 0.5, the preferences differed among individual mice. The preference decreased in *As-1* and 2, whereas it was constant in *As-4* and 5. *As-1* and 2 seemed to be very nervous and in fear of the borers and their noises when the borers walked or landed on the wire mesh floor. *As-1* had the relaxed behaviour, grooming, and so forth, just after biting a borer, and *As-2* usually stayed in a corner of the arena but attacked the borer passing in front of it. Conversely, *As-4* first picked up and brought back all

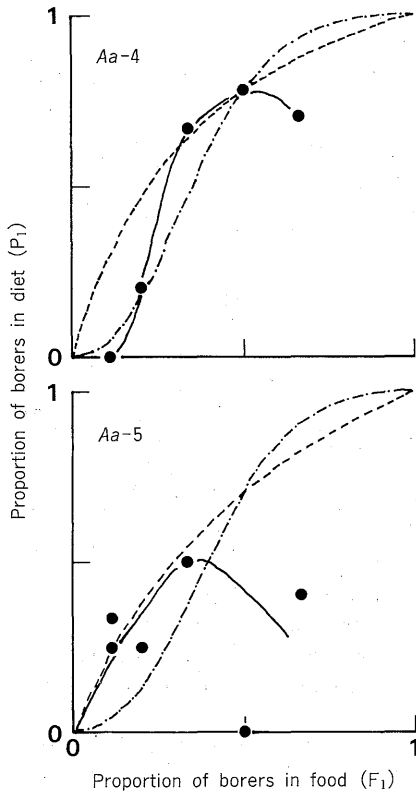


Fig. 5. The relationships between the proportions of borers in the available food (F_1) and those in the diet (P_1) for *A. argenteus* (*Aa*) individuals which ate the borers

Dashed lines show the expectations in the null case. Dash-dot lines are the simple switching curves. See details in the text.

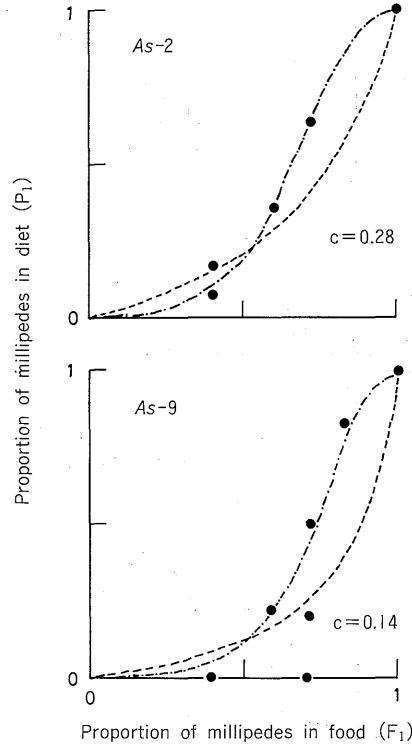


Fig. 6. The relationships between the proportions of millipedes in the available food (F_1) and those in the diet (P_1) for *A. speciosus* (*As*) individuals which ate the millipedes

Dashed lines show the expectations in the null case. Dash-dot lines are the simple switching curves. See details in the text.

of the peanuts in the arena to its nest; then it began very actively to attack and eat the borers. *As-5* also attacked and ate some borers when their density was rather high, but its attack and feeding were not as active as *As-4*. However, all four *A.s.* showed most preference for the borers when their proportion in available food (F_1) was less than 0.33 (P_1 values were plotted at higher points than the null-case curve).

With *A.a.*, *Aa-4* did not attack the borer in the experiment with one borer. After it first ate one borer in the experiment with two borers, it attacked and ate borers before peanuts and looked for borers at a corner of the arena where it could encounter the borers most frequently in the following experiments with four or more borers. Thus, P_1 increased with F_1 and reached the expected values of the null case when F_1 was less than 0.5. This suggests that the preference for the borer increased with the increases in the borer densities, whereas *Aa-5* preferred peanuts more at all densities of borers. It attacked and ate only borers which its body was touched. Thus, P_1 changed with F_1 along the null-case curve when F_1 was less than 0.33, suggesting equal preference for the borer. Both individuals had values of P_1 less than the null case when F_1 was more than 0.5. This result shows that the preference for the borer decreased when the borer density became high.

Figure 6 shows the relationships between the proportions of millipedes in the diet (P_1) and the food available (F_1) for two individuals of *A.s.* In both cases, the relationships fitted well to the simple

switching curves where the preference increased linearly with increasing densities of millipedes. Two other individuals of *A.s.* also ate the millipedes, but I could not obtain enough data to analyze the relationships between F_1 and P_1 . The remainder of the *A.s.* (six mice) and all of the ten *A.a.* did not eat the millipedes at any time. One possible reason why *A.a.* did not eat them was because they were of too large a size for *A.a.* to attack and eat them.

IV. Discussion

Many innate and environmental factors can affect the diet composition. In this study, I observed feeding behaviors of two species of granivorous wood mice in a very simple experimental system feeding them peanuts and arthropod prey. A peanut was a more efficient food than a borer for the mice from the viewpoint of energy intake. However, *A.s.* had a greater preference for the borer when the proportion of borers was at a low level in the food. These results suggest that the feeding of *A.s.* should be determined not only by energy intake but also other factors such as nutrient requirements and so forth (STEPHENS and KREBS, 1986). SONÉ *et al.* (1986) reported that *A.s.* had a tendency to eat as many varieties of food as they could in the field. DON (1979) reviewed the reports on the stomach content of wood mice and stated that in Poland *Apodemus* spp. included invertebrates in their diets at all seasons.

In all cases, both species of mice ate peanuts consistently regardless of the numbers of borers and millipedes. Thus, intra- and interspecific differences in diets might be due to those in feeding on the arthropod prey. Although the effects of feeding experience of mice in the field on diet composition were reduced as much as possible before the experiment, the response to borer densities differed among the mice of both species. Their attacks were influenced by the degrees of their aggressiveness, nervousness, and interest in the borers, but not by borer size and sex.

Therefore, the responses of wood mice to a certain food items may be determined by not only food composition (as stated by WATTS (1968), ZEMANECK (1972), and DON (1979)), but also by innate factors, such as nutrient requirement. The innate character of the mice is also a very important factor.

Theoretical and experimental studies on a predator's response to a prey density suggests that its HOLLING's Type III functional response and switching are, at least, necessary conditions for regulation of prey (HOLLING, 1959, 1965; MURDOCH, 1969). MURDOCH (1973) has stated that switching can be led by the tendencies of predators to stay in areas where prey are more abundant and to attack more abundant prey species which can result in a HOLLING's Type III response. Although individual *A.a.* can eat smaller numbers of the borer than *A.s.*, predation by *A.a.* which showed a Type III response as HOLLING (1965) reported for deer mice, *Peromyscus* spp., can be a more possible regulatory factor on the borer than that by *A.s.* (Type II response). More arboreality of *A.a.* may contribute more to predation on adult borers on cedar (*Cryptomeria japonica* D.DON) trunks. Some mice began to search for places with more borers during the experiments (*Aa-4* and *As-5*) and switched their main diet from peanuts to millipedes as the millipede density increased (Fig. 6). Therefore, it can be concluded that some mice of both species of wood mice have characteristics necessary to regulate the borer density and some of *A.s.* mice do the same with millipede.

However, it is rather difficult to evaluate directly the regulatory abilities of the mice against arthropod prey from the results of this study. The experimental system in this study was too simple. In some cases the borer densities were much higher than under natural conditions in cedar plantations, and the sounds of the walking and landing of the borer might have disturbed the behaviors of the mice. Thus, it could be that some nervous mice ate fewer peanuts. Responses to the prey density differed significantly among individual mice of both species. We must know the composition of individuals with different responses in the mice population so as to evaluate the importance of mice populations in the regulation of insect pests. Not only experimental studies in more complex systems in the field but also field observations of the feeding behaviors of the mice should be conducted.

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Literature cited

- DON, B. A. C.: Gut analysis of small mammals during a sawfly (*Cephalcia lariciphila*) outbreak. *J. Zool.*, London **188**: 290~294, 1979
- GRAHAM, S. A.: The influence of small mammals and other factors upon the larch sawfly survival. *J. Econ. Entomol.* **21**: 301~311, 1929
- HAMILTON, W. J., JR., and COOK, D. B.: Small mammals and the forest. *J. For.* **38**: 468~473, 1940
- HANSSON, L.: Small rodent food, feeding and population dynamics. A comparison between granivorous and herbivorous species in Scandinavia. *Oikos* **22**: 183~198, 1971
- HOLLING, C. G.: The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.* **91**: 293~320, 1959
- : The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* **45**: 1~60, 1965
- MORRIS, R. F., CHESHIRE, W. F., MILLER, C. A., and MOTT, D. G.: The numerical response of avian and mammalian predators during a gradation of the spruce budworm. *Ecology* **39**: 487~494, 1958
- MURDOCH, W. W.: Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* **39**: 335~354, 1969
- : The functional response of predators. *J. Appl. Ecol.* **14**: 335~341, 1973
- , and Oaten, O.: Predation and population stability. *In* *Advances in ecological research* (MACFADYEN, A., ed.). 1~131, Academic Press, London, 1975
- SATO, H.: The role of small mammals as predators of sawfly cocoons in northern Honshu, Japan. *Bull. Iwate Pref. For. Exp. St.* **2**: 1~26, 1978 (in Japanese with English Summary)
- SIEGEL, S.: *Nonparametric statistics for the behavioral sciences*. 312 pp, McGraw-Hill, Kogakusha, Tokyo, 1959
- SOLOMON, M. E.: The natural control of animal populations. *J. Anim. Ecol.* **18**: 1~35, 1949
- SONÉ, K., SEKIJIMA, T., and OKUMURA, H.: Stomach contents of the wood mouse, *Apodemus speciosus* TEMMINCK. 97th Trans. *Jpn. For. Soc.*: 467~468, 1986 (in Japanese)
- STEPHENS, D. W., and KREBS, J. R.: *Foraging theory*. 247 pp, Princeton University Press, Princeton, 1986
- WATTS, C. H. S.: The food eaten by wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) in Wytham Woods, Berkshire. *J. Anim. Ecol.* **37**: 25~41, 1968
- ZEMANECK, M.: Food and feeding habits of rodents in deciduous forest. *Acta Theriol.* **17**: 315~325, 1972

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