論　文（Original article）

Population responses of rodents to the mast seeding of dwarf bamboo *Sasamorpha borealis* over the Chubu region of Japan

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Abstract

In 2017, the mass flowering of dwarf bamboo (suzutake, *Sasamorpha borealis*) occurred throughout the Chubu region of Japan after a non-flowering interval of 120 years. Concern is growing that an abundance of seeds produced by the mass flowering could cause an outbreak of rodents and, thereby, damage to the forests. To investigate whether the rodent population would increase from the mast seeding of suzutake, trapping surveys were conducted in the hinoki cypress (*Chamaecyparis obtusa*) plantation forest in the Dando National Forest (Aichi Prefecture), located in the center of the mass flowering. The estimated rodent density did not prominently increase in the fall after mast seeding. The next spring, the density of voles (*Microtus montebelli* or *Eothenomys smithii*), which cause gnawing damage to trees, remained relatively low (3.3–23.3 individuals/ha), whereas the density of two wood mouse species (*Apodemus argenteus* and *A. speciosus*) was greatly increased (53.3–80.0 individuals/ha). These results indicate that the possibility of a widespread vole outbreak caused by mast seeding is low. However, further attention should be paid to population fluctuations in voles because populations may increase in other areas suitable for vole growth and survival.

Key words: mass flowering, pulsed resource, suzutake, vole, wood mouse

1. Introduction

In 2017, the mass flowering of suzutake (*Sasamorpha borealis*), a monocarpic species of dwarf bamboo, occurred in the Chubu region of Japan. The flowering area was estimated to extend over 200,000 km^2, from the southern part of Nagano Prefecture through Aichi Prefecture to the eastern part of Mie Prefecture (Kobayashi 2018, Okamoto et al. 2018). Reviews of ancient documents have revealed that this mass flowering occurred after an interval of 120 years (Okamoto and Saitoh 2017), and it resulted in the production of an abundance of seeds, from late July to August, following the flowering months.

In recent years, the importance of evaluating the responses of rodents to pulsed resources has been recognized in an effort to predict and control the risk of rodent damage to agriculture and forestry, as well as zoonotic infections (Schnurr et al. 2002, Ostfeld et al. 2006). One of the typical examples of pulsed resources is the mast seeding of dwarf bamboos, which is accompanied by mass flowering. The seeds of dwarf bamboos are large and highly nutritious, consisting of carbohydrates as the primary nutrient (Iwata and Nakajima 1942, Kiruba et al. 2007). Thus, they are considered an important resource for rodents. Accordingly, it is expected that the population of rodents will increase after the mast seeding of dwarf bamboos. In fact, outbreaks of rodents have been frequently observed after the mast seeding of bamboos or dwarf bamboos (Ito 1975 in Japan, Gallardo and Mercado 1999 in Chile, Belmain et al. 2010 in Bangladesh, Douangboupha et al. 2010 in Laos, Htwe et al. 2010 in Myanmar). In most cases, the rodent outbreaks cause severe damage to trees and crops cultivated near forests (Belmain et al. 2010, Douangboupha et al. 2010, Htwe et al. 2010). Therefore, studies undertaken to investigate the possibility of rodent outbreaks caused by the mast seeding of suzutake are urgently required.

Two types of rodents inhabit the forests of mainland Japan. One is the wood mouse species, which includes the large Japanese wood mouse *Apodemus speciosus* and the small Japanese wood mouse *A. argenteus* that mainly feed on seeds and small invertebrates (Ohdachi et al. 2015). The other is the vole species, which includes the Japanese field vole *Microtus montebelli*, Smith's red-backed vole *Eothenomys smithii*, and Anderson's red-backed vole *E. andersoni* that mainly feed on grass, herbs, and tree bark and roots (Ohdachi et al. 2015). When

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the population density of these voles increases, they often cause severe damage to young planted trees and crops. According to a previous report, a large increase in population density in response to the mast seeding of dwarf bamboos occurs more frequently in vole species than in wood mouse species (Ito 1975). This observation is likely related to their reproductive characteristics. Voles can mate post-partum, and thus, if other conditions are suitable, many generations can accumulate in a short period (Ando et al. 1988). In contrast, reproduction of the wood mouse species is highly regulated by the ambient temperature (Murakami 1974), which may prevent their prompt response to increased food availability as a result of mast seeding. Therefore, particular attention must be paid to the population dynamics of voles.

In the present study, we conducted rodent trapping surveys in the Dando National Forest, located in the center of the mass flowering area, to investigate whether the rodent population would increase with the mast seeding of suzutake and whether the rodents would damage trees in the area.

2. Materials and methods

2.1 Study site

The field study was conducted in the Dando National Forest (the 96th compartment; 35°11′N, 137°46′E) in Shitara-cho, the eastern part of Aichi Prefecture. This area is located at the center of the suzutake mass flowering. In this area, mass flowering occurred from May to June 2017, and the culms began to decline after flowering. Then, the mature seeds were dispersed from late July to August 2017. A small non-flowering patch of approximately 0.5 ha, in which no flowers were observed and the culms were still alive, was found in this forest, surrounded by flowering patches. This patch could not be used as a control for examining the effects of mast seeding on rodent population dynamics because rodents could easily enter and leave the non-flowering patch. Instead, in order to investigate the habitat use by rodents, two study plots were established for rodent trapping, one in the flowering patch and the other in the non-flowering patch (Fig. 1). In the trapping survey performed in August 2017, the flowering plot was set adjacent to the non-flowering plot but in the surveys after October 2017, the flowering plot was newly established about 100 m away from the non-flowering plot. Since the original plots were relatively small (0.2 ha each) and only one animal was capture in the first survey, we decided to enlarge the survey area not to miss the small changes of population fluctuations in rodents. The information on the trapping survey is shown in Table 1. Both plots were in the hinoki cypress *Chamaecyparis obtusa* (about 50 years old) plantation forests and suzutake was dominant in the undergrowth.

2.2 Trapping survey

Trapping surveys were conducted three times, in August 2017, just after the dispersal of suzutake seeds; in October 2017; and in April 2018. Twenty trap stations were constructed at intervals of about 5–10 m in a grid pattern within each plot and two Sherman-type live traps were baited with oats and sunflower seeds and placed at each station. Trapping was carried out for two or three consecutive days in the surveys of August 2017 and those after October 2017, respectively. The species, sex, body weight, distinction between adult or subadult, and reproductive status of the rodents were recorded upon capture. Reproductively active females were defined as females with perforated vulvae and/or developed mammillae, or in pregnancy or lactation, whereas reproductively active males were defined as males with testis descent. A small portion of the fur of the buttock was cut

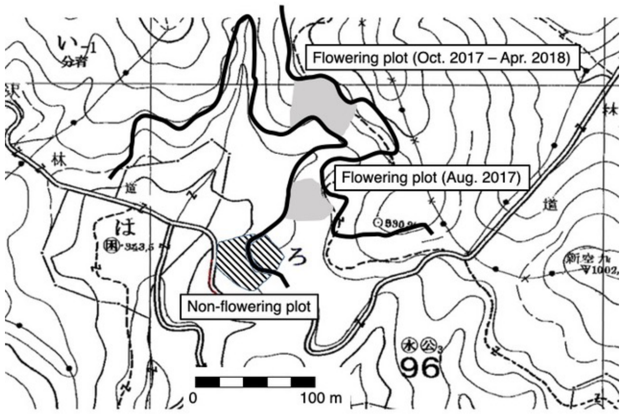

Fig. 1. Trapping plots for investigating rodent abundance in the Dando National Forest.
Suzutake (*Sasamorpha borealis*) flowered throughout this area in 2017 except for the non-flowering patch (shaded area). The flowering plot (grey area) in the first survey (August 2017) was set adjacent to the non-flowering plot. In the subsequent surveys (October 2017 and April 2018), the flowering plot was newly established about 100 m away from the non-flowering plot.

Table 1. Summary of trapping surveys in the Dando National Forest.

Period	Trapping days	Area (ha)	No. of traps
Aug. 8–10, 2017	2	0.2	40
Oct. 16–19, 2017	3	0.3	40
Apr. 17–20, 2018	3	0.3	40

These settings were common both in the flowering and non-flowering plots.

off to distinguish re-captured from newly captured individuals. The population density was estimated using MNA (minimum number alive, Krebs 1999) and expressed as the number of individuals per hectare. The methods of animal handling conformed to the Guidelines for the Procedure of Obtaining Mammal Specimens as Approved by the Mammal Society of Japan. (http://www.mammalogy.jp/en/guideline.pdf, accessed 2017–7–1). Our trapping surveys were permitted by the local government (permission Nos. 29Shin6-1–4 and 29Shin12-1–4).

Four species of rodents are known to be distributed throughout this area, *A. speciosus*, *A. argenteus*, *M. montebelli*, and *E. smithii*. The two *Apodemus* species were able to discriminated by their appearance. Contrary to this, it is difficult to distinguish *M. montebelli* from *E. smithii* by appearance. We adopted the mark-recapture method in this study and thereby did not sacrifice captured animals. Consequently, we could not examine the shape of the skull necessary for species identification. Only females with developed mammillae of these two species can be identified by appearance because characteristics of their mammae differ from each other (Ohdachi et al. 2015). For this reason, we treated both species as voles in the present study. Both vole species are listed in the Red List of Aichi Prefecture as near-threatened species (Red List Aichi 2015, http://www.pref.aichi.jp/kankyo/sizen-ka/shizen/yasei/redlist/, accessed 2017–7–1).

2.3 Nutritional analysis of seeds

To evaluate the potential of suzutake seeds as a food source for rodents, the nutritional composition of the seeds was analyzed using samples collected in August 2017 in the Dando National Forest. Two different samples of about 100 g (samples 1 and 2) were collected at different locations in the forest to serve as analytical replicates. The seed coats were removed before analyses and the crude protein, crude fat, crude ash, and moisture compositions were determined. Nitrogen-free extract (NFE) was estimated as the remainder of the nutrients. Carbohydrate is a major component of NFE. Energy content (kJ/g) was calculated using the following formula: crude protein × 4 + crude fat × 9 + NFE × 4. These analyses were performed by the Japan Functional Food Analysis and Research Center, Inc.

3. Results

In the whole study period, 47 *A. argenteus*, 43 *A. speciosus*, and nine voles were captured. Two of five female voles were identified as *E. smithii* from the mammae formula. In August 2017, just after dispersal of suzutake seeds, only one *A. argenteus* was captured in the flowering plot, which indicated the low density of any species of rodents (Table 2). In October 2017, *A. argenteus* showed an increasing tendency especially in the non-flowering plot (over 20 individuals/ha), but the density of other species remained low (Table 2). However, in April 2018, an increase of population density was observed in all rodent species except for vole spp. in the flowering plot (Table 2). The population of the two wood mouse species grew up to 50–80 individuals in both trapping plots. In addition, most of female mice were reproductively active in this period (Table 3). Contrary to this, the density of voles increased only in the non-flowering plot (Table 2), and the female reproductive ratio remained at 40% in total (Table 3).

In order to examine whether the rodent population structure differed between the flowering and non-flowering plots, the characteristics of captured in the different locations were compared (Table 3). The data for all rodent species collected

Table 2. Changes in rodent density (ha^{-1}) in the Dando National Forest.
The density is expressed in MNA (minimum number alive, Krebs 1999).

a) Flowering plot

	Aug. 2017	Oct. 2017	Apr. 2018
Apodemus argenteus	5.0 (1)	10.0 (3)	66.7 (20)
Apodemus speciosus	0.0 (0)	0.0 (0)	56.7 (17)
Vole spp. †	0.0 (0)	3.3 (1)	3.3 (1)

b) Non-flowering plot

	Aug. 2017	Oct. 2017	Apr. 2018
Apodemus argenteus	0.0 (0)	23.3 (7)	53.3 (16)
Apodemus speciosus	0.0 (0)	6.7 (2)	80.0 (24)
Vole spp. †	0.0 (0)	0.0 (0)	23.3 (7)

Numerals in parentheses represent the number of captured individuals.

†: Two vole species (*Eothenomys smithii* and *Microtus montebelli*), which are difficult to distinguish by appearance, are included.

Table 3. Comparisons of rodent population characteristics between the flowering and non-flowering sites of suzutake (*Sasamorpha borealis*) in the Dando National Forest.

a) *Apodemus argenteus* in fall (Oct. 2017)

	Flowering plot	Non-flowering plot	Statistics [d]
Number of captured individuals	3	7	
Sex ratio (female / total)	0.33 (1/3)	0.71 (5/7)	0.50
Proportion of reproductively active females [a]	1.00	0.80	1.00
Proportion of pregnant or lactating females	0.00	0.60	0.27
Proportion of reproductively active males [b]	1.00	1.00	1.00
Proportion of subadults	0.33	0.00	0.30
Average body weight [c]	19.3 ± 0.4	19.6 ± 1.9	t = 0.28, P = 0.79

b) *Apodemus argenteus* in spring (Apr. 2018)

	Flowering plot	Non-flowering plot	Statistics [d]
Number of captured individuals	20	16	
Sex ratio (female / total)	0.50 (10/20)	0.50 (8/16)	1.00
Proportion of reproductively active females [a]	0.80	1.00	0.48
Proportion of pregnant or lactating females	0.30	0.63	0.17
Proportion of reproductively active males [b]	1.00	0.88	0.27
Proportion of subadults	0.05	0.00	1.00
Average body weight [c]	16.1 ± 2.3	17.5 ± 2.4	t = 1.75, P = 0.09

c) *Apodemus speciosus* in spring (Apr. 2018)

	Flowering plot	Non-flowering plot	Statistics [d]
Number of captured individuals	17	24	
Sex ratio (female / total)	0.41 (7/17)	0.50 (12/24)	0.75
Proportion of reproductively active females [a]	1.00	1.00	1.00
Proportion of pregnant or lactating females	0.17	0.33	0.47
Proportion of reproductively active males [b]	1.00	0.89	0.36
Proportion of subadults	0.24	0.25	1.00
Average body weight [c]	38.9 ± 3.9	37.6 ± 6.9	t = 0.61, P = 0.55

d) Vole spp. in spring (Apr. 2018)

	Flowering plot	Non-flowering plot	Statistics [d]
Number of captured individuals	1	7	
Sex ratio (female / total)	1.00 (1/1)	0.57 (4/7)	1.00
Proportion of reproductively active females [a]	1.00	0.25	0.40
Proportion of pregnant or lactating females	0.00	0.00	1.00
Proportion of reproductively active males [b]	–	0.00	–
Proportion of subadults	0.00	0.00	1.00
Average body weight [c]	32.5	29.7 ± 2.6	t = 1.00, P = 0.36

[a]: calculated without subadult individuals. Reproductively active females were defined as females with perforated vulvae and/or developed mammillae, or in pregnancy or lactation.

[b]: calculated without subadult individuals. Reproductively active males were defined as males with testis descent.

[c]: expressed as mean ± *SD*; calculated without subadult individuals.

[d]: Fisher's exact probability test except for *t*-test in body weight comparisons.

Table 4. Nutritional composition and energy content of suzutake (*Sasamorpha borealis*) seeds

Constituents	Sample 1	Sample 2
Crude protein (%)	9.1	9.3
Crude fat (%)	1.7	1.2
Crude ash (%)	0.9	0.9
Nitrogen-free extracts (%)	76.3	76.9
Moisture (%)	12.0	11.7
Energy (kJ / g)	14.9	14.9

Constituents are expressed as wet weight basis.

in April 2018, as well as the data for *A. argenteus* in October 2017, were analyzed because sufficient numbers of captures had been obtained. The ratio of sexes, proportion of reproductively active males or females, proportion of pregnant or lactating females, proportion of subadults, and average body weight were compared but there were no differences between the two plots.

The nutritional composition of suzutake seeds is shown in Table 4. As predicted, the main nutrient was NFE (carbohydrates), comprising an average of 76.6% of the seed content. The content of crude protein was relatively high for plant materials. The two seed samples showed nearly identical results.

4. Discussion

The population density of rodents did not show a significant increase in the fall after the mast seeding of suzutake, however, a large increase was seen in the density of two *Apodemus* species the next spring. In contrast, the vole density over the entire study area remained low even in the spring and increased moderately only in the non-flowering plot. Ishida et al. (2018) also conducted trapping surveys in 2017 in the same region, the eastern part of Aichi Prefecture, and found results similar to ours. They found an increased density in *Apodemus* species in the fall (10–30 individuals/ha) but no increase in voles. The two results suggest that an outbreak of voles after the mast seeding did not occur, at least not in the study area.

Suzutake seeds were found to be nutritious. The nutritional composition was very similar to that of brown rice (crude protein 6.8%, crude fat 2.7%, NFE 74.3%, crude ash 1.2%, moisture 14.9%, and energy 14.8 kJ/g) according to the 2015 Japan Standard Tables of Food Composition (Seventh Revised Version, http://www.mext.go.jp/a_menu/syokuhinseibun/1365297.htm, accessed 2018–6–1). The nutritious composition of dwarf bamboo seeds, together with the vast amount produced, may have facilitated the increases in rodent populations that have been frequently observed after mast seeding (Ito 1975, Gallardo and Mercado 1999, Belmain et al. 2010, Douangboupha et al. 2010, Htwe et al. 2010).

Ito (1975) investigated the population fluctuation of rodents in 17 areas after the mast seeding of dwarf bamboos (*Sasa kurilensis* and *Sasa kurokawana*) which occurred in the Kansai and Chugoku regions in 1967–70. Of those 17 study areas, we reviewed data from five areas where the number of trapped individuals was represented by each species. In four areas, *M. montebelli* started to increase the fall after the mast seeding (40–240 individuals/ha) and a high density of this species (20–120 individuals/ha) was maintained until the next spring in two areas. An increase in *A. speciosus* the following autumn was also recognized in two areas (40–80 individuals/ha), whereas no noticeable increases were observed in *A. argenteus* and *E. smithii* populations. Similarly, another qualitative observation has reported large increases in vole numbers in the fall after the mast seeding of dwarf bamboos (Inukai 1955).

Compared to those observations, the population fluctuation of rodents observed in this study was quite different. First, no noticeable increase in the vole population was detected in our study. Although there was a moderate increase in the number of voles in the non-flowering plot in the spring, the population density did not seem to increase over a wide range. The observation that majority of voles were reproductively inactive also supports this idea. Both vole species, *E. smithii* and *M. montebelli*, are rare in this region, so the source population that would respond to mast seeding may have already been diminished. Accordingly, no noticeable increase in the vole population occurred. Voles were more abundant in the non-flowering plot than in the flowering plot. This is probably because they preferred habitat with a dense understory of dwarf bamboos. Forests with dense understories are, in general, a preferred habitat for rodents (Tanaka et al. 2006), because the vegetation can provide both food and refuge from predators.

On the other hand, the two *Apodemus* species markedly increased their density the next spring. Was this phenomenon related to the mast seeding of suzutake? Since there are no data regarding rodent density in this study site in normal (non-dwarf bamboo flowering) years, it is difficult to discriminate the effects of the mast seeding from commonly observed, seasonal population fluctuations.

The present study suggested that the possibility of a vole outbreak over a wide range caused by the mast seeding of suzutake was low. However, attention should be paid to the population fluctuation of voles because vole outbreaks may still occur in areas where voles are not rare or in habitats preferred by voles, such as orchards, grasslands, and young plantations, or in cases where mass flowering lasts for more years, gradually changing the flowering areas.

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中部地方で発生したスズタケ（*Sasamorpha borealis*）一斉結実に対する野ネズミ個体群の反応

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要旨

2017年中部地方の広い範囲で、120年振りにスズタケ（*Sasamorpha borealis*）の一斉開花が生じた。スズタケの一斉開花、そしてその後の一斉結実にともなって、野ネズミの個体数が増加し、森林への被害が生じるのではないかという懸念が広まっていた。そこで、一斉結実による野ネズミの大発生が生じるかどうかを明らかにするため、愛知営林署管内段戸国有林ヒノキ人工林において、野ネズミの捕獲調査を実施した。野ネズミは、一斉結実直後の2017年秋には顕著な増加を示さなかった。2018年春には、林木被害を引き起こすハタネズミ・ヤチネズミ類（*Microtus montebelli* または *Eothenomys smithii*）の密度は比較的低いままであったが（3.3–23.3個体/ha）、アカネズミ類（*Apodemus argenteus* および *A. speciosus*）の密度は大幅に増加した（53.3–80.0個体/ha）。これらの結果は、スズタケ一斉結実に起因してハタネズミ・ヤチネズミ類が大発生し、森林被害が広範囲で発生する可能性は低いことを示している。しかし、よりハタネズミ・ヤチネズミ類の増加に適した地域において大発生が生じる可能性は残っているため、個体数変動には今後も注意を払う必要がある。

キーワード：一斉開花、変動する資源、スズタケ、ハタネズミ・ヤチネズミ類、アカネズミ類

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