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How does the 120-year cycle mast seeding of dwarf bamboo affect the rodent population?

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Abstract

Background: In 2017, large-scale flowering, seeding, and dying events of dwarf bamboo (*Sasa borealis*) occurred in a wide range in central Japan for the first time in 120 years. This phenomenon of *S. borealis*, like the mast seeding of trees, could be expected to provide a large amount of food for seed-eating rodents and gradually affect their ecology and population dynamics. We captured rodents in survey plots in a secondary broad-leaved forest with the phenomenon from 2018 to 2019 to investigate the species, the number of individuals, growing stage, sex, and body mass. In addition, we also compared the capture data for 2 years (2018–2019) with that for the mast seeding year (2017) and 6 years before it (2011–2016).

Results: The mast seeding of *S. borealis* greatly increased the population size of rodents, especially *Apodemus speciosus* and *A. argenteus*. Conversely, *Eothenomys smithii* did not show such an increase. Most of the captured rodent individuals were already adults at the time of new capture, and the proportion of male juveniles was extremely low. These results suggest that the mast seeding of *S. borealis* created unusually rich food availability for the population concentration of rodents due to their immigration. However, body mass was not significantly different before and after the mast seeding. In addition, the increased populations of the two *Apodemus* species did not decline 2 years after the *S. borealis* masting, contrary to the previously reported decrease of rodent populations after tree masting.

Conclusions: Our results indicate that the mast seeding of *S. borealis* affected the population dynamics of *Apodemus* species over a long time and their individual composition of different growth stages. However, it did not affect their body mass.

Keywords: *Apodemus speciosus*, *Apodemus argenteus*, *Eothenomys smithii*, Mast seeding, Population dynamics, Predator satiation hypothesis, *Sasa borealis*

Introduction

In 2016, the flowering of *Sasa borealis*, a dwarf bamboo species, was confirmed in northeastern Aichi Prefecture, central Japan. It was the first time in 120 years in this region (Chubu Forest Service 2016). In the following year, 2017, large-scale flowering, seeding, and dying events (hereinafter referred to as “mast seeding”) occurred in a wide range. In general, many of the woody bamboo

species belonging to the subfamily Bambusoideae of the family Gramineae, including dwarf bamboos, show the “monocarpic” breeding. Therefore, they have a long span of alternate generations, ranging from several decades to more than a hundred years (Kobayashi 2017). Janzen (1976) describes the ecological significance of mast seeding as the predator satiation hypothesis, that is, the partial fruit crops are more likely to be eaten up by predators, but widespread concurrent fruit crops reduce the predation risk and increase the probability of contributing to the next generation.

However, various scholars have argued that the predator satiation hypothesis also applies to a phenomenon called masting in seed production of trees, which is a

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repetition of large-yield year and small-yield year. The masting has been identified in many species, including acorn-producing trees of the family Fagaceae, and it affects the ecology of the mammals and arthropods that inhabit in the forest composed of the tree species (Sakai 2013). In particular, since the population of the rodents eating the seeds as the staple food is greatly affected, monitoring has been carried out in various places around the world (Minokuchi 1988; Zwolak et al. 2016, 2018; Gasperini et al. 2016; Ogawa et al. 2017). The results show that rodent populations increase significantly in the year following the masting, but start declining 2 years after (Miguchi 1988; Zwolak et al. 2016, 2018). The relationship between tree masting and the adult body mass of rodents has also been studied, and Conrod and Reitsma (2015) found an increase in the body mass of myomorph rodents during spring, which was triggered by the rich production of acorns compared to the previous year, and a significant decrease after several months (in the summer of the current year). Similarly, the mast seeding of Bambusoideae increases the body mass index of frugi-/granivore rodents (Bovendorp et al. 2020).

It has also been reported that the rodent outbreaks (rapid increase in population) associated with increases in food sources can be caused by the mast seeding of Bambusoideae, including dwarf bamboos, similar to the masting of trees (Ito 1975; González et al. 2000; Bovendorp et al. 2020). The population fluctuation of rodents has received attention, because they cause agricultural and forestry damage and transmit diseases (Ito 1975; Jaksic and Lima 2003; Kumawat et al. 2014; Ojeda and Chazarreta 2018). Particularly, voles are forestry pests, and their outbreak has been associated with the mast seeding of dwarf bamboo (Ueda 1982). However, only a few studies have taken into account population changes before and after mast seeding. Shimada et al. (2019) found that the mast seeding of *S. borealis* resulted in an increase of forest mouse (the genus *Apodemus*) population, but not voles in *Chamaecyparis obtuse* plantation forest. However, this was based on a capture study conducted in the year immediately after the mast seeding; therefore, it only examined a single-year effect on the mice. Similar to the masting of acorn-producing tree, the mast seeding of dwarf bamboo may change the habitat of rodents after 2 years.

In this study, a survey site was set up in the secondary broad-leaved forest, where the mast seeding of *S. borealis* was observed in 2017, and rodents were captured from 2018 to 2019 to evaluate the impact of the mast seeding by comparing with pre-mast seeding capture data.

Methods

Survey site

The survey site was set up in the Takatokke district of Nagoya University Forest (the Inabu Field affiliated with the Graduate School of Bioagricultural Sciences, Nagoya University), located in the northeastern part of Aichi Prefecture, central Japan. The elevation is about 1050 m. In 2019, the annual precipitation was 2334 mm and the average annual temperature was 10.1 °C. The site is a secondary forest composed of deciduous broad-leaved trees mainly of *Quercus crispula* and *Castanea crenata* species, adjoining artificial forests of coniferous trees of *Larix kaempferi* and *Chamaecyparis obtusa*. Notably, no tree masting has occurred at the site since 2017.

Setting up survey plots

In 2018, four 15 × 15 m (0.0225 ha) plots (plots A, B, C, and D) were set up in the site (35° 13' 03.0" N, 137° 34' 22.0" E), where the mast seeding of *S. borealis* was observed in 2017 (Fig. 1). The criteria of the plot establishment included a similar forest type and density of dead *S. borealis* culms and flat sites. Using the seed production data of *S. borealis* in Aichi Prefecture (Saitoh Tomoyuki, unpublished data), we estimated that approximately 16,000 seeds/m² were supplied in this study area in 2017. Plots A and C were enclosed by a polyethylene net (height: 1.2 m, mesh size: 13 cm) with the support of wooden stake and ting to keep out middle- and large-sized mammals, such as Sika deer (*Cervus nippon*). However, the net in no way affected the coming and going of rodents. All the plots adjoin or contain a stream or wetland.



Fig. 1 Spikelets of *Sasa borealis*

Capture of rodents

Data were collected using a capture–mark–recapture method. The trapping was conducted for two nights of the three days (trapping session), every month from June to November in 2018 and from May to December in 2019, resulting in 14 trapping sessions. On the first day of each trapping session, nine live traps (Sherman traps) were set up in a grid point of 7.5 m intervals in each plot. In the trap, about 30 sunflower seeds were introduced as attractant baits. At the setup after November, foam–polystyrene sheets were placed in the traps to prevent freezing to death. Checking the trap (presence or absence of rodents) was carried out daily from 8:00 to 11:00 a.m. The species of the captured rodents was identified, their sex and body mass were recorded, and they were finally marked by toe-clipping. After the individual recognition, the marked rodents were released at the captured trap point.

The monthly rodent population was considered as the total number of rodents captured over the trapping session in each survey month. If the same rodent was captured on two consecutive nights, the number was assumed one. *Apodemus speciosus* and *A. argenteus* were defined as adult rodents weighing 30 g or more and 14 g or more, respectively (Miguchi 1988). The captured rodents were classified into three growing stages: (1) adults, (2) settled juveniles (those that were juveniles at the first capture and were recaptured after growing into adults), and (3) emigrated juveniles (those that were juveniles at the first time of capture but were never recaptured after growth). By distinguishing between (2) and (3), we examined whether there were differences in the proportion of individuals that remained in the mast-seeding area among species, sex, or year of capture.

Comparison between pre-mast years, mast year and after-mast years

Using the capturing data of the rodents from 2011 to 2017 in the area that includes Plot A, used in this study, we investigated the dynamics of the population and the change of the body mass before and after the mast seeding. The capture method was the same as in 2018 and 2019. From 2011 to 2016 (Period I), 14 traps were set up at the grid pattern of 10 m intervals over an area of 0.0700 ha. In 2017 (Period II), 40 traps were set up at the grid pattern of 2 m intervals over an area of 0.0140 ha. For 2018 and 2019 (Period III), only data from plot A was used, which overlaps with the site of Periods I and II. The study sites of Periods I, II and III partially overlap, have the same tree species composition and environment, and probably have the same rodent fauna.

The comparison of rodent populations was made based on the total number of individuals caught from July to October from 2011 to 2019. Since the area and number of traps used were different among the three periods, the value of the rodent population was normalized. Thus, we used two values for the comparison. The one is y , which was converted per the area of Period III (0.0225 ha). The other is y' , which was converted per the area of Period III (0.0225 ha) and the number of capture trials (9 traps \times 2 nights \times 4 months = 72 trap nights). The changes in body mass observed before (2015, 2016) and after (2018, 2019) the mast seeding were compared using data from July to November in adults of the most abundant rodent species (i.e., *A. speciosus* and *A. argenteus*).

Data analysis

The proportions (%) of individuals in different growing stages (adults, settled juveniles, and emigrated juveniles) of the captured rodents from June to November for each year were calculated for both males and females of *A. speciosus* and *A. argenteus*, and were tested for significance using Fisher's exact test. The mean values of their body mass before and after the mast seeding were compared using the Student's T test. The statistical software R ver. 3.5.1 (R Development Core Team 2018) was used for all the analyses.

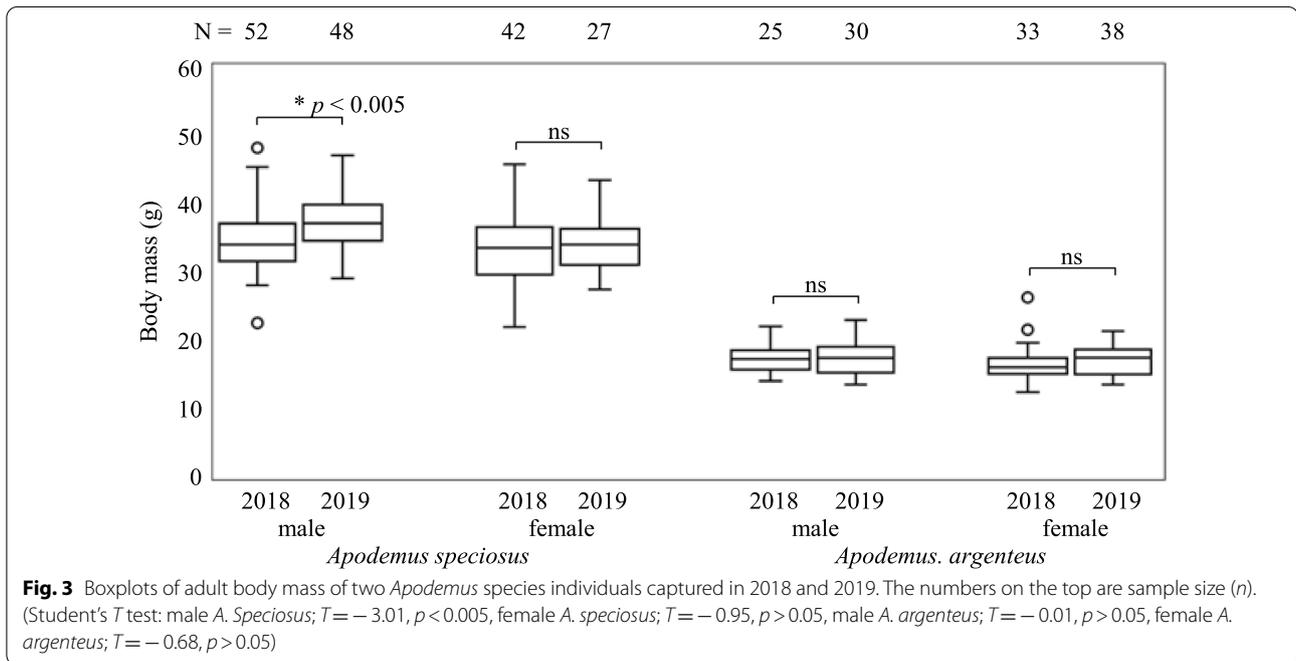
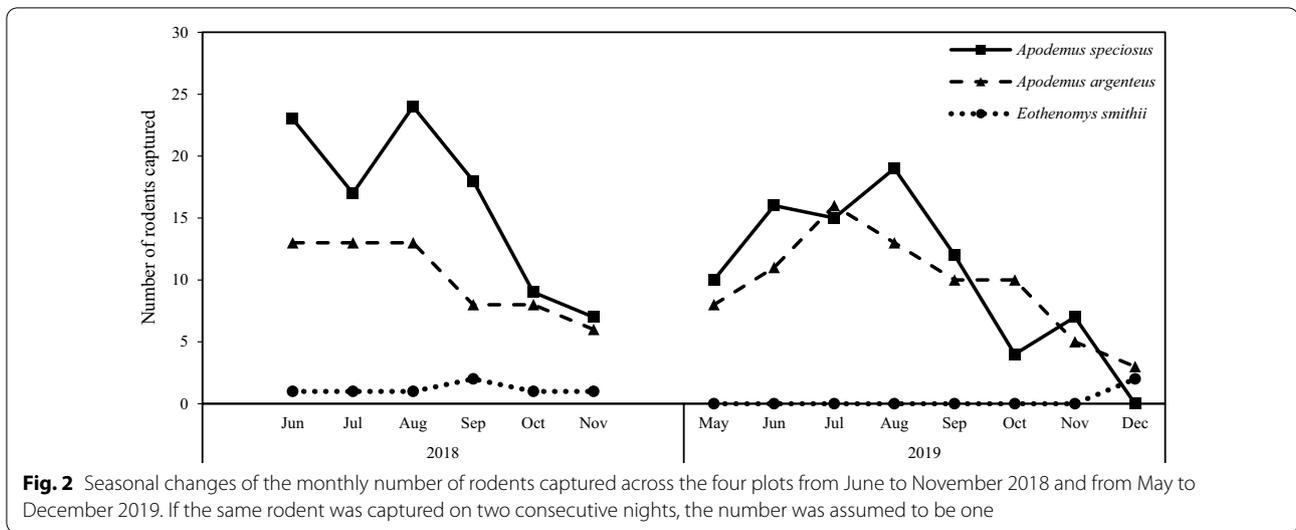
Results

Ecology of rodents in 2018–2019

The captured rodents were of three species: *A. speciosus*, *A. argenteus*, and *Eothenomys smithii*. Within 2 years, the total number of catches was 418, and the total number of marked rodents was 147 for the 1008 trap nights (Additional file 1: Table S1-a and S1-b). *A. speciosus* and *A. argenteus* were captured in all the plots in both years, but *E. smithii* were found in plot B and plot C in 2018 and only in plot A in 2019. The total number of the catches of *A. speciosus* and *A. argenteus* was 129 times and 76 times in 2018, and 106 times and 96 times in 2019, respectively. The values of *A. speciosus* were higher than those of *A. argenteus* in both years. The total number of the catches of *E. smithii* was much less than that of the two *Apodemus* species, and it was nine in 2018 and two in 2019.

In 2018 and 2019, the *A. speciosus* population showed a dramatic declining trend from September to October (Fig. 2). However, the *A. argenteus* population gradually decreased from September to December. Only two individuals of *E. smithii* were captured in each year.

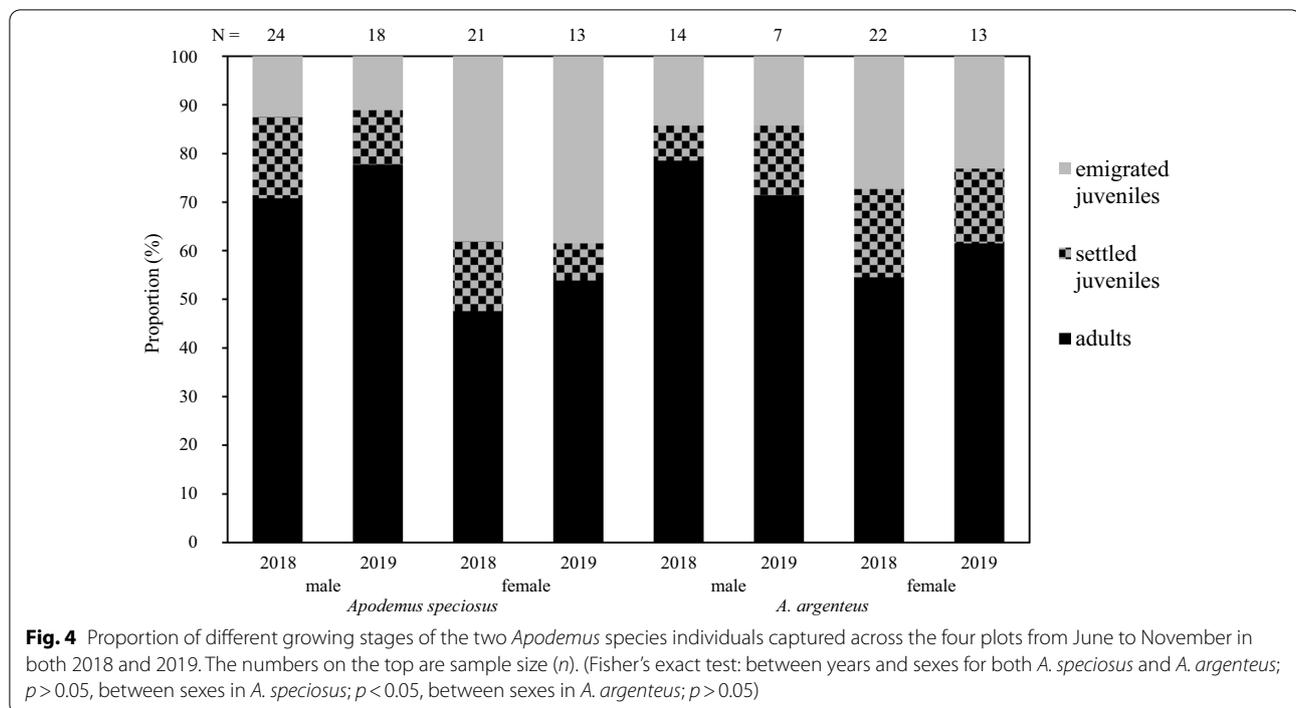
In 2018 and 2019, the mean body mass of adults from June to November was 34.6 ± 4.4 g (\pm SD, $n=52$) and 37.1 ± 3.6 g ($n=48$) for male *A. speciosus*; 33.3 ± 5.5 g ($n=42$) and 34.5 ± 4.1 g ($n=27$) for female *A. speciosus*; 17.2 ± 2.0 g ($n=25$) and 17.2 ± 2.4 g ($n=30$) for male



A. argenteus; and 16.6 ± 2.9 g ($n = 33$) and 17.0 ± 2.1 g ($n = 38$) for female *A. argenteus*, respectively (Fig. 3). In male *A. speciosus*, the body mass in 2019 was significantly higher than that in 2018 (Student's *T* test: $T = -3.01, p < 0.005$). In the other cases, there was no significant difference in the body mass between the years but female *A. speciosus* and *A. argenteus* showed a slight increase from 2018 to 2019.

There was no significant difference in proportions of adults, settled juveniles, and emigrated juveniles of the captured rodents from June to November between 2018

and 2019 for each sex *A. speciosus* and *A. argenteus*, respectively (Fig. 4). In all the categories, the proportion of adults was the highest. In *A. speciosus*, the proportion of adults was over 70% in males, while it was around 50% in females, recording a significant difference between the sexes when the data of 2 years were combined (Fisher's exact test, $p < 0.05$). Conversely, the proportion of its juveniles tended to be higher in females than in males, although there was no significant difference. A similar trend was also observed in *A. argenteus*. No significant differences were observed in the proportion of juveniles



that continued to stay or emigrated among species, sex, or year of capture.

Population dynamics of the rodents from 2011 to 2019

The annual number of captures of the three rodent species—*A. speciosus*, *A. argenteus*, and *E. smithii*—from 2011 to 2019 changed strongly after the period of the mast seeding (Fig. 5; Additional file 1: Table S2). The number of *A. speciosus* and *A. argenteus* increased sharply in the conversion per area (y) in 2017, when the mast seeding occurred, with a 493% and 239% increase compared with the average from 2011 to 2016. The conversion per area and number of capture trials (y') increased substantially in 2018, the year after mast seeding, increasing by 756% and 239% in each species, compared with the average from 2011 to 2016. In 2019, 2 years after the mast seeding, these populations did not return to their previous values before the rapid increase, and the number of *A. argenteus* increased from 2018. *E. smithii*, on the other hand, was not caught between July and October since 2017.

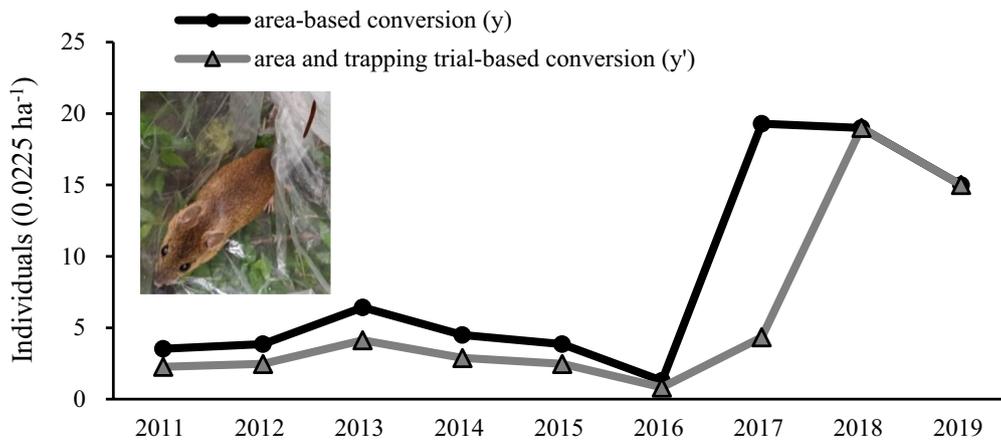
The mean body mass of the adults before (2015 and 2016) and after the mast seeding (2018 and 2019) was 37.8 ± 4.0 g (\pm SD, $n=8$) and 35.6 ± 4.7 g ($n=23$) for male *A. speciosus*; 35.2 ± 2.1 g ($n=9$) and 32.8 ± 3.9 g ($n=10$) for female *A. speciosus*; 18.7 ± 4.3 g ($n=37$) and 16.1 ± 1.6 g ($n=9$) for male *A. argenteus*; and 16.6 ± 2.9 g ($n=26$) and 16.6 ± 2.2 g ($n=23$) for female *A. argenteus*, respectively (Fig. 6; Additional file 1: Table S1-c and

S1-d). Body mass tended to decrease after mast seeding and in both sexes of *A. speciosus* and for male *A. argenteus*, although no significant differences were observed.

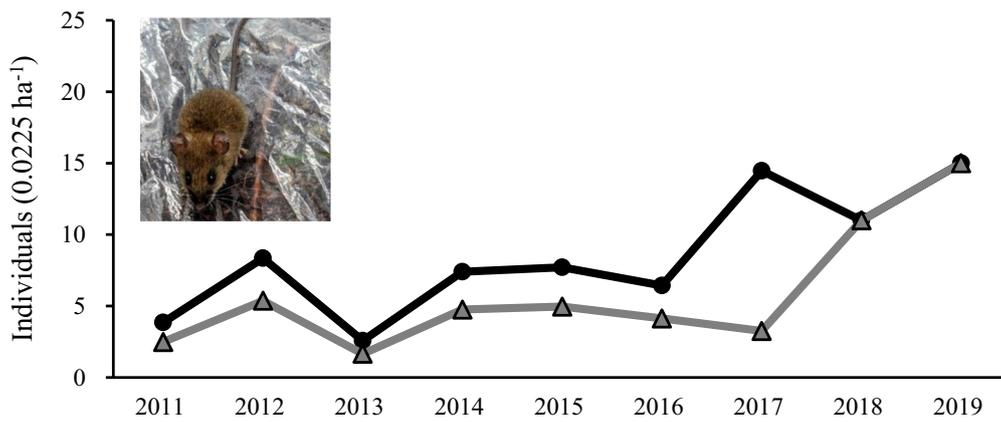
Discussion

Based on a comparison of the number of individuals captured before and after 2017, both *Apodemus* species, *A. speciosus* and *A. argenteus*, increased dramatically after the mast seeding of *S. borealis* (Fig. 5). Conversely, *E. smithii* did not show such an increase. Therefore, the mast seeding significantly contributed to the increase in the populations of *A. speciosus* and *A. argenteus*, but did not affect the reproduction of *E. smithii*. The response in abundance of the two *Apodemus* species in this study is similar to that seen after the mast seeding of trees. Miguchi (1988) reported that *Microtus montebelli* and *A. speciosus* had an outbreak in the year following the masting of *Fugus crenata* in Japan. Similarly, Zwolak et al. (2016) revealed that in Poland, the numbers of *A. agrarius* and *Myodes glareolus* (a species of the vole) increased after the masting of *F. sylvatica*. In the case of bamboo, Bovendorp et al. (2020) reported an increase in the number of rodents after the mast seeding of the subfamily Bambusoideae in Brazil. In addition, Shimada et al. (2019) conducted a rodent-capture survey at other *S. borealis* deadlands in 2017, the same year as in this study, and the findings revealed that in the year following the masting, *A. speciosus* and *A. argenteus* increased, while *E. smithii* remained low density. The findings of this study showed

A *Apodemus speciosus*



B *Apodemus argenteus*



C *Eothenomys smithii*

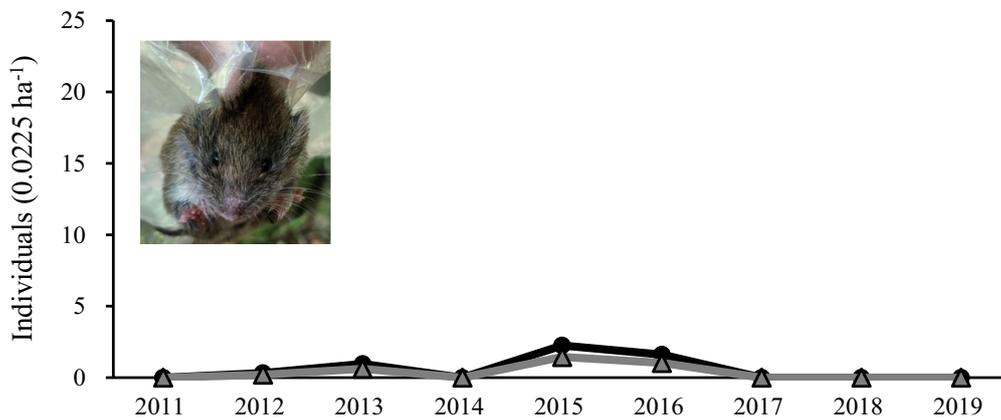
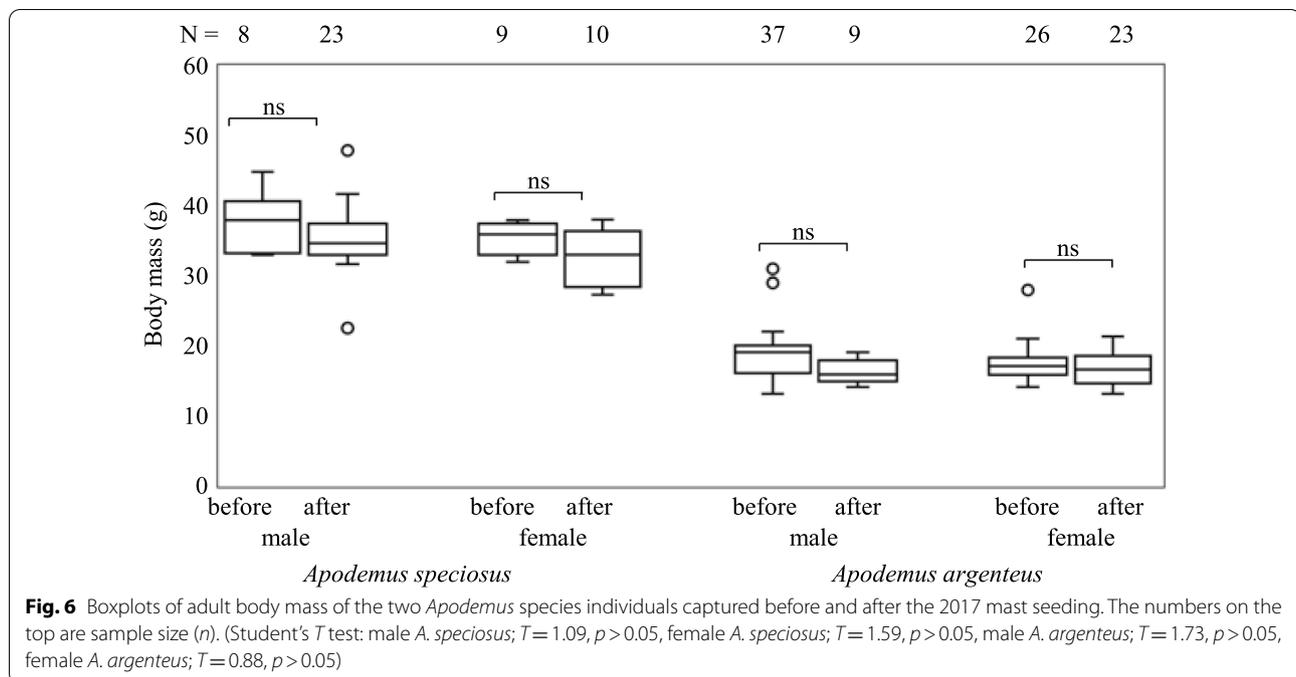


Fig. 5 Population dynamics of the three rodent species in the annual number captured for 9 years from 2011 to 2019 before and after the mast seeding. **A** *Apodemus speciosus*, **B** *Apodemus argenteus*, and **C** *Eothenomys smithii*. Black (y) and gray (y') lines represent values per the unit area (0.0225 ha) and the unit area (0.0225 ha), inclusive of trapping trial (72 trap nights), respectively



a faster population increase in *Apodemus* species than that in Shimada et al. (2019). The response time differs owing to the differences in the habitat conditions of the rodents at the study sites. Our study site is a secondary broad-leaved forest with the original rodent populations, whereas that of Shimada et al. (2019) is a planted coniferous forest, to which numerous rodent individuals migrated from the surrounding original habitat after the mast seeding. Regarding *E. smithii*, which did not increase in our study, a large outbreak, however, was observed in Tokushima Prefecture, western Japan. This phenomenon occurred in the same year as the simultaneous fruiting of dwarf bamboo but was limited to some survey sites and considered not directly related (Tanaka 1967). *E. smithii* gets nourishment from the green part of plants and the starch of seeds (Kaneko 2005). Since more than 76% of the nutrients of *S. borealis* seeds are nitrogen-free extracts (carbohydrates) (Shimada et al. 2019), it is entirely possible that voles eat them as food. However, *E. smithii* prefers moist areas (Tanaka and Shibata 2006), so that its habitat is more limited than that of the two *Apodemus* species. Therefore, despite the large supply of *S. borealis* seeds, the *E. smithii* population may have not increased because of the difficulty of external immigration, which is likely to occur in *A. speciosus* and *A. argenteus*. In addition, Conrod and Reitsma (2015) reported that in an American forest, where three species of rodents existed together, only *Napaeozapus insignis* was no longer captured due to interference among the species after masting. Fasola and Canova (2000) also

found that the exclusion of a species of the genus *Apodemus* increased the population density of bank voles, while the vole exclusion had little effect on the *Apodemus* species, which implies that asymmetrical competition was established between the two species in Italy. These facts suggest that in this study area, *E. smithii* may have been suppressed by *A. speciosus* and *A. argenteus*, both of which increased rapidly in the population density, and could not inhabit the surveyed areas.

It is well known that rodent populations increase significantly in the year following tree mast events, but decrease after 2 years (Miguchi 1988; Zwolak et al. 2016, 2018). Conversely, our study found that in 2019, 2 years after the mast seeding of *S. borealis*, the increased populations of *A. speciosus* and *A. argenteus* remained the same (Fig. 2). This difference may be attributed to the fact that the food supply associated with the mast seeding of *S. borealis* was more persistent than that of the trees. It is also reported that most of the fallen acorns are eaten by rodents or the black bear (*Ursus thibetanus*), even in the case of a good harvest year, and then the rest germinates the following spring (Kikuzawa 1988; Ida and Nakagoshi 1996). However, we observed many *S. borealis* seedlings even in 2019 at the survey sites examined in this study, suggesting that most of its seeds have remained on forest floors for a few years.

In this study, regardless of the species (*A. speciosus* and *A. argenteus*) or sex of rodents, the body mass were not significantly different before and after mast seeding (Fig. 6). These results suggest that the increase in food

sources due to mast seeding did not contribute to body mass gain. It is also worth noting that the body mass decreased slightly after mast seeding (Fig. 3), which seems to be slightly similar to the pattern (Krebs 2013) that in the increasing population of rodents, females mature earlier and become smaller. On the other hand, from 2018 to 2019 (the period after mast seeding), there was a significant increase in the mean body mass of *A. speciosus* adult males (Fig. 3). These results can be explained by the fact that there were many *S. borealis* seeds on forest floor at the end of the 2-year period, which may have resulted in higher intake by the rodents in 2019. Conrod and Reitsma (2015) showed that the mean body mass of adults for three rodent species, *Peromyscus* sp., *Napaeozapus insignis*, and *Myodes gapperi*, was heavier in the post-masting spring than in the pre-masting spring of trees. However, in the current summer following this response, *N. insignis* disappeared completely from their study area, and then the mean body mass of *M. gapperi* and *Peromyscus* sp. was found to have decreased—probably due to low food-availability and density-dependent competition for the vacant niches. In addition, Scarlett (2004) found a significant mean body mass loss in *P. leucopus* in the first of the two straight years of low acorn yield, compared to the masting year, but no difference in the second of the two straight years of low acorn yield, which suggests that factors other than acorn availability may affect the body mass change of the rodents. Therefore, patterns of the body mass change associated with masting are not consistent for dwarf bamboo and trees. Further investigations are needed to explain the mechanism, including the dynamics of other food sources.

The proportion of adults was already high at the time of new capture in both *A. speciosus* and *A. argenteus* (Fig. 4), suggesting immigration. It is evident that juveniles of *A. speciosus* tend to disperse and move away from their birth sites (Miguchi 1988; Sekijima 2008). Therefore, the proportion of juveniles in the study area may have decreased because of their natal dispersal. Moreover, the survey plots used for the capture process in this study were flatter and had a higher density of dead *S. borealis* culms than the surrounding areas did, suggesting that a high seed density was produced. The relative dominance of food sources in the plots may have led to the increase in the migration from the surroundings. In fact, Miguchi (1988) found that an increase in acorn supply due to the masting of *F. crenata* resulted in the concentration of *A. speciosus*, which is likely to actively get around. Ogawa et al. (2017) categorized the effects on the population dynamics of rodents depending on the abundance of seeds as food sources: (1) increased growth, (2) increased survival, and (3) increased immigration. Among them, the third effect, increased immigration, was observed in

Pinus strobus seeds, which were particularly abundant. Therefore, the effect of *S. borealis* seeds on rodent population is considered similar to that of *P. strobus* seeds. Furthermore, males tended to have a higher proportion of adults than females in both *A. speciosus* and *A. argenteus* (Fig. 4). These results may also be explained by the differences in mobility (females < male).

In this study, the proportion of juveniles was different between males and females in both 2018 and 2019, with higher values being recorded for females (Fig. 4). In *A. argenteus*, female juveniles increased when seeds, which they ate as food, were abundant and conditions for female breeding were good (Shibata and Kawamichi 2009). In the survey sites used in this study, the food amount was much higher than before due to the mast seeding of *S. borealis*, and the breeding conditions for females in *A. argenteus* as well as *A. speciosus* improved. Therefore, the *S. borealis* masting clearly caused an increase in female juveniles. If so, since this food abundance did not change between 2018 and 2019, the breeding female rodents were still in good condition after 2 years of mast seeding. Furthermore, it has been reported that the sex ratio of *A. argenteus* captured usually tends to be higher in males (Kinoshita and Maeda 1961; Miyao et al. 1963). In this study, the results were the opposite—more females were caught in each year, which may be due to the unusual (the 120-year cycle) mast seeding of *S. borealis*.

Conclusions

The findings of the present study revealed that the mast seeding of *S. borealis* greatly affected the population growth of rodents, especially *A. speciosus* and *A. argenteus*. The increased populations did not return to their previous levels 2 years after the *S. borealis* masting, which contrasts the findings in the case of the tree masting. Most of the captured rodents were adults already at the time of new capture, and the proportion of male juveniles was extremely low. Even after 2 years of masting, many *S. borealis* seeds remained despite the rapid increase in seed-eating rodents. These facts support the predator satiation hypothesis proposed by Janzen (1976). However, the rodents might have a weak preference for *S. borealis* seeds. Therefore, it is important to investigate their preference in future studies to elucidate the impact of the seeds on rodents. In addition to food availability, other factors, such as environmental conditions and the presence of predators, are strongly associated with the dynamics of rodent populations after masting, as shown in this study, for seeds of dwarf bamboos and acorns of trees (Thakur and Firake 2014; Kumawat et al. 2014; Selås 2016). Therefore, future studies should also consider the relative contribution of other potential factors to the rodent outbreak.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-022-00385-x>.

Additional file 1: Table 1. Data (sex, individual number, and weight) on individuals captured in 2016, 2015, 2018, and 2019 for three rodent species. **Table 2.** Number of captured populations of the three rodent species in each month from 2011 to 2019 before and after the mast seeding.

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Author contributions

HS, HaK and HiK conceived the ideas and designed the study. HS and HaK collected field data. HS analyzed the data and led the writing of the first draft of the manuscript. HiK substantially contributed to revising the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The data sets supporting the conclusions of this article are included within the article and its additional files.

Declarations

Ethics approval and consent to participate

The capture of rodents in this survey site and toe-clipping for individual recognition was carried out with the permission of Aichi Prefecture.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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