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Wood Mice Utilize Understory Vegetation of Leafless Dead Dwarf Bamboo Culms as a Habitat and Foraging Site

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Abstract: In this study, we conducted a field survey in Aichi Prefecture, central Japan, to clarify whether rodent activity is affected by the presence or absence of dead culms of the dwarf bamboo *Sasa borealis*, a species characterized by a 120-year cycle of large-scale flowering, seeding, and dying. We found that a relatively larger number of wood mice, *Apodemus speciosus* and *Apodemus argenteus*, were caught using Sherman live traps in areas with dead *S. borealis* culms than in areas lacking the culms, thereby indicating that *S. borealis* culms, even if dead and leafless, can function as shelters in which the mice can evade predation. However, in the years when *A. speciosus* was abundant, *A. argenteus* avoided areas inhabited by *A. speciosus* and was restricted to areas lacking dead culms, which were devoid of shelter. A feeding experiment using *Castanea crenata* acorns clearly revealed that a larger number of acorns were foraged by mice in areas containing dead culms. Moreover, in the area with dead culms, the mice preferentially removed sound acorns prior to taking acorns that had been vacated by infesting moth larvae. These findings indicate that the shelter function of dead culms enables mice to carefully select sound acorns, which are nutritionally more beneficial than those that have been infested by moth larvae.

Keywords: acorn; *Apodemus argenteus*; *Apodemus speciosus*; dead culm; dwarf bamboo; habitat; *Sasa borealis*; shelter; wood mouse

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1. Introduction

For small-sized rodents, vegetation cover serves as a shelter from predators [1,2]. Given that the risk of predation is higher in open areas [3–5], it can be predicted that rodent activity would be notably reduced in such areas. The presence or absence of grass [6], fallen trees [7], and dwarf bamboos such as *Sasa* spp. [8,9] have been shown to influence rodent activity. In East Asia, forest floors are often covered with *Sasa* bamboos, and in previous studies, a higher *Sasa* coverage has been shown to be associated with an increase in rodent density [8,10]. Moreover, significant increases in the foraging behavior of rodents have been observed in the presence of *Sasa* bamboo, which in turn has important implications for tree regeneration [9].

Rodent activity is also influenced by the availability of light, including moonlight [11,12]. The foliage of *Sasa* bamboo effectively intercepts light [8], resulting in darker environments in which rodents prefer to forage [13–15], given that higher light levels enhance the visual acuity of predators [16].

In 2017, for the first time in 120 years, large-scale flowering, seeding, and death of *Sasa borealis*, a dwarf bamboo species, occurred in the northeastern region of Aichi Prefecture in central Japan. This event accordingly resulted in the mass deposition of seeds on the forest floor and consequently led to a rapid increase in *Apodemus* mouse populations [17,18]. Subsequently, the dead culms of the bamboos remained standing. Despite completely lacking in leaves to provide coverage of the forest floor, the presence of rodents has been recorded in these forest areas [19]. However, there is still no proof to indicate whether these dead culms also provide shelter for rodent populations. We have observed that the dead culms in this area remained standing in 2021 (four years after 2017), although to the best of our knowledge there is no literature indicating the potential length of time such dwarf bamboo remnants remain.

In this study, we sought to clarify whether the activities of two wood mice species, *Apodemus speciosus* and *Apodemus argenteus* (Figure 1), are influenced by the presence or absence of dead *S. borealis* culms. To this end, we compared the numbers of *Apodemus* mice captured in areas with and without dead culms over a 3-year period. We reasoned that if foraging is more frequent in areas with dead culms than in areas without these culms, this would infer that dead culms play an important role in the habitat selection and foraging activities of these mice. We also conducted a feeding experiment with acorns to examine their foraging activity in more detail, in which mice were given the opportunity select between two types of acorn, namely, sound and previously insect-infested. If the sound acorns were removed preferentially, it could be assumed that the mice were able to safely assess acorn quality.

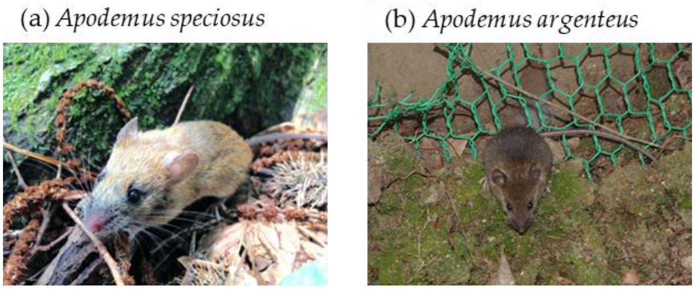


Figure 1. Wood mice, (**a**) *Apodemus speciosus* and (**b**) *Apodemus argenteus*.

2. Materials and Methods

2.1. Study Site and Rodent Species

The study was conducted between 2019 and 2021 in a site of the Takatokke district of the Nagoya University Forest (Inabu Field), located in the northeastern part of Aichi Prefecture, central Japan. The site, which has an elevation of approximately 1050 m, has an average annual temperature and rainfall of approximately 9.4 °C and 2100 mm, respectively. Three species of small rodents, namely, the two wood mice *A. speciosus* and *A. argenteus* and the vole *Eothenomys smithii*, have been confirmed to inhabit this district [18]. *A. speciosus* and *A. argenteus* are sympatric and endemic species that are widely distributed in Japan, wherein they feed on the seeds of a range of plant species, mostly acorns produced by trees in the family Fagaceae [20].

Within the study site, we established a 50 m × 50 m plot (Figure 2) comprising two areas, one of which contained a large number of dead culms (hereafter referred to as the DC area) and the other encompassing an area with no or few dead culms (hereafter referred to as the NDC area) (Figure 3). The culm density (no./m^2) of the DC and NDC areas was 12.42 ± 3.99 and 0.89 ± 1.55 (mean ± SD), respectively. Within the plot, the tall tree layer comprised *Castanea crenata*, *Quercus crispula*, and *Pinus densiflora*, whereas *Lindera triloba* was the main species growing in the shrub layer. With the exception of *S. borealis*, the understory vegetation was comparatively sparse. Moreover, we did not find any live *S. borealis* specimens within or surrounding the plot.

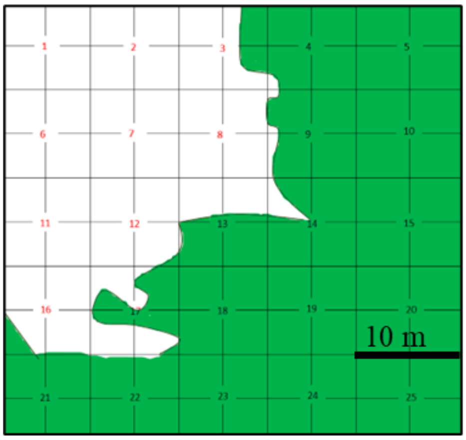
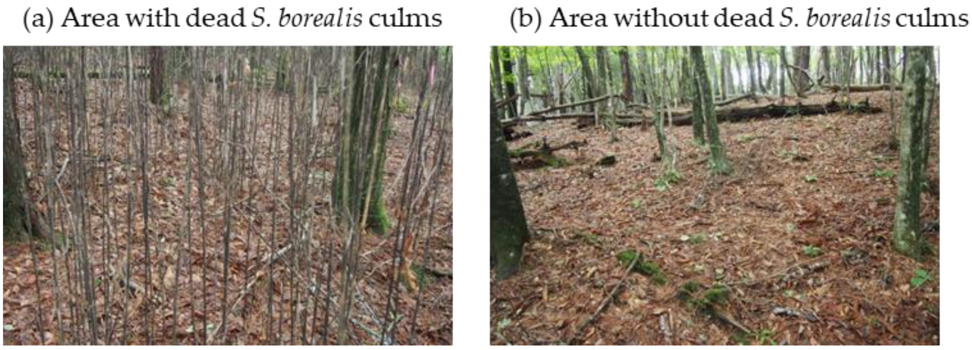


Figure 2. Design of the study plot. The green portion of the plot denotes the area containing dead *Sasa borealis* culms, and the white portion denotes the area devoid of *S. borealis* culms. Digits: trap points.


(a) Area with dead *S. borealis* culms

(b) Area without dead *S. borealis* culms

Figure 3. Photographs showing representative sections of the forest floor in areas (**a**) with and (**b**) without dead *Sasa borealis* culms in the study plot.

2.2. Effects of Dead Culms on Rodent Abundance

For the purposes of capturing rodents, we used Sherman live traps (67 mm × 90 mm × 290 mm), which were placed at grid points spaced at 10-m intervals (16 and 9 traps in the DC and NDC areas, respectively) (Figure 2). Over the 3 years of the study period, traps were installed for three consecutive nights at approximately 4-week intervals between late June and early October, with sunflower seeds being used as bait. On each of the two trapping days, the traps were inspected between 08:00 and 12:00 h for the presence of rodents. At each trap point, we recorded the species, sex, and body weight of any captured rodents; prior to their release, we marked the captured mice by toe-clipping (permission was obtained from Aichi Prefecture). Having confirmed the identity of individuals, the marked rodents were released at the point of capture. Adult *A. speciosus* and *A. argenteus* were defined as those mice weighing 30 g or more and 14 g or more, respectively [21]. For individuals captured on two consecutive nights, the average body weight for each day was calculated to determine whether they were adults. In that case, if the mouse had been captured within the previous month and recorded as an adult, it was recorded as an adult. If it was not possible to determine whether the mouse was an adult, it was recorded as unknown. In addition, individuals with a clearly small body size were recorded as juveniles. Body weight was not measured when it rained. The breeding season was estimated from the number of adults and juveniles captured during each period. As a measure of population density, capture numbers were converted to the number of individuals per hectare for each mouse species and separately for the males and females of each species.

2.3. Effects of Dead Culms on Rodent Foraging Behavior

In October 2021, for both the DC and NDC areas, we conducted feeding experiments using sound *C. crenata* acorns, along with those that had previously been infested with moth larvae. The latter are characterized by large exit holes of approximately 5 mm in diameter and can thus be readily identified visually. One of each of the two acorn types was placed on the same trays (food stations), which were set up at approximately 16:00 h, and these were continuously monitored using video cameras (Hyke SP2; Hyke, Inc., Hokkaido, Japan) until the following next morning. The images obtained were subsequently reviewed, and the type of acorn removed by mice and the order of removal were determined. Given that we initially established the positions (right or left) of the two types of acorns on the tray for each station, in cases in which both acorns had been removed, it was possible to determine which type of acorn was the first to be selected by the rodents. In total, fifteen and eight such trials were conducted in the DC and NDC areas, respectively.

2.4. Statistical Analysis

To determine whether the rodents of each species visited the DC or NDC areas more frequently, we compared the capture rate [number of trap nights (trap number multiplied by night times) in which rodents were captured/all number of trap nights assessed] using Fisher's exact test. To evaluate whether rodents were able to preferentially select sound acorns, we calculated standardized scores [19] based on the removal order data, in which the acorns removed first and second were assigned scores of 2 and 1, respectively, and all non-removed acorns were assigned no score. The Mann–Whitney *U*-test was used to compare the scores obtained for the two acorn types, with a significantly higher score indicating a higher preference.

All analyses were performed using R ver. 3.6.1 [22].

3. Results

Over the 3-year period of monitoring in this study, we captured both *A. speciosus* and *A. argenteus* within the study plots, whereas no *E. smithii* individuals entered traps. In both 2019 and 2020, the population density of *A. speciosus* was particularly high for both sexes, although numbers declined markedly in 2021 (Table 1). Comparatively, the population density of *A. argenteus* remained relatively stable over the 3 years, with numbers exceeding those of *A. speciosus* in 2021 (Table 1). The population of *A. speciosus* was found to increase during the summer (late July to early September) and thereafter decline (Figure 4a). However, whereas *A. argenteus* showed a similar trend in 2019, in 2020 and 2021, we observed a slight tendency for the population to decline in summer (Figure 4b). Juveniles of *A. speciosus* were generally captured from the end of June to the beginning of September, whereas the trends for *A. argenteus* showed inter-annual variation (Figure 4). The mean body weights of the adult males, adult females, juvenile males, and juvenile females of *A. speciosus* were approximately 34–45 g, 39 g, 21–22 g, and 27–28 g, respectively (Table 2), whereas the corresponding weights for *A. argenteus* were approximately 16–18 g, 18–20 g, 12–14 g, and 12 g (Table 2). Therefore, even the juveniles of *A. speciosus* weighed more than *A. argenteus* adults. In all 3 years, the capture rate of mice (*A. speciosus* + *A. argenteus*) in the DC area was significantly higher than that in the NDC area ($p < 0.05$, Figure 5). In terms of the individual mouse species, rate of *A. speciosus* capture in the DC area was significantly higher than that in the NDC area in 2019 and 2020 ($p < 0.005$, Figure 6a). In contrast, for *A. argenteus*, there was no significant difference in the capture rates between the DC and NDC areas in 2019 and 2020 ($p = 0.5761$ and 0.4063, respectively; Figure 6b). However, in 2021, when *A. argenteus* was relatively more abundant than *A. speciosus*, the rate of capture in the DC area was significantly higher than that in the NDC area ($p < 0.001$; Figure 6b).

Table 1. Population densities of the two *Apodemus* species of wood mice in each of the three study years.

Year	**Population Density (No./ha)**					
	A. speciosus			***A. argenteus***		
	♂	♀	**Total**	♂	♀	**Total**
2019	56.3	18.8	75.1	31.3	6.3	37.6
2020	50.0	50.0	100.0	43.8	12.5	56.3
2021	12.5	0.0	12.5	31.3	25.0	56.3

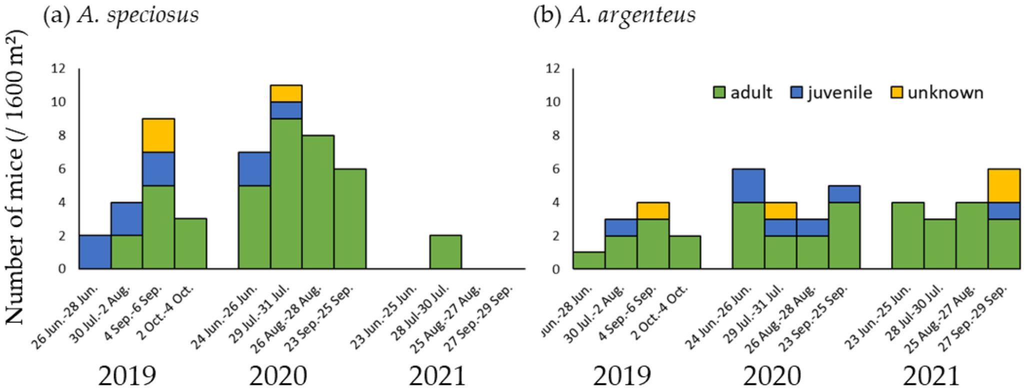


Figure 4. Seasonal changes in the population densities of adult and juvenile (**a**) *Apodemus speciosus* and (**b**) *Apodemus argenteus*. "unknown" indicates an individual that we were unable to identify as an adult or juvenile.

Table 2. Body weights of the two *Apodemus* species in terms of growth stage and gender for each of the three study years. The numbers (n) in the parentheses are sample size (individuals). ND indicates that no mice were captured.

Year	**Body Weight (g) (mean ± SD)**							
	A. speciosus				***A. argenteus***			
	Adult		**Juvenile**		**Adult**		**Juvenile**	
	♂	♀	♂	♀	♂	♀	♂	♀
2019	33.9 ± 2.3 (n = 7)	39.4 ± 1.8 (n = 4)	21.9 ± 5.6 (n = 7)	28.0 ± 0.0 (n = 1)	17.4 ± 2.2 (n = 8)	20.3 ± 1.8 (n = 2)	12.5 ± 0.0 (n = 1)	ND
2020	39.0 ± 6.8 (n = 14)	38.7 ± 5.4 (n = 20)	21.5 ± 5.5 (n = 2)	26.9 ± 0.0 (n = 1)	16.1 ± 1.6 (n = 14)	18.8 ± 2.3 (n = 2)	13.5 ± 0.4 (n = 3)	12.3 ± 1.3 (n = 4)
2021	44.8 ± 1.8 (n = 2)	ND	ND	ND	17.8 ± 2.0 (n = 11)	18.5 ± 2.7 (n = 10)	ND	ND

Inspection of video recordings revealed that the presented acorns were removed by mice (*A. speciosus* or *A. argenteus*, which were difficult to distinguished in videos) and Eurasian jays (*Garrulus glandarius*), and were also consumed at the stations by raccoon dogs (*Nyctereutes procyonoides*) and sika deer (*Cervus nippon*) (Figure S1). In the DC area, acorns were removed by mice in all 14 trials. Notably, the removals of sound acorns were significantly higher than those of acorns previously infested with moth larvae ($p < 0.005$; Figure 7). Interestingly, the video captured the mice smelling the acorns prior to carrying them away (Video S1). Contrastingly, in the NDC area, acorns were removed by mice in only one of the five successfully conducted trials.

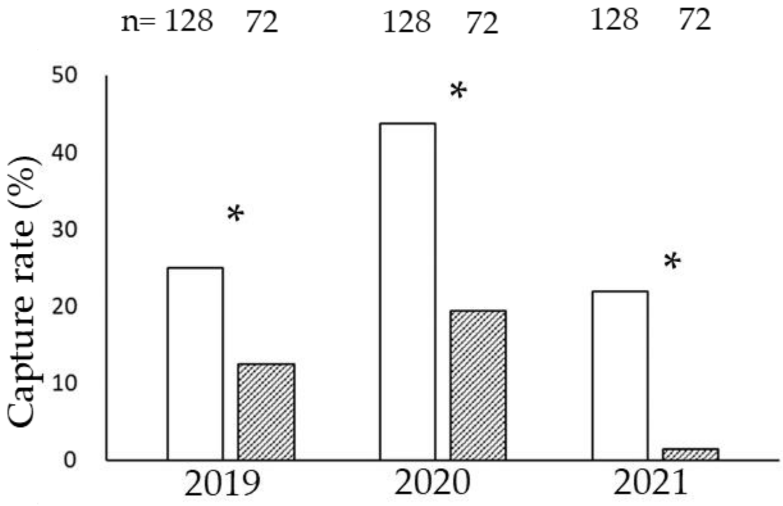
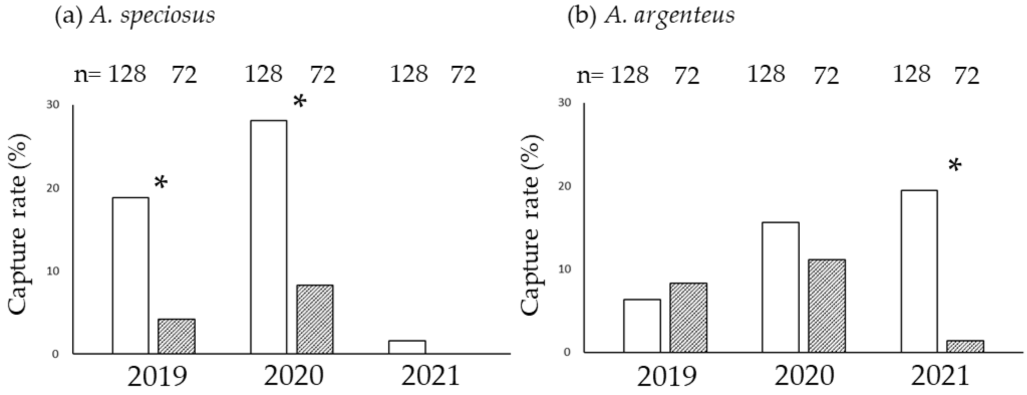


Figure 5. Relationships between the presence or absence of dead *Sasa borealis* culms and the rate of wood mouse capture. Open bars: area with dead *S. borealis* culms (DC). Shaded bars: area lacking dead *S. borealis* culms (NDC). The numbers (n) on the top are sample size (trap nights). Asterisks (*) indicate significant differences between the DC and NDC areas.


(a) *A. speciosus*

(b) *A. argenteus*

Figure 6. Relationships between presence or absence of dead *Sasa borealis* culms and the rate of (**a**) *A. speciosus* and (**b**) *A. argenteus* capture. Open bars: area with dead *S. borealis* culms (DC). Shaded bars: area without dead *S. borealis* culms (NDC). The numbers (n) on the top are sample size (trap nights). Asterisks (*) indicate significant differences between the DC and NDC areas.

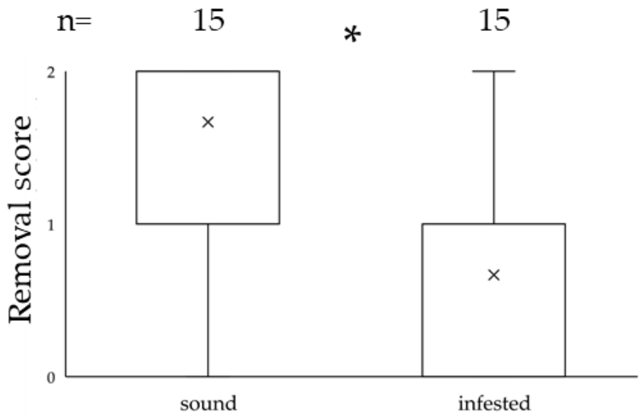


Figure 7. A comparison of the removal scores recorded for sound and infested (moth larvae) *Castanea crenata* acorns in area with dead *Sasa borealis* culms. The numbers (n) on the top are sample size (trials). The asterisk (*) indicates a significant difference in the removal score between sound and previously infested acorns.

4. Discussion

In this study, we sought to determine whether a leafless understory vegetation comprising dead *S. borealis* culms would provide a suitable habitat for rodents. Our results clearly indicated that both *A. speciosus* and *A. argenteus* were more abundant in areas with dead culms compared with an area devoid of these culms. To avoid predation, rodents typically conceal themselves amongst the leaves of understory vegetation [8,23], and our findings in the present study tend to indicate that even dead *S. borealis* culms can provide adequate shelter for mice for at least 4 years after the *S. borealis* bamboos had died, although long-term monitoring studies are needed to determine how long this remnant vegetation would provide sufficient cover.

Foraging activity has been shown to be enhanced in areas with understory vegetation comprising species such as *Sasa* dwarf bamboos. [8,9]. Our findings in the present study also revealed that foraging of acorns by mice (probably only *A. argenteus* in 2021 when the feeding experiment was conducted, based on capture data) was higher in areas with dead *S. borealis* culms, which were more shaded than the areas without the dead culms, being is consistent with the fact that both *A. speciosus* and *A. argenteus* are more active in darker environments [24]. Specifically, these findings tend to indicate that the fate of *C. crenata* acorns differs depending on the type of forest floor onto which they drop. Acorns placed at stations in the NDC area were observed to be consumed by raccoon dogs and deer, which, unlike mice and jays, do not cache acorns, whereas acorns placed in the DC area were frequently removed by mice that habitually cache acorns. Accordingly, it is reasonable to assume that acorns shed in the DC area would have a greater probability of successful germination than those shed in the NDC area. Moreover, given their more extensive distribution range, caching Eurasian jays have the potential to disperse acorns over a considerably greater distances than mice. In addition, we established that mice preferentially removed sound acorns prior to removing acorns that had previously been infested with moth larvae, smelling them in the area with dead culms. Similarly, the findings of previous studies have revealed that rodents preferentially select sound seeds over insect-infested seeds [25,26] and that their behavior in examining the status seeds is influenced by the potential risk of predation [27]. Hence, we speculate that the sheltering function of dead *S. borealis* culms enables mice to exercise greater care in selecting sound acorns. This is a highly advantageous foraging strategy for mice given that a majority of the internal contents of infested acorns have been consumed by larvae and these acorns contain large amounts of larval feces, thereby rendering them less nutritionally beneficial for mice.

With regards to the relationship between the two mouse species, in 2021, when the abundance of *A. speciosus* was lower than that in 2019 and 2020, *A. argenteus* was captured at a significantly higher frequency in areas containing dead *S. borealis* culms than in areas lacking this dead vegetation, thereby implying a change in activity patterns. Specifically, in the two years when *A. speciosus* was abundant, *A. argenteus* tended to avoid areas populated by *A. speciosus*, thereby restricting them to less suitable areas without dead *S. borealis* culms, even though these culms provide a valuable source of shelter. These distribution patterns are presumably a consequence of competitive exclusion. Compared with *A. argenteus*, *A. speciosus* individuals are larger in body size (even at the juvenile stage) and hence assumed to be competitively superior [28]. However, *A. argenteus* has a semi-arboreal habit [29,30], and whereas this species can coexist on the forest floor in spring, *A. argenteus* moves to the trees in summer as a consequence of heightened competition [31]. Thus, in 2019 and 2020, *A. argenteus* could well have been active in areas with dead culms, although it may have been largely restricted to arboreal habitats. Further study is accordingly required to gain a better understanding of this interspecific competition for habitat.

Fluctuations in rodent populations are closely associated with the abundance of food [32,33]. In the case of *A. speciosus*, it has been established that population size is significantly influenced by the production of *Q. crispula* acorns [34], which is a source of food exclusively consumed by *A. speciosus* given the tolerance of these mice to the tannins contained within these acorns [35]. Consequently, it can be speculated that a poor *Q. crispula* acorn crop in 2020 contributed to a decline in the *A. speciosus* population in 2021; however, given the lack of data on acorn production within the study area, we are unable to confirm this conjecture.

In conclusion, our findings in this study provide evidence to indicate that *S. borealis* culms, even those devoid of leaves, play an important role in the activity of wood mice. *S. borealis* not only produces copious amounts of seeds, thereby providing substantial nutritional resources that would contribute to an increase in the wood mouse population [17,18], but also provide valuable shelter that enables wood mice to evade predators when the culms die after seeding. It can be assumed that so long as these dead culms remain in situ, they will serve as a refuge in which mice can safely forage until the next generation of bamboo seedlings grow.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16080458/s1, Figure S1: Animals that foraged *Castanea crenata* acorns in NDC area; Video S1: Behavior of mice smelling *Castanea crenata* acorns prior to carrying them away.

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Data Availability Statement: The original data presented in the study are openly available in [FigShare] at [https://figshare.com/s/23d173f95c8d6879ea11 (accessed on 21 June 2024)].

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Conflicts of Interest: The authors declare no conflicts of interest.

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