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Different nest site selection of two sympatric arboreal rodent species, Siberian flying squirrel and small Japanese field mouse, in Hokkaido, Japan

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Numerous vertebrates use tree cavities as nest resources. Mammals such as Carnivora (Zalewski 1997; Wilson and Nielsen 2007), rodents (Taulman 1999; Shibata et al. 2004; Holloway and Malcolm 2007), bats (Sedgeley and O'Donnell 1999; Boonman 2000; Willis and Brigham 2007), and marsupials (Lindenmayer et al. 1991; Smith et al. 2007; Crane et al. 2010), as well as birds (Aitken et al. 2002; Martin et al. 2004; Adamík and Král 2008), use tree cavities for daily rest, reproduction, and/or overwintering. Sympatric cavity-users often partition their nest cavities to avoid interspecific competition (van Balen et al. 1982; Martin et al. 2004; Shafique et al. 2009).

In Hokkaido, northern Japan, there are two cavity-nesting rodents, the Siberian flying squirrel (*Pteromys volans*) (Nakama and Yanagawa 2009; Suzuki et al. 2011) and the small Japanese field mouse (*Apodemus argenteus*) (Nakata et al. 2009). There may be competition between these two rodents for tree cavities, but their favored nest sites have not yet been compared. Do they select tree cavities of different types, and, if so, what characteristics are their selections based on?

These rodents have different physical and ecological characteristics. *Pteromys volans* (weight, 110 to 142 g; head and body length, 130 to 167 mm; Hanski et al. 2000; Asari et al. 2007; Oshida 2009) is 5 to 14 times heavier than *A. argenteus* (weight, 10 to 20 g; head and body length, 65 to 100 mm; Nakata et al. 2009).

In addition, *P. volans*, which is an aerial and arboreal user, spends most of its time in the canopy and almost never walks on the ground, even when crossing wide fields (Selonen and Hanski 2003, 2004). *Apodemus argenteus* also uses arboreal space (Imaizumi 1978; Abe et al. 1989; Sekijima 2004), and it is able to climb to a height of 18 m (Ida et al. 2004). However, it more frequently uses foods on and under the ground than above the ground (Abe 1986). These differences in size and

habit between the two species may result in different choices of tree cavities.

Larger species of cavity-nesting mammals and birds tend to nest in larger cavities with larger entrances (Martin et al. 2004). Larger flying squirrels use larger trees with larger entrances than do smaller flying squirrel species (Shafique et al. 2009). Larger bird species also nest in larger entrance cavities than do smaller species (van Balen et al. 1982).

Thus, we hypothesized that *P. volans*, with a larger body than that of *A. argenteus*, would nest in trees with greater diameters at breast height and in larger cavities with larger entrances. In addition, we hypothesized that *P. volans*, which is usually active in the upper layer of trees, would nest in higher cavities than *A. argenteus*, which commonly lives on and under the ground. We examined these hypotheses by surveys of tree cavities and nest boxes.

Methods

Study area

Tree cavities and wooden nest boxes were observed within a total of approximately 27 ha of urban, wind-break, and riparian forests (42°51' to 42°53'N, 143°09' to 143°11'E) in Obihiro City, eastern Hokkaido, northern Japan. The forests are chiefly comprised of Korean pine (*Pinus koraiensis*), eastern white pine (*Pinus strobus*), Japanese larch (*Larix leptolepis*), Japanese white birch (*Betula platyphylla*), Manchurian walnut (*Juglans mandshurica*), and Japanese emperor oak (*Quercus dentata*). The proportion of conifers was 29%, and that of broad-leaved trees was 71%, and tree density averaged 692 individuals/ha. Tree height in the forests averaged 15.3 ± 5.6 (SD) m, and diameter at breast height (DBH) averaged 26.0 ± 11.3 cm (Suzuki et al. 2012).

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Cavity survey

We checked 136 individual tree cavities a total of 483 times from May to October 2009 and May to October 2010. Each cavity was checked two to five times at intervals of more than two months. Because of access difficulties, we could not examine tree cavities located more than 3 m above the ground. We recorded the animals and the nest materials in the cavities. DBH of cavity trees (cm) and entrance size (smallest diameter of entrance, cm) were used as indicators of differences in cavity selection according to differences of body size, and the height of bottom of the tree cavity above the ground (m) was used as an indicator of selection according to the animals' patterns of space use.

The species using the tree cavities was specified with the following three criteria: 1) when an animal was found in a tree cavity, that species was regarded as the user of the cavity; 2) when no animals were found and new fallen leaves were present as nest materials in the cavity, *A. argenteus* was considered as the user of this cavity; and 3) when neither animals nor fallen leaves as nest materials were found in the cavity, the cavity user was not identified.

When no animals were found and torn barks were present as the materials in the box, *P. volans* was considered as the user of the box. Cavity use of *A. argenteus* was limited to only the breeding season, however *P. volans* uses them in all seasons. Thus, to unify period of cavity use, nest materials of *P. volans* were not used as criterion. Nest materials were not removed from the cavities.

Nest box survey

In the cavity survey, it was difficult to do examinations to test separating two hypotheses separately. Thus, to examine only the hypothesis of differences of nest site height based on their space use, in June 2010 we installed 87 uniform nest-boxes (approximately 3.2 boxes per ha) at various heights. The boxes were randomly installed 0.7 to 2.8 m above the ground at distances apart of > 20 m; they were then observed once a month in July, September, and October 2010. The DBH (mean \pm SD) of the trees to which the boxes were attached was 25.1 ± 8.8 cm, and the mean entrance height was 1.6 ± 0.5 m. The volume of each box was $3,456 \text{ cm}^3$ ($24 \times 8 \times 18$ cm), and the diameter of the circular entrance was 4.5 cm.

The species using the nest box was specified with the following four criteria: 1) when an animal was found in a

nest box, that species was regarded as the user of the box; 2) when no animals were found and fallen leaves were present as nest materials in the box, *A. argenteus* was considered as the user of this box; 3) when no animals were found and torn barks were present as the materials in the box, *P. volans* was considered as the user of the box because the season in which the materials were brought in was clear; and 4) when neither animals nor these as nest materials were found in the box, the box user was not identified. Nest materials were not removed from the boxes.

Captured *P. volans* were marked with individually numbered ear tags (KN-295-A, Natsume Seisakusho Co., Ltd) and released onto the trees where they had been captured. In contrast, *A. argenteus* were released without marking. The number of *P. volans* captured was considered to represent the minimum number of individuals present, and the number of *A. argenteus* found on the same day was taken to represent the minimum number of individuals present. The rodents were captured with permission (Hokkaido permit no. 511). Animals were handled according to the Mammalogical Society of Japan's guidelines for handling mammal samples (The Mammalogical Society of Japan 2009).

Data analysis

We used logistic regression analysis to clarify the differences in nest sites between *P. volans* and *A. argenteus*. Data on cavities and nest boxes were analyzed separately. Dependent variables replaced *P. volans/A. argenteus* by 1/0 as dummy variables in both analyses. In the tree cavity study, we compared the nest sites of both species by the cavity trees' DBH, entrance size, and cavity height above ground as independent variables. In addition, correlations and multicollinearities between these independent variables were checked by correlation coefficients and variance inflation factors (VIFs). In the nest box study, entrance height above the ground was used as an independent variable. If both species used the same cavity or nest box, the data were not used in the analyses.

Results and discussion

From May to October in the two years, we discovered 35 nest cavities with *P. volans* and 21 with *A. argenteus*. The mean DBH of cavity trees was 30.2 (range: 19.9 to 47.7) cm for *P. volans* and 26.8 (12.7 to 47.8) cm for *A. argenteus*. The entrance size was 4.5 (range: 3.0 to 9.5)

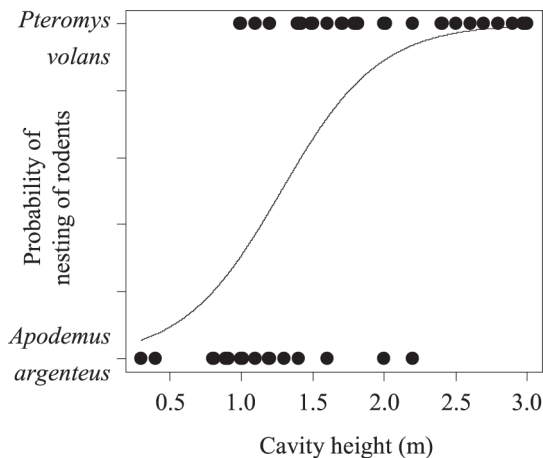


Fig. 1. Probability of nesting of rodents in relation to cavity height using logistic regression analysis.

cm for *P. volans* and 3.9 (1.5 to 5.5) cm for *A. argenteus*. The height of the cavity above the ground was 1.9 (range: 0.7 to 3.0) m for *P. volans* and 1.2 (0.3 to 2.3) m for *A. argenteus*. Only four cavities were used by both species, however the two species were not found in the same nest on the same day.

There were no strong correlations between these independent variables (DBH vs. entrance size, $R = 0.03$; DBH vs. cavity height above the ground, $R = 0.26$; entrance size vs. cavity height above the ground, $R = 0.32$). In addition, multicollinearities were not found among all variables according to the VIFs (DBH, 1.08; entrance size, 1.12; cavity height above ground, 1.20).

The results of the analysis showed that the model was significant ($\chi^2 = 18.81, P < 0.01$); *P. volans* nested in

Table 1. Summary of logistic regression analysis using diameter at breast height (DBH), entrance size, and cavity height as independent variables in tree cavities

	Coefficient	SE	χ^2	P-value
DBH	0.07	0.06	1.67	0.20
Entrance size	0.51	0.50	1.01	0.32
Cavity height	2.86	1.00	8.11	<0.01

higher cavities than *A. argenteus* (Fig. 1), but there was no significant difference in DBH or entrance size (Table 1). These results indicate that the two species select different nest cavities according to height, irrespective of DBH or entrance size.

Through the study period, more than 11 *P. volans* used 40 nest boxes and 5 *A. argenteus* used 14 nest boxes. The mean entrance height above the ground of the boxes used by *P. volans* was 1.9 (range: 1.1 to 2.8) m, and that of *A. argenteus* boxes was 1.4 (0.7 to 1.9) m. Only four boxes were used by both species (Fig. 2).

Pteromys volans used most boxes at ≥ 2 m height, whereas they did not use the boxes at < 1 m height (Fig. 2). On the other hand, *A. argenteus* used only nest boxes at < 2 m height. As in the tree cavity study, the results of the analysis showed that this model was significant ($\chi^2 = 11.37, P < 0.01$) and *P. volans* used higher boxes than *A. argenteus* (coefficient = 3.34, $SE = 1.26, \chi^2 = 7.06, P < 0.01$).

There have been a few studies of nest site selection by *P. volans* (Nakama and Yanagawa 2009; Kadoya et al. 2010), but little known of nest site selection by *A. argenteus*. Although there may be competition

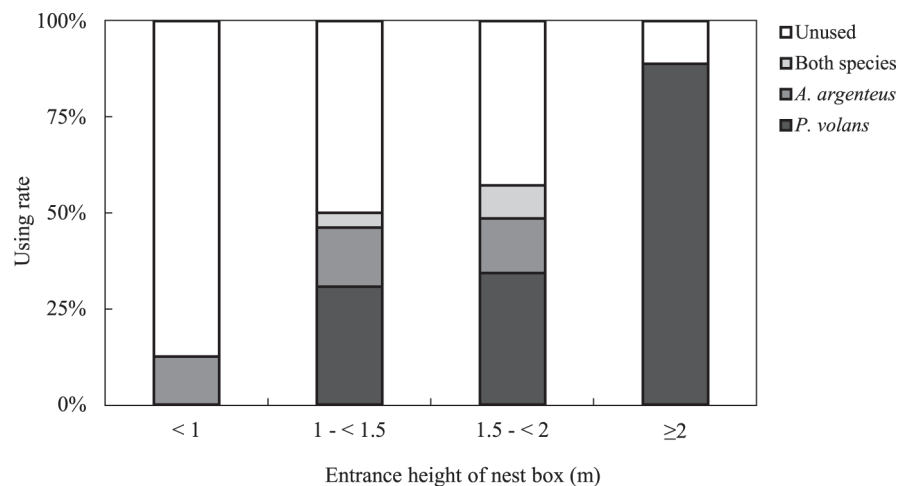


Fig. 2. Relationship between entrance heights of nest boxes and user rates per species (*Pteromys volans* and *Apodemus argenteus*). The number of boxes was 8 in the < 1 m class, 26 for $1 - < 1.5$ m, 35 for $1.5 - < 2$ m, and 18 for ≥ 2 m.

between these two rodents for tree cavities, their nest sites have hitherto not been compared or reported.

In both the tree cavities and the nest boxes, these two rodents' nest site selections had similar patterns: *P. volans* nests tended to be located in higher positions than those of *A. argenteus* (Figs. 1 and 2). Nest boxes installed 2 m or higher above the ground were almost all used by *P. volans* (Fig. 2). Although the survey of this study was limited to cavities under 3 m in height, the observed pattern of the nest use by these two species would not change if the range of the survey had been extended to heights over 3 m. This is because nest boxes installed 2 m or more above the ground were almost all used by *P. volans* (Fig. 2) and, furthermore, a previous study reported that the mean above-ground nest cavity height of *P. volans* was 5.4 m in the same area (Asari et al. 2009).

Another reason for these results is likely to be the difference in feeding sites. *Pteromys volans* feeds on the buds and male flowers of conifers, and on the leaves, seeds, and catkins of deciduous trees (Hanski et al. 2000); these food items are bitten off the branches. In contrast, *A. argenteus* frequently takes food on and under the litter (Abe 1986).

Pteromys volans travels between trees by gliding (Asari et al. 2007; Suzuki et al. 2012). It generally starts gliding from a high position in the trees and rarely lands on tree trunks at heights < 1 m (Suzuki et al. 2012). In contrast, *A. argenteus* walks on the ground between trees. It thus appears that the different nest site selection shown by these two rodents is derived from their different uses of space.

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