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Characteristics of tree cavities used by *Pteromys volans orii* in winter

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Flying squirrels, such as northern flying squirrels (*Glaucomys sabrinus*), southern flying squirrels (*G. volans*), and Siberian flying squirrels (*Pteromys volans*) often use tree holes or abandoned bird nests as nesting sites (Taulman 1999; Goldingay 2000; Airapetyants and Fokin 2003). There have been several reports on the characteristics of the tree cavities used by flying squirrels (e.g. Taulman 1999; Meyer et al. 2005). Although the Hokkaido-native *Pteromys volans orii* is also known to nest in tree cavities (Muraki and Yanagawa 2006), there have been no detailed investigations of the cavities that can be used by these animals.

Flying squirrels consume more energy at low temperatures due to their gliding membranes that add considerably to their surface area-to-volume ratio (Stapp et al. 1991). In these species, to minimize this energy loss, adaptive features such as reduced activity time in winter (Yamaguchi and Yanagawa 1995) and group nesting (Layne and Raymond 1994; Carey et al. 1997; Masuda 2003a), have been observed. In addition, requirements for nesting sites in winter may be more specific than those in other seasons. A warmer nest, which can reduce the animals' energy consumption, was assumed to be required in winter. Here we investigated the conditions required for tree cavities used by *P. v. orii* in winter by comparing the characteristics and inside temperatures of tree cavities used in winter with those in other seasons.

Study area and methods

The survey was performed in the natural forests and windbreak forests of *Larix leptolepis* in Inada-cho, Obihiro City, Hokkaido (42°51'N, 143°10'E) from December 2005 to October 2006. These natural forests consist of tree species such as *Quercus dentata*, *Alnus japonica* and *Fraxinus mandshurica* var. *japonica*. The total area of the investigation sites was 20.4 ha. In these forests, the average (\pm SD) tree height was 7.9 ± 5.7 m, and the average (\pm SD) diameter at breast height (DBH)

was 27.1 ± 8.4 cm. Tree cavities below four meters above the ground were targeted for investigation and all the cavities at each site surveyed were checked twice a month. A cavity confirmed to be inhabited by flying squirrels was classified as "Used." The survey period was divided into two phases, "winter" (from December to March) and "other seasons" (from April to October). The cavities investigated were classified into two groups: the "Used during winter (Used)" group, in which use by *P. v. orii* was confirmed during investigation in winter and "Not used in the winter (Not used)" group, in which use was confirmed in the other seasons, but not in winter. The "Used" group was defined as including the holes used in both seasons.

The cavities confirmed to be used by *P. v. orii* were evaluated according to the following characteristics, determined with reference to Nakano et al. (1991) and Masuda (2003b), to compare the results obtained from the "Used" group and the "Not used" group. Compared were status of the cavity tree (live or dead tree), tree height (m), DBH (cm), diameter at cavity height (DCH; cm), cause of the cavity (abandoned woodpecker nests, sockets left by fallen branches, decay originating in splits caused by frost cracks), direction of the entrance (cardinal points), lengths of the major and minor axes of the entrance (mm) and entrance length (a), horizontal depth (b) and vertical depth (c) which representing the size of the cavity (cm) (Fig. 1). Regarding statistical analysis, a χ^2 test of independence for direction of the entrance, Fisher's Exact test for status of the cavity trees and cause of the cavity, and the Mann-Whitney's *U* test for the other measurements were used.

A temperature data logger (KN Laboratories, Inc., Thermocron Type-G) was used for measuring temperature. The data logger was 17 mm in diameter, 6 mm in thickness and 3.3 g in weight, and specifies a resolution of 0.5°C and an accuracy of $\pm 1^\circ\text{C}$ within the operating range of -30°C to 60°C . The temperatures in the tree cavities in the "Used" group and the "Not used" group

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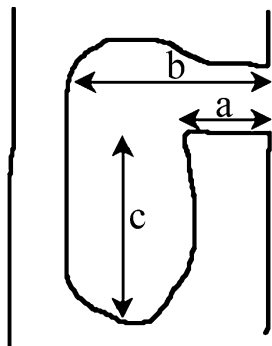


Fig. 1. Measured positions of tree cavity. a, Entrance length; b, Horizontal depth (from the entrance to the back wall of the cavity); c, Vertical depth (from the bottom of the cavity entrance to the bottom of the cavity).

were compared using the following method. First, monthly mean temperatures from December to March in winter were calculated. Three days were then selected from each month based on the daily mean temperature closest to the monthly mean temperature (four months \times three days = 12 days). The data of mean in-cavity temperatures in the 12 days selected as described above was averaged for the “Used” group and for the “Not used” group. However, data obtained while *P. v. orii* was present in the tree cavities was excluded. The mean daily temperatures were compared between the “Used” group and the “Not used” group using the Mann-Whitney’s *U* test on a day-by-day basis.

Results

We found a total of 150 tree cavities at sites that appeared to be available for use by Siberian flying squirrels. Of the 150 cavities investigated in our survey, only 34 were confirmed to be used by *P. v. orii*. The density of the tree cavities available to the Siberian flying squirrels was 7.35/ha and that of the tree cavities actually used by them was 1.66/ha. Of these 34, 17 holes were used in winter and the remaining 17 were used in seasons other than winter. Most cavities ($n = 16$) used in winter were used also in seasons other than winter.

Both consisted of four live trees and 13 dead trees making a total of 17 trees. There was no difference in the status of cavity-bearing trees between the “Used” group and the “Not used” group (Fisher’s Exact test, $P > 0.05$). As for the cause of the cavity, no statistical difference was observed between the two groups: three of the 17 cavities in the “Used” group were caused by decayed branch sockets left by lost branches, while the

remaining 14 cavities were abandoned woodpeckers’ nests. In the “Not used” group, five cavities of the total of 17 resulted from decay that had originated in scars left by lost branches, while the remaining 12 cavities were abandoned woodpeckers’ nests ($P > 0.05$). There was no statistical significance to the direction of the entrance of the cavity ($\chi^2 = 1.63$, $df = 3$, $P > 0.05$). There was a significant difference in the vertical depth (c) between the two groups, i.e. the cavities in the “Used” group tended to be deeper ($z = 2.05$, $P < 0.05$) than the “Not used” group. However, no significant differences were observed in tree height, DBH, DCH, lengths of major and minor axes of the entrance, the entrance length (a) and the horizontal depth (b) ($P > 0.05$; Table 1).

The average ambient temperatures of months measured in the study area, ranged 2.38–21.00°C from April to November. Average monthly ambient temperatures were -6.91 , -10.19 , -7.25 and -0.98 °C in December, January, February, and March, respectively. When the temperatures inside the cavities were compared on all the 12 days during which the mean daily temperatures were closest to the average monthly temperature in each month, there were no differences between the “Used” group and the “Not used” group ($P > 0.05$ for all the comparisons: Table 2).

Discussion

It was believed in the past that in winter, *P. v. orii* used tree cavities, which would be warmer than other types of nest, to reduce their energy consumption. Observing the use of nest boxes by *P. v. orii* revealed that during the winter (December to March) their use plunged significantly (Yanagawa 1994). Asari and Yanagawa (2008) studied the use of tree cavities, nest boxes and dreys by *P. v. orii* and found that the tree cavities and the dreys are frequently used in winter, but that the nest boxes and cavities are chiefly used during the other seasons. These studies showed that in winter, warm nests are preferred by *P. v. orii* (Asari and Yanagawa 2008).

A study of cavities in Sapporo, Hokkaido by Maeda (1974) found that during the winter, the temperature in cavities in living trees falls less than those in dead trees. Similarly, a study by Maeda and Sato (2008) on Rishiri Island, Hokkaido, using a data logger showed that temperatures inside cavities in living firs, *Abies sachalinensis* are more stable and less affected by outdoor temperatures than those in dead firs. These results

Table 1. Comparison of measurements of the tree cavities between the “Used (used during winter)” group and the “Not used (not used in the winter)” group

		Used (<i>n</i> = 17)		Not used (<i>n</i> = 17)		<i>z</i> *	<i>P</i> *
		mean	<i>SD</i>	mean	<i>SD</i>		
Cavity-bearing tree	Tree height (m)	13.2	6.6	13.3	6.6	0.05	n.s.
	DBH (cm)	28.9	6.8	32.6	7.9	1.29	n.s.
	DCH (cm)	28.5	6.8	32.2	8.0	1.22	n.s.
Tree cavity	Entrance						
	Major axis (mm)	43.7	7.1	49.2	13.8	1.26	n.s.
	Minor axis (mm)	39.1	7.9	40.9	9.4	0.34	n.s.
	a (cm)	6.1	2.7	6.2	2.8	0.03	n.s.
	b (cm)	17.8	2.6	17.9	3.3	0.28	n.s.
	c (cm)	20.2	4.6	16.3	5.5	2.05	< 0.05

*Mann-Whitney's *U* test.

Table 2. Comparison of in-cavity temperatures between the “Used” group and the “Not used” group

	Used (<i>n</i> = 17)	Not used (<i>n</i> = 17)	<i>z</i> *	<i>P</i> *
	mean (°C)	mean (°C)		
2005.12.16	-8.05	-7.18	1.14	n.s.
2005.12.17	-7.08	-6.48	0.27	n.s.
2005.12.23	-5.30	-5.38	0.25	n.s.
2006.1.13	-8.26	-7.87	1.76	n.s.
2006.1.16	-11.60	-10.77	0.30	n.s.
2006.1.20	-6.49	-6.50	0.14	n.s.
2006.2.4	-6.98	-7.09	1.07	n.s.
2006.2.13	-8.56	-8.71	0.32	n.s.
2006.2.20	-3.30	-2.87	1.04	n.s.
2006.3.2	-1.37	-1.64	0.23	n.s.
2006.3.5	-0.33	-0.91	1.24	n.s.
2006.3.20	-0.04	-0.20	1.69	n.s.

*Mann-Whitney's *U* test.

suggest, Maeda and Sato (2008) maintain, that bats are more likely to spend the winter in cavities in living trees.

These data had led us to conclude that *P. v. orii* also would select cavities in living trees as their winter nests, due to their preferable conditions. However, the results of this study did not concur with those of Maeda and Sato (2008). Furthermore, no difference was found between the temperatures measured in the actually used cavities during the winter and those not used, suggesting that *P. v. orii* selected the cavities for the winter nest using criteria other than the temperatures inside the cavities.

On the other hand, regarding the characteristics of the cavities chosen by *P. v. orii* in winter, a significant difference was observed in the vertical depth: *P. v. orii* tended to use deeper cavities in winter. In flying squir-

rels distributed in the Holarctic region, it has been confirmed that animals share nests in winter (Layne and Raymond 1994). Stapp et al. (1991) studied the energy preservation benefits of nesting in groups in *G. volans*. According to their results, shared nesting by three or six individuals when outside temperatures were around 9°C could reduce energy consumption by 27% and 36%, respectively, compared with energy consumption by a single animal. Therefore, tree cavities with a sufficient depth which *P. v. orii* chose in winter in this study may enable a greater number of animals to share. Group nesting of flying squirrels in winter has been noted in a substantial number of reports (Muul 1968; Carey et al. 1997; Masuda 2003a) and appears to be an important overwintering strategy for these animals.

One of the reasons the cavities of thicker trees or liv-

ing tress were not selected during winter in the current research is considered to be that the investigation sites were secondary forests in the urban areas where available nest resources are limited. In terms of quantity, there were as many as 150 tree cavities in forests usable by Siberian flying squirrels. However, it may be that these nest resources did not show a significant qualitative difference between “Used” and “Not used” tree cavities. In other studies on *P. v. orii* (Nakano et al. 1991), the average DBH (55.9 ± 26.0 cm) in the trees whose cavities were used in winter was much larger than that in the present study. The most common causes of the cavities were sockets of lost branches or frost cracks, and tree cavities produced by woodpeckers included those excavated by a large species, *Dryocopus martius* (Masuda 2003b). In other words, it was possible for the structural characteristics of the tree cavities investigated in these studies to be of various types. In contrast to these studies, most of the sites investigated in this study, which was located in the suburbs of Obihiro City in Hokkaido, were secondary forests and windbreak forests in which only the middle-sized *Dendrocopos major* and the smaller *D. minor* woodpeckers lived. The tree cavities used by *P. v. orii* in this study showed no distinct differences in characteristics other than their vertical depth, since such resource-limited forests might not feature a sufficiently varied range of tree cavities to allow *P. v. orii* to demonstrate preferences in their overwintering quarters.

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