

ORIGINAL ARTICLE

Secondary users of Great Spotted Woodpecker (*Dendrocopos major*) nest cavities in urban and suburban forests in Sapporo City, northern Japan

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Abstract Old nest cavities excavated by Great Spotted Woodpeckers (GSW) *Dendrocopos major* were examined in two study areas (urban and suburban forests) in Sapporo, the capital city of Hokkaido, northern Japan. Five avian and one mammalian secondary cavity user (SCU) species occupied 47 of 101 GSW cavities inspected. The species composition differed between urban and suburban forests. Avian SCU species occupied GSW cavities more frequently in the urban than in the suburban forests. Tree Sparrows *Passer montanus* and Chestnut-cheeked Starlings *Sturnus philippensis* were the only dominant cavity breeding species in the severely fragmented urban forests. Flying Squirrels *Pteromys volans* were the most dominant users of GSW cavities in the suburban forests. The density of GSW cavities depends not only on natural processes but also on human activities. The suitability of the GSW cavities for certain SCU species decreases with time. To maintain the diversity of cavity-nesting wildlife in urban and suburban areas of Sapporo, preservation of existing trees with GSW cavities as well as providing suitable habitat conditions to support continued production of new cavities is essential.

Key words *Dendrocopos major*, Nest webs, Sapporo City, Secondary cavity user, Urban area

Cavity-nesting species comprise a major component of the forest wildlife community (Scott et al. 1980). Martin and Eadie (1999) proposed as a direct analogy to ‘food webs’ that cavity-nesting bird communities are organized in ‘nest webs’ with the cavities as the central resource, around which inter-specific and intra-specific interactions occur. In such a web structure, a certain species may have disproportionate importance if it constitutes a key component of the cavity resources. Primary cavity nesters (PCNs, e.g. woodpeckers) are such key components that excavate cavities used as nests or roosts by secondary cavity users (SCUs) including not only bird but also many other wildlife species. The SCUs rely on the cavities created by PCNs or on natural holes formed through other processes. The number of

available nesting cavities has been considered to be a major factor limiting the population size of SCU bird species (Haartman 1957; Perrins 1979; Newton 1994). Thus, the density and diversity of woodpeckers may have a strong influence on the richness and abundance of other SCU species (Martin & Eadie, 1999).

In recent years in Hokkaido, northern Japan, GSW is the only PCN species regularly breeding in urban areas (Yamauchi et al. 1997). In fact, GSW is now the most abundant and often the only PCN species in the urban area of Sapporo, the capital city of Hokkaido (Kotaka & Kameyama in press). In urban areas, GSW may affect entire communities of cavity-nesters through the excavation of nest cavities. However, information on the importance of GSW cavities for other species so far has been just anecdotal, and few studies have quantified utilization of GSW cavities by SCU species in urban areas of modern large cities such as Sapporo. The composition of the nest webs

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may also vary with habitat features such as forest type or landscape pattern.

In this paper, we compare the availability of GSW cavities and their actual occupation frequency by SCU species in two different types of forest (urban and suburban area) in Sapporo to develop a better understanding of the ecological role of GSWs within the nest webs.

STUDY AREAS AND METHODS

The GSW nest cavities were surveyed in two different types of landscapes in Sapporo; a highly fragmented forest in an urban area (HKD) and a less fragmented forest in an agricultural suburban area (HJO). Both areas are characterized by a relatively flat topography. The former (HKD) includes the University of Hokkaido Campus and its Botanical Garden located in the center of Sapporo (43°04'N, 141°20'E) and totalling 271 ha. This area is characterized by highly fragmented woodland (21.3% of tree coverage) comprising woodland with dense undergrowth, open woodland with little undergrowth, hedgerows, farmland, sports grounds, lawns and buildings. Dominant tree-species are *Acer mono* and *Ulmus japonica*. The latter (HJO) is situated in the grounds of the Hokkaido National Agricultural Experiment Station and the Forestry and Forest Products Research Institute, totalling about 380 ha, located in the southeastern part of Sapporo about 8 km from HKD. This area is characterized by farmland used mainly for crop production and grazing. The tree coverage is about 39.8%, and dominant tree species are *Quercus mongolica* and *Acer mono*.

Both study sites were searched for all new GSW nests (HKD in 1994–1997 and HJO in 1995–1998). Locations of the nest cavity-trees were mapped, and each tree was classified as living or dead. The GSW cavities were revisited and examined at least twice in late May and June during the period 1995–1998 in HKD and in 1999 in HJO. Use of the cavities was examined by climbing the trees to inspect cavities with a dentist's mirror. If adults, eggs or young of certain species were found, the cavity was classified as 'occupied'. The users of those cavities were identified through observation with binoculars. The nest cavities inspected were further classified into two categories according to their age, "1 year-old" if they were examined one year after excavation and "2–4 year-old" if they were examined two to four years after excavation. When we observed cavity usurpa-

tions between cavity users during our survey, we recorded which species were involved. All visits were made during daylight so we have no information on cavity utilization at night. Some GSW cavities were lost due to natural events or logging, and we classified the former as "broken" and the latter as "logged." Line transects for bird censuses were established in both study sites: 50 m wide and 1.4 km long in HKD and 50 m wide and 3.4 km long in HJO. At each study site, line transect surveys were conducted from 05:00 to 08:00 in the morning during late May (1995–1998 for HKD and 1999 for HJO).

RESULTS

1) Cavity loss, reuse by GSWs and availability to SCUs

Through the survey, we found 24 (5, 7, 6, and 6 for 1994, 1995, 1996 and 1997) and 42 (7, 8, 15 and 12 for 1995, 1996, 1997 and 1998) new GSW nests in HKD and HJO, respectively. The proportion of dead trees among the nest trees was significantly higher in HJO (45.2%) than in HKD (4.2%) (Fisher's exact test, $P < 0.01$).

We inspected 59 nest cavities (1 year-old=24; 2–4 year-old=35) in total for HKD (1995–1998) and 42 nest cavities (1 year-old=12; 2–4 year-old=30) for HJO (1999). Some nest cavities or whole trees with nest cavities were lost due to human activity or natural events. The losses amounted to 12.5% of the 1 year-old and 17.1% of the 2–4 year-old cavities in HKD. The primary cause of cavity losses in this area was logging in the course of road or building construction (6 of 8); the other two were lost when trunks broke at a cavity (Fig. 1). In HJO, all cavity losses (16.7% for 1 year-old and 20.0% for 2–4 year-old cavities) were caused by natural events (mainly strong winds) (Fig. 1).

We found four cases of cavity reuse for breeding by GSW (1 in HKD and 3 in HJO, Fig. 1). Cavities were not considered available for SCU when GSWs were using them for nesting.

Finally, we found that the proportions of GSW cavities available for SCU species were 87.5% (1 year-old) and 80.0% (2–4 year-old) in HKD, and 66.7% (1 year-old) and 76.7% (2–4 year old) in HJO.

2) Cavity use by SCUs and nest webs

Cavity-nesting bird species are a major component of the bird communities in both of our study sites. From the line transect surveys, the proportion of cav-

Secondary Users of Great Spotted Woodpecker Cavities

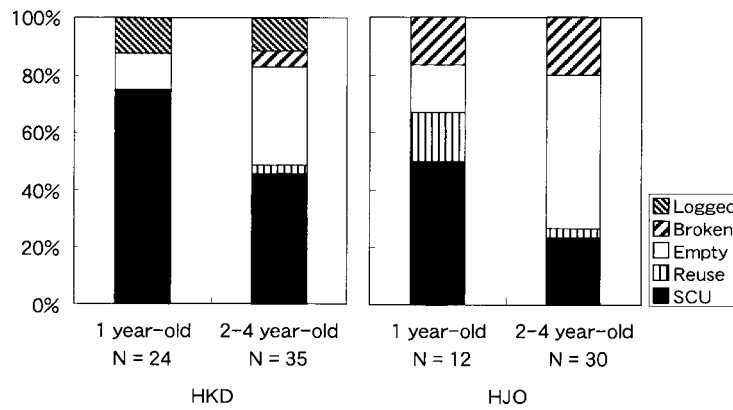


Fig. 1. Status and utilization of 1 year-old and 2–4 year-old GSW cavities in urban (HKD) and suburban (HJO) forests.

ity-nesting bird species among all recorded individuals was 75.5% (total bird density: 8.65/ha) for HKD and 62.0% (5.08/ha) for HJO (Table 1). Two species of PCN, GSW and Japanese Pygmy Woodpecker *Dendrocopos kizuki* were observed at our study sites. For both sites, the GSW was the dominant PCN species (Table 1). Overall, five avian and one mammalian SCU species used 47 (34 for HKD and 13 for HJO) GSW nest cavities (Fig. 2).

Within the available nest cavities, 1 year-old cavities were occupied more frequently than 2–4 year-old cavities (Fisher’s exact test, HKD: $P=0.06$; HJO: $P<0.05$, Table 2). The number of nest cavities in the two different “cavity age groups” used by each species at both study sites, elucidating the shift from GSW to SCU, can be seen in Figure 2.

The composition of the “nest webs” differed fundamentally between HKD and HJO. In HKD, avian species that used GSW nest cavities were Tree Sparrow *Passer montanus*, Chestnut-cheeked Starling *Sturnus philippensis* and Nuthatch *Sitta europaea*. The Tree Sparrows and Chestnut-cheeked Starlings were the dominant GSW cavity users and occupied 94.1% (16 for Tree Sparrow and 16 for Chestnut-cheeked Starling) of 34 cavities used by SCUs. Although the density of the Tree Sparrows (4.01/ha) was about five times as high as that of the Chestnut-cheeked Starlings (0.80/ha), we found the occupation rate of the GSWs nest cavities by Chestnut-cheeked Starlings was disproportionately higher than that by Tree Sparrows (G-test, $df=1$, $G=37.4$, $P<0.001$, Fig. 2). One mammalian species (the Flying Squirrel *Pteromys volans*) was the most dominant user of GSW cavities in HJO, followed by avian species (Nuthatch, Great Tit *Parus major* and Russet Spar-

Table 1. Bird density (no/ha) of HKD (averaged 1995–1998) and HJO (1999)

Bird Species		HKD (no/ha)	HJO (no/ha)
PCNBs	<i>Dendrocopos major</i>	0.16	0.20
	<i>D. kizuki</i>	0.01	0.04
	Total PCNBs	0.17	0.24
SCUs	<i>Passer montanus</i>	4.01	—
	<i>Sturnus philippensis</i>	0.80	—
	<i>Parus major</i>	0.65	0.71
	<i>Sturnus cineraceus</i>	0.62	—
	<i>Parus palustris</i>	0.10	0.75
	<i>Ficedula narcissina</i>	0.09	0.24
	<i>Sitta europaea</i>	0.02	0.31
	<i>Parus varius</i>	0.01	0.08
	<i>Passer rutilans</i>	—	0.51
<i>Parus ater</i>	—	0.08	
	Total SCUs	6.29	2.68
Others		2.18	2.17
	Total	8.65	5.08

row *Passer rutilans*). The Flying Squirrel occupied 61.5% (8 of 13) of the GSW cavities used by SCU.

It is to be noted that 85.7% (1 year-old) and 57.1% (2–4 year-old) of all the available GSW cavities examined were occupied in HKD, while in HJO only 25.0% (1 year-old) and 13.0% (2–4 year-old) were occupied by avian SCU species (Fisher’s exact test, 1 year-old: $P<0.005$; 2–4 year-old: $P<0.005$).

The Nuthatch was the only SCU species that used the GSW cavities at both study sites. Although Great Tits were found at both of our study sites, we could not find any nest belonging to this species among the available cavities in HKD. One of the five Great Tit

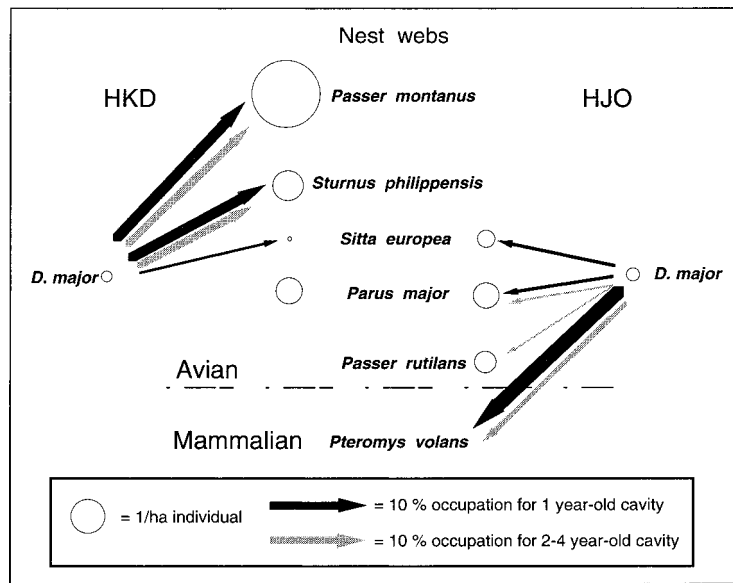


Fig. 2. Turnover of species using GSW nest cavities in urban (HKD) and suburban (HJO) forests. Arrows connect species that use resources provided by GSW. The size of the circles indicates the bird density (no/ha) of each species and the width of the arrows shows the percentage of occupancy of available GSW cavities for each species. The sample sizes for the SCU species are 21 (1 year-old) and 28 (2–4 year-old) for HKD and 8 (1 year-old) and 23 (2–4 year-old) for HJO.

Table 2. Utilization of GSW cavities in relation to nest age in urban (HKD) and suburban (HJO) forests.

Nest age	HKD		HJO	
	1 year	2–4 year	1 year	2–4 year
Occupied	18	16	6	7
Empty	3	12	2	16

in HKD was in a cavity of unknown origin and the others were in natural or artificial holes.

3) Interactions and cavity usurpations

In HKD, cavity usurpations between SCU species were observed. Chestnut-cheeked Starlings drove five pairs of Tree Sparrows out of their nest sites, and Chestnut-cheeked Starlings and Tree Sparrows replaced one and two pairs of Great Tits, respectively.

GSWs aggressively harassed Chestnut-cheeked Starlings, Tree Sparrows, and Great Tits when these species approached their nests. In spite of these attempts to defend their nest sites, 28.6% (6 of 21) of newly excavated GSW nest cavities were usurped by Chestnut-cheeked Starlings. Three of the six pairs whose cavities were taken over attempted to excavate new nest cavities, but the others did not. Only one of the pairs that made new cavities succeeded in raising

their offspring while the others abandoned their nests.

In HJO, we did not observe direct competition between SCU species and GSW for nest cavities.

DISCUSSION

In our study sites, we found that five avian and one mammalian species used GSW cavities. Thus, the GSW may function as a keystone species, in the urban as well as suburban areas of Sapporo, by providing a critical resource—nesting cavities—for SCUs. Woodpecker cavities can enhance breeding success and reduce predation risk (Rendell & Robertson 1989; Li & Martin 1991), and they may provide thermoregulatory advantages for some SCU species, including Flying Squirrels (Carey et al. 1997).

With the exception of the Nuthatch, none of the species using GSW nest cavities in HKD was found to use them in HJO, and vice versa. It is interesting to note that in HKD where the woodland was highly fragmented, the GSW cavities were frequently occupied by avian SCU species, but almost none by mammalian SCU species.

The competition for GSW cavities may be severer in HKD, reflecting its poor habitat quality. In this area Chestnut-cheeked Starling is the largest user of GSW cavities. In HKD, Chestnut-cheeked Starlings

occupied the same number of GSW cavities as Tree Sparrows did, because they are probably the dominant species in competition for the cavities.

In HKD, Chestnut-cheeked Starlings even usurped GSW newly excavated cavities. Ingold (1994) suggested that woodpeckers (Red-bellied Woodpecker *Melanerpes carolinus*, Northern Flicker *Colaptes auratus*, Red-headed Woodpecker *M. erythrocephalus*) can avoid competition with European Starling *Sturnus vulgaris* and may not have suffered reductions in fecundity, because at least some of these pairs were successful in building new nests later in the season. However, the success rate of the re-nesters was only 17% (1 of 6) in HKD; pairs of GSW were unable to avoid competition with Chestnut-cheeked Starlings and suffered apparent reductions in fecundity.

In HJO, the Flying Squirrel was the main user of GSW cavities. In North America, Flying Squirrels are seen as major predators or competitors of nesting Red-cockaded Woodpeckers *Picoides borealis* (Loeb 1993; Loeb & Hooper 1997; but see Mitchell 1999). Dominant competitors (e.g. Chestnut-cheeked Starlings or Flying Squirrels) may affect utilization and nest-site selection of other SCU species as well as PCNs through their ability to win the competition for cavities. Johnsson et al. (1993) found that the most competitive species, Jackdaws *Corvus monedula* usually used the best old Black Woodpecker *Dryocopus martius* holes, while other subordinate species used inferior holes in a Swedish forest. Further research on species-specific cavity selection and ability of competing for nest cavities would help to determine functional relationships between GSW and SCU species.

The significant difference in the utilization frequencies between 1 year-old and 2–4 year-old cavities suggests that the suitability of GSW nest cavities deteriorates with time elapsed after excavation. Some of the old GSW nest cavities could obviously not be used by SCU species any more because they were clogged with mushrooms, or because the size and shape of the entrance had changed as the living tissues of the tree around it kept growing. Old GSW cavities in living trees seemed to have narrower openings than newly excavated ones, probably due to the lateral growth of the stems.

Another factor that has been reported to prevent repeated use of nest holes is infection with pathogenic organisms or parasites. If old nest material contains larger parasite loads (Perrins 1979; Møller 1989), the lower occupation rate for older (2–4 year-old) cavities might be an indirect effect of parasite avoidance.

In addition to losses of GSW cavities due to natural events, human activities can be of major importance, especially in or near urban areas. Human impact is responsible mostly for decreases in the number of available nest cavities, whereas natural processes influence also the suitability of a given nest hole for repeated use.

Most woodpecker species use trees for nesting, foraging and communication, and they are extremely sensitive to extensive forest harvesting (Winkler et al. 1995). If local extinction of a keystone species, such as GSW, occurred, we predict that the wildlife community will face a catastrophic ecological cascade. To maintain the diversity of wildlife in urban areas, city planners should protect existing GSW cavity trees and maintain a sustainable breeding habitat for continued production of new cavities.

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