Tree cavity abundance and nest site selection of cavity nesting birds in a natural boreal forest of West Khentey, Mongolia

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1 INTRODUCTION

1.1 Roles of Cavity-Nesting Birds

Cavity-nesting birds (CNBs) comprise a major component of many forest bird communities. In Europe and North America, 14% and 10% of the avifauna use tree cavities for breeding (NEWTON 1994). If confined to forest avifauna, CNBs generally constitute about 20 – 30% of breeding bird species in Palaearctic and Nearctic forests (VON HAARTMAN 1957, MCCLELLAND et al. 1979, GIBBS et al. 1993, MARTIN et al. 2004).

Cavity-nesting species can be classified into different guilds according to their mode of cavity acquisition. Woodpeckers, or primary cavity nesters (PCNs), excavate cavities in trees for nesting and roosting. Secondary cavity nesters (SCNs) require cavities but cannot excavate by their own, and thus rely on the cavities constructed by excavators or formed through decay process. In recent years, some studies suggested the division of a third group, weak primary cavity nesters (WPCNs). These birds may excavate their own cavities in decayed trees, use naturally occurring ones, or use cavities from other species. Due to their potential flexibility, they may have different relationships with birds in other guilds, or show different response to the changing availability of nest site resources. Therefore some authors strongly suggested to consider them as a separate group when studing the structure within CNB communities (MARTIN & EADIE 1999, MARTIN et al. 2004).

Great research efforts have been placed in the study of CNBs for the following reasons:

- **CNBs as interesting groups for comparative studies**

Due to their difference in nest site, CNBs and open-nesters may face different constraints, such as nest predation pressure, nest-site availability and microclimate of their nest sites (BRUSH 1983, BRAWN & BALDA 1988, MARTIN & GHALAMBOR 1999, SANIGA 2003). PCNs and SCNs may further differ from each other, as the former are less dependent on existing cavities and their nest site seems to be safer (LI & MARTIN 1991). With that background many hypotheses were tested, e.g. for clutch size (VON HAARTMAN 1957, SLAGSVOLD 1982, MARTIN & LI 1992, MARTIN 1993, MARTIN &

CLOBERT 1996), duration of incubation and nestling periods (MARTIN & LI 1992, MARTIN & CLOBERT 1996), egg colour (VON HAARTMAN 1957), sexual dimorphism (SIGURJÓNSDÓTTIR 1981, MARTIN & BADYAEV 1996, FIGUEROLA & GREEN 2000), courtship and territory behaviour (VON HAARTMAN 1957), foraging behaviour (ALERSTAM & HÖGSTEDT 1981, GREENWOOD 1985), incubation feeding (MARTIN & GHALAMBOR 1999) and coloniality (EBERHARD 2002).

- **CNBs as biological indicators**

For their close association with trees and cavities, CNBs are one of the most sensitive groups to the alteration of forest structure (SCOTT & OLDEMEYER 1983, IMBEAU et al. 1999, 2001). Thus they are suggested to be indicators suitable for detecting and monitoring impacts of forestry (WINKEL 1996, HAUSNER et al. 2003). Among them, the habitat requirements of woodpeckers have been most detailed studied. Many woodpecker species depend on certain tree resources, e.g. large trees, decayed trees or deciduous trees, which are often firstly removed in managed forests (WESOLOWSKI & TOMIALOJC 1986, AULÉN 1988, BLUME 1990, STENBERG 1990, PECHACEK 1995). Several species specialise on certain stages of succession, which are often eliminated due to human intervention in natural dynamics (JAMES et al. 1997, MIKUSINSKI 1997). Therefore woodpecker diversity or the occurrence of certain woodpecker species is considered as indicators of several forest qualities, such as tree species diversity, density of snags or stand age (ANGELSTAM 1990, WEISS 1990, MIKUSINSKI & ANGELSTAM 1998, SCHERZINGER 1998, NILSSON et al. 2001, WÜBBENHORST & SÜDBECK 2003, LAMMERTINK 2004). Woodpecker species richness is also suggested as an indicator of forest bird diversity (MIKUSINSKI et al. 2001).

- **The needs for conservation**

As another consequence of their sensitivity to forest structure alteration, modern forestry exerts great influence on CNBs. The plantation of conifers, fragmentation of landscape and installation of nest boxes do cause the expansion of some species which inhabit coniferous stands, prefer forest edges or are well adapted to nest boxes (VAN BALEN et al. 1982, WESOLOWSKI & TOMIALOJC 1986, MIKUSINSKI 1995). However, many CNB species decline in numbers or even go regionally extinct, as the result of lacking suitable nest sites, lacking suitable foraging substrates or increased

competition with edge species (PETTERSSON 1985, REED 1990, HAVELKA & RUGE 1993, WESOLOWSKI 1995a, JEDICKE 1997, MIKUSINSKI & ANGELSTAM 1997, WIKTANDER et al. 2001, KOENIG 2003). Such situation in Europe is profound due to long-term anthropogenic habitat change. At the continent scale, six out of ten European woodpecker species showed negative trends over the last decades (RUGE 1993, SAARI & MIKUSINSKI 1996, MIKUSINSKI & ANGELSTAM 1997). In Germany, 15 CNB species are placed in the Red List. In the forest bird community of Germany, about 29% of CNB species are placed in the Red List, while only 16% of open nesting species are in the list (BAUER et al. 2002).

1.2   Present Studies about Cavity-Nesting Birds

As the consequence of their importance in scientific study, conservation and management, CNBs have become one of the most intensively studied bird groups. However, our knowledge of them is still far from complete, and in some aspects even heavily biased, as data from natural cavities and natural forests are rare, quantitative information is usually incomplete, and the relationships among species are largely ignored.

- **Lack of studies with natural cavities**

So far most of our knowledge about CNBs is gathered from the studies of birds in nest boxes. Nest box studies of birds are very productive, because boxes can usually be designed to attract the desired species, and provide large samples of easily found nests in accessible and standardised sites. Moreover, the catch of individuals, the monitoring of breeding success and the manipulation of nest-site variables can be handled without difficulty. Therefore, since 1920s, the studies with nest boxes have become popular, especially in the managed forests of Europe (MØLLER 1989, NEWTON 1994, WESOLOWSKI & STANSKA 2001). Not surprisingly, some box-nesting species, such as the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca*, are now some of the best-known birds in the world. The long-term data from nest boxes have further formed the basis for the development of many important ideas in several fields, such as population regulation, sexual selection, habitat selection, site fidelity and life history evolution (e.g. LACK 1966, MINOT 1981,

ALATALO et al. 1986, GUSTAFSSON 1986, NUR 1986, KRIŠTÍN & ŽILINEC 1997, TRIPET & RICHNER 1997).

However, there are substantial differences between the characters of nest boxes and that of natural cavities. Nest boxes are usually designed to be safer from predation. The old nests in nest boxes are often artificially removed, which may influence parasite loads. The microclimate in the nest boxes may differ from that in natural cavities. Nest boxes tend to be uniform, with usually one variable of dimension or location experimentally manipulated each time. While natural cavities occur in diverse shape, dimension and location, and these properties are correlated. Furthermore, nest boxes usually cause higher density of specific host species population in the nest box area, which may influence the predation and parasitism patterns as well as behaviour of box users (VAN BALEN et al. 1982, NILSSON 1984a, GREENWOOD 1985, WESOLOWSKI et al. 1987, MØLLER 1989, WESOLOWSKI & STANSKA 2001, MITRUS 2003). Recent comparative studies have found that laying date, clutch size, predation rate, main predator species, parasite loads, breeding success and population fluctuations differed between the nest box populations and those breeding in natural cavities (PURCELL et al. 1997, CZESZCZEWIK et al. 1999, WESOLOWSKI & STANSKA 2001, EVANS et al. 2002, CZESZCZEWIK 2004), and the response differed from species to species.

As nest boxes have not become widely available until several decades ago, some traits of the birds breeding in nest boxes may not yet be adaptive, and the sequential generalisations might be misleading. Though some CNB species may locally breed almost exclusively in nest boxes, the majority of the individuals of any species still breed in natural cavities. Thus the observations of box-breeding populations may not represent the species properly (WESOLOWSKI & STANSKA 2001). Therefore studies of CNBs breeding in natural cavities are highly in need (VAN BALEN et al. 1982, WESOLOWSKI 1989)

- **Lack of studies in natural forests**

As the importance of the studies with natural cavities is gradually being concerned, most of the studies were carried out in managed woodlands, especially in Europe (WESOLOWSKI 1989). In managed forests, several important factors may be totally

different to the primeval conditions. Managed forests usually have impoverished snag density and cavity abundance (MORIARTY & MCCOMB 1983, ZEEDYK 1983, NEWTON 1994, GRAVES et al. 2000). Predator abundance and potential predator species also differ between managed forests and natural ones. Even in unmanaged forest fragments surrounded by modified landscape, forest edge species usually dominate CNB communities (VAN BALEN et al. 1982, JOHNSSON et al. 1993), and the extent and the pattern of predation may differ from that under natural conditions (SANDSTRÖM 1991, WALANKIEWICZ 2002a, WESOLOWSKI 2002). Actually, to what extent and in which direction does the situation in managed forests differ from that in pristine conditions are still largely unknown, as there is too few information available about the CNBs breeding in the primeval habitats (WESOLOWSKI 1989).

As species were evolved in and adapted to natural habitats, evolutionary interpretations should be preceded by observations in natural habitats (CZESZCZEWIK & WALANKIEWICZ 2003). From the viewpoint of conservation, with the emergence of the idea of ecological forestry since 1990s, the goal of forest management is aimed towards a "near-nature" system (HANSEN et al. 1991, FUJIMORI 2001). However, this could not be achieved without knowledge of natural conditions. Thus there is an increasing and urgent need of understanding biodiversity and its maintenance in natural forests, so that such knowledge can be incorporated into management guidelines.

In boreal forests, one further point addresses the importance of studying CNBs in natural forests. Boreal forests have been a dynamic system in the past due to fire. Due to their close association with forest structure, CNBs as a group is highly sensitive to post-fire succession (MURPHY & LEHNHAUSEN 1998, SAAB & DUDLEY 1998, IMBEAU et al. 1999, SAAB et al. 2004). However, large areas of boreal forests are no longer dynamic in natural process. Fire suppression is conducted in managed forests as well as most of the protected areas in Europe and North America (CHANDLER et al. 1983, GOLDAMMER & FURYAEV 1996, MCRAE & LYNHAM 2000, GRANSTROM 2001). In Fennoscandia, for example, it is nearly impossible to find sufficient successional stages for ecological study (HELLE & NIEMI 1996). Information from forests not only of natural structure but also under natural processes is necessary to evaluate the consequence of human intervention in natural dynamics.

- **Lack of quantitative habitat survey**

A further flaw in the studies of CNB nest-site selection is that most studies did not quantitatively survey the forest structure and cavity availability (e.g. MCCLELLAND et al. 1979, WESOLOWSKI & TOMIALOJC 1986, WESOLOWSKI 1989, JOHNSSON et al. 1993, MEYER & MEYER 2001, WIESNER 2001, GIBBONS et al. 2002). The availability of suitable trees for nest excavation and the availability of suitable nesting cavities have often been suggested as the factor limiting the population of several PCN and SCN species, respectively (GUSTAFSSON 1986, AULÉN 1988, HÅLAND & UGELVIK 1990, POGUE & SCHNELL 1994, POYSA & POYSA 2002). But this point was often assumed instead of proved. Data on availability of nest substrates or nest cavities were largely lacking.

The information on forest structure and cavity availability according to different tree attributes is also essential to demonstrate the preference of birds. The observed pattern of PCN species frequently using certain trees might be due to the abundance of such trees in the habitat. As cavities occurrence highly dependant on tree species, age and decay condition (VAN BALEN et al. 1982, NOEKE 1990), the observed tree utilisation pattern of SCN species is further confounded by the availability of cavities. Without taking the entire resource availability into account, the selection or preference cannot be properly clarified. This is especially important in the natural forests, as trees and cavities are present in diverse forms, and many attributes are correlated. Yet nest-site selection studies with consideration on resource availability were few (SANDSTRÖM 1992, WALANKIEWICZ 1991).

- **Lack of information at the community level**

Though the nest-site selection of CNBs has been intensively investigated, most studies focused only on single species (e.g. KOROL & HUTTO 1984, DOW & FREDGA 1985, MULDAL et al. 1985, BELTHOFF & RITCHISON 1990, RUDOLPH & CONNER 1991, DAILY 1993, SMITH 1997, ROLSTAD et al. 2000, MITRUS & SOCKO 2004). These efforts resulted in detailed information valuable for setting up individual conservation guidelines. However, analyses of nest-site use at the community level were few, and interspecific relationships were largely ignored (MARTIN & EADIE 1999, BEDNARZ et al. 2004). Some studies filled the gap by surveying the nest sites of several sympatric

PCNs or SCNs, which provided the information to investigate the relative preference of each species, extent of niche overlap and the potential for competition (e.g. VAN BALEN et al. 1982, STAUFFER & BEST 1982, PETERSON & GAUTHIER 1985, WESOLOWSKI 1989, CARLSON et al. 1998). While CNBs were composed of PCNs and SCNs, which have different constraints but are intimately related, an overall consideration is critical for demonstrating ecological links among species and drawing up comprehensive conservation plans.

Some recent trends of studying CNBs within broader ecological context include studies of sequential cavity use and nest web analysis. Patterns of cavity reuse are central to understand the population ecology and evolution of cavity nesting birds (SEDGWICK 1997). Yet studies on cavity reuse were mostly focused on the reuse tendency of certain species (e.g. BARCLAY 1988, MAZGAJSKI 2003, STANBACK & ROCKWELL 2003), or the sequential use of specific woodpecker holes (e.g. KÜHLKE 1985, JOHNSSON et al. 1993, BONAR 2000, MEYER & MEYER 2001, WIESNER 2001, KOTAKA & MATSUOKA 2002). Only since SEDGWICK (1997) has the reuse pattern of the whole CNB community been concerned. Nest web is a newly emerged approach in structuring CNB communities analogous to food webs (MARTIN & EADIE 1999). It reveals direct and indirect interactions among species and may predict the response of the community to perturbations or change. Yet so far only the nest web of British Columbia has been worked out (MARTIN & EADIE 1999, AITKEN et al. 2002)

1.3   Objectives of this Study

The objectives of this study were:

– to investigate cavity abundance in different types of natural boreal forest,
– to identify the characteristics of cavity trees,
– to survey CNB composition in different types of natural boreal forest,
– to observe the characteristics of trees and cavities utilised by CNBs,
– to study the nest-site selection of individual species,
– to investigate the pattern of sequential cavity use, and
– to construct the nest web for the CNB community.

2 STUDY AREA

2.1 Natural Environment of Mongolia

2.1.1 Geographic location and landform

Bordering the Russian Federation in the north and the People's Republic of China in the east, south and west, Mongolia is a landlocked country which covers an area of 1.56 million km^2. It extends 1236 km from north to south, stretches 2405 km from east to west, and is the seventh largest country in Asia (MNE et al. 1998).

Mongolia is a typical highland (Fig. 2.1). About 85% of its territory is situated higher than 1000 m, and the average elevation is 1580 m above sea level. The relief is characterised by a highly wavy plateau which is crossed by the Altai mountains in the west and the Khangai-Khentey mountain area in the north. The rivers originating from the northern slopes of the Khangai-Khentey mountains flow into the Arctic Ocean. The area east of the Khentey mountains belongs to the drainage basin of the Pacific Ocean. The central and southern parts of the country have few rivers and other water resources, and they usually situated in depressions without any outflow, forming part of inland drainage of Central Asia (MNE et al. 1998).
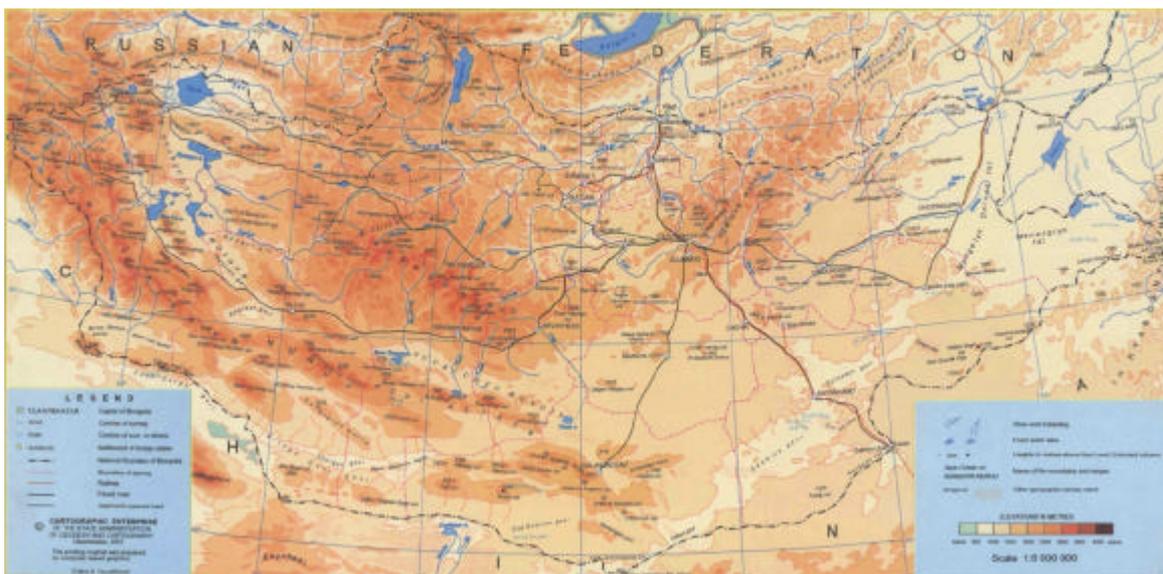
Fig. 2.1   Physical map of Mongolia (OYUNKHAND 2001).

2.1.2   Climate

The main characteristics of Mongolia's harsh continental weather are long and cold winter, low precipitation and great annual and diurnal fluctuations in temperature. The mean temperature in January is -20 to -35°C, but the extreme temperature ever recorded reaches -58°C. In July, the mean temperature ranges between 15°C in the mountains and 20 to 30°C in the south, while the extreme temperature higher than 40°C has been recorded (MNE et al. 1998).

The annual precipitation averages approximately 400 mm in the northern mountainous region and decreases to less than 100 mm in the south. 75 to 85 percent of the precipitation falls in the three summer months (MNE et al. 1996, 1998).

2.1.3   Vegetation zones

Mongolia can be divided into six basic vegetation zones: alpine, mountain taiga, mountain forest steppe, arid steppe, desert-steppe and desert (Fig. 2.2). These zones differ in their flora, fauna and soil quality, which are adapted to the geographic and climatic conditions (LAVRENKO 1979; MNE et al. 1996, 1998).
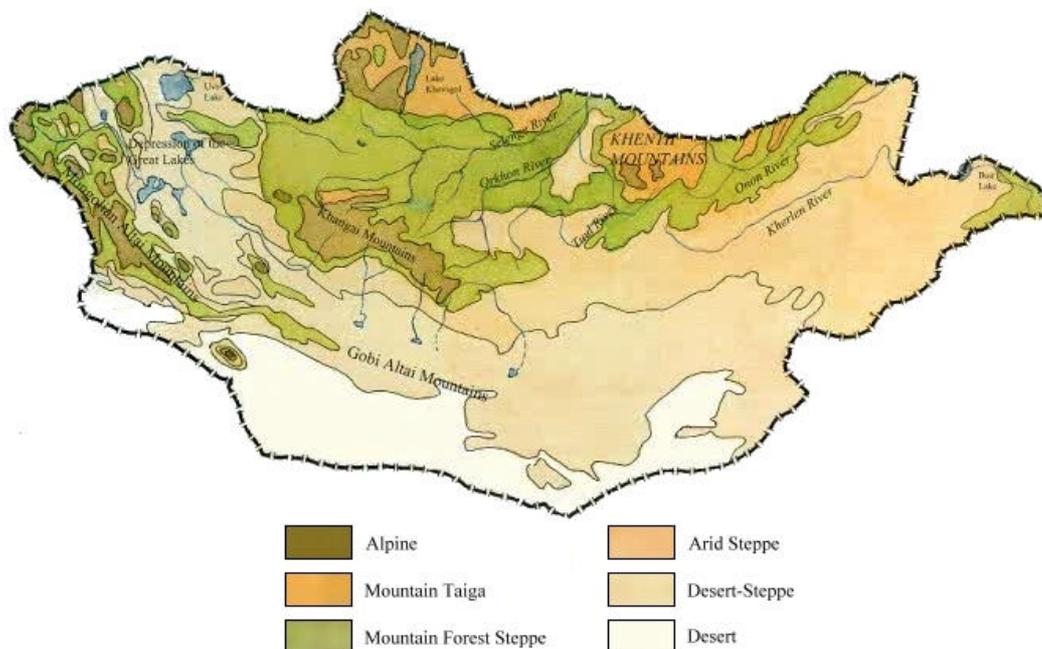
Fig. 2.2   The vegetation zones of Mongolia (MNE et al. 1996).

The alpine zone rises above the tree line in the Altai, Khangai and Khentey mountains. It is characterised by tundra, alpine-sedge meadows and highland swamps. The mountain taiga zone of Mongolia is the southern edge of the Siberian taiga, the largest continuous forest system in the world. The forests in this zone consist mainly of Siberian pine *Pinus sibirica* and Siberian larch *Larix sibirica*, and hold a relatively rich flora and fauna. The mountain forest steppe zone is the ecotone of Siberian taiga and Central Asian steppe. The taiga tree species distribute over the northern slopes, while the steppe vegetation occupies the southern slopes. This zone covers about 26% of Mongolia's area. The arid steppe zone is characterised by flat plains and rolling hills covered in feather grass and shrubs. The vegetation in desert-steppe zone is dominated by low grasses and semi-shrubs. In the desert zone, the extreme climate hinders the growth of plants. Most parts consist of bare sandy plains and rocky mountains (MNE 1996).

2.2   The Khan Khentey Strictly Protected Area

2.2.1   Geographic location, topography and hydrology

The Khan Khentey Strictly Protected Area (KKSPA), situated in the northeast of Mongolia, was founded in 1992 (Fig. 2.3). This huge uninhabited area, stretching from the Russian border to the northeast of Ulaanbaatar, lies between 48°N and 49°N and extends from 107°E to 110°E. It covers 1.2 million ha and is the fourth largest protected area in Mongolia (MYAGMARSUREN 2000). Compared with the protected boreal ecosystems in Europe, it is as large as the complete protected forests of Fennoscandia (VON VELSEN-ZERWECK 2002). Under the cooperation of the Göttingen University and the Ulaanbaatar University, in 1999 the research station Khonin Nuga was established by the side of the Eröö river in the western buffer zone of the KKSPA (Fig. 2.3).

The KKSPA comprises the rugged Khentey mountains, a northeast-southwest branch of Transbaikal mountain range. The terrain undulates from around 900 m at the river valleys to almost 2800 m at the highest peak (MNE & WWF 1994). As the region where the watersheds of the Arctic Ocean and the Pacific Ocean intersect, it plays important hydrological roles. In the western part of the area, the rivers Eröö, Minsh
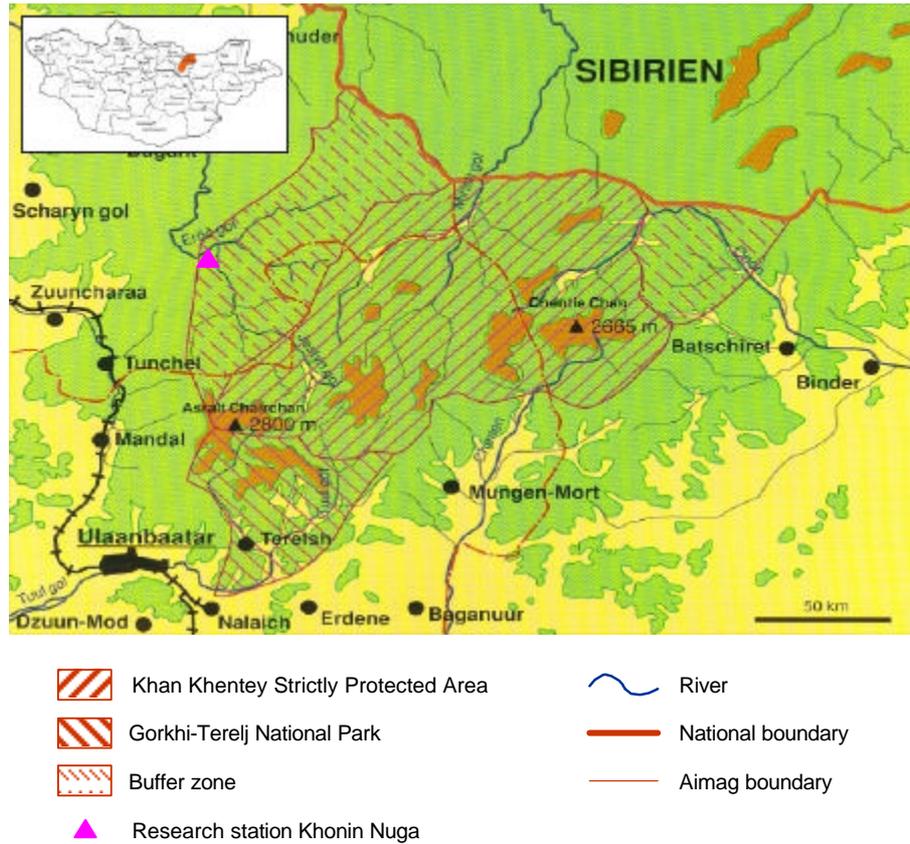
Fig. 2.3   The location of Khan Khentey Strictly Protected Area and research station Khonin Nuga (after MNE & WWF 1994).

and Tuul originate. These rivers form the headwaters of the Selenge river, which is the major inflow of the Baikal Lake. Thus the KKSPA is interlinked with the largest and oldest freshwater lake on earth (MÜHLENBERG et al. 2001). In the eastern part, the rivers Onon and Cherlen run eastwards through the eastern steppes of Mongolia, then pour into the Amur river, which flows into the Pacific Ocean. Therefore the KKSPA is crucial in nourishing the large area of Mongolia's eastern steppes with precious water resource (VON VELSEN-ZERWECK 2002).

2.2.2   Climate

Situated more than 1400 km away from the closest ocean, the climate of the Khentey mountains is strongly continental. Under the influence of the Siberian high pressure, the winter is cold, clear and dry with little snowfall. In summer, the warm air from Central Asia meets the cold air of the north, and the precipitation increases. Thus the climate of the KKSPA is characterised by moderate, humid, short summer and cold,

dry, long winter. The mean temperature in July is about 12°C. In January, the mean temperature averages -24°C, but can drop to the extreme of -45°C. The annual precipitation reaches 400-500 mm in the higher zone, which is one of the precipitation-richest areas in Mongolia. 80% of the precipitation falls in July and August (DöLLE et al. 2002).

The local climate varies greatly according to elevation and aspect. Temperature drops and precipitation rises with increasing altitude. The northern slopes are the windward side in the region, while the southern slopes expose to the sun. Therefore the northern slopes are cooler and have relatively higher precipitation. These variations shape the characteristic mosaic of vegetation cover (DULAMSUREN 2004).

2.2.3   Vegetation types

The KKSPA defines the southern edge of Siberian taiga and is the transition zone where the vast Siberian taiga meets the broad Central Asian steppe. This region belongs predominantly to the mountain taiga zone, with the mountain forest steppe in the south and the alpine zone at the high peaks (LAVRENKO 1979).

The mountain taiga zone surrounding Khonin Nuga is classified into three groups: the upper mountain level at the elevation 1200-1600 m, the lower mountain level at 900-1300 m and the riparian vegetation at the riverside (DULAMSUREN 2004). The upper mountain level is covered by dark mountain taiga mainly dominated by Siberian pine. In the lower mountain level, forests cover only the northern slopes, while shrubs or herbs occupy the drier southern slopes. In more shaded and humid stands with fertile soil, the forests of the northern slopes is dark mountain taiga dominated by Siberian spruce *Picea obovata* and Siberian fir *Abies sibirica*. The most widespread forest type is, however, light subtaiga, consisting mainly of whitespire birch *Betula platyphylla* and Siberian larch *Larix sibirica*. The riparian vegetation appears in diverse forms, including riparian forests, bushes and riverine meadows. The riparian forest is dominated by birch, spruce, Scots pine *Pinus sylvestris*, laurel poplar *Populus laurifolia* or willow *Salix spp.* depending on soil conditions (DöLLE et al. 2002, DULAMSUREN 2004).

2.2.4 Bird community

In the whole Khentey mountains, 253 bird species have been recorded, among which 180 species breed in the area (BOLD 1984). 185 species of 38 families have been registered around Khonin Nuga, with 137 species as breeding birds (WICHMANN & POKROVSKAYA 2004). The high number of breeding species is contributed by the high habitat diversity and naturalness (WICHMANN 2001).

The biogeographic component of breeding bird community is primarily Palaearctic (45%). The rests are composed mainly of Holarctic (17%), Central-and-East Asian (14%) and Southeast Asian (14%) species. Main bird species in the open area are Black-faced Bunting *Emberiza spodocephala*, Yellow-breasted Bunting *E. aureola*, Dusky Warbler *Phylloscopus fuscatus*, Common Rosefinch *Carpodacus erythrinus* and Daurian Redstart *Phoenicurus auroreus*. Dominant species in the most prevalent forest type, the birch-larch forest, are Willow Tit *Parus montanus*, Nuthatch *Sitta europaea*, Red-throated Flycatcher *Ficedula albicilla*, *P. auroreus*, Olive-backed Pipit *Anthus hodgsoni* and Pallas's Warbler *Phylloscopus proregulus* (WICHMANN 2001).

2.3 Study Stands

Considering the representative forest types and their accessibility, the field work was carried out in four different forest stands, including two birch-larch forests of different successional stages, the riparian mixed forest and the spruce-fir coniferous forest (Fig. 2.4). The former three stands are situated close to the research station Khonin Nuga, while the coniferous stand is located about 20 km southeast from the others, because around the Khonin Nuga the birch-larch forests cover most of the area.

2.3.1 Mature birch-larch forest (BLm; Fig. 2.5(a)):

This deciduous stand lies on a gentle northern slope. The surveyed area covered about 52 ha, and the elevation ranges from 950 to 1100 m. Canopy is dominated by birch with scattered emergent larch trees. Aspen is patchily abundant.

The ground cover is characterised by rich and diverse herbs. The main species include brome *Bromopsis pumpellianus*, sedge *Carex amgunensis*, dwarf iris *Iris ruthenica* and vetchling *Lathyrus humilis*.
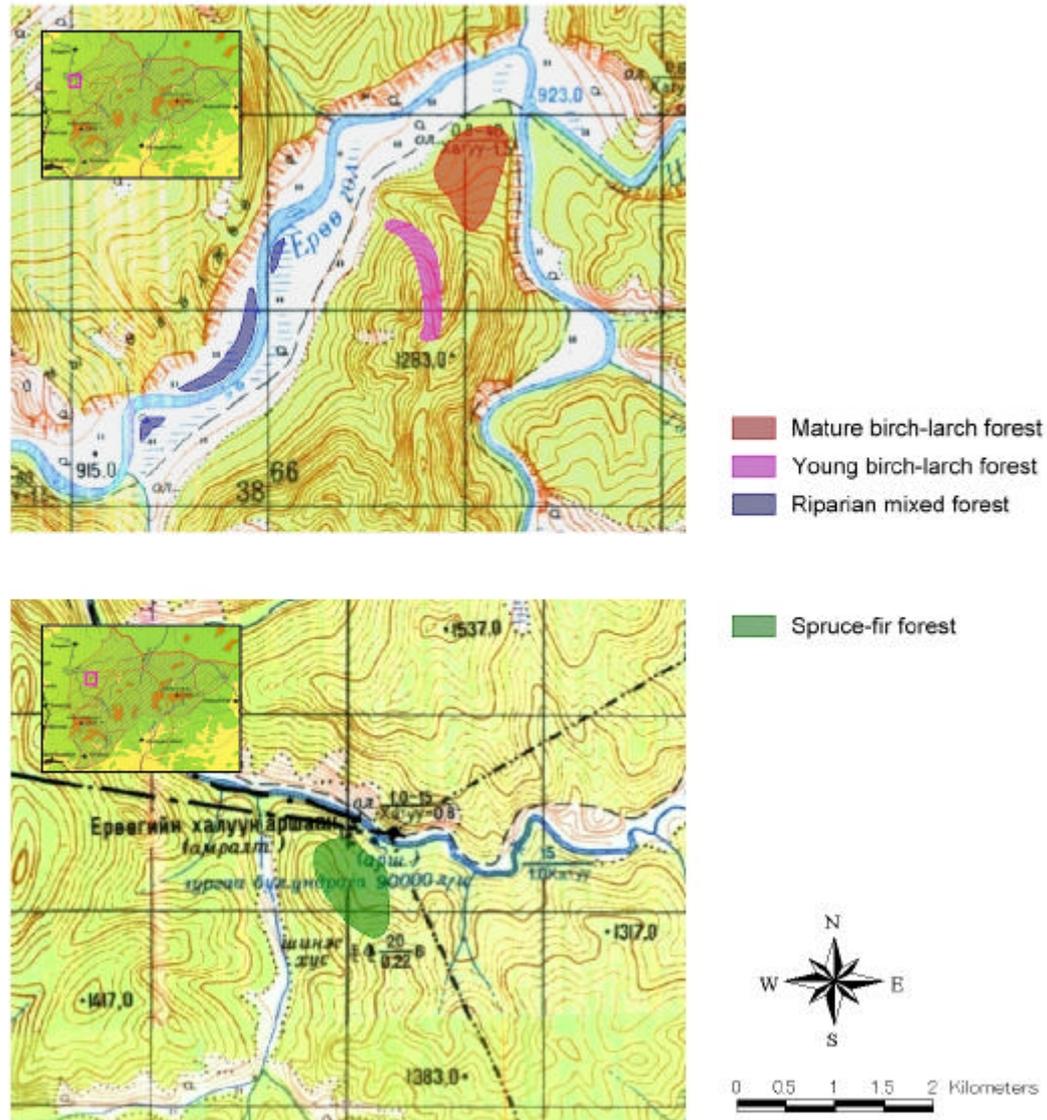
Fig. 2.4   The location of study stands.

2.3.2   Young birch-larch forest after recent fire (Bly; Fig. 2.5(b)):

This stands is located on a steep northeastern slope with an area of approximately 25 ha. The elevation ranges between 1000 and 1250 m. The dominance of birch is similar to that in the previous habitat, but is composed of thinner and closely spaced stems. Larch scatters among the birch, large Scots pine patchily dominates the upper part of eastern slope, and aspen forms small and disperse patches.

This stand is characterised by obvious signs of fire. Over 95% of all living stems, even the young ones, were scarred by fire. The impact of fire is spatially

heterogeneous: in some patches and along the ridge, most of the trees were killed and canopy is open; while close to the valley, the fire progressed in the form of surface fire, keeping most trees alive with fire scars at the bottom. Density of standing dead trees is high.

The composition of ground cover is similar to that in the previous habitat. In patches where the canopy is open, shrubs such as Dauricum rhododendron *Rhododendron dauricum* and prickly rose *Rosa acicularis* form dense clumps.

2.3.3   Riparian mixed forest (RM; Fig. 2.5(c)):

This habitat forms thin belts on the alluvial side of rivers. The surveyed area included three blocks, with a total area of 23 ha. The relief is rather flat, and the elevation lies at about 920 m. Tree species composition and forest structure are diverse. Birch, poplar and Scots pine dominate different patches, while willow, larch and spruce are also patchily frequent.

Shrub layer is well developed in the riparian mixed forest. The main species include redhaw hawthorn *Crataegus sanguinea*, bird cherry *Padus asiatica*, bush cinquefoil *Potentilla fruticosa*, red currant *Ribes rubrum* and bridewort *Spiraea salicifolia*.

2.3.4   Spruce-fir coniferous forest (SF; Fig. 2.5(d)):

This coniferous stand is situated on a moderate northeastern slope. The surveyed area covered approximately 53 ha. The dominant tree species is spruce. Fir, Siberian pine, birch and old larch are scattered, and Scots pine occupies upper slopes. Deadfalls (dead wood on the ground) are abundant.

Moss forms the characteristic ground layer in this habitat. Typical species include bog groove-moss *Aulacomnium palustre*, tree-moss *Climacium dendroides*, crisped fork-moss *Dicranum bonjeanii* and spiky bog-moss *Sphagnum squarrosum*.
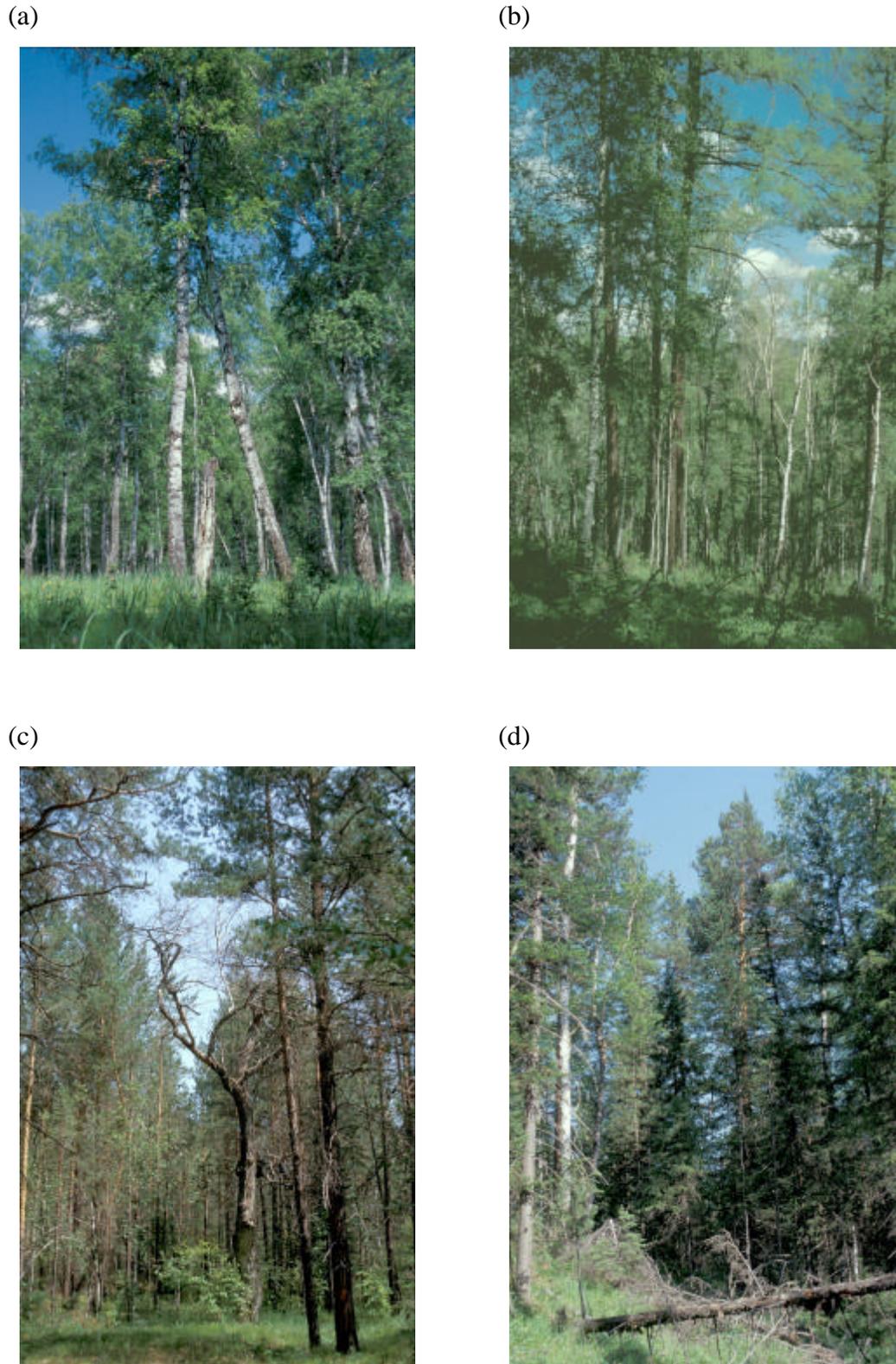
Fig. 2.5 **The study stands (a) the mature birch-larch forest, (b) the young birch-larch forest, (c) the riparian mixed forest, and (d) the spruce-fir coniferous forest.**

3 METHODS

3.1 Field Work

3.1.1   Habitat measurement

In each of the four habitats, five 1 ha plots (50 × 200 m) were established for detailed study and quantitative comparison among habitats. The plots were orientated so that the distance between neighbouring plots was at least 100 m. Each plot was marked at intervals of 25 m along the boundary and the long axis, in order to help locating individual trees and mapping the territories of birds.

In each plot, two points on the long axis, each of which lied 50 m apart from one end, were taken for carrying out habitat measurements. Elevation, slope, topographic position, canopy height, shrub coverage, amount of lying dead wood were registered at each sampling point (see Table 3.1 for description). Standing stems (diameter at breast height (DBH) ≥ 5 cm) were sampled by the plotless method with the help of a dendrometer (GROSENBAUGH 1952). This method was adopted instead of the fixed-area plot sampling, because the probability a tree being sampled is proportional to its DBH in the former method. Therefore it is more efficient in collecting the information of large trees, especially in heterogeneous natural forests where the occurrence of a tree is usually negatively correlated to its DBH. The data at each sample point can be transformed into per unit area based information without bias (AKÇA 2000). For each sampled tree, the following items were recorded:

(1) tree species;
(2) DBH, registered in 5 cm rank;
(3) tree condition, categorised as 1. healthy living tree, 2. living tree, in state of decline, 3. dead tree, branches intact, 4. dead tree, few or no branches, 5. dead tree, broken top, 6. dead tree, shortened snag (Fig. 3.1; after MASER et al. 1988, GUNN and HAGAN 2000);
(4) if the tree had fire scars; and
(5) if the tree carried fruit bodies of fungi.

These single-tree measurements were then sorted into forest structure variables of each sampling point as listed in Table 3.1.

Table 3.1   The habitat variables recorded in each sampling point.

Variable	Definition
Elevation	Measured with a GPS (m)
Slope	Measured with a clinometer (degree)
Topographic position	Assigned to one of the five levels: 1: ridge, 2: upper slope, 3: middle slope, 4: lower slope, 5: flat plain
Canopy height	Measured with a dendrometer (m)
Shrub coverage	Percentage of shrub (height = 50 cm)-covered area in a circle of 10 m radius (%)
Lying dead wood	Number of woody debris (diameter = 15 cm) in a circle of 10 m radius
Stem density	Number of standing stems pro hectare (n/ha)
Prop. decid.	Percentage of deciduous stems (%)
Prop. large	Percentage of trees with DBH = 40 cm (%)
Prop. dead	Percentage of dead trees (tree condition category = 3) (%)
Prop. fire	Percentage of stems with fire scars (%)
Prop. fungi	Percentage of stems with fungi conk (%)
Birch	Basal area of birch (m^2/ha)
Aspen	Basal area of aspen (m^2/ha)
Poplar	Basal area of poplar (m^2/ha)
Willow	Basal area of willow (m^2/ha)
Rowan	Basal area of rowan (m^2/ha)
Larch	Basal area of larch (m^2/ha)
Scots pine	Basal area of Scots pine (m^2/ha)
Siberian pine	Basal area of Siberian pine (m^2/ha)
Fir	Basal area of fir (m^2/ha)
Spruce	Basal area of spruce (m^2/ha)
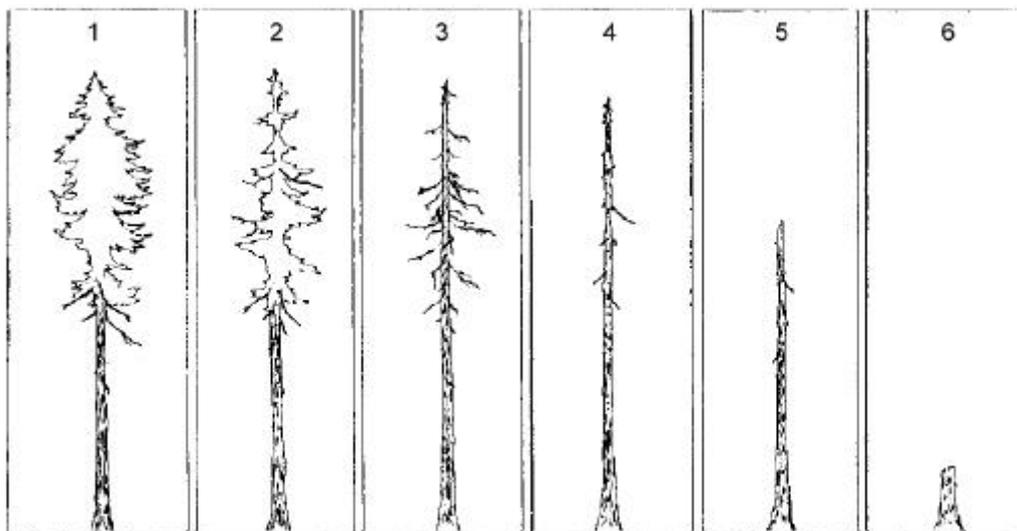
Fig. 3.1   Tree condition: 1. healthy living tree, 2. living tree, in state of decline, 3. dead tree, branches intact, 4. dead tree, few or no branches, 5. dead tree, broken top, 6. dead tree, shortened snag (after MASER et al. 1988, GUNN and HAGAN 2000).

3.1.2   Cavity search

Each standing stem sampled in habitat measurement was searched for cavities in autumn 2002, when deciduous trees had lost their leaves. Cavities were located by examining from the ground with the help of a binocular, and each tree was observed from at least three directions. Trees with cavities found were referred as cavity trees.

Cavities were classified into one of the following types (after CARLSON et al. 1998):

(1) Woodpecker hole (Fig. 3.2(a)): excavated by woodpeckers for nesting or roosting. In the study area, this might be constructed by the Black Woodpecker *Dryocopus martius*, the Grey-headed Woodpecker *Picus canus*, the Great Spotted Woodpecker *Dendrocopos major*, the White-backed Woodpecker *D. leucotos*, the Lesser Spotted Woodpecker *D. minor* or the Three-toed Woodpecker *Picoides tridactylus*.

(2) Other bird-induced hole (Fig. 3.2(b)): including all other excavated cavities that were apparently not the nesting or roosting holes of woodpeckers. This category included cavities excavated by the Willow Tit *Parus montanus* for nesting and cavities of any origin but followed by the destruction of woodpeckers.

(3) Branch hole (Fig. 3.2(c)): originating from a fallen limb and showing no signs of processing by birds.

(4) Bark crevice (Fig. 3.2(d)): formed under loose bark.

The former two types were referred as excavated cavity, and the others as non-excavated cavity. The excavating species, including six woodpecker species and *P. montanus*, were referred as primary cavity nesters (PCNs). The other non-excavating species were referred as secondary cavity nesters (SCNs). In the analysis of sequential cavity use (Section 4.7) and nest web (Section 4.8), *P. montanus*, which could either excavate by itself or use existing cavities, was referred separately as weak primary cavity nester (WPCN).

(a)

(b)

(c)

(d)
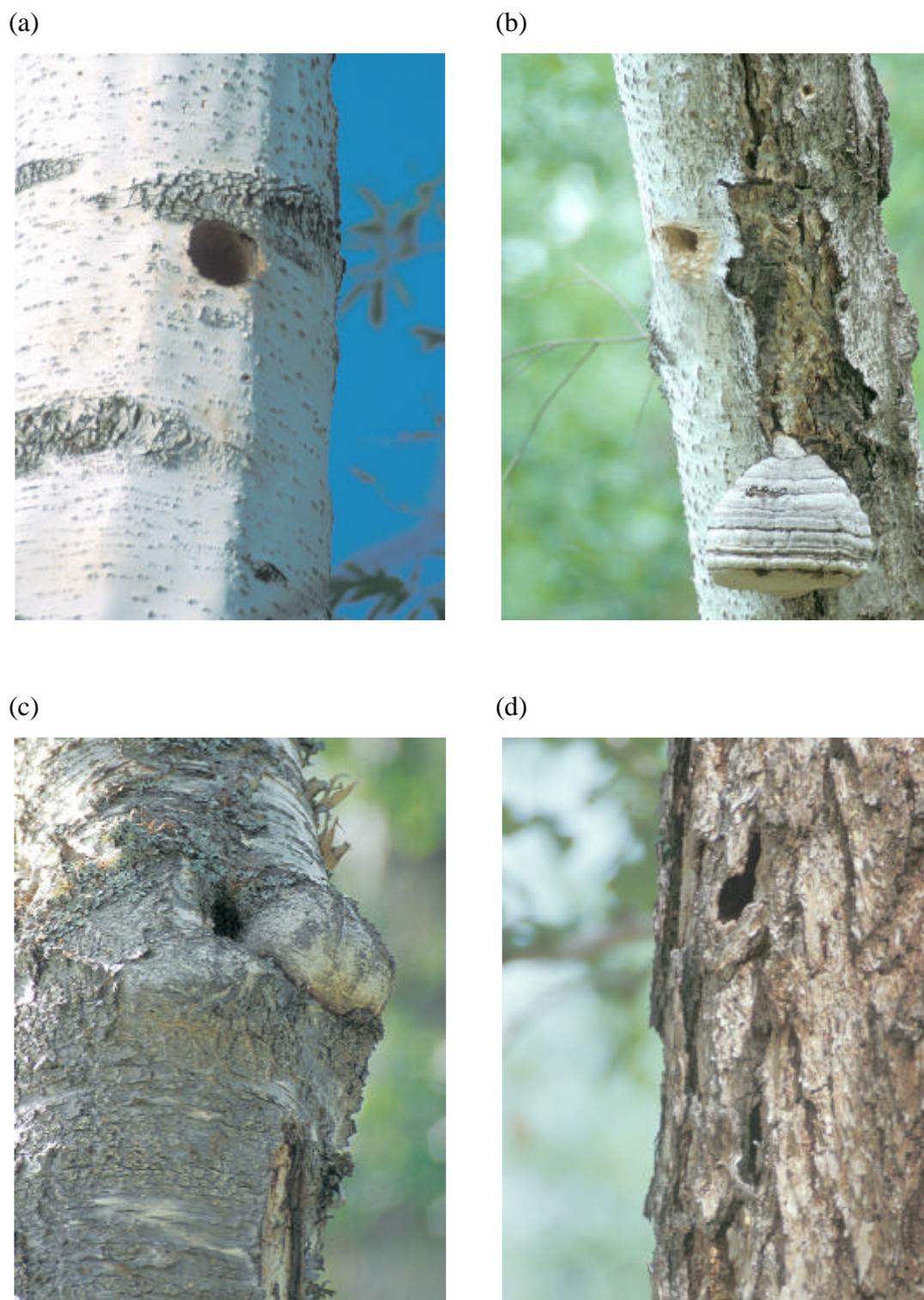
Fig. 3.2   Different cavity types: (a) woodpecker hole, (b) other bird-induced hole, (c) branch hole and (d) bark crevice.

3.1.3   Nest cavity search and measurement

Nests of all cavity-nesting bird (CNB) species were searched from the last week of April to the first week of July in 2002 and 2003. Given the northern latitude, harsh winter and late-coming spring of the study area, most resident and migratory CNBs did not begin nesting until the first week of May (WICHMANN, pers. com.). This was in correspondence to the phenology of CNBs in the boreal forests of Fennoscandia (CARLSON et al. 1998) and Canada (MARTIN et al. 2004).

Nests were located by observing breeding behaviour, listening for excavating PCNs or begging chicks and scratching or knocking cavity trees. A nest cavity was defined when an adult bird was observed bringing in nesting material or food. For species such as *D. martius*, *P. canus* and the Wryneck *Jynx torquilla*, of which the food carriage could hardly be observed, frequently entering a cavity was taken as the evidence of an active nest. As for ducks such as *B. clangula*, of which the youngs fledge soon after hatched, the female entering a cavity in the daytime was regarded as the presence of a nest. The observations of birds displaying or defending a cavity were not considered as signs of cavity occupancy (WESOLOWSKI 1989, MARTIN & EADIE 1999, BONAR 2000). In the quantitative plots, nest search was confirmed with territory mapping, in order to locate all the nest cavities in the plots. Nest cavities found outside the plots were recorded as well. A tree with a nest cavity was referred as the nest tree, and the part of trunk or branch in which the nest cavity was located was referred as the substrate.

For each nest, variables were recorded according to three different scales (GIBBONS et al. 2002):

(1) Habitat variables: the same procedure as taking habitat measurement was carried out, but using the nest tree as the centre point instead (POGUE & SCHNELL 1994, MARTIN & EADIE 1999). Elevation, slope, topographic position, canopy height, shrub coverage, amount of lying dead wood and composition of surrounding standing stems were registered (see Section 3.1.1).

(2) Nest tree variables: tree species, tree DBH (in cm), tree condition (as defined in Section 3.1.1), the presence of fire scars and fruit bodies of fungi were recorded;

(3) Nest cavity variables: including cavity type, cavity height above ground, substrate
     diameter, substrate condition (categorised as living or dead), cavity opening
     length and cavity opening width.

The types of nest cavities were categorised into woodpecker hole, other bird-induced
hole, branch hole and others. The former four types followed the definition as
described above, while the last category "others" covered all other less common nest
sites, which encountered in this study included bark crevices, hollows on broken top
(chimneys), holes originated from side fire and vertical slits in trunk due to the shear
force when the snag broke.

The cavity height was measured from the ground to the middle of the cavity opening
with a dendrometer. The substrate diameter, cavity opening length and cavity
opening width were estimated from ground using the size of adult birds as a reference
(PETERS & GRUBB 1983). The ratio of opening length to opening width was
calculated as an index of opening shape. The opening shape of a cavity was termed
"slit-like" when the ratio was larger than 1.25, "flat" when the ratio was smaller than
0.8, and "round" for an intermediate value.

The distance and direction to the next plot mark of each nest tree were recorded.
Together with the tree and cavity variables recorded, all nest cavities could be
relocated (SEDGWICK 1997). The nest cavities found in 2002 were checked in 2003,
and the utilisation of each was recorded as occupied, unoccupied or unusable.
Unusable cavities included those that had destructed walls or those that were lost due
to the collapse of the tree or limb containing the cavity (SEDGWICK 1997). The nest
cavities located outside the plots were revisited less often, thus a nest which failed in
the early stage of breeding might not be observed.

3.2   Statistical Analysis

3.2.1   Habitat structure

Kruskal-Wallis test was used to compare habitat variables among four habitats (ZAR 1999). When the among-habitat difference of a variable was found (significance level 0.05), Mann-Whitney U test was further applied for pairwise comparison.

A habitat could be viewed as a complex of all the interlinked variables, which were individually measured (POGUE & SCHNELL 1994, ROTENBERRY & WIENS 1998, MCGARIGAL et al. 2000). Thus the principal component analysis (PCA) was applied to the correlation matrix of 22 habitat variables (Table 3.1), for summarising the variations of these variables. The major trends of variation were represented in the first few principal components. These principal components could be interpreted by their component loadings. Each of the 20 plots was then projected onto the main components according to its component score. Such a graphic could represent the ecological relationship among habitats and indicate the important dimensions of available habitat space (ROTENBERRY & WIENS 1998).

3.2.2   Cavity abundance

To compare the density of different cavity types and the cavity density in different habitats, Kruskal-Wallis test (for number of groups > 2) and Mann-Whitney U test (for number of groups = 2) were applied.

The relationship between cavity abundance and habitat variables was checked with correlation analysis (SANDSTRÖM 1992). Pearson correlation coefficients between the density of each cavity type and habitat variables were calculated. Bonferroni probability was used to test the null hypothesis of zero correlation.

Cavity density was also correlated with major principal components from the PCA of habitat structure. Cavity density of each plot was projected onto the main components, for representing the variation of cavity abundance across major environmental gradients.

3.2.3 Cavity occurrence and tree characters

While the previous section was to exam cavity occurrence at habitat level, here the cavity occurrence according to five tree-level variables: tree species, tree DBH, tree condition, the presence of fire scars and the presence of fungi conks was examined.

The distribution of cavities across each tree variable was compared to the distribution of all sampled stems across the same variable with chi-square test (ZAR 1999). If significant difference was found (significance level 0.05) and the variable had more than two classes, further comparisons were conducted with one class versus other classes pooled, for identifying whether the class was disproportionately rich or poor in cavities. Two classes were compared pairwise when the difference of cavity occurrence between specified classes was interested. Comparisons were also conducted between excavated cavities and non-excavated cavities. In all above comparisons, Yates corrected chi-square test was applied when a 2×2 table was encountered.

Cavity holding rate was defined as the percentage of stems with cavities, which was calculated by the number of cavity-holding stems divided by the number of total stems. This was different from the number of cavities divided by the number of stems, since one stem might hold more than one cavity.

Tree DBH was grouped into five classes in the analysis, i.e. < 15 cm, $15 - 30$ cm, $30 - 45$ cm, $45 - 60$ cm and > 60 cm. Tree condition was treated as six classes (Fig. 3.1) in the overall analysis. When examining the interactions between variables, tree condition was further pooled into three classes: living tree (classes 1 and 2 in Fig. 3.1), dead tree with intact top (class 3 and 4) and dead tree with broken top (class 5 and 6), to avoid too small sample size in each class.

After considering the five tree variables separately, stepwise logistic regression was applied to model the probability of cavity occurrence in a tree (JOBSON 1992). Whether the tree was deciduous (binary variable), tree DBH (in 5 ranks), tree condition (in 3 ranks), the presence of fire scars (binary variable), the presence of fungi conks (binary variable) and the habitat where the tree stood (as 3 dummy

variables), were used as independent variables. Backward stepwise selection was
used to select the variables (significance level 0.05).

3.2.4   Composition of CNB community

Density of CNBs was compared between habitats with Mann-Whitney U test. To
compare the species composition in different habitats, Sorensen's similarity
coefficient were applied (KREBS 1989):

$$S_s = \frac{2c}{a+b}$$

where S_s = Sorensen's similarity coefficient

       a = number of species in habitat A

       b = number of species in habitat B

       c = number of species in habitat A and B (joint occurrences)

Correlation analysis was than applied between CNB density and habitat variables,
habitat principal components and cavity density. CNB density was then projected
onto the main components to investigate the variation of CNB density across major
environmental gradients.

The species abundance distribution of the CNB community was compared with
lognormal and logseries model with chi-square goodness of fit test (MAGURRAN
1988). Comparisons of species abundance pattern with other studies were also
conducted, including the CNB communities in natural forests, in managed woodlands
and the CNBs nesting in nest boxes.

3.2.5   Utilisation of trees and cavities by CNBs

In this section, CNBs were considered as a whole instead of individual species. The
main purpose was to determine to which extent the trees and cavities were utilised by
CNBs, and whether the utilisation was related to tree variables (tree species, tree
DBH, tree condition, presence of fire scars and fungi conks) and cavity type.

Data from different habitats were pooled. Only the nests located in plots were
included in the analysis, so that nest data from each habitat had the same contribution

and could be compared with the pooled tree measurements. The difference between years was firstly examined. Since the utilisation pattern of each variable did not differ between years, data for both years were pooled. Utilisation patterns of PCNs and SCNs were also compared, and they were treated separately if there was a significant difference.

For each variable, the distribution of nests was compared with the distribution of all sampled stems. When significant difference arose for a variable of more than two classes, comparison of one class versus other classes pooled was conducted to find out whether the class was utilised overproportionally or underproportionally. The distribution of SCN nests was further compared with the distribution of cavities across the same variable to test whether cavities were selected according to the variable concerned. Chi-square test was used in all above comparisons, and Yates correction was applied when a 2×2 table was encountered.

3.2.6   Nest site selection of individual species

Both nests located inside and outside the plots were used in this part of analysis. Bird species of sample size less than 10 were excluded. Thus only 9 species were studied, including 3 PCNs (*D. major*, *D. minor* and *P. montanus*) and 6 SCNs (the Daurian Redstart *Phoenicurus auroreus*, the Red-throated Flycatcher *Ficedula albicilla*, the Coal Tit *Parus ater*, the Great Tit *P. major*, the Nuthatch *Sitta europaea* and the Treecreeper *Certhia familiaris*).

For each tree and cavity variable, comparison were conducted between bird species to reveal their relative preference. For the variables tree species, tree DBH, tree condition and cavity type, of which the availability were known, the utilisation pattern of each bird species was also contrasted with the availability to investigate the real selection. However, for variables such as tree species, which differed greatly among habitats, comparison could not be made directly, since this would be largely influenced by the number of nests found in each habitat.

For continuous variables, Mann-Whitney U test was applied to compare between species, and F test was applied to compare the variance, which indicated the niche

breadth. For categorical variables, chi-square test was used. Niche breadth was measured by Levins' index (KREBS 1989):

$$B = \frac{1}{\sum\limits^{n} p_i^2}$$

where B = Levins' measure of niche breadth

p_i = proportion of individuals found in or using resource state i

n = total number of resource states

The range of Levins' B is between 1 and n. Minimum occurs when all individuals use only one resource state, and maximum occurs when the same numbers of individuals are found in each resource state.

Niche overlap was indicated by the Renkonen index of percentage similarity (KREBS 1989):

$$P_{jk} = \left[\sum\limits^{n} \min(p_{ij}, p_{jk}) \right] \times 100$$

where P_{jk} = percentage overlap between species j and k

p_{ij} , p_{ik} = proportions resource state i is of the total resources used by species j
and species k

n = total number of resource states

ABRAMS (1980) recommended the Renkonen index of percentage similarity as the best measure of niche overlap. One strength of this index is that it is not sensitive to how one divides up the resource states, since human observers may recognise resource categories different from that animals or plants do.

After checking each variable separately, a cluster analysis was applied to summarise the overall similarity of nest sites among species (JOBSON 1992). Tree species (as 5 dummy variables), tree DBH, tree condition (in 3 ranks), cavity type (as 3 dummy variables), cavity height above ground, substrate diameter, substrate condition (binary variable), cavity opening length and cavity opening width were used to calculate the nest site similarity between species.

A discriminant function analysis was then performed based on these 15 variables (JOBSON 1992). Backward selection was used to select the variables which maximised separation among bird species. The reclassification matrix from discriminant functions could imply the extent of niche overlap between species.

3.2.7   Sequential cavity use

This part of analysis was based on all the nests found in 2002. Beside overall reuse rate, proportion of reuse by the same species (constancy) and reuse by different species (usability) were considered (SEDGWICK 1997). The reuse pattern was compared at both guild level (between PCN, WPCN and SCN) and at species level with chi-square test.

All tree and cavity variables of reused cavities were compared with that of cavities which were not reused. Continuous variables were compared with Mann-Whitney U test, and categorical variables with chi-square test. Logistic regression with backward stepwise selection was than applied to determine which variables could best predict the reuse of cavities.

3.2.8   Nest web analysis

While the previous section was a time sequence observation of interspecific links from cavity suppliers' side, the nest web analysis was a snap shot approach from cavity demanders' view. All the nests found in both years were used in the analysis.

Actors in the nest web included all CNB species as well as trees and cavities which were utilised by CNBs (MARTIN & EADIE 1999, MARTIN et al. 2004). Tree species formed the fundamental level in the nest web. PCNs and non-excavated cavities constituted the second level. A PCN species was linked to a tree species if it excavated in the tree. The strength of the linkage was indicated by the proportion of nests of this PCN species excavated in this tree species. Non-excavated cavities were also linked to tree species depended on the proportion of cavities located in each tree species. SCNs represented the third level in the nest web. A SCN species was linked to a PCN species if it utilised the cavity created by the PCN, or linked to non-excavated cavities if it nested in them. The strength of linkage was also decided by

the percentage of nest use. However, when a SCN was found nesting in a middle-sized woodpecker hole, in most of the cases the excavator species could not be confirmed. Thus middle-sized woodpeckers were grouped when linked with SCNs. WPCNs stood at an intermediate level between PCNs and SCNs. They might be linked to a tree species when they excavated in the tree by their own, or be linked to a PCN species or to non-excavated cavities, when they nested in the cavity created by the PCN in non-excavated cavities, respectively.

The nest web was than applied to test the roles of woodpeckers and some tree species in the CNB community.

4 RESULTS

4.1 Habitat Structure

The mature birch-larch forest (BLm) contained 724 stems/ha (Table 4.1). About 68% was deciduous trees composed of birch, and the remaining 32% was larch. Aspen, Scots pine and few young spruce also occurred in this habitat, but was not included in the sample due to the limited sample size. Of all the standing stems, 5% were large trees of DBH > 40 cm, 3% were dead, and about 31% showed signs of past fire.

The young birch-larch forest (BLy) had 725 stems/ha (Table 4.1). Birch (70%) and aspen (1%) comprised the deciduous part, and the remainders were larch (23%) and Scots pine (6%). Only about 2% of the trees had DBH > 40 cm, which were mainly old larches and Scots pines surviving the past fires. This habitat contained highest proportions of standing dead stems (35%; Kruskal-Wallis, $H = 10.04$, $df = 3$, $p < 0.05$) and fire-scarred trees (96%; Kruskal-Wallis, $H = 14.61$, $df = 3$, $p < 0.01$).

The tree density in the riparian mixed forest (RM) was 591 stems/ha (Table 4.1). Tree composition in descending order of stem number was birch (55%), Scots pine (23%), poplar (8%), spruce (7%), willow (6%) and larch (1%). But when considering the basal area, Scots pine (5.8 m^2/ha), birch (5.1 m^2/ha) and poplar (4.5 m^2/ha) formed co-dominance. 6% of the standing stems were large trees, 9% were dead, and 21% were scarred by fire. Shrub coverage in this habitat (46%) was the highest (Kruskal-Wallis, $H = 10.72$, $df = 3$, $p < 0.05$).

The spruce-fir forest (SF) contained 1560 stems/ha, denser than other habitats (Table 4.1; Kruskal-Wallis, $H = 8.15$, $df = 3$, $p < 0.05$). The proportion of deciduous trees (13%) was the lowest (Kruskal-Wallis, $H = 9.63$, $df = 3$, $p < 0.05$), and was comprised exclusively of birch. The coniferous part was made up of spruce (39%), fir (25%), Siberian pine (17%), Scots pine (4%) and larch (2%). About 2% of the standing stems were large trees, and 14% were dead. Signs of past fire were inconspicuous in this habitat, with only about 4% of the stems showing fire scars (Kruskal-Wallis, $H = 14.61$, $df = 3$, $p < 0.01$).

Table 4.1   Stem density (DBH > 5 cm), proportion of deciduous stems (= Prop. decid.), proportion of large trees (= Prop. large), proportion of dead trees (= Prop. dead), proportion of trees with fire scars (= Prop. fire) and shrub coverage in each habitat.

Habitat	Stem density* (/ha)	Prop. decid.* (%)	Prop. large (%)	Prop. dead* (%)	Prop. fire** (%)	Shrub coverage* (%)
BLm	724.5	67.8	5.5	2.9	31.2	6.9
BLy	725.3	71.0	1.9	35.4	95.5	10.0
RM	590.7	68.8	6.5	8.9	20.7	45.6
SF	1560.2	12.9	2.5	14.4	4.0	13.1
Grand mean	900.2	56.2	4.1	15.4	37.8	18.9

Kruskal-Wallis test, * p < 0.05, ** p < 0.01.

Table 4.2   Results of principal component analysis based on 22 habitat variables.

	Component					
	1	2	3	4	5	6
Eigenvalue	6.74	4.83	2.17	2.07	1.64	1.12
% of total variance	30.62	21.96	9.86	9.39	7.45	5.09
Cumulative variance	30.62	52.58	62.44	71.83	79.28	84.37
Component loadings						
Elevation	0.908**	0.177	0.210	0.170	0.017	0.059
Slope	0.853**	-0.392	0.107	0.189	-0.050	-0.019
Topographic position	-0.944**	0.097	0.125	0.053	0.013	-0.043
Canopy height	0.596*	0.323	0.479	-0.073	-0.286	0.234
Shrub coverage	-0.767**	0.219	0.042	0.397	0.141	0.301
Lying dead wood	0.473	0.306	-0.275	0.675*	-0.195	0.114
Stem density	0.535	0.605*	-0.005	-0.294	0.411	0.036
Prop. decid.	-0.572*	-0.625*	-0.214	0.121	-0.060	0.075
Prop. large	-0.539	-0.110	-0.067	0.130	-0.651*	-0.010
Prop. dead	0.351	-0.412	0.141	0.624*	0.382	-0.197
Prop. fire	0.193	-0.868**	0.108	0.197	0.006	-0.145
Prop. fungi	0.249	-0.722**	0.019	0.484	0.249	-0.075
Birch	0.158	-0.542	-0.570*	-0.181	0.236	0.241
Aspen	0.316	-0.460	0.688**	-0.079	0.024	0.262
Poplar	-0.718**	0.131	0.382	-0.021	-0.068	-0.437
Willow	-0.677*	0.205	0.197	0.174	0.346	0.150
Rowan	-0.531	0.155	0.004	0.331	0.063	0.660*
Larch	0.485	-0.350	-0.067	-0.586*	0.088	0.246
Scots pine	-0.094	0.098	0.863**	-0.093	0.177	0.031
Siberian pine	0.525	0.638*	-0.005	0.089	-0.047	0.032
Fir	0.472	0.680**	-0.002	0.151	-0.114	-0.132
Spruce	0.444	0.747**	-0.022	0.228	-0.161	-0.043

Bonferroni probability, * p < 0.01, ** p < 0.001.

From the principal component analysis, the first six principal components had eigenvalues greater than 1, and the first two summarised 52.6% of the total variance in 22 habitat variables (Table 4.2). Principal component 1 had eigenvalue 6.74 and alone explained 30.6% of the total variance. This component, with high positive loadings of elevation and slope and high negative loadings of topographic position, shrub coverage and the basal area of poplar, reflected the gradient from the riparian forest to the mountain taiga (Fig. 4.1). The eigenvalue of principal component 2 was 4.83, which accounted for 22.0% of the total variance. This component, having high positive loadings of the basal areas of spruce and fir and high negative loadings of the proportions of stems with fire scars and fungi conks, indicated the gradient from the light subtaiga to the dark mountain taiga.
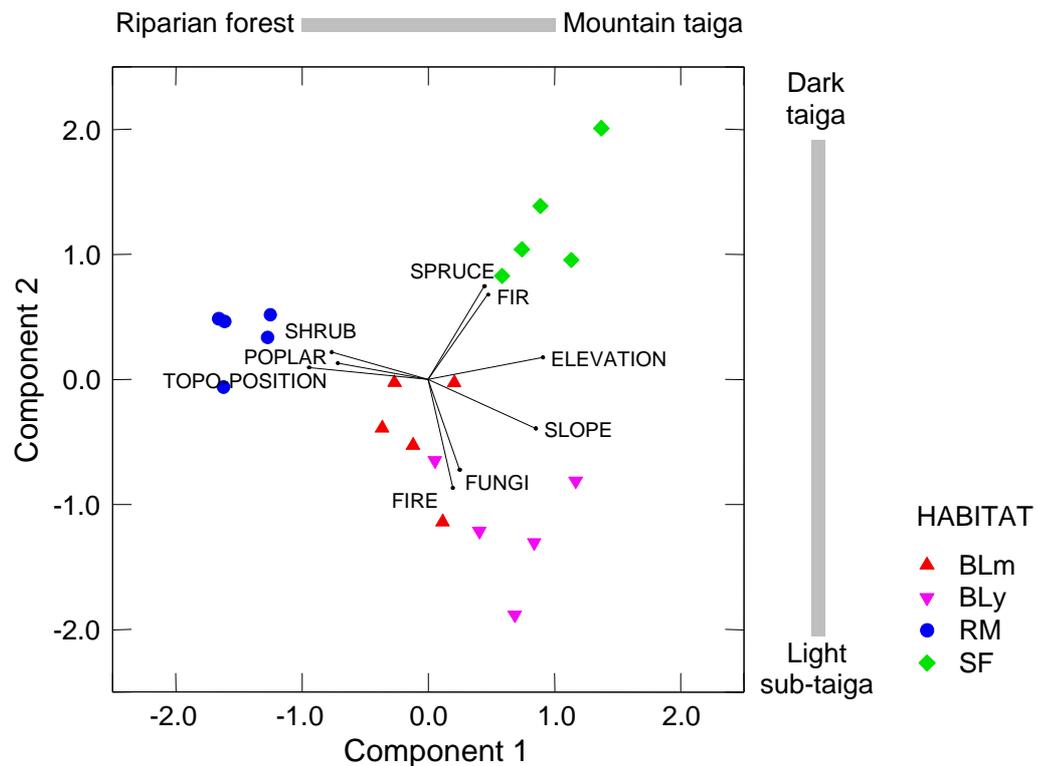

Fig. 4.1   Component loadings and projections of 20 plots onto principal components 1 and 2, based on the principal component analysis of 22 habitat variables. Only variables of highly significant correlation (p < 0.001) to component 1 or 2 were shown.

4.2   Cavity Abundance

The average density of tree cavities in the study area approached 30 cavities/ha (Table 4.3). The most numerous cavity type was branch hole (Kruskal-Wallis, H = 9.17, df = 3, p < 0.05). It averaged to 16 cavities/ha, and comprised 54% of the total cavities found. Bark crevice was the scarcest cavity type (about 1 cavity/ha), which accounted for 5% of the total. When pooling the cavity types into excavated and non-excavated cavities, there was no significant difference between the abundance of excavated cavities and non-excavated ones (Mann-Whitney, U = 5.00, df = 1, p = 0.386).

Observing each habitat separately, in both mature and young birch-larch forests, branch hole was the most numerous cavity type (Kruskal-Wallis, H = 8.77, df = 3, p < 0.05 in the mature one; H = 8.06, df = 3, p < 0.05 in the young one). It comprised approximately 60% of the total cavities in both habitats. In the riparian mixed forest, though branch hole was still the most frequent cavity type (48%), woodpecker hole also showed high abundance (26%). And there was no significant difference among the densities of different cavity types (Kruskal-Wallis, H = 6.04, df = 3, p = 0.110). In the spruce-fir forest, other bird-induced holes (49%) and branch holes (44%) had similar shares, and the densities of different cavity types did not differ significantly (Kruskal-Wallis, H = 7.22, df = 3, p = 0.065).

Table 4.3   Density (mean ± SD) of each type of cavity (n/ha) in each habitat.

| Habitat | Cavity type | | | | Total |
| | Excavated | | Non-excavated[2] | | |
	Woodpecker hole	Other bird-induced hole	Branch hole[1]	Bark crevice	
BLm	1.2 ± 2.7	8.0 ± 10.6	15.0 ± 10.6	0.0 ± 0.0	24.2 ± 22.0
BLy	2.7 ± 6.1	9.2 ± 12.0	22.2 ± 12.6	2.8 ± 5.5	36.9 ± 15.9
RM	10.3 ± 9.4	7.2 ± 8.0	18.9 ± 11.0	2.9 ± 2.9	39.2 ± 18.8
SF	1.2 ± 2.0	8.9 ± 13.5	7.9 ± 5.2	0.0 ± 0.0	18.1 ± 18.0
Grand mean	3.9 ± 4.3	8.3 ± 0.9	16.0 ± 6.1	1.4 ± 1.6	29.6 ± 10.1

[1] BLy > SF; Mann-Whitney, U = 22.00, df = 1, p < 0.05.
[2] BLy > SF; Mann-Whitney, U = 24.00, df = 1, p < 0.05.

Among the four habitats, the riparian mixed forest had the highest cavity density, approaching 40 cavities/ha, owing to the abundance of woodpecker hole in this

habitat. Total density in the young birch-larch forest (37 cavities/ha) was close to the former one, due to plentiful branch holes. The spruce-fir forest had lowest cavity density (18 cavities/ha), due to less branch holes in this habitat. The density of other bird-induced hole kept moderate values in all habitats, while the density of bark crevice was low in all habitats. Because cavity density varied greatly among the plots in the same habitat, i.e. having high intra-habitat variance, statistically significant difference only arose in that the young birch-larch forest had more branch hole (Mann-Whitney, $U = 22.00$, df $= 1$, $p < 0.05$) and non-excavated cavity (Mann-Whitney, $U = 24.00$, df $= 1$, $p < 0.05$) than the spruce-fir forest.

Correlating cavity density to habitat variables, the density of woodpecker hole showed high positive correlation with shrub coverage (Table 4.4). The densities of branch hole and non-excavated cavity altogether were positively correlated with the proportion of trees with fire scars. The abundance of other cavity types and the overall density were not significantly correlated with the habitat variables concerned.

Table 4.4   Correlation coefficients between density of each cavity type and habitat features, including proportion of deciduous stems (= Prop. decid.), proportion of large trees (= Prop. large), proportion of dead trees (= Prop. dead), proportions of trees with fire scars (= Prop. fire), shrub coverage, and component scores of principal component 1 (= Prin. comp. 1) and 2 (= Prin. comp. 2).

	Excavated cavity			Non-excavated cavity			Overall
	Woodpecker hole	Other bird-induced hole	Sum	Branch hole	Bark crevice	Sum	
Prop. decid.	0.297	-0.213	-0.019	0.209	0.298	0.276	0.153
Prop. large	0.313	-0.333	-0.109	0.197	0.113	0.214	0.058
Prop. dead	-0.129	0.093	0.009	0.170	0.104	0.186	0.118
Prop. fire	-0.144	-0.043	-0.110	0.404*	0.318	0.462**	0.206
Shrub coverage	0.801**	-0.152	0.293	0.069	0.191	0.117	0.261
Prin. comp. 1	-0.552**	0.149	-0.166	-0.230	-0.252	-0.282	-0.278
Prin. comp. 2	0.063	-0.027	0.011	-0.355	-0.217	-0.389*	-0.227

Bonferroni probability, * $p < 0.1$, ** $p < 0.05$.

Applying correlation analysis between cavity densities and component scores of the first two principal components, the density of woodpecker hole was correlated with the principal component 1 (Table 4.4 and Fig. 4.2(a)). Higher density of woodpecker hole occurred in the plots with negative scores of component 1, which were the

riparian plots. Component 1 could explain 30% of the variation in the abundance of woodpecker hole. Density of non-excavated cavity was negatively correlated with component 2, due to lower abundance of such cavity in the spruce-fir forest (Table 4.4 and Fig. 4.2(b)). Component 2 summarised 15% of the variation in the density of non-excavated cavity.
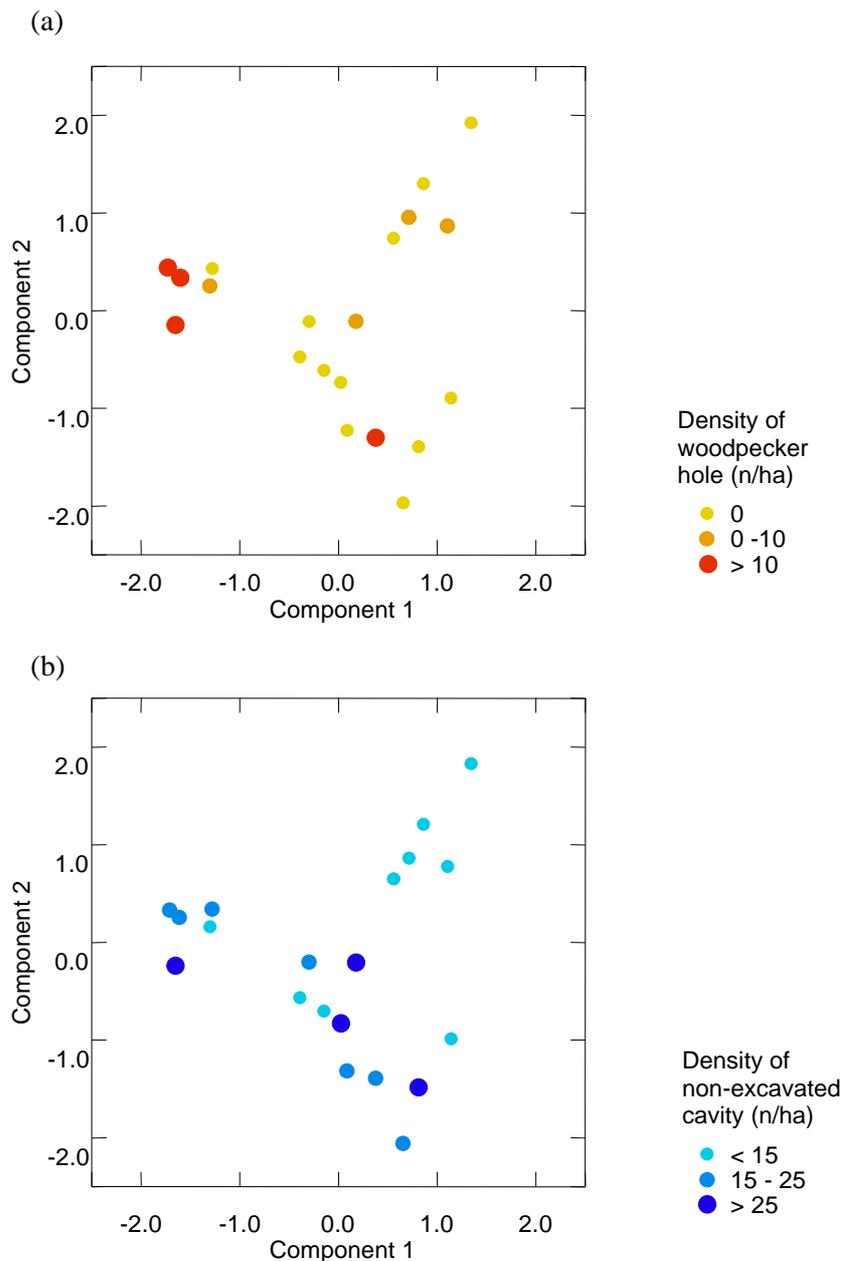

Fig. 4.2   Densities of (a) woodpecker hole and (b) non-excavated cavity of each plot projected onto principal components 1 and 2.

4.3   Cavity Occurrence and Tree Characters

4.3.1   Cavity occurrence and tree species

Cavities occurred with different frequency in different tree species ($x^2 = 248.85$, df = 9, $p < 0.001$). Birch was the most important cavity tree. Over 50% of the cavities were found in this species, which comprised only 37% of the standing stems (Table 4.5). About 4% of birch stems hold cavities. Poplar accounted for one fourth of the total cavities. Related to its abundance, poplar was the most cavity-rich tree species (x^2 test with Yates correction, $p < 0.001$ with each of other species except aspen and rowan, which had very small sample sizes). About one third of poplar stems hold cavities, and a poplar with cavity usually had more than one cavity per tree, in average 2.3. Other deciduous tree species, including aspen, willow and rowan, were only seldom sampled. Altogether these trees contributed about 1% to the total cavities.

Larch was the third important cavity tree species, accounted for 14% of total cavities. Cavities could be found in about 1% of larch stems, which was the most cavity-rich conifer species (x^2 test with Yates correction, $p < 0.05$ with Scots pine, $p < 0.01$ with Siberian pine, $p < 0.001$ with fir and spruce). Scots pine contributed 2% to the total cavities. No cavity was found in Siberian pine, fir and spruce, though these species made up 35% of the standing stems. In summary, poplar and birch supplied cavities over-proportionally (x^2 test with Yates correction, $p < 0.001$ for both), larch and other deciduous trees supplied cavities in proportion to their abundance, while Scots pine, Siberian pine, fir and spruce supplied cavities under-proportionally (x^2 test with Yates correction, $p < 0.05$ for Scots pine, $p < 0.001$ for others).

Table 4.5   The percentage constitution of all sampled stems (= Prop. stem), the percentage contribution to total cavities found (= Prop. cavity), and the cavity holding rate of each tree species.

	Tree species								N
	Poplar	Birch	Other deciduous trees	Larch	Scots pine	Siberian pine	Fir	Spruce	
Prop. stem	2.7	36.8	1.2	16.2	7.7	7.4	11.2	16.9	863
Prop. cavity	25.8	56.9	1.0	14.3	2.0	0	0	0	157
Cavity holding rate	38.4	3.8	1.1	1.2	0.3	0	0	0	863

Taking cavity type into account, birch hold bulk of both excavated (46%) and non-excavated (64%) cavities (Fig. 4.3). Poplar accounted for 22% and 28% of excavated and non-excavated cavities, respectively, and was the most cavity-rich tree species related to its abundance. Larch held similar amount of excavated cavities as poplar (28%), but stocked relatively less non-excavated ones (6%). Excavated and non-excavated cavities showed no significant difference in their distribution across tree species while taking all species into account ($x^2 = 0.00$, df = 9, p = 1.000). But when considering only species with cavities found, i.e. willow, poplar, birch, larch and Scots pine, these two types of cavity differed in their occurrence in tree species ($x^2 = 17.93$, df = 4, p < 0.01). Non-excavated cavity occurred relatively more frequently in birch (Yates corrected $x^2 = 4.52$, df = 1, p < 0.05) and less frequently in larch (Yates corrected $x^2 = 11.56$, df = 1, p < 0.01) than excavated one.
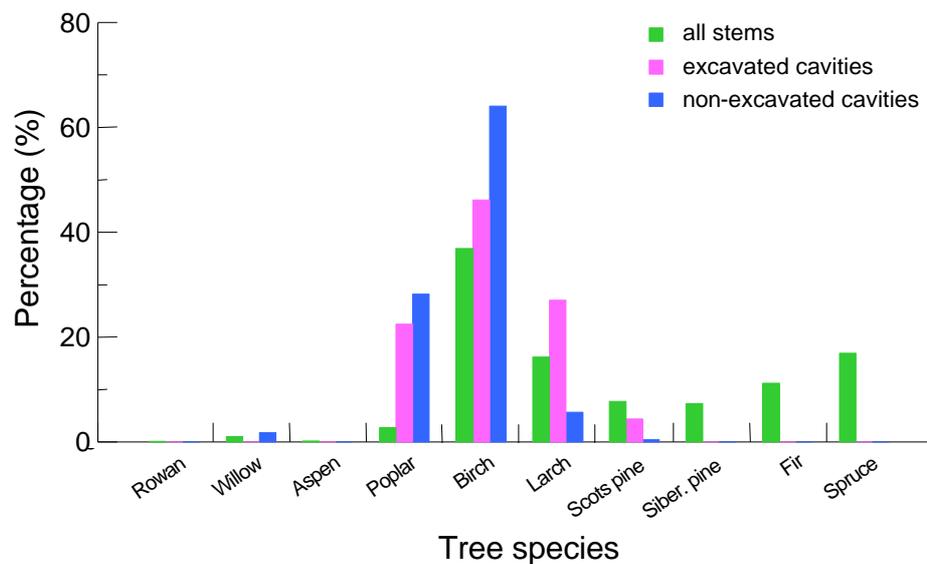
Fig. 4.3   The percentage constitution of all sampled stems (green bars; n = 863), the percentage of excavated cavities (red bars; n = 76), and the percentage of non-excavated cavities (blue bars; n = 81) according to tree species.

Each tree species played different roles in different habitats due to difference in species composition of each habitat. In the mature birch-larch forest, all the cavities found were located in birch. In the young birch-larch forest, birch also supplied bulk of the cavities (74%), and larch accounted for 24%. In the riparian forest, poplar was

the most important cavity tree. 78% of the cavities found in this habitat were located in poplar, and 16% in birch. In the spruce-fir forest, birch again served most often as the cavity tree, accounted for 58% of the cavities found. The remainder cavities in this habitat were located in larch.

4.3.2   Cavity occurrence and tree DBH

Cavity occurrence differed significantly across DBH classes (Fig. 4.4; $?^2$ = 413.01, df = 4, p < 0.001). Cavities presented under-proportionally in trees of DBH < 15 cm (Yates corrected $?^2$ = 226.25, df = 1, p < 0.001), and over-proportionally in trees of DBH larger than 30 cm ($?^2$ test with Yates correction, p < 0.001 for each class above 30 cm). Trees of DBH < 15 cm comprised over 60% of the standing stems, but no cavity was found in them. Most of the cavities (41%) were located in trees of DBH 30 - 45 cm, which accounted for only about 5% of the standing stems. Though just about 9% of the cavities were found in trees of DBH > 60 cm, these large trees were most cavity-rich relative to their occurrence in the forest (0.4%). About one third of these trees hold cavities. Cavity holding rate rose with ascending DBH (Fig. 4.4, blue line). Excavated cavity and non-excavated cavity did not differ in their occurrence across DBH class (Yates corrected $?^2$ = 0.00, df = 4, p = 1.000).
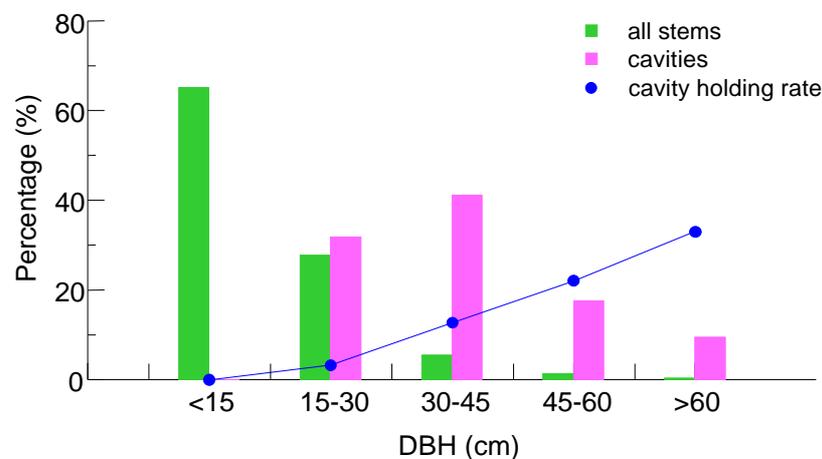
**Fig. 4.4   The percentage constitution of all sampled stems (green bars; n = 863), the percentage of total cavities (red bars; n = 157), and cavity holding rate (blue line; n = 863) according to tree DBH.**

Consider the main cavity tree species (i.e. poplar, birch, larch and Scots pine) separately, the cavity holding rate increased with raising diameter in all species (Fig. 4.5). But the increase in Scots pine was not significant ($?^2$ = 24.39, df = 4, p = 0.356), due to very low cavity holding rate in all DBH class. The cavity holding rate did not differ among tree species when DBH was under 30 cm ($?^2$ = 2.74, df = 3, p = 0.433). Above 30 cm, cavity holding rate showed among species differences ($?^2$ test, p < 0.001 for each class above 30 cm). Poplar and birch acquired cavities more often than larch and Scots pine. In each DBH class, cavity holding rate showed no significant difference between the two deciduous species, nor between the two coniferous species ($?^2$ test with Yates correction, p > 0.05 for each pairwise comparison).
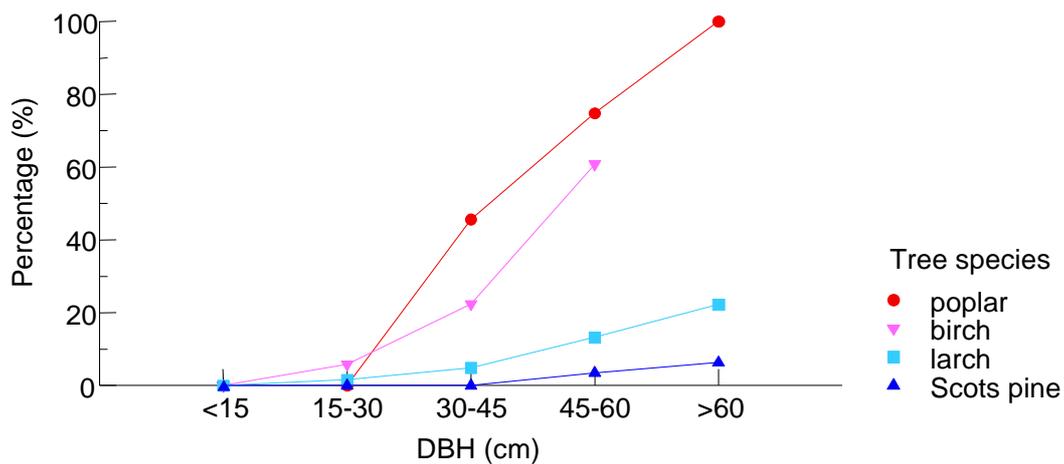
Fig. 4.5   The cavity holding rate of poplar (n = 45), birch (n = 327), larch (n = 166) and Scots pine (n = 125) in each DBH class.

The cavity occurrence across DBH classes showed different patterns among habitats (Fig. 4.6), which was shaped by the DBH distribution of each component tree species in each habitat. In the mature birch-larch forest, up to 79% of the cavities were located in trees of DBH 30 - 45 cm. In the young birch-larch forest, the bulk of cavities (59%) occurred in trees of DBH 15 - 30 cm, because of the higher abundance and higher cavity holding rate of such trees in this habitat. In the riparian forest, most cavities (39%) were located in trees of DBH 30 - 45 cm, while larger trees (DBH 45 -

60 cm and DBH > 60 cm) had relatively great contribution compared to the former two habitats. This was contributed by the cavity-rich large poplar trees, which occurred only in this habitat. In the spruce-fir forest, the cavity abundance showed a bimodal distribution across DBH class. About 51% of the cavities found in this habitat were located in trees of DBH 15 - 30 cm, which were exclusively contributed by birch. Larger birch trees were rare in this habitat. The substantial amount of cavities found in trees of DBH 45 - 60 cm (28%) and DBH > 60 cm (14%) were mainly contributed by old larch trees.
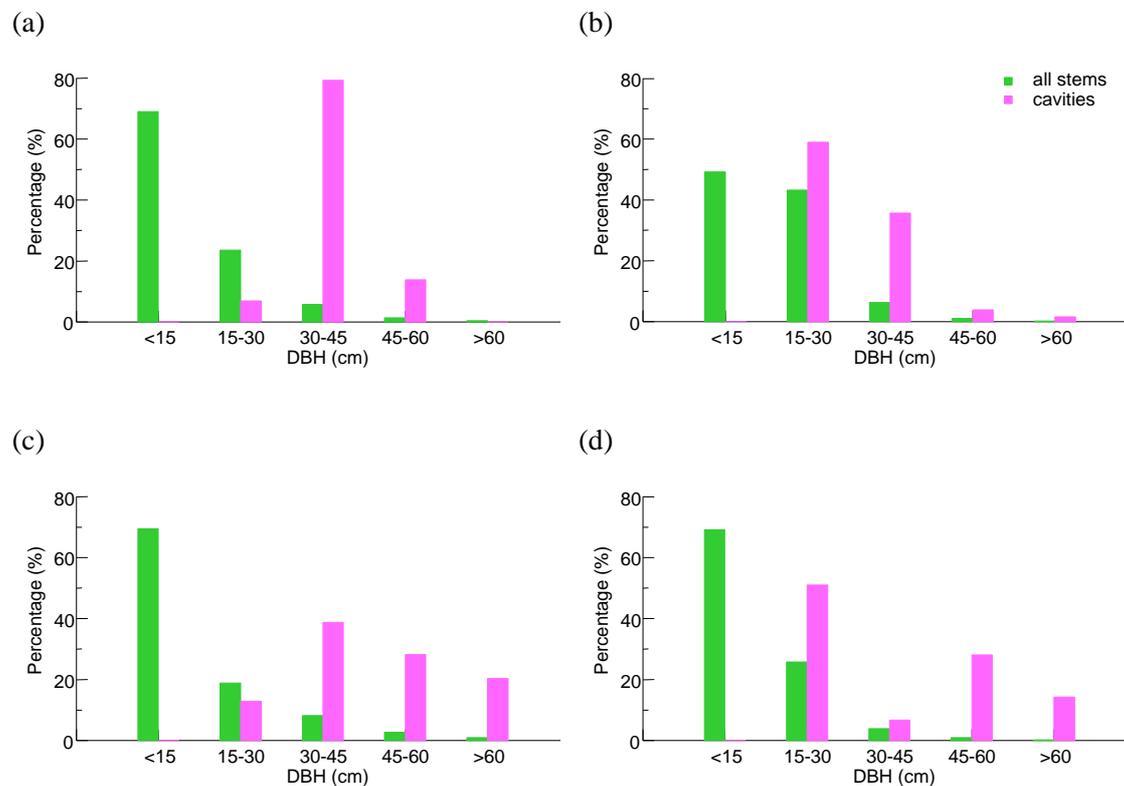

Fig. 4.6   The percentage constitution of all sampled stems (green bars) and the percentage of total cavities (red bars) according to tree DBH in each habitat: (a) the mature birch-larch forest, (b) the young birch-larch forest, (c) the riparian mixed forest and (d) the spruce-fir forest.

4.3.3   Cavity occurrence and tree condition

Most of the cavities (45%) were found in healthy living trees (class 1; Table 4.6).

Considering the abundance of such stems in the forests (84%), cavities occurred

under-proportionally in such trees (Yates corrected $?^2$ = 113.04, df = 1, p < 0.001).

Tall snags with broken top (class 5), which comprised only about 4% of the standing

stems, accounted for 31% of total cavities (Yates corrected $?^2$ = 137.83, df = 1, p <

0.001). About 12% of these tall snags had at least one cavity, in average 3.2

cavities/stem. Cavities were also relatively frequently found in living trees in state of

decline (class 2; Yates corrected $?^2$ = 9.20, df = 1, p < 0.01) and shortened snags

(class 6; Yates corrected $?^2$ = 18.69, df = 1, p < 0.001).

Table 4.6   The percentage constitution of all sampled stems (= Prop. stem), the percentage contribution to total cavities found (= Prop. cavity), and the cavity holding rate of trees in different condition. (Codes for tree condition: 1. healthy living tree, 2. living tree, in state of decline, 3. dead tree, branches intact, 4. dead tree, few or no branches, 5. dead tree, broken top, 6. dead tree, shortened snag.)

| | Tree condition | | | | | | N |
	1	2	3	4	5	6	
Prop. stem	83.6	1.5	5.9	3.8	3.5	1.8	863
Prop. cavity	45.0	5.8	4.3	5.5	31.3	8.1	157
Cavity holding rate	1.3	8.3	1.0	1.7	11.9	13.6	863

Excavated cavities and non-excavated cavities showed different distribution across

tree condition (Fig. 4.7; $?^2$ = 41.40, df = 5, p < 0.001). Though both types of cavity

occurred seldom in healthy living trees in relation to the abundance of such trees,

excavated cavities were even fewer in theses trees comparing to non-excavated ones

(Yates corrected $?^2$ = 24.58, df = 1, p < 0.001). 61% of non-excavated cavities were

located in healthy living trees, while only 22% of excavated cavities were found in

them. In tall snags with broken top, both types of cavity were relatively common, but

excavated cavities were even more frequent (Yates corrected $?^2$ = 17.83, df = 1, p <

0.001). These trees accounted for 51% of excavated cavities and 18% of non-

excavated ones. Excavated cavities were also relatively more frequent in trees of

class 4 (few or no branches, without broken top) than no-excavated ones (Yates

corrected $?^2$ = 7.87, df = 1, p < 0.01).
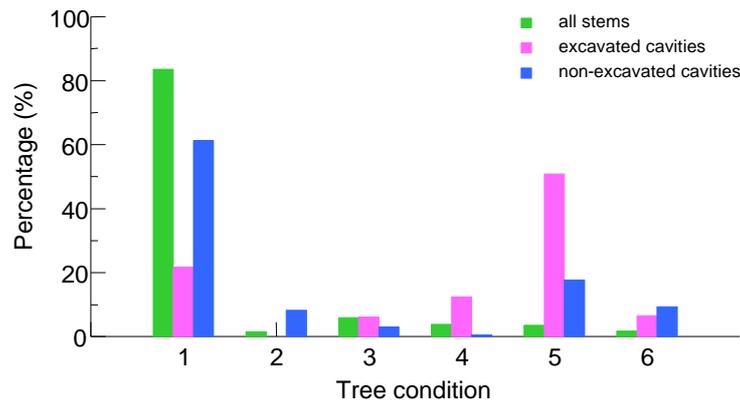
Fig. 4.7   The percentage constitution of all sampled stems (green bars; n = 863), the percentage of excavated cavities (red bars; n = 76), and the percentage of non-excavated cavities (blue bars; n = 81) according to tree condition.
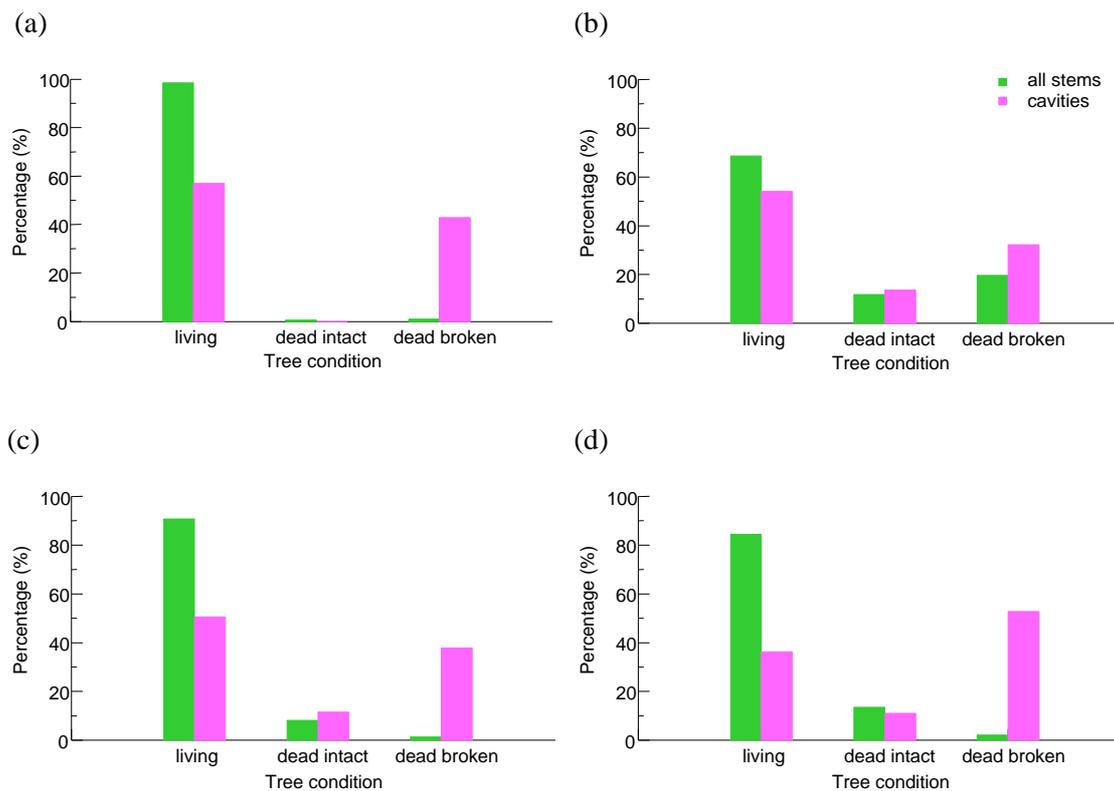
Fig. 4.8   The percentage constitution of all sampled stems (green bars) and the percentage of total cavities (red bars) according to tree condition in each habitat: (a) the mature birch-larch forest, (b) the young birch-larch forest, (c) the riparian mixed forest and (d) the spruce-fir forest.

To investigate cavity occurrence across tree condition in each habitat, tree condition was further pooled into three classes: living tree, dead tree with intact top and dead tree with broken top, to avoid too small sample size. In all habitats, the cavity occurrence pattern was similar in that most of the cavities were found in living stems and broken snags (Fig. 4.8). In the mature birch-larch forest, the riparian mixed forest and the spruce-fir forest, cavity occurrence across tree condition was not in proportion to the abundance of trees of each condition ($?^2$ test, p < 0.001 for each habitat). Living trees supplied cavities under-proportionally while broken snags did over-proportionally, as indicated above in the overall pattern. But in the young birch-larch forest, trees of each condition supplied the cavities in proportion to its abundance ($?^2$ = 2.44, df = 2, p = 0.296). There was a high density of broken snags in this habitat, and the cavity holding rate of these trees was lower than that in other habitats (Yates corrected $?^2$ = 5.09, df = 1, p < 0.05). This was mainly due to that most of the broken snags in this habitat (71%) had DBH < 15 cm, which seldom possessed any cavities.

4.3.4   Cavity occurrence and fire

Cavities occurred more frequently in trees with fire scars (Fig. 4.9, Yates corrected $?^2$ = 133.64, df = 1, p < 0.001). Trees with fire scars comprised only 28% of the standing stems, while about 76% of the cavities were located in them. This pattern was similar for both excavated cavities and non-excavated ones (Yates corrected $?^2$ = 0.62, df = 1, p = 0.433). The cavity holding rate of trees without fire scars was 0.7%, while that of fire-scarred trees was 5.4%, which was 7 times higher.

This overview might overestimate the influence of fire, however, due to the confounding effects of tree species. Spruce, fir and Siberian pine, in which no cavities were observed, were also rarely scarred by fire (< 1% of the standing stems of these three species pooled). When considering only the four main cavity tree species (poplar, birch, larch and Scots pine), altogether trees with fire scars comprised 44% of the standing stems and accounted for 76% of the total cavities (Yates corrected $?^2$ = 53.80, df = 1, p < 0.001). The cavity holding rate of these trees was about 5.5%, 3.8 times higher than those without fire scars (1.4%).
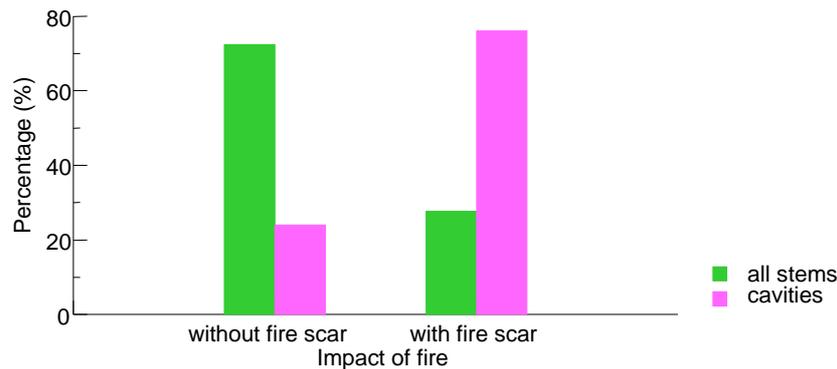
Fig. 4.9   **The percentage constitution of all sampled stems (green bars; n = 863) and the percentage of total cavities (red bars; n = 157) according to the presence of fire scars.**

Considering these four species separately, larch and Scots pine acquired cavities only in stems with fire scars (Table 4.7). For poplar and birch, the cavity holding rate of trees with fire scars was about 3 times higher than that of trees without fire scars. For all species except Scots pine, cavities occurred more frequently in fire-scarred stems relative to their abundance (Yates corrected $?^2$ test, df = 1, p < 0.05 for poplar, p < 0.001 for birch and larch).

Table 4.7   **The cavity holding rate of trees without and with fire scars of each tree species.**

Tree species	Cavity holding rate of trees		n
	without fire scars	with fire scars	
Poplar	18.9	59.8	45
Birch	2.0	6.1	327
Larch	0.0	3.4	166
Scots pine	0.0	0.5	125

4.3.5   Cavity occurrence and fungi

Cavities occurrence was also related to the presence of fungi conks on the tree (Fig. 4.10). Only about 5% of the sampled stems had fungi conks, while these trees accounted for 29% of the total cavities (Yates corrected $?^2$ = 90.10, df = 1, p < 0.001).

The cavity holding rate of conk-bearing stems was 10.8%, seven times higher than that of stems without fungi conks (1.5%).

Though both types of cavity were relatively more frequent in conk-bearing stems, excavated cavities had even higher co-occurrence with fungi conks than non-excavated ones (Fig. 4.10, Yates corrected $?^2 = 10.31$, df = 1, p < 0.01). 44% and 19% of excavated and non-excavated cavities, respectively, were located in conk-bearing stems. For excavated cavities, the cavity holding rate of conk-bearing stems was 16.9 times higher than that of stems without fungi conks. And for non-excavated cavities, the cavity holding rate of conk-bearing stems was only 4.7 times higher.
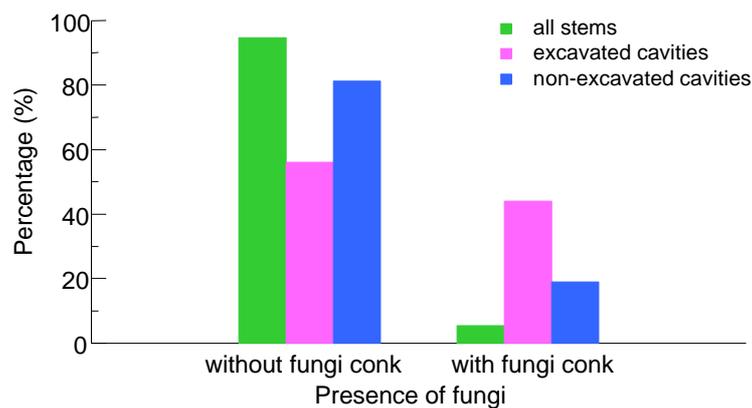
**Fig. 4.10   The percentage constitution of all sampled stems (green bars; n = 863), the percentage of excavated cavities (red bars; n = 76), and the percentage of non-excavated cavities (blue bars; n = 81) according to the presence of fungi conks.**

Of all sampled stems, fungi conks were only found in poplar, birch, larch and willow. The sample size of willow was too small for analysis. When considering only polar, birch and larch, the percentage of conk-bearing stems was 10%, and accounted for 30% of cavities (Yates corrected $?^2 = 39.45$, df = 1, p < 0.001). The cavity holding rate of conk-bearing stems was four times higher than that of stems without fungi conks. For birch and larch, cavities occurred more frequently in conk-bearing stems relative to their abundance (Yates corrected $?^2$ test, df = 1, p < 0.001 for both species). While for poplar, the difference was not significant (Yates corrected $?^2 = 1.53$, df = 1, p = 0.216).

4.3.6   Predicting cavity occurrence with tree characters

Applying logistic regression to predict the probability a tree possessing cavities, the backward stepwise selection identified three variables as predictors: if the tree was deciduous, tree DBH and tree condition (Table 4.8; log likelihood = -157.62, $?^2$ = 222.20, df = 4, p < 0.001). The presence of fire scars and fungi conks, though individually having significant influence to the occurrence of cavities (p < 0.001 for each), did not add significant contribution to the multivariate model. The model could correctly predict whether or not a tree holding cavities in 89% of the cases.

Table 4.8   The coefficient estimates, standard errors, chi-square values and p-values for logistic regression models of the probability a tree holding cavities.

| Variable	Coefficient	Std. error	$?^2$	p
Probability a tree holding cavities				
Deciduous	3.677	0.463	7.947	0.000
DBH	1.734	0.190	9.148	0.000
Tree Condition				
living	-1.988	0.399	-4.977	0.000
dead intact	-0.754	0.570	-1.323	0.186
Constant	-8.168	0.891	-9.170	0.000
Probability a tree holding excavated cavities				
Deciduous	1.499	0.551	2.721	0.007
DBH	1.694	0.252	6.731	0.000
Tree Condition				
living	-2.637	0.546	-4.833	0.000
dead intact	-0.403	0.650	-0.620	0.535
Fungi	0.899	0.564	1.594	0.111
Constant	-8.021	1.160	-6.914	0.000
Probability a tree holding non-excavated cavities				
Deciduous	4.888	0.648	7.547	0.000
DBH	1.593	0.202	7.876	0.000
Tree Condition				
living	-1.006	0.454	-2.215	0.027
dead intact	-0.543	0.716	-0.759	0.448
Fire	0.900	0.415	2.168	0.030
Constant	-10.589	1.155	-9.167	0.000

(a)

(b)
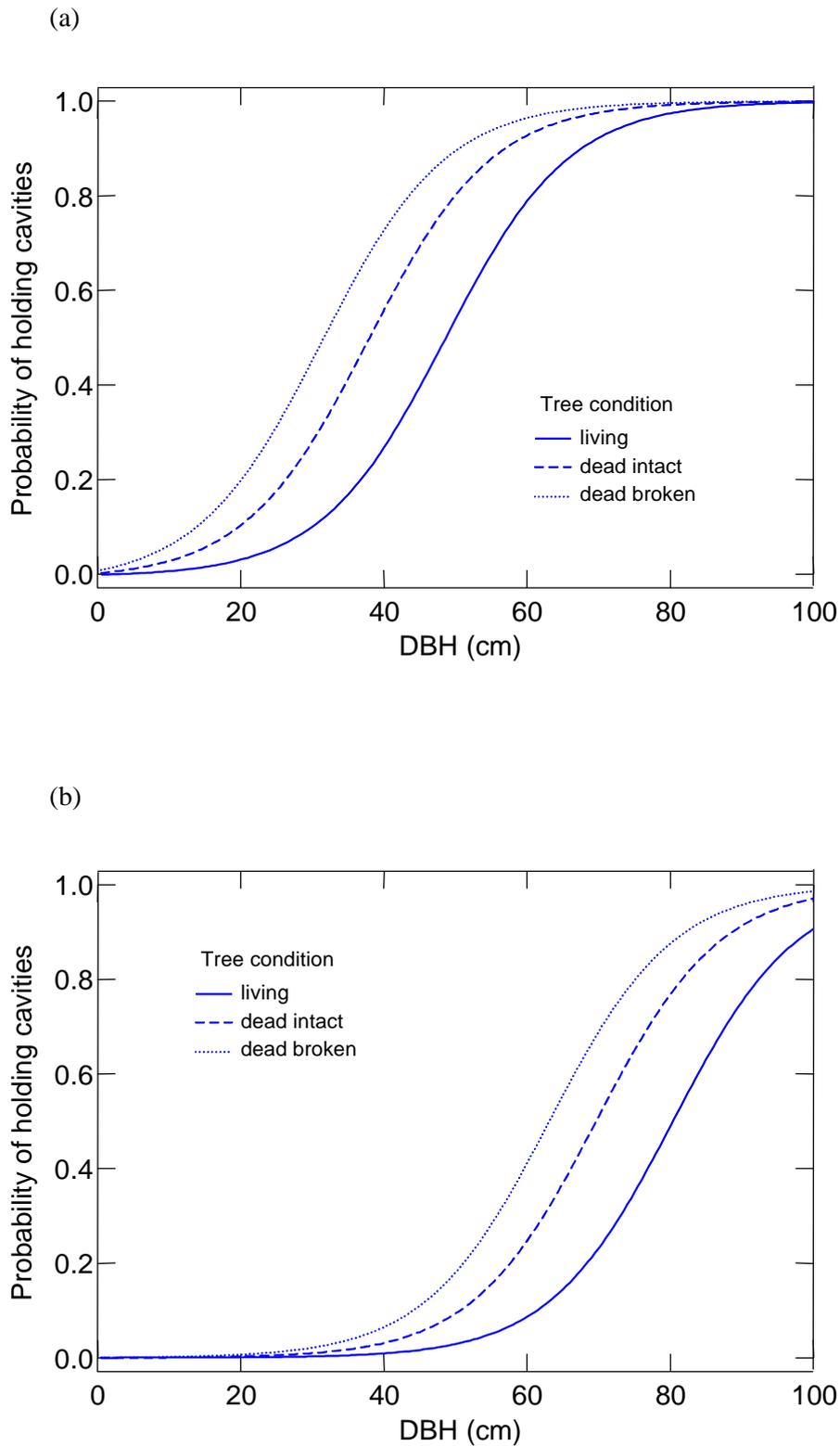
Fig. 4.11   Predicted probability of cavity occurrence in (a) deciduous trees and (b) coniferous trees, in relation to tree DBH and tree condition.

From this model, it was clear that the probability of holding cavities rose as tree DBH increased (Fig. 4.11). For trees of the same DBH, probability of holding cavities was higher for trees of more decayed condition. Deciduous trees (Fig. 4.11(a)) were much more likely to acquire cavities than coniferous trees (Fig. 4.11(b)) of the same size and the same condition. The probability of holding cavities rose notably at DBH 30 – 50 cm for deciduous trees, while for conifers this stage only started at DBH about 60 – 80 cm.

When modelling the probability a tree holding excavated cavities, the presence of fungi conks was included in the model additionally (Table 4.8; log likelihood = -75.90, $?^2$ = 115.32, df = 5, p < 0.001). This model could correctly predict the occurrence of excavated cavities up to 95%. Tree condition had great influence on the occurrence of excavated cavities (Fig. 4.12). Living trees were much less likely to hold excavated cavities than dead ones, except when the trees were extremely small or large. For trees of DBH 50 cm without fungi conks, the probability of holding excavated cavities was about 0.07 for living trees, six times less than that of dead intact trees (0.39) and seven times less than that of broken snags (0.49). The presence of fungi conks raised the cavity holding probability. For trees of DBH 50 cm, those with fungi conks were approximately twice more likely to hold excavated cavities than those without.

In the model of the probability a tree holding non-excavated cavities, the presence of fire scars was included instead of the presence of fungi conks (Table 4.8; log likelihood = -128.15, $?^2$ = 194.76, df = 5, p < 0.001). With this model, whether a tree holding non-excavated cavities or not could be correctly predicted in 92% of the cases. When compared with the pattern of excavated cavities, the difference resulted from tree condition was relatively less strong (Fig. 4.13). For trees of DBH 50 cm without fire scars, the probability of holding non-excavated cavities was about 0.35 for living trees, slightly less than that of dead intact trees (0.47) and broken snags (0.60). The presence of fire scars increased the cavity holding probability. Living trees with fire scars had probability of holding non-excavated cavities similar to that of broken snags without fire scars. For trees of DBH 50 cm, those with fire scars were about 1.5 times more likely to hold non-excavated cavities than those without.
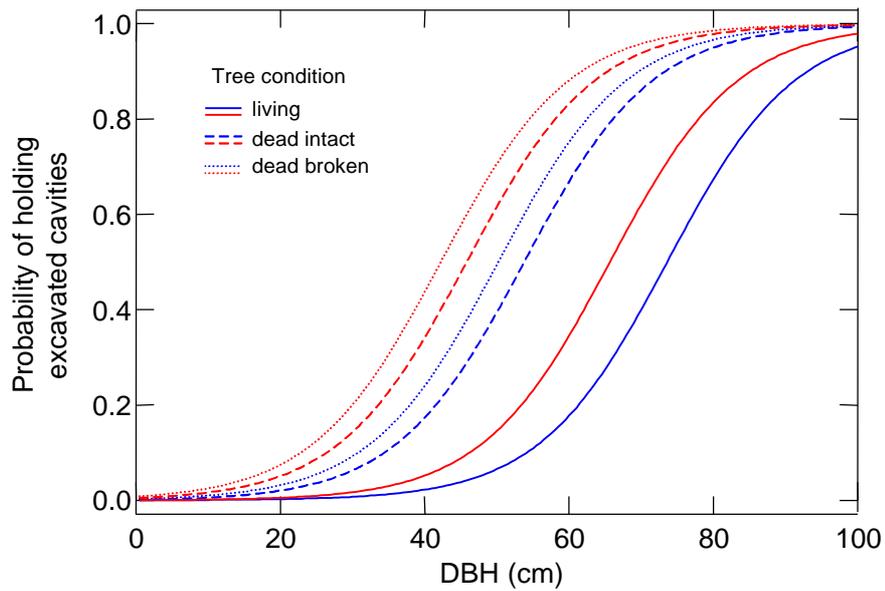
Fig. 4.12 **Predicted probability of the occurrence of excavated cavities in deciduous trees with (red) and without (blue) fungi conks, in relation to tree DBH and tree condition.**
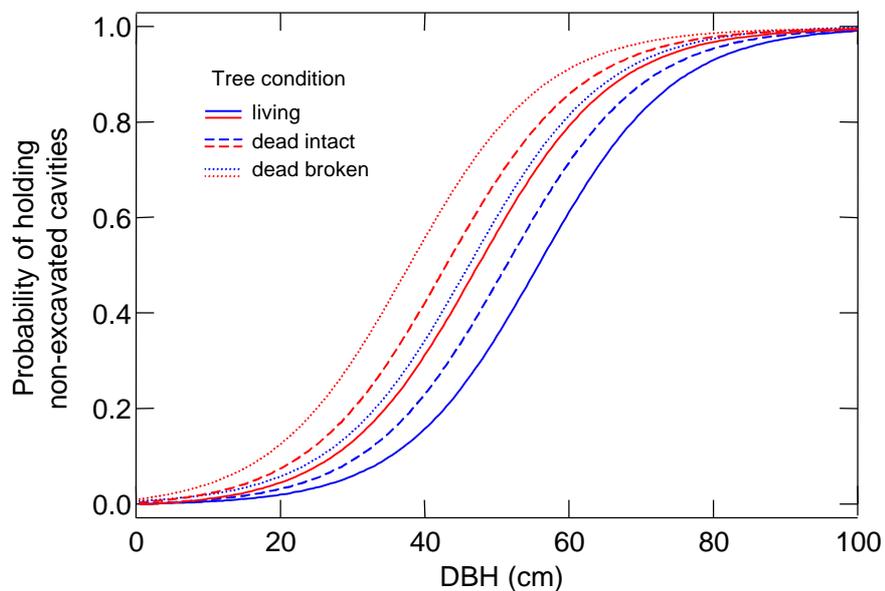

Fig. 4.13 **Predicted probability of the occurrence of non-excavated cavities in deciduous trees with (red) and without (blue) fire scars, in relation to tree DBH and tree condition.**

4.4 Composition of CNB Community

4.4.1 CNB composition in the study area

A total of 259 nests from 16 cavity nesting bird species were found in the study period, including 6 species of primary cavity nesters (PCNs) and 10 species of secondary cavity nesters (SCNs; Table 4.9). 49 and 48 nests were located in the sampling plots (total area 20 ha) in 2002 and 2003 respectively, and others were found outside the plots. In each habitat, neither the number of nests nor the number of species showed significant difference between years, so the data for both years were pooled.

Table 4.9   Number of nest of each species found in each habitat.

	Bird species	Nests in plots								Nests off plots	Sum
		2002				2003					
		BLm	BLy	RM	SF	BLm	BLy	RM	SF		
PCN	*Dryocopus martius*			1						2	3
	Picus canus					1				4	5
	Dendrocopos leucotos									3	3
	Dendrocopos major						1			12	13
	Dendrocopos minor	2	1					1		9	13
	Parus montanus	2	3	6	2	4	4	5	2	36	64
SCN	*Bucephala clangula*			1				1			2
	Jynx torquilla									2	2
	Phoenicurus auroreus	1		1		1	1	1		18	23
	Phoenicurus phoenicurus		1							1	2
	Turdus ruficollis									3	3
	Ficedula albicilla	1	3	1		2	2	2		14	25
	Parus ater	5	4	5	3	4	3	5	3	21	53
	Parus major	1		1				2		12	16
	Sitta europaea		1	1			1	1		17	21
	Certhia familiaris	1	1			1				8	11
	Total number of nests	13	14	17	5	13	12	18	5	162	259
	Total number of species	7	7	8	2	6	6	8	2	15	16

The density of cavity-nesting birds in the study area averaged 2.4 nests/ha, which varied from 1.0 nest/ha in the spruce-fir forest to 3.5 nests/ha in the riparian mixed forest (Table 4.10). The spruce-fir forest had both lower density and fewer species number than the other three habitats (Mann-Whitney U test, $p < 0.01$ with each of other habitats), while there were no significant differences among the three deciduous stands. The density of PCNs and the density of SCNs were positively correlated

(Pearson correlation r = 0.830, p < 0.05). When considering *P. montanus* separately as WPCN, there were weak positive correlations between PCN and SCN (Pearson correlation r = 0.730, p = 0.120) and between WPCN and SCN (Pearson correlation r = 0.662, p = 0.222), while no correlation between PCN and WPCN (Pearson correlation r = 0.221, p = 1.000).

Species composition of the three deciduous habitats was quite similar (Sorensen's similarity coefficient = 0.67 - 0.71), while the spruce-fir forest was distinct from the others (Sorensen's similarity coefficient = 0.36 - 0.40).

Table 4.10   Density of nests and hole-nesting species (mean per ha ± SD) and cavity occupancy (%) by SCNs in each habitat.

Habitat	No. of nests (/ha)	No. of species (/ha)	Cavity occupancy (%)
BLm	2.6 ± 0.8	2.4 ± 0.8	7.0
BLy	2.6 ± 1.3	2.4 ± 1.0	4.6
RM	3.5 ± 1.5	3.1 ± 1.3	5.6
SF	1.0 ± 0.7	1.0 ± 0.7	3.3
Overall	2.4 ± 1.0	2.2 ± 0.9	5.2

Cavity occupancy was estimated by dividing the mean cavity density (Table 4.3) by SCNs density in each habitat. The overall occupancy in the study area was 5.2%. Occupancy was highest in the mature birch-larch forest and lowest in the spruce-fir forest (Table 4.10).

4.4.2   Relationship between CNB abundance and habitat variables

Correlating CNB density with habitat variables, the proportion of deciduous stems and shrub coverage showed significant relationships with CNB density (Table 4.11). Both PCNs and SCNs were more abundant in stands with more deciduous trees. PCNs also had higher density in stands with higher shrub coverage. The densities of neither PCNs nor SCNs were related to cavity abundance. Considering species richness, there were more CNB species in stands with higher deciduous components.

Table 4.11   Correlation coefficients between density of CNBs, number of CNB species and habitat features, including proportion of deciduous stems (= Prop. decid.), proportion of large trees (= Prop. large), proportion of dead trees (= Prop. dead), proportions of trees with fire scars (= Prop. fire), shrub coverage, component scores of principal component 1 (= Prin. comp. 1) and 2 (= Prin. comp. 2), and cavity density.

	Density of			Number of CNB species
	PCN	SCN	All CNBs	
Prop. decid.	0.509*	0.535*	0.645**	0.544*
Prop. large	0.278	0.251	0.323	0.168
Prop. dead	-0.009	-0.102	-0.079	0.122
Prop. fire	0.069	0.254	0.220	0.289
Shrub coverage	0.566**	0.261	0.475*	0.305
Prin. comp. 1	-0.507*	-0.454*	-0.586**	-0.469*
Prin. comp. 2	-0.173	-0.397	-0.376	-0.416
Cavity density	0.220	0.259	0.299	0.314

Bonferroni probability, * $p < 0.1$, ** $p < 0.05$.
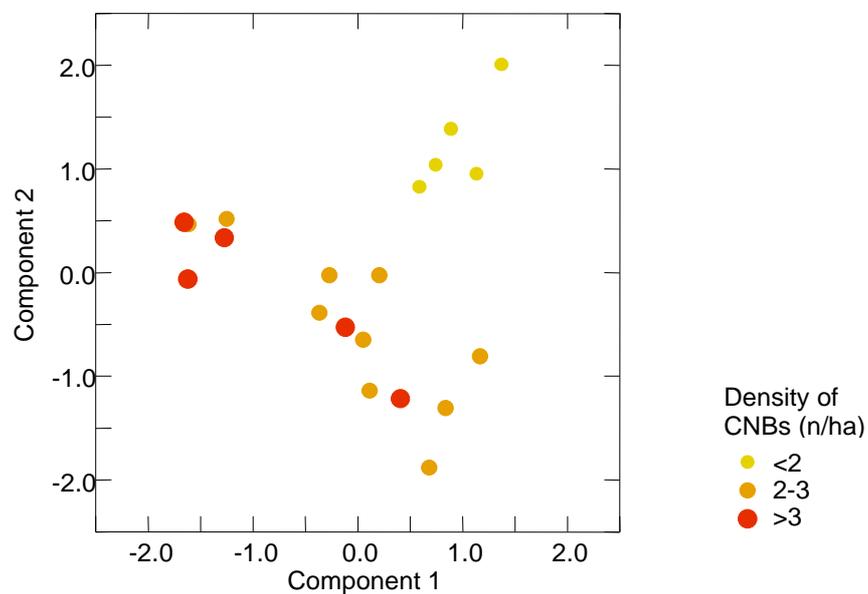
Fig. 4.14   Densities of cavity-nesting birds of each plot projected onto principal components 1 and 2.

The density of CNBs was negatively correlated with principal component 1 (Table 4.11 and Fig. 4.14). Both PCN and SCN densities were higher in the riparian stands, as well as the species richness. Component 1 could explain 34% of the total variation in overall CNB density. CNB density and number of CNB species were not correlated with principal component 2 when all habitats were considered. However, when excluding the riparian stands and considering only the plots in mountain taiga, both SCN density and overall CNB density were negatively correlated with component 2 (Pearson correlation r = -0.611, p < 0.05 for SCN, r = -0.641, p < 0.05 for overall density), as well as the species number (Pearson correlation r = -0.581, p < 0.05). Lower CNB density and less CNB species occurred in dark taiga.

4.4.3   Species abundance distribution

The species abundance distribution of each habitat could not be examined separately, due to the limited sample size. Since the mature and the young birch-larch forests had similar species composition, and no CNB species showed different abundance in these two habitats (Table 4.9), the data of both birch-larch forests and of both years were pooled and used in the following analysis.

The species abundance pattern in the birch-larch forest was plotted in Fig. 4.15(a). *P. ater* and *P. montanus* were the dominant species. This pattern showed no difference from lognormal distribution ($?^2$ = 3.11, df = 4, p = 0.539), nor from logseries distribution ($?^2$ = 4.67, df = 4, p = 0.323).

The species abundance distributions of other seven CNB communities were also plotted for comparison. This included the CNB communities of the natural oak forest in Andersby, Sweden (Fig. 4.15(b); CARLSON et al. 1998), the natural ash-alder forest (Fig. 4.15(c)) and oak-hornbeam forest (Fig. 4.15(d)) in Bialowieza, Poland (WESOLOWSKI et al. 2002), the managed larch-Douglas fir forest in Montana, USA (Fig. 4.15(e); MCCLELLAND et al. 1979), the beech-oak wooded area near Arnhem, Netherlands (Fig. 4.15(f); VAN BALEN et al. 1982), and the CNBs using nest boxes in deciduous wooded area in Hoge Veluwe (Fig. 4.15(g)) and Warnsborn (Fig. 4.15(h)), Netherlands (VAN BALEN et al. 1982). The species abundance distribution of Mongolian birch-larch forest did not differ from that of other CNB communities
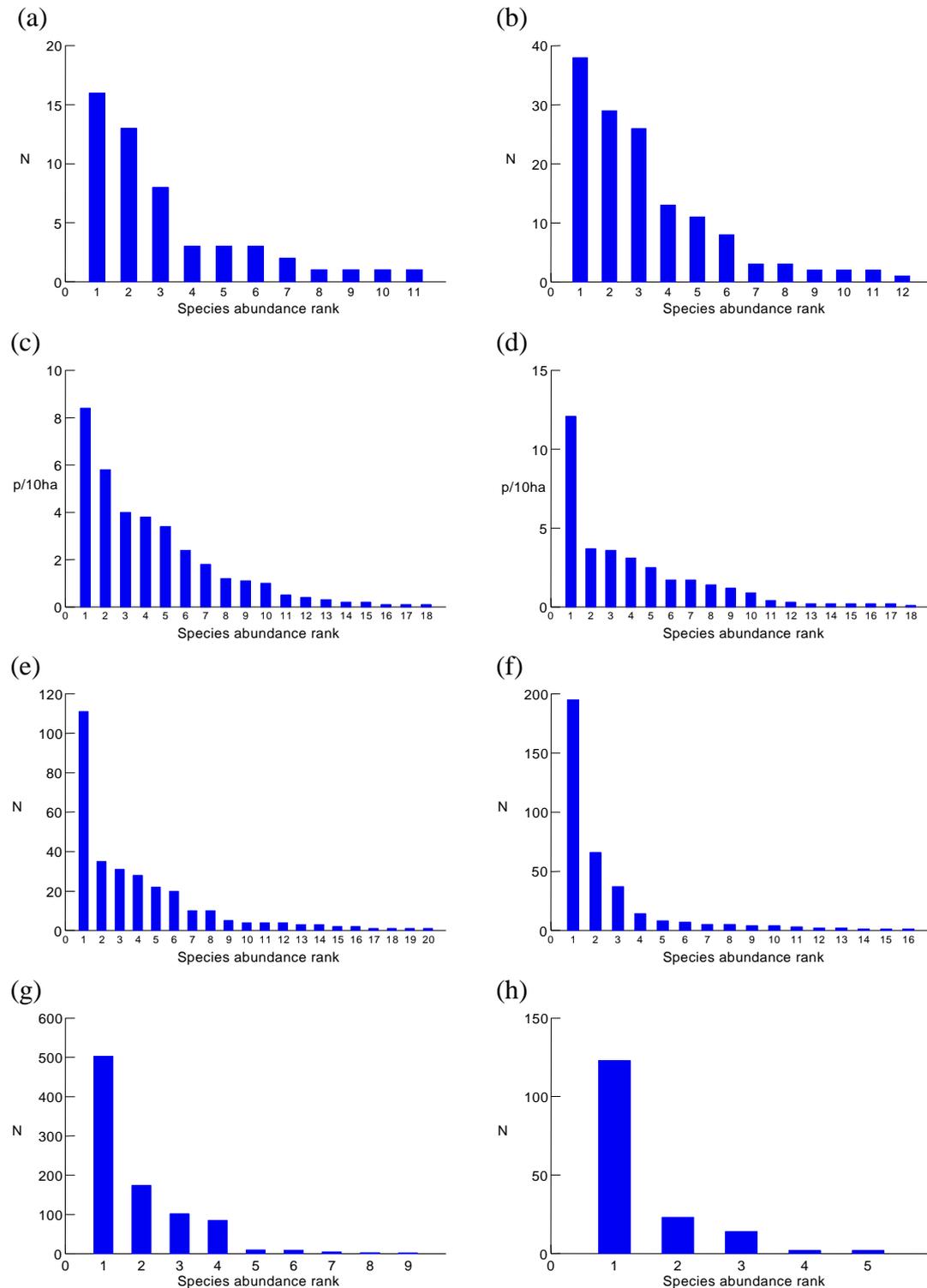
Fig. 4.15 **Species abundance distribution of CNBs of (a) birch-larch forest in West-Khentey, (b) natural oak forest in Andersby, Sweden (CARLSON et al. 1998), (c) natural ash-alder forest in Bialowieza, Poland (WESOLOWSKI et al. 2002), (d) natural oak-hornbeam forest in Bialowieza, Poland (WESOLOWSKI et al. 2002), (e) managed larch-Douglas fir forest in Montana, USA (MCCLELLAND et al. 1979), (f) beech-oak wooded area in Arnhem, Netherlands (VAN BALEN et al. 1982), (g) nest boxes in deciduous wooded area in Hoge Veluwe, Netherlands (VAN BALEN et al. 1982), and (h) nest boxes in deciduous wooded area in Warnsborn, Netherlands (VAN BALEN et al. 1982).**

breeding in natural cavities (Fig. 4.15(b) - (f); $?^2$ test, $p > 0.05$), but significantly differed from that of CNBs using nest boxes (Fig. 4.15(g) - (h); $?^2$ test, $p < 0.001$).

The species abundance pattern of Mongolian birch-larch forest was most similar to those of Swedish natural oak forest and Polish natural ash-alder forest. The species abundance decreased in a gradual manner from common species to rare species (Fig. 4.15(a) - (c)). In Polish natural oak-hornbeam forest, American managed larch-Douglas fir forest and Dutch beech-oak wooded area, there were a protrusive dominant species in the CNB community (Fig. 4.15(d) - (f)). This single dominant species accounted for 36%, 37% and 55% of the individuals in these CNB communities, respectively, and was about three times more abundant than the second common species. While in the first three CNB communities, the abundance of the first dominant species was only about 1.2 - 1.4 times of the second one.

Fewer species inhabited nest boxes, and one of them appeared as a protrusive dominant (Fig. 4.15(g) - (h)). The first dominant species represented 56% and 75% of all the individuals using nest boxes in the two Dutch wooded areas, and was 3 - 5 times more abundant than the second common species.

4.5   Utilisation of Trees and Cavities by CNBs

4.5.1   Tree species

Of the 97 nests located in plots, 68% were found in birch trees (Table 4.12). Eight out
of 13 bird species utilised birch. Poplar was the second important nest tree species,
accounted for 13% of the nests and was used by 6 bird species. No nests were found
in rowan, Siberian pine, fir and spruce. PCNs and SCNs showed similar patterns in
tree species utilisation ($?^2 = 5.63$, df = 5, p = 0.344), and were pooled in the following
analysis.

Table 4.12   Species composition (%) of nest trees used by PCNs and SCNs.

	Tree species						N
	Willow	Aspen	Poplar	Birch	Larch	Scots pine	
PCNs	2.9	5.7	20.0	65.7	2.9	2.9	35
SCNs	1.6	1.6	9.7	69.4	9.7	8.1	62
Overall	2.1	3.1	13.4	68.0	7.2	6.2	97

The species composition of nest trees differed from the relative abundance of tree
species in the forests ($?^2 = 144.10$, df = 9, p < 0.001). Poplar, which comprised only
3% of the standing stems (Table 4.5), was strongly selected by CNBs (Yates corrected
$?^2 = 57.80$, df = 1, p < 0.001). Birch, which was frequent in the forest (37%), was also
used overproportionally (Yates corrected $?^2 = 34.18$, df = 1, p < 0.001). Siberian pine,
fir and spruce were used underproportionally ($?^2$ test with Yates correction, p < 0.05
for Siberian pine, p < 0.001 for fir and spruce).

Comparing the species composition of cavity trees (Table 4.5) with that of nest trees,
no significant difference were found ($?^2 = 0.00$, df = 9, p = 1.000). Most of the
cavities were located in birch, so were the nests. Poplar and larch were the next
important cavity tree species, and were thus frequently served as nest trees.

Tree species differed among habitats, but the utilisation of nest tree species followed
some general rules. In each habitat, PCNs and SCNs had similar patterns in their use

of tree species (x^2 test, p > 0.05 in each habitat). And this pattern differed from the tree species composition in the corresponding habitat (x^2 test, p < 0.01 in each habitat). In both the mature and the young birch-larch forests, birch was used overproportionally. In the riparian forest, poplar was used overproportionally and birch was only used in proportion to its abundance. In the spruce-fir forest, both birch and larch were used overproportionally, and Siberian pine, spruce and fir were used underproportionally. Species composition of nest trees did not differ from that of cavity trees in each habitat (x^2 test, p > 0.05 in each habitat).

4.5.2 Tree DBH

Trees of different DBH were used disproportional to their abundance in the forests (x^2 = 232.66, df = 2, p < 0.001). Most of the nests (60%) were located in trees of DBH 25 - 50 cm, which accounted for only about 10% of the standing stems. Trees of DBH larger than 50 cm, containing 13% of the nests, were even more strongly selected relative to their abundance (1%). Trees of DBH under 25 cm, accounting for 88% of the standing stems and 27% of the nests, were used underproportionally.
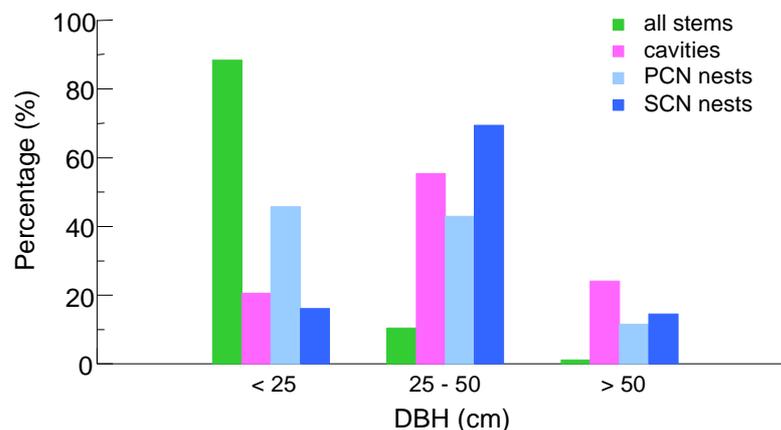
Fig. 4.16 **The percentage constitution of all sampled stems (green bars; n = 863), total cavities (red bars; n = 157), nests of PCNs (cyan bars; n = 35) and nests of SCNs (blue bars; n = 62) according to tree DBH.**

The DBH distribution of nest trees differed between PCNs and SCNs (Fig. 4.16, cyan and blue bars; x^2 = 10.09, df = 2, p < 0.01). Both group of birds used small trees underproportionally (Fig. 4.16, green bars), but SCNs used even less small trees than

PCNs. 46% of PCN nests were located in trees of DBH < 25 cm, while only 20% of SCN nests were found in these trees (Yates corrected $?^2$ = 8.53, df = 1, p < 0.01). The DBH distribution of SCN nest trees was not significantly different from the DBH distribution of cavity trees (Fig. 4.16, red bars; $?^2$ = 3.82, df = 2, p = 0.148).

4.5.3   Tree condition

63%, 13% and 24% of CNB nests were located in living trees, intact dead trees and broken snags, respectively. Compared with the tree condition constitution in the forests (85%, 10%, 5%, respectively; Fig. 4.17, green bars), living trees were used underproportionally (Yates corrected $?^2$ = 28.56, df = 1, p < 0.001), and broken snags were used overproportionally (Yates corrected $?^2$ = 42.56, df = 1, p < 0.001). The nest holding rate of broken snags was six times higher than that of living trees, and 3 times higher than that of intact dead trees.
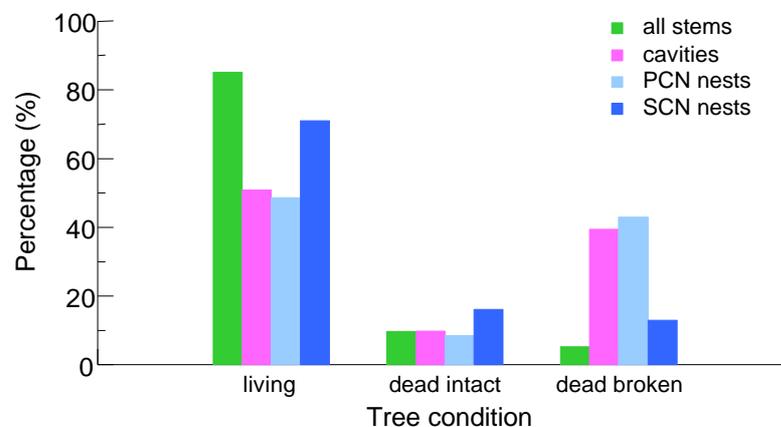
Fig. 4.17   The percentage constitution of all sampled stems (green bars; n = 863), total cavities (red bars; n = 157), nests of PCNs (cyan bars; n = 35) and nests of SCNs (blue bars; n = 62) according to tree condition.

PCNs and SCNs differed in their nest tree condition (Fig. 4.17, cyan and blue bars; $?^2$ = 11.20, df = 2, p < 0.01). Both group of birds used living trees underproportionally and used broken snags overproportionally, while PCNs avoided living trees and preferred broken snags further than SCNs. Living trees contained 71% of SCN nests but only 49% of PCN nests (Yates corrected $?^2$ = 3.90, df = 1, p < 0.05). Broken

snags accounted for 13% of SCN nests, while 43% of PCN nests were established in them (Yates corrected $?^2$ = 9.50, df = 1, p < 0.01).

SCNs did not use cavities in trees of different condition according to their availability (Fig. 4.17, red bars). Cavities in living trees were used overproportionally (Yates corrected $?^2$ = 6.46, df = 1, p < 0.05), and those in broken snags were used underproportionally (Yates corrected $?^2$ = 13.25, df = 1, p < 0.001).

4.5.4   Presence of fire scars

Most of the nests (64%) were located in trees with fire scars, which comprised only 28% of the standing stems (Yates corrected $?^2$ = 51.92, df = 1, p < 0.001). Nest holding rate of fire-scarred trees was 5 times higher than that of trees without fire scars.
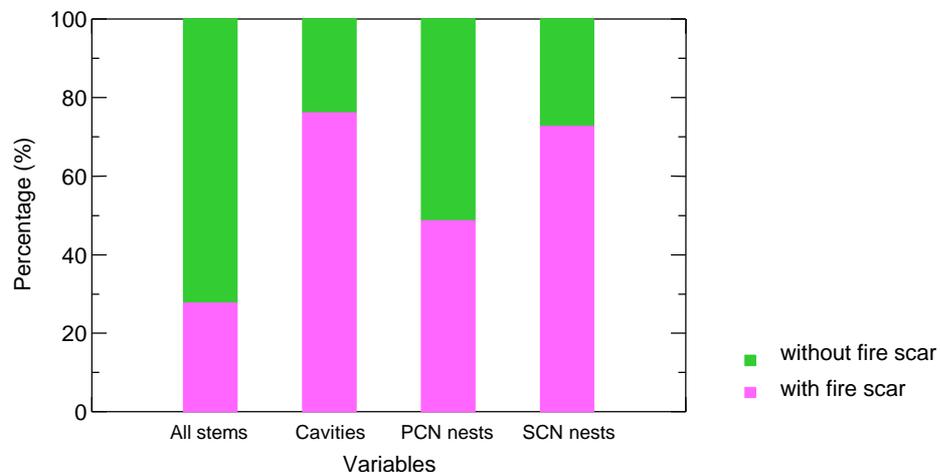
Fig. 4.18   **The percentage of all sampled stems (n = 863), total cavities (n = 157), nests of PCNs (n = 35) and nests of SCNs (n = 62) according to the presence of fire scars.**

Both PCNs and SCNs utilised fire-scarred trees overproportionally (Yates corrected $?^2$ = 6.30, df = 1, p < 0.05 for PCNs, Yates corrected $?^2$ = 53.07, df = 1, p < 0.001 for SCNs), while SCNs nested in these trees even more frequently than PCNs (Fig. 4.18; Yates corrected $?^2$ = 4.60, df = 1, p < 0.05). For SCN nests, the nest holding rate of

fire-scarred trees was 7 times higher than that of trees without fire scars, while for PCN nests only about 2 times higher. The extent SCNs using fire-scarred trees (73%) was similar to the cavity availability in these trees (76%; Yates corrected $?^2 = 0.53$, df = 1, p = 0.468).

4.5.5   Presence of fungi conks

38% of the nests were found in conk-bearing trees, which accounted for only 5% of the standing stems (Yates corrected $?^2 = 144.76$, df = 1, p < 0.001). Nest holding rate of trees with fungi conks was 11 times higher than that of trees without.

PCNs showed higher tendency to use conk-bearing trees than SCNs (Fig. 4.19; Yates corrected $?^2 = 7.16$, df = 1, p < 0.01). 57% and 27% of PCN and SCN nests, respectively, were established in trees with fungi conks. Conk-bearing stems held PCN nests 23 times more frequently, and held SCN nests 7 times more frequently, than those without conks did. The proportion SCNs using conk-bearing trees was similar to cavity availability in these trees (29%; Yates corrected $?^2 = 0.01$, df = 1, p = 0.911).
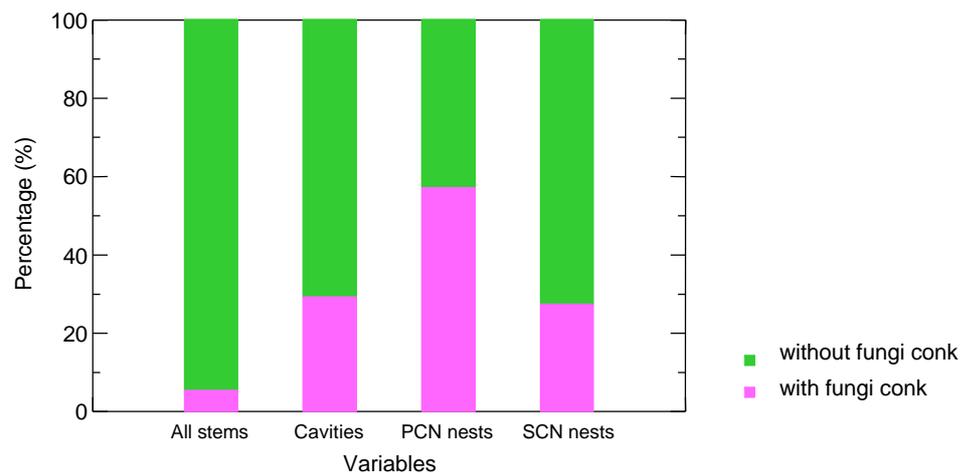
**Fig. 4.19   The percentage of all sampled stems (n = 863), total cavities (n = 157), nests of PCNs (n = 35) and nests of SCNs (n = 62) according to the presence of fungi conks.**

4.5.6   Cavity type

PCNs and SCNs differed in their use of cavity type (Fig. 4.20, cyan and blue bars; $?^2$ = 47.69, df = 3, p < 0.001). PCNs mostly nested in cavities excavated by themselves or other PCNs, while in few cases (11%) *P. montanus* also utilised branch hole. For SCNs, the majority (71%) of their nests were established in branch hole, and 18% in woodpecker hole.

In comparison to the relative abundance of each cavity type (Fig. 4.20, red bars), branch hole was used overproportionally (Yates corrected $?^2$ = 4.53, df = 1, p < 0.05) and other bird-induced hole was used underproportionally by SCNs (Yates corrected $?^2$ = 10.86, df = 1, p < 0.01). Woodpecker hole and bark crevice were utilised in proportion to their availability (Yates corrected $?^2$ = 0.55, df = 1, p = 0.458 for woodpecker hole, Yates corrected $?^2$ = 0.00, df = 1, p = 1.000 for bark crevice).
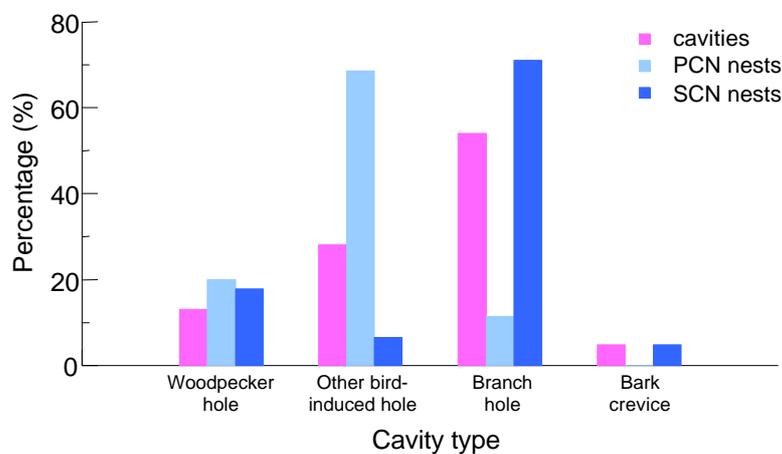
Fig. 4.20   The percentage constitution of total cavities (red bars; n = 157), nests of PCNs (cyan bars; n = 35) and nests of SCNs (blue bars; n = 62) according to cavity type.

4.6   Nest Site Selection of Individual Species

4.6.1   Selection of nest tree

Tree species

The preference for nest tree species differed among bird species (Table 4.13; $?^2 =$ 181.60, df = 40, p < 0.001). Three bird species showed patterns distinct from that of others. *C. familiaris* placed 64% of its nests in larch, *D. major* preferred aspen, and *S. europaea* used both larch and aspen overproportionally. All other six species established most of their nests in birch, with proportions from 69% in *D. minor* to 96% in *F. albicilla*. Thus these six species mainly using birch had smaller niche breadth, and showed high niche overlap between each other (Fig. 4.21). *C. familiaris*, *D. major* and *S. europaea* had larger niche breadth, and had less overlap with the former group.

Table 4.13   Species composition of nest trees (in %) used by each bird species.

Bird species	Tree species						N	Levins' B
	Willow	Aspen	Poplar	Birch	Larch	Scots pine		
Dendrocopos major	-	53.8	-	30.8	-	15.4	13	2.45
D. minor	-	15.4	7.7	69.2	7.7	-	13	1.94
Phoenicurus auroreus	4.3	-	4.3	73.9	17.4	-	23	1.72
Ficedula albicilla	-	4.0	-	96.0	-	-	25	1.08
Parus ater	-	1.9	3.8	86.8	3.8	3.8	53	1.32
P. major	-	-	18.8	81.3	-	-	16	1.44
P. montanus	3.1	-	12.5	81.3	3.1	-	64	1.48
Sitta europaea	-	23.8	-	19.0	38.1	19.0	21	3.64
Certhia familiaris	-	9.1	-	18.2	63.6	9.1	11	2.20

Birch comprised 13% to 68% of the standing stems across different habitats (see Section 4.1), thus the high use rates of birch by *P. auroreus*, *F. albicilla*, *P. ater*, *P. major* and *P. montanus* suggested use over its availability. Larch, comprising 1% to 32% of the standing stems, was overproportionally used by *C. familiaris*. Poplar, which occurred only in the riparian mixed forest and constituted about 8% of the stems there, was used by *P. major* and *P. montanus* overproportionally. Aspen
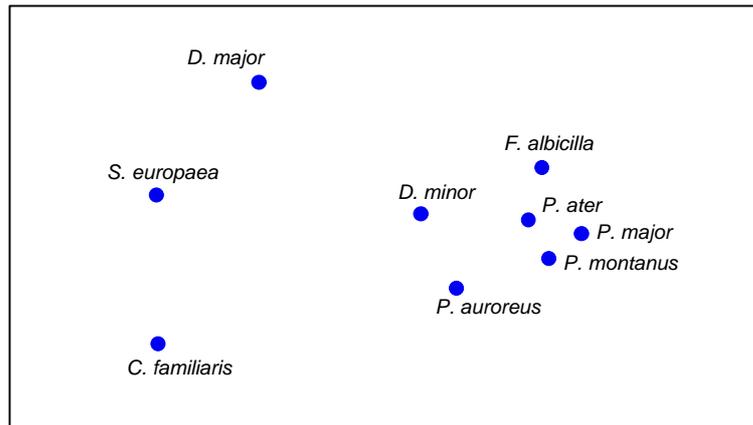
Fig. 4.21   The Renkonen similarity of nest tree species between bird species.

formed small patches in birch-larch forests, and its availability (0 - 1%) could be biased due to its highly patchy distribution and the small sample size. However, the very high use rates of aspen by *D. major*, *D. minor* and *S. europaea* related to its availability suggested an overproportional use. Spruce, fir and Siberian pine occurred mainly in the spruce-fir forest and altogether comprised 81% of the trees there, but no nest was found in them. *D. minor*, *P. auroreus* and *P. major* were never observed in this habitat, and *F. albicilla* occurred only very seldom. For other species, these three conifers were used underproportionally.

Taking cavity availability into consideration, overall 57% (16 - 100% across different habitats) of the cavities were located in birch, 26% (0 - 78%) in poplar, and no cavities were found in spruce, fir and Siberian pine (see Section 4.3.1). Thus the tree species use of most SCNs reflected the cavity availability in different tree species. The preference for cavity regarding tree species occurred in that *C. familiaris* preferred cavities in larch and *S. europaea* preferred those in aspen.

Tree DBH

The DBH of nest trees ranged from 12 cm for *P. montanus* to 91 cm for *P. ater*. *P. montanus* differed from all other species in that they placed their nests in thinnest trees (Table 4.14; Mann-Whitney U test, $p < 0.05$ with *F. albicilla*, $p < 0.001$ with each of other species). *D. major*, *S. europaea* and *C. familiaris* never utilised trees thinner than 25 cm, and the latter two showed highest preference for large trees (Mann-Whitney U test, $p < 0.001$ with each of other species except *D. major*).

Table 4.14   Mean (± SD) and the percentage in 25 cm ranks of nest tree DBH of each bird species.

Bird species	DBH (cm)				N
	mean	< 25	25 - 50	> 50	
D. major	38.5 ± 7.2	0.0	7.7	92.3	13
D. minor	33.2 ± 9.9	15.4	7.7	76.9	13
P. auroreus	35.0 ± 11.5	17.4	13.0	69.6	23
F. albicilla	28.1 ± 7.8	40.0	0.0	60.0	25
P. ater	34.0 ± 15.5	24.5	11.3	64.2	53
P. major	35.1 ± 8.5	12.5	6.3	81.3	16
P. montanus	24.6 ± 11.1	60.9	4.7	34.4	64
S. europaea	46.9 ± 14.5	0.0	33.3	66.7	21
C. familiaris	46.5 ± 10.6	0.0	27.3	72.7	11

In the study area, the percentages of trees of DBH < 25 cm, 25 - 50 cm and > 50 cm were 88%, 10% and 1%, respectively (see Section 4.5.2). Grouping DBH of nest trees into the same interval for comparison, all species used large trees overproportionally (x^2 test, df = 2, p < 0.001 for each species). 21%, 55% and 24% of the cavities were found in trees of DBH < 25 cm, 25 - 50 cm and > 50 cm, respectively (see Section 4.5.2). Among SCNs, *F. albicilla* used cavities in thinner trees overproportionally (x^2 = 9.50, df = 2, p < 0.01), while the others were not selective to cavities according to tree diameter.

Tree condition

The nest tree condition differed significantly among bird species (Table 4.15; x^2 = 82.13, df = 16, p < 0.001). *P. ater* and *P. major* highly preferred living trees and thus had smaller niche breadth. They had high niche overlap with each other and were distinct from others (Fig. 4.22). *D. major* and *S. europaea* utilised living trees and intact dead trees more often and used broken snags only seldom. *P. auroreus*, *F. albicilla* and *C. familiaris* also placed most of their nests in living trees, while, in contrast to the former two groups, broken snags were often used. *D. minor* and *P. montanus* established most of their nests in broken snags.

Table 4.15   Condition of nest trees (in %) used by each bird species.

Bird species	Tree condition			N	Levins' B
	living	dead intact	dead broken		
D. major	61.5	30.8	7.7	13	2.09
D. minor	30.8	15.4	53.8	13	2.45
P. auroreus	47.8	13.0	39.1	23	2.51
F. albicilla	52.0	16.0	32.0	25	2.51
P. ater	96.2	3.8	-	53	1.08
P. major	87.5	6.3	6.3	16	1.29
P. montanus	43.8	4.7	51.6	64	2.18
S. europaea	61.9	33.3	4.8	21	2.01
C. familiaris	45.5	27.3	27.3	11	2.81
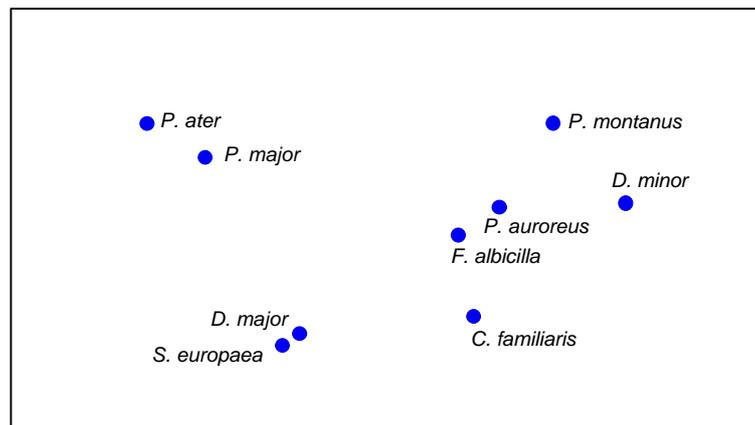
Fig. 4.22   The Renkonen similarity of nest tree condition between bird species.

Living trees, intact dead trees and broken snags comprised 85%, 10% and 5% of the standing stems, respectively (see Section 4.5.3). Thus all species except *P. ater* and *P. major* utilised living trees underproportionally (x^2 test, df = 2, p < 0.05 for *D. major*, p < 0.01 for *S. europaea*, p < 0.001 for others). 51%, 10% and 39% of the cavities were found in living trees, intact dead trees and broken snags, respectively. *P. ater* and *P. major* preferred cavities in living trees ($x^2 = 35.5$, df = 2, p < 0.001 in *P. ater*, $x^2 = 8.1$, df = 2, p < 0.05 in *P. major*), while *S. europaea* preferred cavities in fresh dead trees and avoided those in snags ($x^2 = 15.0$, df = 2, p < 0.001). Other SCNs were not selective to cavities according to tree condition.

4.6.2   Selection of nest cavity

Cavity type

The preferences for cavity type were distinct among most bird species (Table 4.16, $?^2$ = 539.95, df = 24, p < 0.001). Woodpecker species were persistent in using woodpecker holes. Though being an excavator as well, only 84% of *P. montanus* constructed nest cavities by their own. Among them 51 nests were completely excavated by themselves, and 3 were modified from branch holes. One out of the

Table 4.16   Cavity type (in %) used by each bird species.

Bird species	Cavity type				N	Levins' B
	woodpecker hole	other bird-induced hole	branch hole	others		
D. major	100.0	-	-	-	13	1.00
D. minor	100.0	-	-	-	13	1.00
P. auroreus	17.4	21.7	56.5	4.3	23	2.51
F. albicilla	32.0	56.0	12.0	-	25	2.32
P. ater	-	-	100.0	-	53	1.00
P. major	-	-	100.0	-	16	1.00
P. montanus	1.6	84.4	14.1	-	64	1.37
S. europaea	85.7	-	14.3	-	21	1.32
C. familiaris	-	-	-	100.0	11	1.00
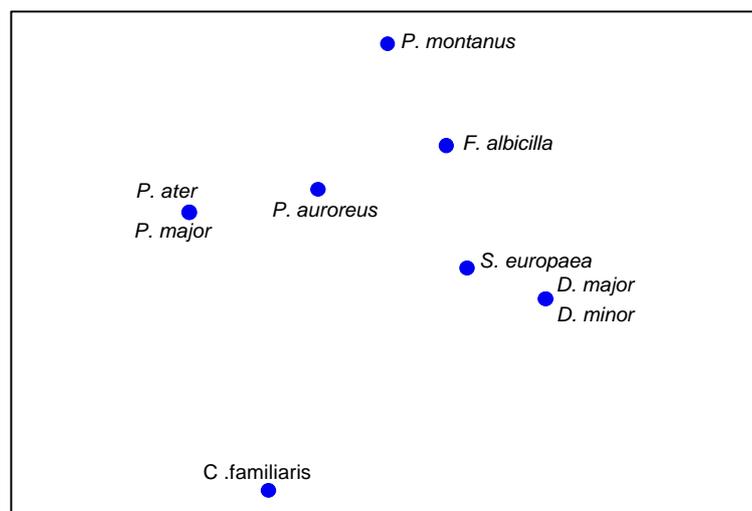
Fig. 4.23   The Renkonen similarity of nest cavity type between bird species.

total 64 nests of *P. montanus* were found in a woodpecker hole after the entrance modified by *S. europaea*, and 9 were found in branch holes of which no sign of further excavation was observed. *S. europaea* preferred using woodpecker holes and had high similarity with woodpeckers (Fig. 4.23). *F. albicilla* placed most of their nests in other bird-induced holes and thus had high niche overlap with *P. montanus*. *P. ater* and *P. major* used exclusively branch holes. *C. familiaris* utilised special cavity types: 8 out of the 11 nests found were located in bark crevices, 2 in vertical slits in trunk due to the shear force when the snag broke, and 1 in trunk fissure originated from side fire. *P. auroreus* was the only species that utilised all types of cavities. Except for *P. auroreus* and *F. albicilla*, niche breadths for others were small since each preferred specified cavity type. All SCNs except *P. auroreus* utilised cavity types differed from their availability ($?^2$ test, df = 2, p < 0.01 for *P. major*, p < 0.001 for the others).

Height above ground

The height above ground of nest cavities varied between 0.1 m (*P. auroreus*) and 20 m (*S. europaea*). The three PCNs as well as *S. europaea* and *F. albicilla* nested in higher cavities (Table 4.17). Among them *S. europaea* nested higher than *D. major* (Mann-Whitney U = 75.00, df = 1, p < 0.05), and *F. albicilla* higher than *P. montanus* (Mann-Whitney U = 1024.50, df = 1, p < 0.05). *D. major*, *D. minor* and *S. europaea* never nested in cavities lower than 4 m. *P. auroreus*, *P. ater*, *P. major* and *C. familiaris* utilised lower cavities and showed no difference between each other. *P. montanus* nested in cavities of more variable height than *D. major*, *P. auroreus*, *P. ater* and *P. major* (F test, p < 0.05).

Substrate diameter

The substrate diameter ranged from 8 cm for *P. montanus* to 96 cm for *P. ater*. *C. familiaris* nested in thicker part of tree than all other species (Table 4.17; Mann-Whitney U test, p < 0.05 with each of other species). *D. minor*, *F. albicilla* and *P. montanus* established their nests in thinner part of tree than others , while *F. albicilla* and *P. montanus* further used thinner part than *D. minor* (Mann-Whitney U = 230.00, df = 1, p < 0.05 for *F. albicilla*, Mann-Whitney U = 656.00, df = 1, p < 0.01 for *P. montanus*). Other five species utilised cavities with similar substrate diameter. *P.*

auroreus, *P. ater* and *C. familiaris* could utilise cavities with more variable substrate diameter than the others (F test, p < 0.05).

Table 4.17   Mean (± SD) of cavity height above ground, substrate diameter, cavity opening length and cavity opening width of each bird species.

Bird species	cavity height (m)	substrate diameter (cm)	opening length (cm)	opening width (cm)	N
D. major	8.4 ± 2.2	27.2 ± 5.4	4.7 ± 0.3	4.7 ± 0.3	13
D. minor	8.8 ± 3.6	20.9 ± 4.5	3.4 ± 0.3	3.4 ± 0.3	13
P. auroreus	4.4 ± 3.0	30.6 ± 13.6	8.1 ± 4.6	6.5 ± 3.2	23
F. albicilla	9.2 ± 3.5	17.2 ± 5.8	3.8 ± 1.0	3.9 ± 0.8	25
P. ater	4.2 ± 3.2	30.5 ± 15.1	6.2 ± 3.1	3.1 ± 0.7	53
P. major	5.0 ± 2.7	27.1 ± 6.7	7.0 ± 3.0	4.1 ± 1.3	16
P. montanus	7.3 ± 4.6	15.7 ± 7.5	3.5 ± 0.9	3.4 ± 0.5	64
S. europaea	11.3 ± 3.9	29.1 ± 6.8	5.1 ± 0.7 3.0 ± 0.2[†]	4.9 ± 0.3 3.1 ± 0.2[†]	21
C. familiaris	4.3 ± 3.6	41 ± 14.1	18 ± 20.7	3.1 ± 0.9	11

[†] After minimisation by *S. europaea*.

Substrate condition

P. ater differed from all other species in their high preference for cavities in living parts of trees (Table 4.18; x^2 test with Yates correction, p < 0.01 with *P. major*, p < 0.001 with the others). *D. minor*, *F. albicilla* and *P. montanus* preferred to nest in dead parts. *D. minor* excavated exclusively in dead substrates. *P. montanus* used also only dead substrates when they excavated the cavities by themselves, but their nest cavities that were not self-excavated all occurred in living substrates. The comparison with the nest tree condition (Table 4.15) indicated that *F. albicilla* and *P. montanus* preferred a broken top or a dead branch when using a living tree ($x^2 = 9.5$, df = 1, p < 0.01 for *F. albicilla*, $x^2 = 10.8$, df = 1, p < 0.01 in *P. montanus*). Other five species used cavities in living or dead substrates more evenly and thus had larger niche breadth.

Table 4.18   Substrate condition (in %) used by each bird species.

Bird species	Substrate condition		N	Levins' B
	living	dead		
D. major	38.5	61.5	13	1.90
D. minor	-	100.0	13	1.00
P. auroreus	39.1	60.9	23	1.91
F. albicilla	8.0	92.0	25	1.17
P. ater	96.2	3.8	53	1.08
P. major	62.5	37.5	16	1.88
P. montanus	15.6	84.4	64	1.36
S. europaea	42.9	57.1	21	1.96
C. familiaris	45.5	54.5	11	1.98

Dimension and shape of cavity opening

The length of cavity opening varied greatly (Table 4.17), ranged from 2.4 cm (*F. albicilla*) to 74 cm (*C. familiaris*). *D. minor*, *F. albicilla* and *P. montanus* nested in cavities with smallest opening length. *S. europaea* used cavities with opening length similar to that of *D. major*, *P. ater* and *P. major*, but it minimised the opening length to the smallest of all. *C. familiaris* could utilise cavities with most variable length (F test, $p < 0.001$), while *D. major* and *D. minor* were most strict in opening length (F test, $p < 0.01$).

Table 4.19   Shape of nest cavity opening (in %) of each bird species.

Bird species	Shape of cavity opening			N	Levins' B
	flat	round	slit-like		
D. major	-	100.0	-	13	1.00
D. minor	-	100.0	-	13	1.00
P. auroreus	17.4	26.1	56.5	23	2.39
F. albicilla	8.0	88.0	4.0	25	1.28
P. ater	7.5	15.1	77.4	53	1.60
P. major	12.5	18.8	68.8	16	1.91
P. montanus	6.3	79.7	14.1	64	1.52
S. europaea	-	90.5	9.5	21	1.21
C. familiaris	-	-	100	11	1.00

The width of cavity opening showed less variability than length (Table 4.17), ranged from 2 cm (*P. ater*, *P. montanus* and *C. familiaris*) to 18 cm (*P. auroreus*). *P. auroreus* bred in cavities with widest opening, and was the only species utilised cavities with opening wider than 8 cm. *D. major* and *S. europaea* utilised cavities with similar opening width which was wider than that of other six species. *S. europaea* then minimised the opening width to one of the smallest, similar to that of *P. ater* and *C. familiaris*. The nest cavities of *P. auroreus* had the largest variance in opening width (F test, $p < 0.001$), while those of *D. major*, *D. minor* and *S. europaea* showed least variance (F test, $p < 0.05$).

The preference for cavity opening shape showed two distinct patterns (Table 4.19). *D. major*, *D. minor*, *F. albicilla*, *P. montanus* and *S. europaea* preferred cavities with round openings, while others utilised mostly slit-like ones. Cavities with flat opening shape were seldom used by any species.

4.6.3   Multivariate summary of nest niche overlap

Cluster analysis
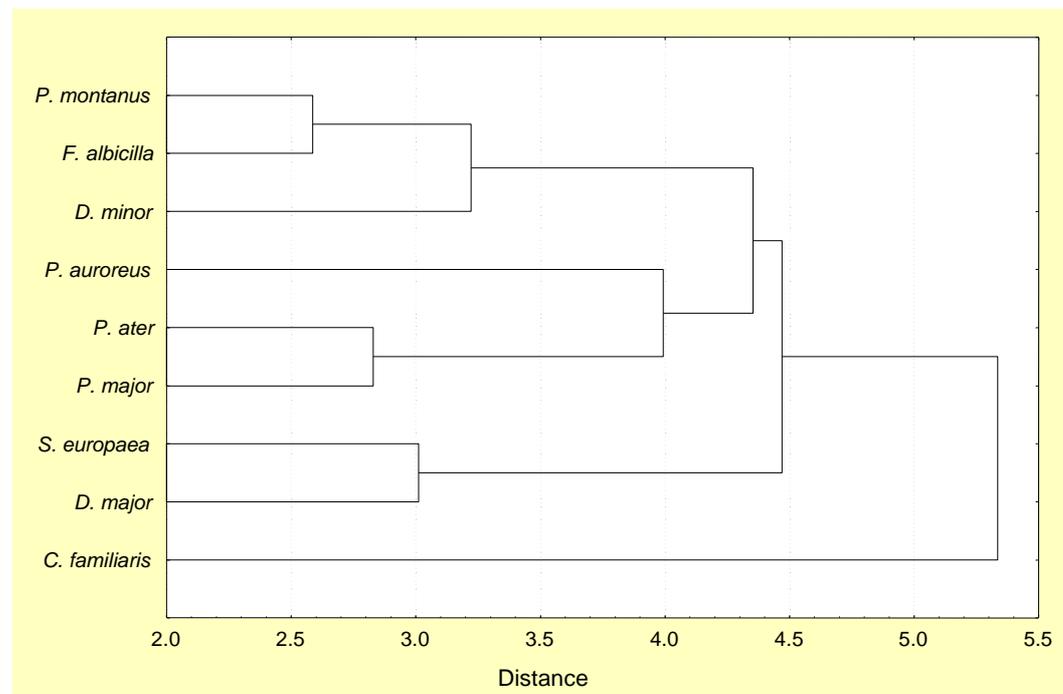
Fig. 4.24   The dendrogram of single linkage cluster analysis.

The overall similarity of nest sites among bird species was summarised and visualised in the cluster tree (Fig. 4.24). Greatest similarity occurred between *F. albicilla* and *P. montanus*, while the nest site of *C. familiaris* was most distinct. Four groups could be identified: *D. major* with *S. europaea*, *D. minor* with *F. albicilla* and *P. montanus*, *P. auroreus* with *P. ater* and *P. major*, and *C. familiaris* alone.

Discriminant function analysis

A discriminant function analysis was performed to investigate the extent of niche overlap among species, and to identify the nest attributes most discriminate among species. A full model with all 15 variables resulted in 67% of correct classification. When a backward stepwise selection was applied, the three cavity type variables and the cavity opening width alone reached an accuracy of 66%, i.e. over 98% of the discriminant power of the full model. Thus this model was adopted.

From the classification matrix (Table 4.20), the nest sites of *D. major* and *S. europaea* were indistinguishable. Low classification accuracy also occurred in *P. auroreus*, *F. albicilla* and *P. major*. The nest site of *P. auroreus* overlapped with that of *P. ater*, *P. major*, *P. montanus*, *S. europaea* and even *C. familiaris*. The nest site of *F. albicilla* was mainly confounded with that of *P. montanus*, and also overlapped with *D. minor*, *P. ater* and *S. europaea*. The nest site of *P. major* was mainly confounded with *P. ater*.

Table 4.20   Classification matrix from discriminant function analysis based on cavity type and cavity opening width. Boldface marked the diagonal elements of correct classification, and italic type marked the high overlap between species.

		Classified									Accuracy (%)
		D. major	*D. minor*	*P. auroreus*	*F. albicilla*	*P. ater*	*P. major*	*P. montanus*	*S. europaea*	*C. familiaris*	
	D. major	**0**	0	0	0	0	0	0	*13*	0	0.0
	D. minor	0	**12**	0	0	0	0	0	1	0	92.3
	P. auroreus	0	0	**8**	0	6	1	3	4	1	34.8
Observed	*F. albicilla*	0	2	0	**0**	3	0	*14*	6	0	0.0
	P. ater	0	0	0	0	**53**	0	0	0	0	100.0
	P. major	0	0	2	0	*12*	**2**	0	0	0	12.5
	P. montanus	0	1	0	0	8	1	**54**	0	0	84.4
	S. europaea	0	0	0	0	2	0	0	**18**	0	90.0
	C. familiaris	0	0	0	0	0	0	0	0	**11**	100.0

4.7   Sequential Cavity Use

4.7.1   Sequential use at guild level

37% of the nest cavities found in 2002 were reused in 2003. Cavities previously used by PCNs, WPCNs and SCNs had reuse rate 31%, 16% and 46%, respectively (Fig. 4.25). The reuse rate of previous WPCN cavities was significantly lower than that of SCN cavities (Yates corrected $?^2$ = 5.85, df = 1, p < 0.05).

Constancy, or reuse of cavities by the same species, for SCN cavities was 45%, higher than that of PCN cavities (Yates corrected $?^2$ = 8.89, df = 1, p < 0.01) and WPCN cavities (Yates corrected $?^2$ = 19.77, df = 1, p < 0.001). Thus old cavities of PCNs and WPCNs were more available to other bird species, while old SCN cavities tended to be reused by the same species that previously occupied the cavity.
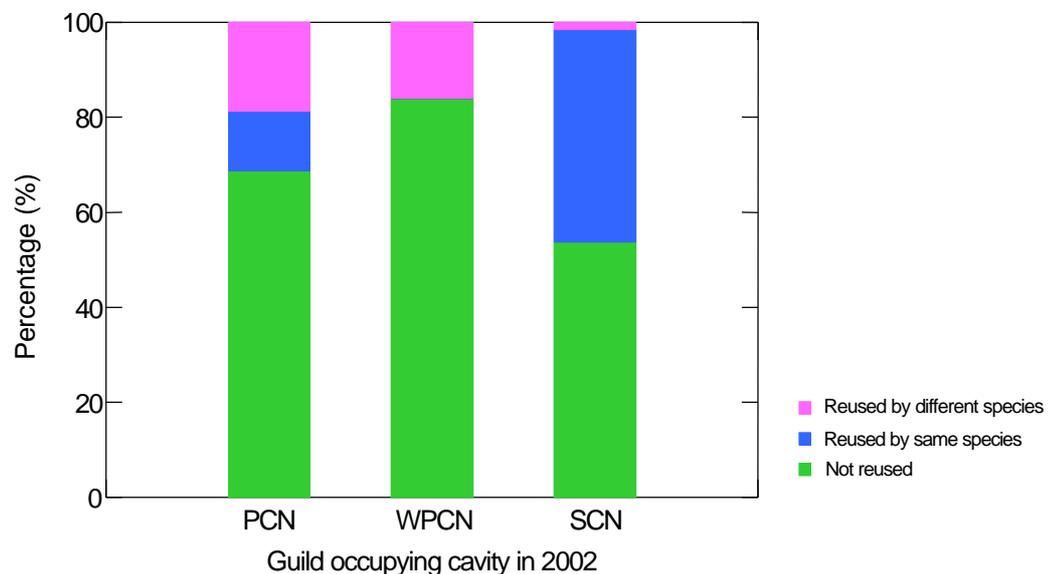
Fig. 4.25   Reuse pattern of nest cavities (in %) for PCNs (n = 16), WPCNs (n = 25) and SCNs (n = 67).

4.7.2 Sequential use at species level

Among PCNs, cavities previous occupied by *D. major* were more frequently reused (Table 4.21). It was also the only woodpecker species of which the reuse its own cavity was found in the study period (Fig. 4.26). Two out of 6 *D. major* nest cavities in 2002 were utilised by the same species in 2003, 2 were utilised by *S. europaea*, resulted in a reuse rate of 67%. For *D. minor*, of which also 6 nest cavities were found in 2002, only one was used by *F. albicilla* in the following year, and the reuse rate was 17%. For other woodpecker species, only 1 or 2 nests of each species were found in 2002, due to their lower density in the study area. No difference in the cavity reuse rate between woodpecker species could be found owing to the small sample size. Four out of 25 *P. montanus* nest cavities in 2002 were occupied in 2003, and the subsequent users were all *F. albicilla*. The reuse rate of *P. montanus* cavity (16%) was lower than that of *D. major* (Yates corrected $?^2 = 4.11$, df = 1, p < 0.05).

Table 4.21   Reuse pattern of nest cavities (in %) for each species.

Occupant 2002	No. of nests found in 2002	Reuse (%) in 2003		
		not reused	by same species	by different species
PCN				
D. martius	1	100	0	0
P. canus	2	100	0	0
D. leucotos	1	100	0	0
D. major	6	33	33	33
D. minor	6	83	0	17
WPCN				
P. montanus	25	84	0	16
SCN				
B. clangula	1	0	100	0
P. auroreus	10	70	30	0
P. phoenicurus	2	100	0	0
T. ruficollis	1	100	0	0
F. albicilla	12	100	0	0
P. ater	26	23	77	0
P. major	7	71	29	0
S. europaea	5	0	80	20
C. familiaris	3	100	0	0

Occupant 2002		Occupant 2003
D. martius		D. martius
P. canus		P. canus
D. leucotos		D. leucotos
D. major		D. major
D. minor		D. minor
P. montanus		P. montanus
B. clangula		B. clangula
J. torquilla		J. torquilla
P. auroreus		P. auroreus
P. phoenicurus		P. phoenicurus
T. ruficollis		T. ruficollis
F. albicilla		F. albicilla
P. ater		P. ater
P. major		P. major
S. europaea		S. europaea
C. familiaris		C. familiaris

Fig. 4.26   The reuse of nest cavities of 2002 in 2003. Dotted lines: reuse rate < 25%, thin lines: reuse rate 25 - 50%, thick lines: reuse rate > 50%.

Among the SCNs, the cavities of *B. clangula*, *P. ater* and *S. europaea* showed high constancy. Only one nest of *B. clangula* was found in 2002 and could not be concluded. Of the 26 *P. ater* nest cavities found in 2002, 20 were reused by the same species, and the reuse rate was 77%. All five nest cavities of *S. europaea* were reused, four by the same species, and one was occupied by *P. montanus*. This was the only case observed between the two years that a previous SCN nest was reused by a different species. 30% and 29% of the nest cavities previously occupied by *P. auroreus* and *P. major*, respectively, were reused by the same species. No reuse of *F. albicilla* cavities was observed, and the reuse rate of previous *F. albicilla* cavities was lower than that of *P. ater* and *S. europaea* (Yates corrected $?^2$ = 16.52, df = 1, p < 0.001 with *P. ater*, Yates corrected $?^2$ = 12.52, df = 1, p < 0.001 with *S. europaea*).

4.7.3   Characters of reused cavities

There were significant associations between cavity reuse and tree condition, presence of fungi conks, cavity type and substrate condition (Table 4.22). Most of the reused cavities (80%) were located in living trees. And cavities in living trees were reused more frequently (47%) than cavities in broken snags (16%). Only 27.5% of reused cavities were situated in trees with fungi conks, while 58.8% of those not reused were

Table 4.22   Comparisons of reused and not reused cavities.

Attributes (in %)	Nest cavities of 2002		$?^2$	p value
	reused (n = 40)	not reused (n = 68)		
Tree condition			9.092	< 0.05
living	80.0	51.5		
dead intact	7.5	11.8		
dead broken	12.5	36.8		
Presence of fungi			8.698	< 0.01
without fungi conk	72.5	41.2		
with fungi conk	27.5	58.8		
Cavity type			12.555	< 0.01
woodpecker hole	27.5	22.1		
other bird-induced	12.5	36.8		
branch hole	60.0	33.8		
others	0.0	7.4		
Substrate condition			16.454	< 0.001
living	70.0	27.9		
dead	30.0	72.1		

in conk-bearing trees. Regarding cavity type, most reused cavities were branch holes, while other bird-induced holes were reused underproportionally. 42% and 51% of woodpecker holes and branch holes in 2002, respectively, were reused in the following year. These were higher than the reuse rate of other bird-induced holes (16%). Cavities in living substrates were more frequently reused than those in dead substrates.

No relationship was found between cavity reuse and tree species ($?^2$ = 8.14, df = 5, p = 0.15), tree DBH (t = -0.66, df = 106, p = 0.51), presence of fire scars on the tree (Yates corrected $?^2$ = 0.00, df = 1, p = 1.00), cavity height above ground (t = 0.75, df = 106, p = 0.46), substrate diameter (t = -1.50, df = 106, p = 0.14), cavity opening length (t = 0.29, df = 106, p = 0.77), opening width (t = 1.04, df = 106, p = 0.30) and opening shape ($?^2$ = 3.10, df = 2, p = 0.21).

Using backward stepwise logistic regression to determine the variables that could best predict cavity reuse, substrate condition came to be the only significant predictor in the model (log likelihood = -61.96, $?^2$ = 18.46, p < 0.001).

4.8   Nest Web Analysis

4.8.1   Nest web of CNB community in West Khentey

Integrating tree and cavity characteristics across the CNB community, the nest site use of CNBs was summarised in the nest web (Fig. 4.27). The links indicated the proportion of tree or cavity use of each bird species. Such a graphic visualised the linkage and interdependence among species.

Considering the linkage between level one (trees) and level 2 (PCNs, WPCNs and non-excavated cavities), birch played the most important role. All excavating species except *D. martius* utilised birch. *D. leucotos*, *D. minor* and *P. montanus* were highly dependent on this tree species, among them the nests of *D. leucotos* were only found in birch (n = 3). It also supported the majority (73%) of the non-excavated cavities
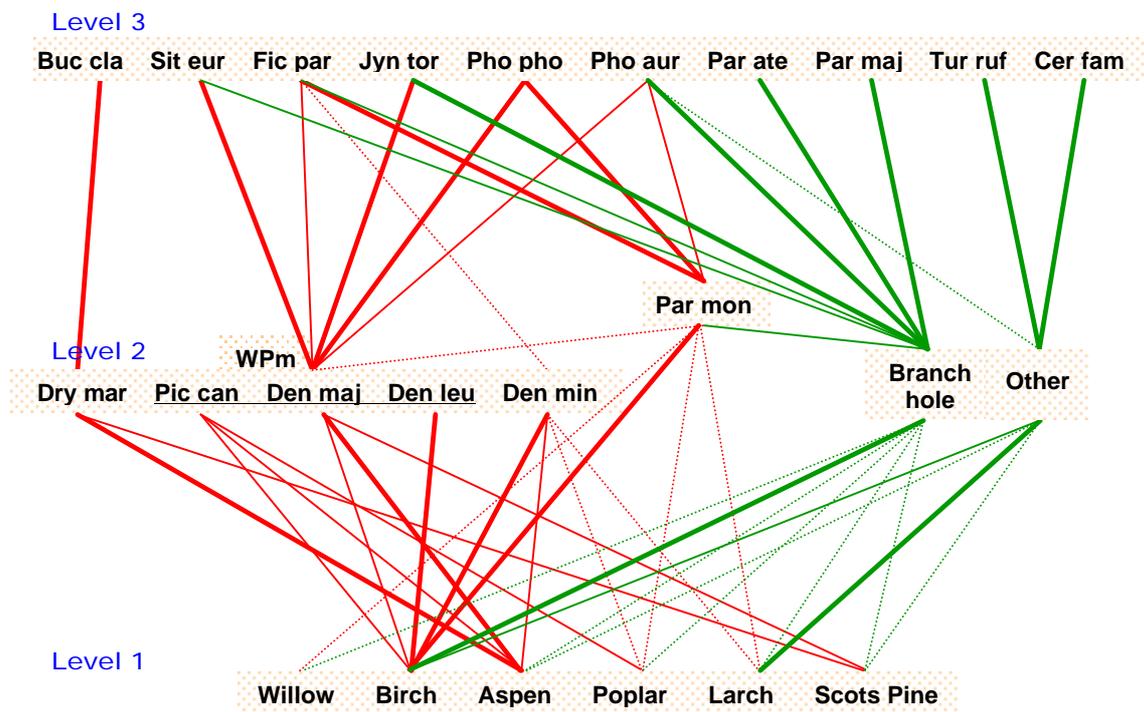

Fig. 4.27   Nest flow in the nest web. Cavity type was indicated by red (excavated cavities) and green (non-excavated cavities). The proportion of nest use was indicated by dotted lines (< 10%), thin lines (10 - 50%) and thick lines (> 50%). Bird species were abbreviated by the first three letters of the genus and species names. WPm referred to middle-sized woodpecker holes pooled.

which were used by SCNs and *P. montanus*. Aspen was important tree species for *D. martius* and *D. major*. Spruce, fir and Siberian pine did not enter the nest web, since no nests were found in them.

Between level two and level three (SCNs), the large-sized woodpecker holes from *D. martius* were only used by *B. clangula*, and this duck depended exclusively on this resources (n = 2). Middle-sized woodpecker holes supported more diversified users, including *S. europaea*, *F. albicilla*, *J. torquilla*, *P. phoenicurus*, *P. auroreus* and the WPCN *P. montanus*, but none of these users focused entirely on this resource. The sample size for *J. torquilla* and *P. phoenicurus* was small (n = 2 for each), and for both species one of the two nests found were in middle-sized woodpecker holes. *S. europaea* showed highest dependence on this resource, in which 86% of their nests were established. The small-sized woodpecker holes from *D. minor* were only utilised by *F. albicilla*.

Cavities from *P. montanus* were the main resource for *F. albicilla*, supporting 56% of their nests. In some cases, usually after the cavity openings were enlarged by woodpeckers or due to other causes, *P. montanus* cavities were also utilised by *P. phoenicurus* and *P. auroreus*.

Except *B. clangula* and *P. phoenicurus*, all other SCNs and *P. montanus* utilised non-excavated cavities. *T. ruficollis* was not an obligate cavity nester. *P. ater*, *P. major* and *C. familiaris* depended exclusively on this resource, while others had alternative choices.

Among SCNs, *F. albicilla* and *P. auroreus* used more diversified cavities, behaving as generalists in cavity use. *B. clangula*, *P. ater*, *P. major* and *C. familiaris* behaved as specialists.

4.8.2 Simulation I: roles of woodpeckers

The nest web could be applied to investigate the roles of woodpeckers in the CNB community. Supposing that *D. martius* was removed from the system, according to the nest web (Fig. 4.27), it was most likely that *B. clangula* would disappear as well. However, other parts of the CNB community were basically unaffected.

In the case that all middle-sized woodpecker species were excluded from the CNB community, the influence would be more complicated (Fig. 4.28). First, this could affect other members in the same level. *D. minor* and *P. montanus* might gain some advantages due to the release of competition for nest substrates. However, their benefit might not be substantial. The preferred nest site of *D. major* did not greatly overlap with that of *D. minor* and *P. montanus* (see Section 4.6). Other middle-sized woodpecker species only appeared with low density in the study area. It also affected the resource availability of SCNs. Of the five SCN species nesting in middle-sized woodpecker holes, none was totally dependent on such cavities. *S. europaea*, which had the highest preference for middle-sized woodpecker holes, could also well use branch holes.

With the simplified assumption that each of the users of middle-sized woodpecker cavities simply shift to its alternative resources proportionally, the users of *D. minor*
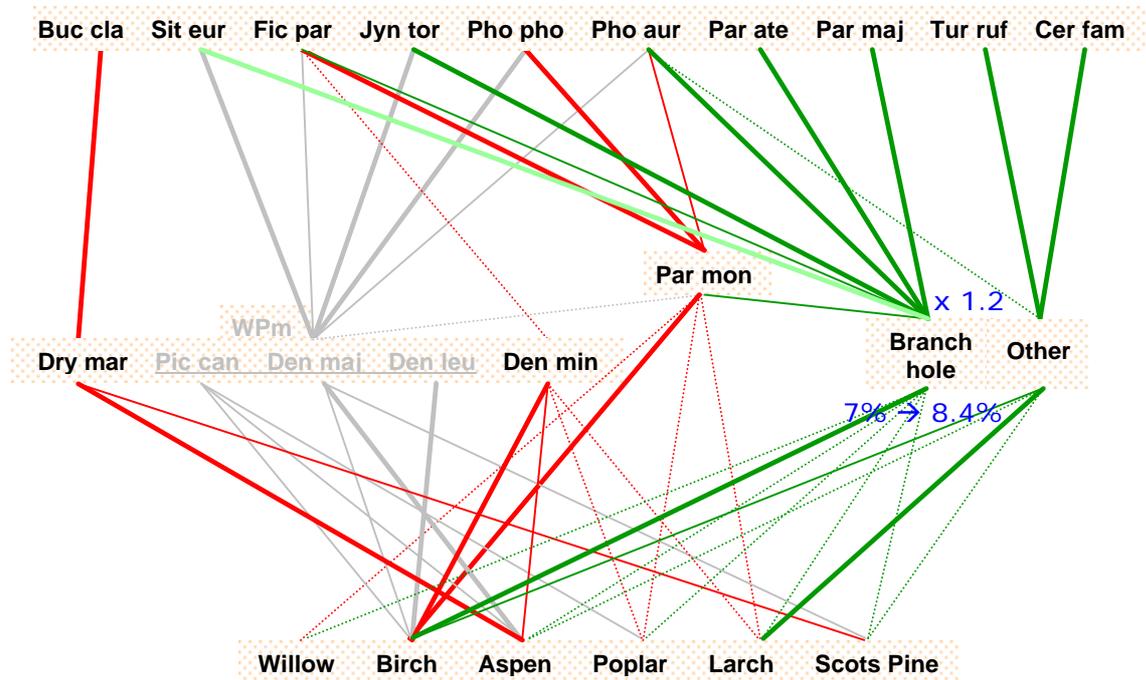

Fig. 4.28   **The supposed nest web in the case that middle-sized woodpeckers were excluded from the system.**

cavities and *P. montanus* cavities would become 1.3 times more, and that of branch holes 1.2 times more. Branch hole was originally the cavity type most heavily used by SCNs (see Section 4.5.6). The original occupancy of branch hole was approximately 7%. This would rise to 8.4% when middle-sized woodpecker holes were no more available. These numbers indicated that there might still be enough available branch holes to buffer the lost of middle-sized woodpecker holes.

The removal of *D. minor* seemed to cause few stirs to the nest web. Only *F. albicilla* used *D. minor* holes. And in the study area, there were abundant *P. montanus* cavities, which served as an alternative for *F. albicilla*.

4.8.3   Simulation II: roles of some tree species

Nest web could also be applied to observe the importance of each tree species to the CNB community. From the nest web (Fig. 4.27), it was clear that the removal of spruce, fir and Siberian pine had no direct impact on the CNBs, from the viewpoint of cavity supply.

If birch was removed from the system and replaced by, for example, spruce, far-reaching influences could arise (Fig. 4.29). Firstly, birch was the main nesting substrate for several PCNs and WPCNs, supporting 65% of their nests. *D. leucotos*, *D. minor* and *P. montanus* were highly dependent on birch. Though these excavators could shift their resource use, the impact was not likely to be fully adjusted. Aspen and poplar were the favourite alternatives for *D. minor* and *P. montanus* (see Section 4.6.1), but these tree species had either low abundance or limited distribution. Thus the intra- and interspecific competition among PCNs and WPCNs would rise.

Another critical function of birch was that it supplied large amount of non-excavated cavities. About 80% of the branch holes utilised by SCNs were located in birch. When birch was excluded from the system, the abundance of branch hole would reduced to one-fifth, which indicated the occupancy would rise to five times, given the same amount of users. The original occupancy 7% would than become 35%, which might lead to strong competition among SCNs for cavities of good quality. *P. ater* and P. major, which nested exclusively in branch hole, might suffer the most. For other species, the opportunity of shifting to other resources would be limited as
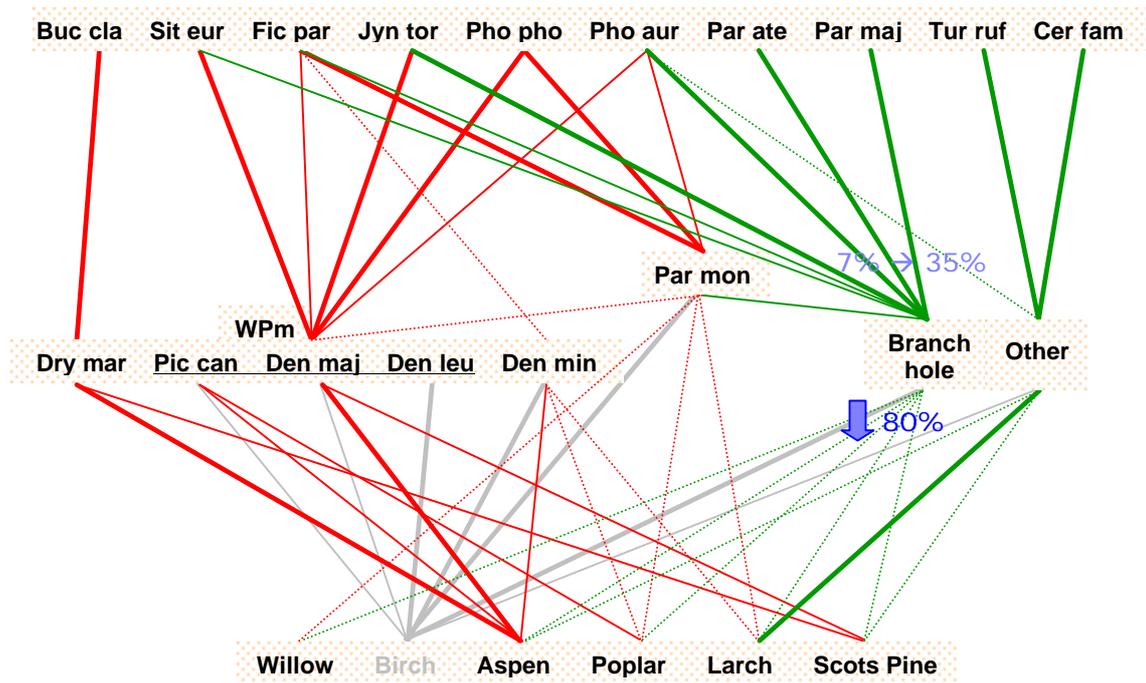
Fig. 4.29   The supposed nest web in the case that birch was excluded from the system.

well, since the availability of PCN and WPCN cavities might also decrease both in number and in spatial distribution.

The removal of aspen would influence mainly *D. martius* and *D. major*. *D. major* was adaptive to diverse tree species. *D. martius* was more limited by the availability of large trees. Suitable alternatives were, however, likely to be available in its large territory. As the result of the adjustability of these PCNs, the influence on SCNs due to the removal of aspen might not be substantial.

The removal of larch would lead to about 67% decrease of special non-excavated cavities. Since *T. ruficollis* was not an obligate cavity nester, only *C. familiars* might suffer to a great extent. Other parts of the CNB community were not likely to be substantially affected.

5   DISCUSSION

5.1   Cavity Abundance in a Forest

5.1.1   Cavity abundance in natural boreal forest

The cavity density estimates reported in the literature ranged widely, from 1 to 60 cavities/ha (Table 5.1). The cavity abundance in the study area (30 cavities/ha) was among the highest reported. Comparisons were approximate as the definitions of cavities and survey methods varied substantially among studies, and locating cavities could be difficult (WATERS et al. 1990). In this study, cavities were located from the ground and inner dimension of cavities was not measured. Thus the cavity abundance might be underestimated due to overlooking some cavities located higher in the trees, while on the other hand might be overestimated due to including some cavities unsuitable for CNBs (e.g. too small chamber, too deep or containing water).

Another constraint for comparisons was the inadequate sample efforts in many studies. Due to the difficulty in locating cavities, most studies had very small sample area or were lack of repeats. Cavities usually occurred in large trees, the density of which in the forests is usually low. Thus insufficient sampling size could not give rise to representative estimates (SANDSTRÖM 1992). As shown in Table 5.1, many studies reported high variance of cavity abundance. In the present study, plotless method was adopted for sampling. This method is efficient in collecting information of large trees and thus especially suitable for surveying cavities (GROSENBAUGH 1952, NOEKE 1989, 1990). But so far this method is more frequently applied in forestry while not well-known by biologist.

The cavity abundance in a stand is also strongly influenced by tree density, age of trees and tree species composition (VAN BALEN et al. 1982), which further made the comparisons among different study sites obscure. The most comparable study to the present one was conducted in boreal forests in Sweden (SANDSTRÖM 1992). The Swedish forests were composed of tree species closely related to those in the taiga of West Khentey. SANDSTRÖM (1992) reported 41.0 (2 – 72) cavities/ha in the natural stands. One possible reason for the higher value in Sweden than in Mongolia was the absence of cavity-rich oaks in the latter. Oak was the main deciduous tree species in

Table 5.1   Cavity density estimates (/ha) in the literature.

Cavity density (/ha)	Forest type	Natural/Managed	Location	References
Conifer dominated stands				
1 – 1.5	Spruce-pine-beech	Managed	Würzburg, Germany	KNEITZ (1961)
1 – 3	Pine-fir, pine-sage	-	Sierra Nevada, USA	RAPHAEL & WHITE (1984)
8.7 (0 – 16)	Spruce-pine	Managed	Ulleråkers Häradsallmänning, Sweden	SANDSTRÖM (1992)[1]
18.1	Spruce-fir	Natural	West Khentey, Mongolia	This study
28.5 (2 – 72)	Spruce, pine	Natural	Fiby and Ola skifte, Sweden	SANDSTRÖM (1992)[1]
Deciduous dominated and mixed stands				
1.1 (0.2 – 2.1)	Honey mesquite, cottonwood	-	Arizona, USA	BRUSH (1983)
4.1 (3.4 – 4.8)	Oak-pine woodland	Unmanaged; grazed	Sierra Nevada, USA	WATERS et al. (1990)[2]
4.2	Cottonwood-willow	-	Colorado, USA	SEDGWICK & KNOPF (1986)[3]
6.2	Mixed (beech-oak-spruce)	Plantations	Arnhem, Holland	VAN BALEN et al. (1982)[4]
7.6	Beech, beech-oak	Managed	Germany	NOEKE (1990)
15.2 (8 – 40)	Beech, mixed, spruce-pine, pine	Managed	Sweden	SANDSTRÖM (1992)[1]
15.5	Birch-ash-alder	Unmanaged for many years	Brecknockshire, UK	EDINGTON & EDINGTON (1972)
19 (9.4 – 30.0)	Beech-oak	Old plantations bordering roads	Arnhem, Holland	VAN BALEN et al. (1982)[4]
21.0	Beech, beech-oak	Natural	Germany	NOEKE (1990)
33.4 (24 – 39)	Birch-larch, birch-pine-poplar	Natural	West Khentey, Mongolia	This study
41.0 (2 – 72)	Deciduous, mixed spruce, spruce-pine	Natural	Sweden	SANDSTRÖM (1992)[1]
52.5 (13 – 92)	Beech-oak	-	Wienerwald, Austria	SACHSLEHNER (1992)
60.4	Oak-maple-lime	Natural	Andersby, Sweden	CARLSON et al. (1998)[5]

[1] Cavity opening diameter at least 25 mm; bottom area at least 22 cm^2; smallest diameter inside the cavity at least 40 mm.

[2] Cavity opening diameter 2.5 – 15 cm; depth 15 – 50 cm.

[3] Cavity opening diameter 3 – 12 cm.

[4] Bottom area at least 25 cm^2; smallest diameter inside at least 4 cm; distance bottom-top at least 10 cm; cavity opening diameter at least 23 mm (if circular), or a width at least 18 mm (if slit like); entrance not so large that the nest is exposed; closed at bottom; without substantial amount of water in the cavity.

[5] Cavity opening diameter at least 25 mm (if circular), or a width at least 18 mm (if slit like); bottom area at least 22 cm^2; smallest diameter inside at least 40 mm.

Table 5.2 **Mean DBH, proportion of dead stems and cavity holding rate of conspecific or congeneric trees in the boreal forest of Mongolia (this study) and Sweden (SANDSTRÖM 1992). For comparison, analysis was confined to trees of DBH = 10 cm.**

Tree species	Location	Mean DBH (cm)	Proportion of dead stems (%)	Cavity holding rate (%)
Populus spp.	Mongolia	37.8	42	34
	Sweden	34.2	20	30
Betula spp.	Mongolia	18.8	13	5
	Sweden	23.6	16	9
Pinus sylvestris	Mongolia	23.8	4	1
	Sweden	23.9	8	2
Picea spp.	Mongolia	18.4	10	0
	Sweden	22.9	4	0.5

several stands of the Swedish study, and the reported cavity holding rate of oak was 18%, which was higher than that of birch (5%), the main deciduous species in West Khentey. Comparing conspecific or congeneric trees of these two sites, tree DBH and proportion of dead trees were correspondent (Table 5.2). And the cavity holding rates of these related species were strikingly similar (Sweden in brackets): 34% (30%) in *Populus spp.*, 5% (9%) in *Betula spp.*, 1% (2%) in *Pinus sylvestris* and 0% (0.5%) in *Picea spp.* In the Swedish study, the inner dimension of cavities was measured, and only cavities considered suitable for CNBs were registered. Thus the cavity abundance reported in the present study could be considered as reasonable estimates of available resources for CNBs. And the cavity holding rates could be taken as reference values of the corresponding genus/species in boreal Eurasia.

5.1.2 Cavity abundance vs. forest type and management

Cavity density in the spruce-fir forest (18 cavities/ha) was lower than that in the three deciduous stands (24 – 39 cavities/ha). Lower cavities densities in coniferous forests than in deciduous ones has been documented in several studies (KNEITZ 1961, SANDSTRÖM 1992, NEWTON 1994). In the literature, the cavity density reported in conifer dominated stands ranged from 1 to 28.5 cavities/ha (Table 5.1). This variance was to a certain extent due to the proportion and the species of deciduous trees in mixture with the conifers. In the spruce-fir forest of West Khentey, the relatively higher density resulted from the presence of scattered birch. An extreme value of 72

cavities/ha was reported in one stand of Sweden (SANDSTRÖM 1992). In this riverine forest, cavity-rich aspen interspersed among spruce and accounted for most of the cavities.

In deciduous dominated stands, cavity abundance varied greatly in the literature, ranging from 1 to 60 cavities/ha (Table 5.1). Some lowest values arose from special site conditions. WATERS et al. (1990) counted 4.1 cavities/ha in oak-pine woodlands with very low tree density (54 stems/ha). SEDGWICK & KNOPF (1986) studied in a cottonwood-willow stand with even sparser trees (23.9 stems/ha), and reported 4.2 cavities/ha. The lowest density (1.1 cavities/ha) was registered by BRUSH (1983) in honey mesquite and cottonwood deltas, of which detailed habitat information was not given. But honey mesquite usually forms sparse large trees or dense shrubs (ANSLEY et al. 1997). Thus data from these studies should not directly be compared with the results of studies conducted in forests.

Another important factor of cavity abundance is the naturalness of the stand (NOEKE 1989, 1990, SANDSTRÖM 1992, NEWTON 1994). Higher densities were mainly recorded in natural forests (Table 5.1). Excluding the sparse study sites described above, cavity abundance was 15 – 60 cavities/ha in natural stands, and 1 – 19 cavities/ha in managed sites. Attention should be paid to the high value (19 cavities/ha) in the plantation reported by VAN BALEN et al. (1982). This sample was based on old deciduous trees bordering the roads. Such tree rows situated in areas otherwise unsuitable for nesting could have higher woodpecker hole density than large uniform area with suitable trees. And in some sites along major roads, the decline of tree condition due to car traffic caused higher cavity holding rate. Thus the linear areas were not representative of forest areas with the same composition (VAN BALEN et al. 1982). The highest cavity density (40 cavities/ha) in the managed forest was documented in one area in Sweden. The author noted that the data were collected from patches difficult to access for forest machines because of the terrain, thus many large deciduous trees were left (SANDSTRÖM 1992).

KNEITZ (1961) concluded that the density of cavity trees was 1 – 1.5 trees/ha in coniferous stands, 5 – 6 trees/ha in mixed stands, and 7 – 10 trees/ha in deciduous dominated stands. This was, however, the picture in managed forests in Germany. WESOLOWSKI (1989) summarised that the cavity density reported in most European

deciduous stands was 5 – 17 cavities/ha, and should be higher in Bialowieza primeval forest. The present study suggested that in primeval boreal forest, 20 – 40 cavities/ha could be considered as a common value in deciduous stands. In coniferous stands with more than 10% of deciduous components, cavity abundance could also well above 10 cavities/ha. In natural old-growth forest containing large snags, MCCOMB & NOBLE (1981) proposed cavity density might exceed 40 cavities/ha.

5.1.3   Abundance of each cavity type

The figures above referred to the total amount of cavities. Taking cavity type into consideration, the abundance of woodpecker holes in the literature ranged from 2.1 to 14.4 cavities/ha (SCHIERMANN 1934, KNEITZ 1961, PRILL 1987, HARESTAD & KEISKER 1989, NOEKE 1990, WATERS et al. 1990, SANDSTRÖM 1992, DOBKIN et al. 1995, CARLSON et al. 1998, HART & HART 2001). The mean density of woodpecker holes in West Khentey was about 4 cavities/ha, which was not high compared to the documented values. Highest abundance of woodpecker holes was found in the riparian forest (10.3 cavities/ha). DOBKIN et al. (1995) reported 7.7 woodpecker cavities/ha as an average in riparian and snowpocket aspen woodland, and HART & HART (2001) recorded 14.1 cavities/ha in riverine aspen stands. The highest woodpecker hole density also occurred in the riverine stand among the diverse forest types studied by SANDSTRÖM (1992).

KNEITZ (1961) suggested lower abundance of woodpecker holes in coniferous forests than in deciduous ones. This could not be confirmed by the present study, since woodpecker hole density in the spruce-fir forest was similar to that in birch-larch forests. This could be partly due to the limitation of small sample size. Another reason might be that in the spruce-fir forest studied, there were enough large larches and Scots pines which supplied suitable nest sites for woodpeckers. In the study of SANDSTRÖM (1992), abundance of woodpecker holes was also not lower in coniferous stands.

The mean density of branch holes in West Khentey was approximately 16 cavities/ha, one of the highest among the documented values 1.3 – 32 cavities/ha (NOEKE 1990, WATERS et al. 1990, SANDSTRÖM 1992, CARLSON et al. 1998). The forest in West Khentey was not composed of especially large trees compared to most European or

American study sites. The possible reasons for the branch hole abundance were the frequent forest fire and extreme climate conditions in the study area. Fire may create openings in trees which initiate cavity formation or form cavities directly (MCCAW 1983, GIBBONS et al. 2002; see also Section 5.2.4). In forests at high latitudes, heavy snow leading to limb breakage may also initiate cavity formation (LOWNEY & HILL 1989). In areas where temperature fluctuations are extreme, which is characteristic in West Khentey, another powerful mechanism of creating cavities is frost crack (Fig. 5.1). The great tension between the frozen outer layers and unfrozen inner layers of wood may lead to the sudden break of wood at a previous wound. When warmer temperatures arrive, the frozen tissues thaw and absorb more water, and the crack closes. However, the heartwood tissues at the crack zone never seal completely, providing the entrance for decay fungi deep into the tree (PIRONE et al. 1988, MARKOVETS 2003).

Fig. 5.1   A nest cavity of *P. ater* formed through frost crack.

5.1.4 Cavity abundance and habitat-level variables

The density of woodpecker holes was positively correlated to shrub coverage of the stand. There could be at least two possible explanations for such a relationship. One is, the higher coverage of shrubs indicates food-rich habitats and profitable nest sites for woodpeckers. In the study area, high shrub coverage and high woodpecker hole density co-occurred in the riparian forest. The periodical flooding in the riparian forest results in nutrient-rich soils, while at the same time such anaerobic condition suppresses the development of dense tree canopy. The fertile soil and sufficient light provide optimum environment for shrub layer development. Riparian forests are usually composed of fine mosaics of different tree and shrub species, due to various soil condition and water level at a relative fine scale. The high structural diversity and species diversity of vegetation form abundant food resources for animals (HUBBARD 1977, BRINSON et al. 1981, MALANSON 1993). Invertebrate communities are usually diverse and abundant in riparian forests, which then support plentiful insectivorous birds (IWATA et al. 2003, ROMANUK & LEVINGS 2003). HOGSTAD & STENBERG (1994) suggested that food resources might be the most important factor of the habitat choice of woodpeckers. Thus riparian forests have been reported as important habitats for many woodpecker species (BLUME 1961, AULÉN 1988, SPITZNAGEL 1990, ANTHONY et al. 1996).

The correlation between shrub coverage and woodpecker hole density could also be explained by simply coincidence. Riparian forests are typically small or linear patches at the alluvial side of rivers. In the study area, they were mostly isolated woodlands surrounded by meadows or bushes, which were unsuitable for woodpeckers nesting but provide food. Thus the density of woodpecker holes might be higher in such linear patches than in large homogeneous areas of similar structure. This was similar to that VAN BALEN et al. (1982) found high woodpecker hole density in tree rows bordering roads. Another suggestion is that the inner condition of trees in riparian areas supports rapid fungal development, and is thus more suitable for cavity excavation (JACKSON & JACKSON 2004). All above explanations may play some roles in the higher woodpecker hole density in the riparian forest.

The abundance of branch holes and non-excavated cavities pooled were positively correlated to the proportion of fire-scarred stems in the stand. Fire is known to cause

tree wounds which initiate cavity formation (McCaw 1983; see also Section 5.2.4). No significant correlation was found between cavity abundance and the proportion of deciduous stems, the proportion of large trees or the proportion of dead trees in the stand. As shown in Section 4.3, these variables (if a tree is deciduous, tree DBH and tree condition) are important factors of cavity occurrence at single tree level. At habitat level, however, these factors interact and the individual effect is blurred. The proportions of deciduous stems were similar in the young birch-larch forest, the mature birch-larch forest and the riparian forest. However, the impact of fire in the young birch-larch forest and the abundance of cavity-rich poplars in the riparian forest caused higher cavity density in these two habitats. Sandström (1992) also didn't find significant correlation between cavity density and the proportion of deciduous stems. At single tree level, cavities are more frequent in larger trees. However, the young birch-larch forest, which was composed of relatively less large trees, had abundant cavities due to fire. Sandström (1992) reported positive correlation between cavity abundance and density of dying and dead wood (including dying stems, snags, stumps and old windthrows). In the present study, the proportion of dead trees was higher in the spruce-fir forest than in the mature birch-larch forest and the riparian forest. However, the dead stems in the spruce-fir forest were mostly young conifers and didn't contribute to cavity abundance.

In managed forests, the role of one single factor to cavity abundance might be more easily revealed, due to the control of other variables: fires are usually suppressed, dying and dead trees are largely removed, and stands are often even-aged and comprised of single or few species. In natural forests, however, cavity abundance is the outcome co-acted by diverse factors, the combination of which resulted from various stand condition and history. Thus it is difficult to be derived from single habitat-level variable. The multifactor consideration with a large amount of data is necessary for understanding the natural patterns.

5.1.5   Cavity abundance and succession

The abundance of woodpecker holes was negatively correlated with the first principal component of environment variables, i.e. the gradient from riparian forest to mountain taiga. The higher woodpecker hole abundance in the riparian forest has been

discussed in the previous section, as the consequence of rich habitat and/or isolated suitable patch.

The abundance of non-excavated cavities was negatively correlated with the gradient from light taiga to dark taiga. Concerning cavity abundance and natural forest succession, NEWTON (1994) suggested two hypothetical models. Fig. 5.2(a) illustrates the condition under the long-term absence of fire or other catastrophes. In the beginning period of stand establishment, cavities are absent since trees are too young for decay to process and too thin for woodpeckers to excavate. Cavity numbers increase progressively as large trees age and die, and then stabilise as large tree mortality rates stabilise. At equilibrium, the annual additions of new cavities (arising mainly through decay and woodpecker activities) approximately match the annual losses (mainly through branch and tree fall). In Fig. 5.2(b), many large trees are periodically killed by fire, and then progressively fall over several decades as new forest develops around them. Years later, another fire sweeps through and the process
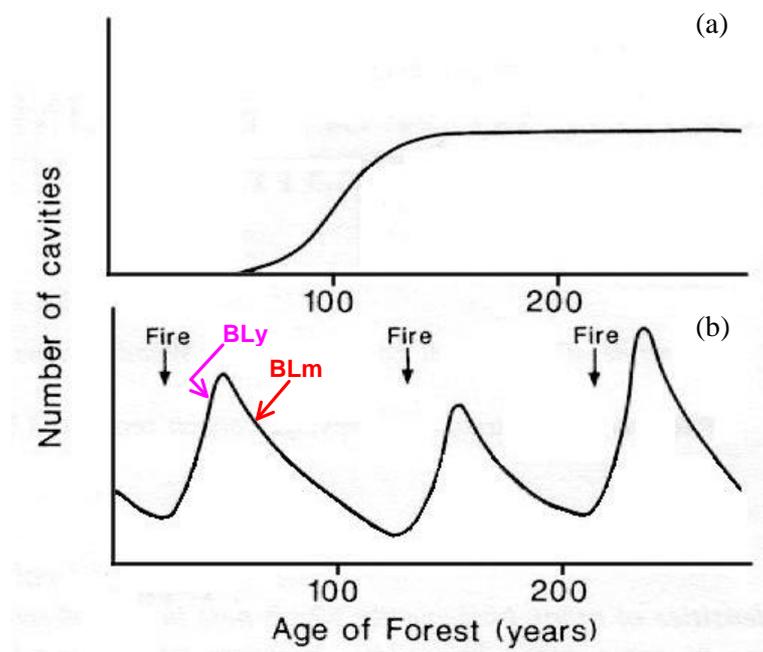

Fig. 5.2 **Hypothetical models of the changing numbers of cavities during natural forest succession: (a) from establishment to maturity in the absence of fire or other catastrophes; and (b) an established forest under the influence of periodic fires. The time scale is set roughly for forest in north temperate regions, but would vary with tree species (modified from NEWTON 1994).**

is repeated. In each cycle, cavity numbers reach a peak some years after fire, as dead standing trees rot, and then decline as these trees fall. The exact pattern depends on the proportion of trees killed by each fire, and on the intervals between successive fires. If fires are too frequent, they prevent any trees from being big enough to provide usable cavities (NEWTON 1994).

In West Khentey, the birch-larch stands, the forests under the influence of periodic fires, may fit to the second model. In the young birch-larch forest of the present study, the cavity density might be close to its peak value. Without measuring the annual addition and loss, it is not clear whether the cavity density is in its increasing or declining phase. In the mature birch-larch forest, many trees scarred by the last fire already fell and new generation develops, thus the cavity density might be in the declining stage (Fig. 5.2(b)).

However, the spruce-fir forest, which represents a condition under the long-term absence of fire, does not fit to the first model. In NEWTON's model, the change of tree species composition during succession, which is the case of the majority of natural successions, is not taken into consideration. Thus here a modified model for boreal Eurasia is proposed (Fig. 5.3). In the beginning period of stand establishment, the
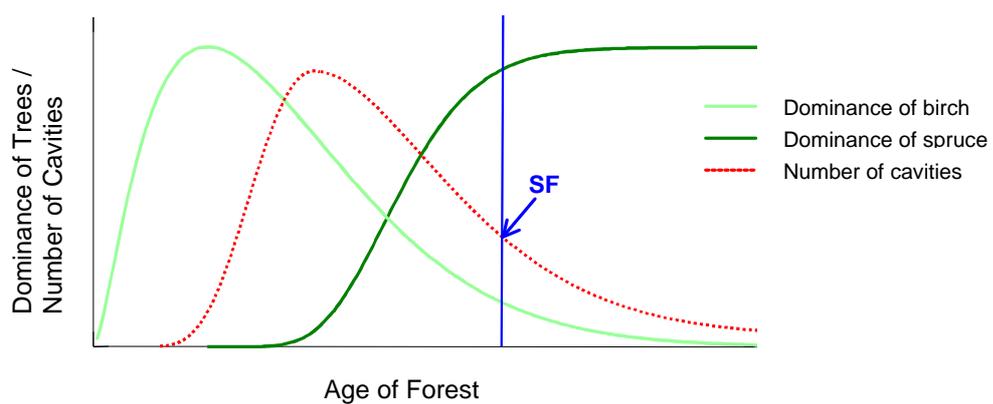

Fig. 5.3   Hypothetical model of the changing numbers of tree species and cavities during natural forest succession. The blue line indicates the approximate stage of the spruce-fir forest in this study (composed of about 13% birch trees), and the arrow marks the theoretical cavity abundance of this stage.

pioneer species, birch, develops. Cavity numbers increase as birches age, weaken and die. The shade-tolerant spruce gradually takes over the forest as succession proceeds. The regeneration of birch cannot recruit the fall of old birch trees, and the spruce is less rich in cavities, thus cavity abundance decreases. In the climax forest, cavities are held by spruce and the scattered birch trees regenerating at forest gaps caused by windthrows. The equilibrium is reached when cavity additions match cavity losses in both spruce and birch parts, with a slower turnover rate in the former and a more rapid turnover in the latter.

5.2   Factors Influencing Cavity Formation in a Tree

5.2.1   Tree species

Deciduous trees are in general more cavity-rich than conifers, corresponding to other studies (VAN BALEN et al. 1982, WATERS et al. 1990, SANDSTRÖM 1992, CARLSON et al. 1998). The most common way decay fungi invading a tree's heartwood is through wounds left by fallen limbs. When a limb of a deciduous tree falls, a protective layer of gum-filled cells develops at the base of the limb. This layer is limited to the sapwood (the living wood tissue), rounding the edges of the wound, leaving the heartwood unprotected from invasion by insects and decay fungi. Conifers develop a protective zone of resin at the base of dead limbs. This resin is not limited to the sapwood but also spreads to the heartwood, providing a greater protection against decay fungi (PEACE 1962, SHIGO & MARX 1977). Thus cavities are more likely to develop in deciduous trees.

Among the deciduous species in this study, poplar has the highest cavity holding rate. *Populus* species (including aspen, poplar and cottonwood) are especially prone to attack by heartrot fungi (HIRATSUKA & LOMAN 1984; PIRONE et al. 1988), and the high cavity occurrence in *Populus* has been frequently documented (CARLSON et al. 1998, MARTIN & EADIE 1999, HART & HART 2001). Birch is the most important cavity tree in West Khentey, holding over 50% of total cavities. It has high cavity holding rate and is common in diverse habitats. Birch accounts for bulk of the cavities in birch-larch forests and plays the subordinate part in the riparian forest. But the most critical role it plays might be in the spruce-fir forest. In a climax coniferous

forest with a slight admixture of deciduous trees, most cavities are located in deciduous trees (HAAPANEN 1965). In the natural boreal forests of Mongolia, it is mainly birch that establishes itself in the gaps of coniferous stands with its very light seeds well capable for dispersal. The distribution of birch (*Betula spp.*) covers most of Scandinavia, the north and middle of Asia and America, and reaches as northward as to the tree line (JALAS & SUOMINEN 1972, SANDSTRÖM 1992, HORA 1993, FARRAR 1995). Birch might be an important cavity tree species in boreal forests in general.

Excavated cavities are also associated with wood decay, because excavators usually prefer to excavate in parts of tree where the wood has been softened by decay (CONNER et al. 1976, HART & HART 2001). Thus excavated and non-excavated cavities are generally similar in their occurrence in tree species. In Sweden, cavities found in aspen were mainly woodpecker holes (SANDSTRÖM 1992). While in West Khentey, non-excavated cavities were frequent in poplar as well. The only difference found is that non-excavated cavities were relatively more frequent in birch and less frequent in larch than excavated ones. This might be related to frost crack, a cavity forming mechanism which may occur in trees without remarkable proceeding of decay and is more common in trees of thin bark (PIRONE et al. 1988). Another reason might be that larch can develop to the size that birch seldom reaches, which allows larger-sized excavators to place their nests.

5.2.2   Tree DBH

Cavity occurrence increases notably with tree DBH. Such association has been well documented (KNEITZ 1961, VAN BALEN et al. 1982, SEDGWICK & KNOPF 1986, NOEKE 1990, SANDSTRÖM 1992, LINDENMAYER et al. 1993, PARKS et al. 1999, GIBBONS et al. 2000, LEHMKUHL et al. 2003). Cavity formation is partly a deterministic process, because trees are predisposed to form cavities as they age, subsequently weaken and senesce. Cavity formation can also be generated by stochastic process (e.g. fire), and therefore cavities can also develop in young trees. However, older trees are more likely to have been exposed to more of such events (GIBBONS et al. 2002). In areas without considerable difference in soil condition, trunk circumference could probably be used as a measure of age (VAN BALEN et al. 1982), thus cavity occurrence increases with tree DBH. In West Khentey, 68% of the cavities were located in trees of DBH >

30 cm. While in Swedish boreal forest, a very similar value 67% was reported (SANDSTRÖM 1992).

For trees of DBH under 30 cm, cavity holding rate is generally low and does not differ significantly between tree species, though birch seems to acquire cavities more often than others at the DBH class 15 – 30 cm. When tree DBH is above 30 cm, the cavity holding rate starts to differentiate among tree species. The cavity holding rate of deciduous trees (poplar and birch) rises remarkably, over the conifers. Birch, when looking each DBH class separately, has cavity holding rate approaching that of poplar. But birch seldom develops to the size which poplar can do, thus the overall cavity holding rate of birch is much lower than that of poplar. It should also be noticed that the relationship between DBH and tree age differs from species to species. *Populus* species are characteristic in their fast growing (PIRONE et al. 1988, HORA 1993). In European managed stands, a 20-year-old *Populus* may reach mean diameter of about 30 cm, while a *Betula* tree of similar size would be already around 80 years old. *Larix* and *Pinus sylvestris* have growth rate approaching or slower than *Betula*, depending on site conditions (SCHOBER 1995). Thus *Populus* can hold cavities at much younger stage than other species, and is much richer in cavities than other species of the same age. In fact, such rapid growth might be related to the characteristic porous, light and soft wood of *Populus*, which leads to more frequent cavity formation.

Due to different site condition and stand history, the DBH distribution of cavity trees differed in different habitats. In the young birch-larch forest, more young trees acquired cavities because of fire. In the riparian forest, many cavities were located in large poplars. While in the spruce-fir forest, cavities occurred either in young birches or in old larches. A cavity in a young living tree could be expected to exist longer, with gradually changing size and shape following the tree's growing up, and might be utilised by different CNBs for following decades. However, if decay proceeds too rapid in a small tree, wind or snow may lead to tree fall at an early stage and cause cavity loss (PARKS et al. 1999). Larger trees remain standing longer even after their death, and can keep cavity stock for longer term (MORRISON & RAPHAEL 1993). Thus DBH distribution of cavity trees in a habitat would influence future cavity availability.

It might also influence the performance of some CNBs that have preference for certain nest tree size (see Section 5.5.2).

5.2.3   Tree condition

Living trees in state of decline have higher cavity holding rate than healthy living trees. A tree of weak physiological condition has a reduced capacity to occlude wounds, and, reciprocally, the invasion of decaying organisms further weaken the tree (GIBBONS et al. 2000). It is well understandable that dead trees have more cavities than living ones, since cavity development proceeds and the number of cavities accumulates, though occasionally there might be loss due to the fall of tree parts containing cavities. Living trees in state of decline (class 2) had higher cavity holding rate than intact dead trees (class 3 and 4). Because most of the trees in the former class already had a broken top and would be grouped into broken tall snags (class 5) as soon as they die.

Occurrence of cavities is in close association with broken top. A broken top not only exposes the heartwood to the invasion of decay organisms, but also often accumulates rain water which further promotes decomposition process (LEHMKUHL et al. 2003). Excavated cavities are relatively even more frequent in tall broken snags than non-excavated ones. MCCLELLAND et al. (1979) suggested that a broken top might be an obvious cue for excavators indicating decayed heartwood in combination with firm sapwood shell.

Due to fire, the living trees in the young birch-larch forest held cavities more frequently than those in other habitats. Cavities in living trees might be valuable, since the expectance of the time they remaining in the forest, and thus usable for CNBs, is longer than those in dead trees. Living trees can isolate fungi-infected sapwood, a process called compartmentalisation. The isolation includes both physical barriers, such as blocking xylem vessels with gum and other tree products, and chemical barriers, such as tannins and phenols (JACKSON & JACKSON 2004). Therefore, though cavity formation progresses very slowly in living trees, a usable cavity in a living tree is long lasting, while cavities in dead tree undergo rapid decay and are prone to loss due to tree or limb fall. But for some tree species with strong compartmentalisation ability, cavities in living trees could also loss due to the sealing

of cavity openings by sapwood growth (SEDGWICK & KNOPF 1991, WESOLOWSKI 1995b). The constitution of cavity tree condition is thus important for cavity dynamics. It might also influence the breeding performance of CNBs since different bird species have different preference for nest tree condition (see Section 5.5.2).

5.2.4   Fire

In West Khentey, about 76% of the cavities were located in trees with fire scars. For the main cavity tree species, fire-scarred trees acquired cavities three to four times more often than those without fire scars. Fire may directly excavate cavities in trees. This often leads to special cavity types which could be utilised by CNBs or other animals. But more often fire causes tree wounds and predisposes trees to the invasion of fungi and termites. Trees with physiological conditions weakened by fire also have reduced recovering capacity against the invasion of decay-causing organisms (MCCAW 1983, GIBBONS et al. 2002, HUNTER & MAZUREK 2003).

Though fire may increase cavity occurrence significantly and allow cavity formation in younger trees, heavily wounded trees might stand only few years in the forest (PARKS et al. 1999, WHITE & SEGINAK 2000, LEHMKUHL et al. 2003). The intensity and type of fire, as well as the pre-burned forest structure, have to be taken into consideration to access the influence of fire to cavity availability.

5.2.5   Fungi

Trees with the presence of fungi conks acquire cavities much more often than those without. In West Khentey, conk-bearing trees, which made up only about 5% of the standing stems, accounted for 29% of the cavities. This is not surprising since fungi are the main decay-causing organisms, which lead to the formation of non-excavated cavities and minimise the excavation burdens of excavators. In aspen woodland, DOBKIN et al. (1995) reported that 75% of cavity holding living trees supported visible fungi.

An interesting phenomenon is that excavated cavities are more closely associated with the presence of fungi conks than non-excavated ones. Many studies have reported the preference for conk-bearing trees of excavators, and the explanation is usually the

dependence of excavators on fungi-softened wood (ERSKINE & MCLAREN 1972, CONNER & LOCKE 1982, WINTERNITZ & CAHN 1983, HOOPER et al. 1991, HART & HART 2001). But if the occurrence of non-excavated cavities could to certain extent indicates the process of fungi-caused decay, then the higher association between excavated cavity and fungi conks suggests that wood softness might not be the only factor. Presence of fungal conks may provide excavators with a visual cue of a suitable nest tree (KILHAM 1971, CROCKETT & HADOW 1975). Excavators may sometimes also become a vector for fungi. Both nest excavation and foraging excavation activities provide openings for invasion of microorganisms. Excavators may further infect the sites they excavate with hyphae or spores that adhere to their bills or feathers (JACKSON 1977, FARRIS et al. 2004).

Type of fungi is important in such associations. Wood-decaying fungi are often specific in their use of tree species, tissues, and sites of entrance. Heartwood fungi and sapwood fungi are usually different, and the previous group is typically more important for excavators (JACKSON & JACKSON 2004). Such fungi cause extensive decay of the heartwood while the sapwood remains intact, protecting the nest cavity (HART & HART 2001). The way fungi invading trees also influence the nest site of excavators. Fungi invading trees from the broken top often lead to excavated cavities formed close to the broken top. New cavities in the same snag are usually excavated below the cavity of the previous year, as the fugal decay grows downwards (CONNER et al. 1975). The root fomes *Heterobasidium annosum* invades spruce from root injuries and can develop up to 5 – 6 m. Consequently woodpecker holes are found in lower parts of trees, and successive cavities are often above previous ones due to the upward growth of fungi (WIESNER 2001).

As the result of all above ecological interactions, certain fungi and certain species of excavators could be intimately linked. In America, the red ring rot fungus *Phellinus pini* is closely associated with the cavity trees of the endangered Red-cockaded Woodpeckers *Picoides borealis* (CONNER et al. 1976, CONNER & LOCKE 1982). Several sapsucker species *Sphyrapicus spp*. select aspen with fruit bodies of the aspen bracket fungi *Phellinus tremulae* (CROCKETT & HADOW 1975, WINTERNITZ & CAHN 1983). In West Khentey, a primary inventory on wood-decaying fungi has been conducted, and 37 species were identified (SUNJIDMAA et al. 2003). Excavated

cavities were mainly associated with hoof fungus *Fomes fomentarius* specializing on birch trees (pers. obs.; Fig. 5.4). The detailed species-specific interaction is in need for further study.

Fig. 5.4   A nest cavity of *D. leucotos* in a birch tree bearing the fruit body of hoof fungus *Fomes fomentarius*.

5.2.6   Predictive model of cavity occurrence

Though cavity abundance of a stand was difficult to quantify by habitat-level variables (see Section 5.1.4), cavity occurrence in a tree could be properly predicted by tree-level variables. The logistic regression models developed here not only summarised the relationship between cavity-holding rate and individual tree characters, but also clarified and integrated the multivariate interactions. Such predictive models are useful tool for conservation and management. They provide quantified estimates of a tree's value, in term of supplying cavities, and could be applied to the practice of snag creation and wildlife tree retention (PARKS et al. 1999). Further models about the longevity of cavity trees should also be generated and taken into consideration when framing conservational plans (BULL 1983).

5.3   Composition of CNBs

5.3.1   Species richness of CNBs

The assemblage of CNBs is rich in West Khentey. During the study period of two breeding seasons, nests of 16 CNB species were found in the study sites. Potentially, this area contains at least 31 CNB species, representing 24% of the breeding bird species (WICHMANN & POKROVSKAYA 2004; Appendix). Among which 24 species are obligate cavity nesters. This includes seven species of woodpeckers (Picidae, including Wryneck), which may occur sympatrically and represent all possible woodpecker species existing in the biogeographic region. It has been suggested that in non-tropical regions of North America and Eurasia, four to five sympatric woodpecker species are typical, while up to eight species may occur at where trees are diverse (SHORT & HORNE 1990). However, the tree species composition in West Khentey is relatively simple.

The total number of 30 CNB species is also one of the highest in the literature. However, comparison is rough since the method differed a lot among studies, and most studies did not consider the entire CNB community. Some studies reported CNB species by conducting census or inventory, while others did through locating nests or identifying traces left in cavities. The definition of CNBs might also differ in including or excluding non-obligatory cavity nesters and/or species nesting in half-cavities or chimneys. Time and spatial scale varied from study to study, and could cause great differences in the number of species found.

In Swedish deciduous forest, 12 CNB species were recorded, including three species of woodpeckers and nine SCNs (CARLSON et al. 1998). In five managed stands in Sweden, 8 CNB species were censused (SANDSTRÖM 1992). Across Norway, seven species of woodpeckers produce cavities used by 21 species of birds and mammals, but not all species live sympatrically (AANDERAA et al. 1996). In German beech forests, eight to ten CNB species were registered (PEITZMEIER 1969, WEISS 1987). In cultural landscape of Netherlands, nests of three PCN and 13 SCN species were found (VAN BALEN et al. 1982). In the primeval temperate forest in Bialowieza, Poland, 25 CNB species were recorded (WESOLOWSKI 1989). In Canadian mixed forest, a rich number of 31 CNB species was reported, including eight species of woodpeckers

(MARTIN et al. 2004). In United States, 20 CNB species were registered in Douglas fir forest (MCCLELLAND et al. 1979), 15 species (6 PCN + 9 SCN) in mixed forest (LI & MARTIN 1991), 12 species in post-fire pine-Douglas fir forest (SAAB et al. 2004), 11 species (5 PCN + 6 SCN) in cottonwood bottomland (SEDGWICK & Knopf 1992), 8 species (3 PCN + 5 SCN) in aspen woodland (LAWLER & EDWARDS JR. 2002), and 8 diurnal SCN species in oak-pine woodland (WATERS et al. 1990). GIBBS et al. (1993) reported that, in New World forests, the number of CNB species increased with decreasing latitude, averaging 33.6 species in tropical and subtropical forests versus 14.8 species in temperate and boreal forests. The number of PCN species was similar between low latitude forests (8.2 species) and high latitude forests (6.0 species).

The mosaic landscape and the naturalness of the study area might contribute to the high CNB species richness. In West Khentey, forest, steppe and shrub form fine natural mosaics. Even inside forests, there are often shrubby or grassy patches due to fire or topography. Dead trees and fire-scarred trees are abundant in natural forests, and are composed of various species, size, height and decay stage. Natural cavities are presented in variable height, inner dimension, opening size and shape. These factors could result in diverse foraging and nesting niches for CNBs, which allow different species to coexist.

5.3.2   CNB density vs. forest type and management

The density of CNBs in the study area averaged 2.4 breeding pairs/ha. This was highest in the riparian forest (3.5 pairs/ha), though the difference to the birch-larch forests (2.6 pairs/ha for both mature and young stands) was not significant. The spruce-fir coniferous forest had lower CNB density (1.0 pair/ha) than the deciduous stands. No apparent fluctuation of CNB density was observed in the study period.

The CNB density in West Khentey corresponded well to the documented values. In Sweden, NILSSON (1979) reported 3.7 territories/ha in natural deciduous forest, and 1.1 territories/ha in managed spruce-pine forest with an admixture of deciduous trees. SANDSTRÖM (1992) found an average of 3.2 pairs/ha in deciduous dominated stands, and 1.1 pairs/ha in conifer dominated ones. In Poland, 2.3 pairs/ha in forest interior and 3.8 pairs/ha at forest edge were reported in Bialowieza (TOMIALOJC et al. 1984). WESOLOWSKI (2002) further documented 3.0 – 3.8 pairs/ha in ash-alder swamp plots,

2.9 – 3.5 pairs/ha in oak-hornbeam plots and 1.3 – 1.4 pairs/ha in coniferous plots. 1.2 pairs/ha was reported in spruce-fir forest in United States (SCOTT et al. 1978).

Coniferous forests generally has lower CNB density than deciduous forests, and the occurrence of deciduous trees in a coniferous forest may be crucial for the abundance of CNBs. In Finland, HAAPANEN (1965) found CNB density in a spruce forest with an admixture of aspen and birch (1.1 pairs/ha) was about twice than in an almost pure spruce stand (0.6 pairs/ha). In United States, both the densities of PCNs and SCNs were higher in pine-oak stands than in pine stands (ROSENSTOCK 1998).

CNB density is usually lower in managed forests. In Finnish pine forests, HAAPANEN (1965) reported 0.4 pairs/ha in natural stands and 0.07 – 0.2 in managed ones. In Sweden, natural forests had, on average, 2.1 – 2.8 times higher density than managed forests (SANDSTRÖM 1992).

Distribution of species abundance is often a more sensitive measure of environmental disturbance than species richness or density alone (MAGURRAN 1988). In natural forests, there are usually not one superior dominant in CNB community (but the high abundance of *F. albicollis* in oak-hornbeam forest in Poland, see WESOLOWSKI et al. 2002). While in managed forests, most of the cavities are usually occupied by one superior dominant species, which, in Europe, is mostly Starling *S. vulgaris* or *P. major*. Nest boxes usually represent an impoverished assemblage. Different species response differently to the addition of nest boxes (BRAWN & BALDA 1988, PURCELL et al. 1997). Except the boxes specially designed for target species, *P. major* or the Pied Flycatcher *Ficedula hypoleuca* usually becomes the superior box nester in most part of Europe (PERRINS 1979, VAN BALEN et al. 1982, CZESZCZEWIK 2004).

5.3.3   CNB abundance and habitat-level variables

In West Khentey, proportion of deciduous trees and shrub coverage were related to the CNB density of a stand. Both PCN and SCN density and number of CNB species were positively correlated with the abundance of deciduous trees. Positive correlation between CNB density and proportion of deciduous trees was also found in Swedish forests (SANDSTRÖM 1992). Deciduous trees hold cavities much more frequent than conifers (see Section 5.2.1). Deciduous trees usually support more invertebrate food

than conifers do (HUHTA et al. 1998). Solitary deciduous trees growing in coniferous forests may increase the species richness of invertebrates by several magnitudes (SANDSTRÖM 1992). Thus deciduous trees are important for CNBs in satisfying both their nesting and foraging needs. This is in accordance with the higher CNB density in deciduous forests and the importance of deciduous trees in coniferous forests to CNB density described in previous section. This also partly explained the lower CNB density in managed forests, since deciduous trees are mostly removed in forestry practice.

PCN density and pooled CNB density were positively correlated with shrub coverage. This was in accordance with the higher abundance of woodpecker holes found in stands with higher shrub coverage, mainly the riparian stands in the study area. And this might be resulted from more than one factor, including rich food resources, edge effect, and fungi-feasible tree condition in riparian sites (see Section 5.1.4). Density of shrubs was found to be associated with the abundance of many bird species, including several CNBs (FLACK 1976, BRAWN 1988, HOBSON & BAYNE 2000). The artificial thinning practice in silviculture, which stimulated vigorous shrub growth, was also suggested to be highly beneficial to numerous breeding bird species (SIEGEL & DESANTE 2003). These observations supported the idea that sites with well-developed shrub understories as richer habitats. Several CNB species were found to prefer nesting near forest edges for reduced travelling time to foraging patches, though also some species preferred forest interior (JOHNSSON et al. 1993, DOBKIN et al. 1995, MARTIN et al. 2004). MARTIN & EADIE (1999) reported that the overall CNB abundance showed positive edge effect in a natural fragmented landscape.

No significant correlation was found between CNB density and the proportion of dead trees. In Sweden, SANDSTRÖM (1992) also found no relationship between density of dying and dead wood and abundance of CNBs. While in plots with different intensity of silvicultural snag removal, ZARNOWITZ & MANUWAL (1985) found both CNB species richness and density increased with increasing snag densities. SHOWALTER & WHITMORE (2002) recorded that the trend of CNB abundance over 16 years followed the abundance of snags killed by Gypsy moth *Lymantria dispar*. In three snag density treatments, HAGGARD & GAINES (2001) reported that stands with medium snag density treatment (15 – 35 snags/ha) had the highest abundance, species richness, and

nesting population of CNBs. RAPHAEL & WHITE (1984) found correlations between CNB density and snag density, with most birds in the plots where there were most snags. But beyond a density of about 7 large snags/ha, bird density levelled off. Thus in most part of the West Khentey forests, the snag density might be high enough and did not become the limiting factor of CNB density.

5.3.4   Cavity occupancy – Are cavities limiting?

In the study area, about 5% of the cavities were occupied by SCNs in each year. The documented cavity occupancy varied greatly, from less than 10% to more than 90%. In unmanaged deciduous forest in Sweden, occupancy of 5.3 – 9.1% was reported (CARLSON et al. 1998). SANDSTRÖM (1992) found about 7% of cavities were occupied by CNBs in both natural and managed forests (6.5 – 7.2 in natural, 6.3 – 6.9 in managed). Occupancy of less than 10% was also reported in mixed hardwood stand (McCOMB & NOBLE 1981). Most documented values lay, however, between, 20% and 60%. In United States, cavity occupancy of 21% was reported in birch-ash woodland (EDINGTON & EDINGTON 1972), 28.9 – 45% in pine-oak woodlands (WATERS et al. 1990), and 38.5 – 46% in cottonwood bottomland (SEDGWICK 1997). In parkland with Douglas fir, pine and aspen in Canada, 57% of the cavities were occupied (PETERSON & GAUTHIER 1985). In Germany, cavity occupancy between 32.6 – 44% was found in beech-fir forest (HOHLFELD 1995), and between 50 – 64.1% was documented in pine forest (SCHIERMANN 1934). Some highest values was reported in Netherlands by VAN BALEN et al. (1982), ranged from 54% to 93% in different years and areas. It was argued that the linear tree rows of the study site probably promoted high occupation, in that birds of a large adjacent area concentrated their breeding attempts in the small strip (VAN BALEN et al. 1982).

The cavity occupancy of West Khentey was among the lowest in the literature. The low occupancy of only 5.2% indicated a large proportion of unoccupied holes, and thus cavity availability might not be a limiting factor of the breeding density of SCNs. The presence of unoccupied cavities has been frequently used as the argument that cavities are not limiting (e.g. EDINGTON & EDINGTON 1972, PETERSON & GAUTHIER 1985, RENDELL & ROBERTSON 1989). However, the inner dimension of cavities was not measured in the present study, and many might be unsuitable or unavailable for SCNs. Some cavities identified from ground might have chambers too shallow or too

narrow to contain a nest. Some cavities might contain rain water at the bottom, have heavy parasite load, or be filled by nesting materials from previous breeding attempts. The acquisition to cavities might also be limited due to the territoriality of birds or the occupation by insects or mammals. Thus the actual availability of nest cavities is often less than the apparent availability, determined simply by counting (NEWTON 1994).

Therefore, the possibility cavity availability as the limiting factor was also discussed through other approaches. First, SCN density was not significantly correlated with cavity abundance in the study area. Positive associations between relative abundance of CNBs and numbers of cavities were reported in some studies regarding natural nest sites (RAPHAEL & WHITE 1983, DOBKIN et al. 1995). Other numerous evidences of positive correlation between SCN density and nest-site availability was mainly based on artificially providing nest boxes. The addition of nest boxes usually resulted in the increase of breeding population of target species (e.g. VON HAARTMAN 1957, ENEMAR & SJÖSTRAND 1972, BRUSH 1983, BRAWN & BALDA 1988, TÖRÖK & TOTH 1988, JÄRVINEN 1989, GUSTAFSSON 1998). However, most of these studies were conducted in forests where previous long-term management might have impoverished the stock of cavities and led to the shortage of nest sites. BRAWN & BALDA (1988) found that CNB density increased after the addition of nest boxes in two plots with intermediate numbers or few natural cavities, bur remained unchanged in the plot with abundant natural cavities. The installation of nest boxes in Bialowieza National Park also caused no increase in Paridae density (WALANKIEWICZ 1991). Nest boxes are often less vulnerable to predation and give rise to higher breeding success (NILSSON 1984a, 1984b). Most western European forest forests contain a lower diversity of predator species, and near human settlement bird food is often provided in winter (TOMIALOJC et al. 1984, WESOLOWSKI et al. 1987). Thus the nest box population may be unnaturally high, due to the release of certain limiting agents which might come into play under natural conditions.

Second, if assuming the proportion of unsuitable cavities was similar among habitats, some clues could be drawn through the comparison of cavity occupancy. Between the mature and young birch-larch forests, which had similar forest composition, the latter possessed more cavities than the former, but the density of SCNs was identical in both

habitats, which resulted in a lower occupancy in the latter. Thus there might be other factors limiting bird populations in the young birch-larch forest. On the other hand, if cavity availability was the limiting factor of SCN density, competition should be the strongest in the spruce-fir forest, where cavities were most scarce. Yet the occupancy in this habitat was the lowest, suggesting that other factors suppressed the bird density.

Third, in comparison with other studies conducted in unmanaged forests, the occupancy in the study area was in accordance to that of Swedish natural forest (5.3 – 9.1%), in which the inner dimensions of all cavities were measured, and more than 50% of them were considered as suitable for nesting (CARLSON et al. 1998). Studies in Bialowieza also suggested that cavity availability was not the limiting factor of SCN density in primeval forest (WESOLOWSKI 1989, WALANKIEWICZ 1991).

Predation, food supply and weather conditions are other possible alternative factors limiting CNB populations. Though tree cavities are usually considered as a safer nesting site than open ones, it is not always safe (NILSSON 1986, MØLLER 1989, MARTIN & LI 1992, MARTIN & CLOBERT 1996, WALANKIEWICZ 2002a, 2002b). Nest predation was found to be a major factor influencing breeding success of several CNB species, and the predation rate is higher in natural cavities than in nest boxes, in natural forests than in managed ones. In Sweden, the predation by the Pine Marten *Martes martes* was the main cause of nesting failure of the nests established in *Dryocopus martius* holes (JOHNSSON et al. 1993). In Bialowieza, predation led to 56% of the brood loss of the Collared Flycatcher *Ficedula albicollis* (WALANKIEWICZ 1991) and 47% of the Pied Flycatcher *Ficedula hypoleuca* (CZESZCZEWIK 2004). The nest site selection of the Marsh Tit *Parus palustris* was best explained by anti-predator adaptations, which also suggested a strong predation pressure (WESOLOWSKI 2002).

Food abundance may also influence CNB density in areas where natural cavities are abundant (HAAPANEN 1965, WATERS et al. 1990). Winter food availability was suggested to be more important in determining *Parus major* density than nest site availability (NILSSON 1979). The yearly variation of the breeding numbers of *C. familiaris* was positively correlated with the abundance of leaf-eating caterpillars (WESOLOWSKI 1994). Population density of *S. europaea* was positively correlated

with the beech crop in the previous year (ZANG 2003). Winter temperatures were found critical for the survival of *S. europaea* and *P. major* (SLAGSVOLD 1975, NILSSON 1987). The breeding densities of *D. martius*, *D. major* and *D. minor* correlated positively with temperatures of preceding winter in Finland (HAVELKA & RUGE 1993), but in Poland the breeding density of *D. major* was not correlated with temperatures of preceding winter (WESOLOWSKI & TOMIALOJC 1986). In the present study, the fact that CNB density was positively associated with proportion of deciduous trees and shrub coverage might suggest the importance of food availability. And winter climate in West Khentey is extremely harsh. Thus several factors may co-act in limiting CNB density, and different species might be influenced by different factors to different extent.

5.3.5   CNB abundance and succession

The abundance of CNBs decreased along the gradient from riparian forest to mountain taiga. The higher CNB density in riparian sites has been discussed in the previous sections (see Section 5.1.4 and 5.3.3). When considering the mountain taiga alone, both the density and species richness of CNBs were higher in the light taiga and lower in the late successional stage, dark taiga.

Post-fire forests have been documented as important habitats for CNB community (BOCK et al. 1978, RAPHAEL & WHITE 1984, HUTTO 1995, SAAB & DUDLEY 1998, KREISEL & STEIN 1999). Fire-scarred trees supply plenty of nesting substrates for PCNs and cavities for SCNs (see Section 5.2.4). Fire-killed snags are rich in larvae of bark beetles and wood-boring beetles (YANOVSKI & KISELEV 1996, MURPHY & LEHNHAUSEN 1998). Fire also further influences nutrient dynamics, changes the composition and distribution of vegetation, and alters insect community. Vegetation regrowth after wildfire generally results in rapid increases of arthropod populations (BEST 1979). Mammal and reptile nest predators are likely absent or have reduced numbers in large, recently burned forests, possibly allowing for higher reproductive success of CNBs (SAAB & VIERLING 2001). Therefore early post fire habitats provide more nesting and foraging opportunities and a reduced risk of predation.

This is only the approximate pattern, however. The responses of bird community to fire vary with size, severity and type of fire, as well as pre- and post-fire cover types

and landscape context of burns (SAAB & DUDLEY 1998, KOTLIAR et al. 2002). Different bird species may also have different response, due to differences in preferred prey abundance or the preferred decay stage of cavity tree, and thus occur in different post-fire successional stages (JAMES et al. 1997, MURPHY & LEHNHAUSEN 1998, SAAB et al. 2004).

Newton (1994) applied the models of changing numbers of cavities during natural succession (see Section 5.1.5) to explain the role of nest site availability as the limiting factor to CNB density (Fig. 5.5). L indicates the level below which CNBs are limited by shortage of nest sites, and above which they are limited by other factors. In Fig. 5.5(a), which illustrates the trend from stand establishment to maturity in the absence of fire or other catastrophes, in period a-b cavities are absent, b-c increasing, and c-d present in excess. So in period a-b CNBs are absent as breeders, in b-c they are present but limited by nest sites, and in c-d present but limited by other factors
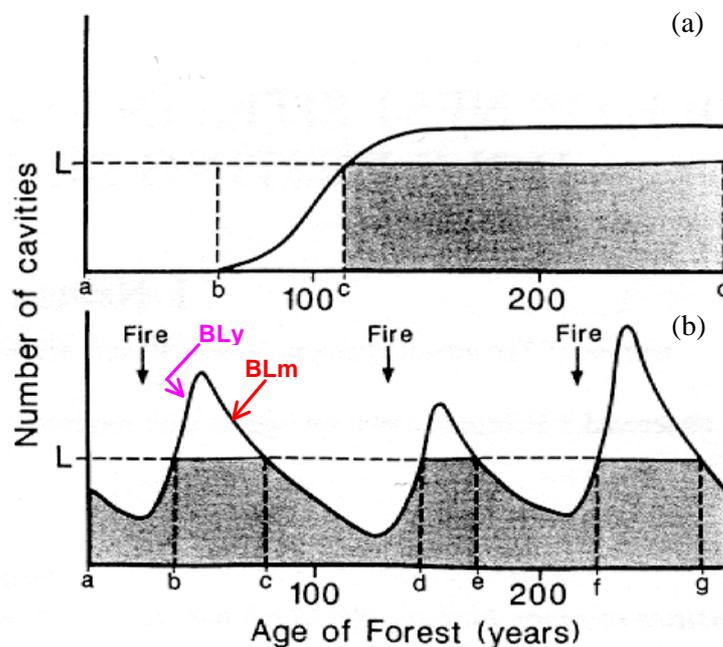
**Fig. 5.5   Hypothetical models of the changing numbers of cavities and cavity-nesting birds during natural forest succession: (a) from establishment to maturity in the absence of fire or other catastrophes; and (b) an established forest under the influence of periodic fires. On the vertical scale, L indicates the level below which cavity-nesting birds are limited by shortage of nest sites, and above which they are limited by other factors (modified from NEWTON 1994).**

below the level that nest sites would permit. Managed forests are usually felled
before stage c, and some even before b, therefore the shortage of nest sites is often
observed. In Fig. 5.5(b), where cavity abundance fluctuates due to periodic fires,
CNBs are limited by nest site availability in periods a-b, c-d and e-f, and by other
factors in periods b-c, d-e and f-g, when cavities are surplus to needs.

The birch-larch forests in the present study may fit to the second model. Cavity
abundance is higher in the young birch-larch forest than in mature one, but is above L
in both stands. CNB abundance is similar in the two habitats, limited by other factors,
and doesn't exploit all available cavities.

For the spruce-fir forest, which represents a stage of the natural succession with
changing tree species composition, the modified model proposed in Section 5.1.5
should be applied. During such type of succession (Fig. 5.6), CNBs might be limited
by cavity availability both in the early phase of stand establishment (period a-b) and
in the late stage of almost pure conifers (period c-d). In period b-c, cavities are
surplus and CNB density is limited by other factors. This model should be further
improved, since during succession with such great change of forest composition, L,
the point at which other limiting factors come into play, is not likely to keep constant
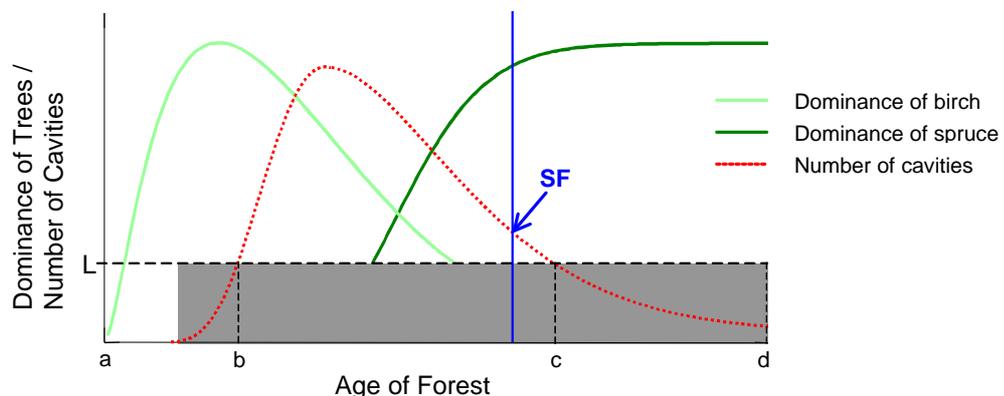
**Fig. 5.6   Hypothetical model of the changing numbers of tree species, cavities and
cavity-nesting birds during natural forest succession. The blue line indicates the
approximate stage of the spruce-fir forest in this study.**

throughout every stage. Coniferous forest might have more limited food supply than deciduous or mixed forest, thus keeps CNBs at a lower density even when cavities are still sufficient, which suggests a lowered L. The exact condition may be dependent on the characteristics of the composition tree species and bird species, as well as specific site conditions. And the detailed information of such systems is still largely unknown.

5.4   Factors influencing Tree and Cavity Use

5.4.1   Tree species

Deciduous trees were used overproportionally by both PCN and SCN, consistent with other studies (VAN BALEN et al. 1982, AULÉN 1988, WESOLOWSKI 1989, STENBERG 1996). PCNs preferred to excavate in decay-feasible deciduous trees, as has been discussed in Section 5.2.1. SCNs, however, did not really have a preference for deciduous trees. The tree species composition of SCN nest trees showed no difference to that of cavity trees, indicating that SCNs were not selective on cavities according to tree species. Thus their overproportional use of certain species simply reflected the higher availability of cavities in these trees. The tree species utilisation of CNBs has been extensively studied, but most studies did not survey the availability of tree species and cavities or did not separated PCNs and SCNs, thus failed to clarify the role of tree species.

WESOLOWSKI (1989) found that, through comparison from two habitats and from the literature, SCNs can utilise totally different tree species, and suggested that tree species was not important factors influencing their nest-site selection. GIBBONS et al. (2002), by identifying animal traces in the cavities in felled trees, found that cavity tree occupancy (including all vertebrate fauna) did not differ significantly between tree species. GUTZWILLER & ANDERSON (1987) and SAAB et al. (2004) also reported tree species was unimportant for cavity occupancy (including both PCNs and SCNs). CARLSON et al. (1998), instead, found cavities in aspen were most frequently used by CNBs. A further examination of this data set showed that SCNs alone still preferred cavities in aspen.

Birch was the most important nest tree species in West Khentey, in that it supported up to two third of CNB nests. Poplar was most extensively used relative to its abundance. Many *Populus* species has been found to be favoured by diverse woodpecker species (AULÉN 1988, HARESTAD & KEISKER 1989, STENBERG 1990, JOHNSSON et al. 1993, CARLSON et al. 1998, AITKEN et al. 2002), as well as important nest tree for CNBs in general (LI & MARTIN 1991, DOBKIN et al. 1995, MARTIN & EADIE 1999).

5.4.2 Tree DBH

Relative to tree abundance, both PCNs and SCNs used large trees overproportionally (DOBKIN et al. 1995). Larger trees, which are usually older, are more often in a weakened stage, at least partly. Large diameter also means higher structural stability of the tree, which may release the risk of tree fall during breeding season. With increasing DBH, the nest cavities can usually be excavated in higher tree positions (WIESNER 2001). Thus large trees were favoured by PCNs. SCNs, however, were not selective on tree DBH. Cavities in trees of different DBH were utilised to a similar extent by SCNs. Thus most of SCN nests were placed in trees of DBH 25 – 50 cm, since large trees were rare and cavities in small trees were few or might be too small.

In Poland, WESOLOWSKI (1989) also found most SCN nests in medium-sized trees (DBH 32 – 47 cm), and suggested this reflecting the cavity availability. In Sweden, CARLSON et al. (1998) reported that tree DBH was unimportant to cavity occupancy (including both PCNs and SCNs). While in Australia, by identifying animal traces in the cavities, a weak positive correlation between cavity occupancy (including all vertebrates) and tree DBH was found (GIBBONS et al. 2002).

SCNs used less small trees than PCNs did in the study area. This partly reflected the rarity of cavities in small trees. Since compared to excavation, formation of non-excavated cavities is a very slow process, and more likely to progress to a usable size in old trees. While excavation can in principal occur in a small tree, as long as the tree is large enough to contain a nest and is in a proper decay stage. However, the difference did not reflect in the tree DBH distribution of excavated and non-excavated cavities (Section 4.3.2). Besides the limited sample size, this might be because most of the excavated cavities in small snags were lost in few years, while those in large

trees still remain. Thus the tree DBH distribution of cavities in stock was different from that of nest cavities in use of a certain year.

5.4.3   Tree condition

Both PCNs and SCNs used dead trees overproportionally. The importance of snags for CNBs has been frequently addressed (MORRISON et al. 1983, SCOTT & OLDEMEYER 1983, PETIT et al. 1985, GIBBS et al. 1993, DOBKIN et al. 1995, HUTTO 1995, BRANDEIS et al. 2002, LAWLER & EDWARDS JR. 2002, MARTIN et al. 2004). And broken snags were considered important for supplying nest sites (SCOTT et al. 1978). However, in the study area, cavities in living trees were preferred by SCNs, while those in broken snags were used underproportionally. In the study of the reuse of *D. major* cavities in German beech and spruce forests, cavities in living trees were found to be occupied more often (GÜNTHER & HELLMANN 1995).

Nesting in living trees has been suggested to have several advantages. Living trees have higher structural stability and are less prone to tree fall. Nests placed in living part of trees suffer less predation (ALBANO 1992, CHRISTMAN & DHONDT 1997, WESOLOWSKI 2002). Larger predators that could not reach the nest through cavity entrance usually destroy the cavity wall, which is less likely to happen when the cavity is surrounded by solid living wood. In the study area, some nests were observed to be lost due to the predation by *Dendrocopos major* or the nest tree falling, and such events happened almost exclusively on snags. Therefore security could be an important advantage of nesting in a living tree. Microclimate inside cavities in living substrates has also been suggested to be more stable. Cavities in decayed substrates reach higher maximum temperatures and have greater daily fluctuations than those in harder wood (WIEBE 2001).

However, for PCNs, excavating in living trees is more energetically costly. Softer wood of a dead tree may allow a larger cavity for a given expenditure. Shorter excavation period means the possibility of earlier breeding and less danger of exposing the excavating adult or nest site. Thus the trade-off may be different among PCN species and study sites, depending on physical excavation ability of the species and environmental conditions. In the study area, about half of the PCN nests were found in living trees. While in the aspen stand in United States, at least 84% of the

cavities were constructed when the tree was alive, since Sapsuckers *Sphyrapicus spp.*
and the Hairy Woodpeckers *Picoides villosus*, which nested almost exclusively in
living trees, were the main PCNs of the area (CROCKETT & HADOW 1975, HART &
HART 2001).

5.4.4   Fire

PCNs used fire-scarred trees overproportionally. This was largely in correspondence
to the tree condition, since trees were often strongly weakened or killed by fire, and
consequently invaded by fungi or other decay organism, giving rise to plenty of
potential nest sites. Fire may also directly induce cavities in trees (Fig. 5.7). SCNs
showed even stronger overproportional use of fire-scarred trees, which accorded with
the abundance of cavities. Thus SCNs were not selective to cavities according to
whether or not the tree was burned. GIBBONS et al. (2002), however, reported that
cavity trees with fire scars were occupied by vertebrates more often in Australia.

**Fig. 5.7   A nest of *T. ruficollis* (left) and a nest of *C. familiaris* (right) located in special
types of cavities induced by fire.**

5.4.5   Fungi

PCNs strongly preferred trees with fungi conks. This was in correspondence to that more excavated cavities were found in conk-bearing trees (Section 4.3.5). The presence of fungi conks not only indicates a tree in decay, but may also be a visual clue of a suitable nest tree for PCNs (KILHAM 1971, CROCKETT & HADOW 1975). The preference for conk-bearing trees of many PCN species has been reported (KILHAM 1971, ERSKINE & MCLAREN 1972, CROCKETT & HADOW 1975, WINTERNITZ & CAHN 1983, HART & HART 2001, WIESNER 2001; see Section 5.2.5 for more detailed discussion). SCNs also used trees with fungi conks overproportionally, to the same extent of cavity occurrence in such trees. Thus SCNs showed no real preference for conk-bearing trees, but simply utilise the trees according to cavity availability.

5.4.6   Cavity type

In the study area, branch hole was the most important cavity type, which supported 71% of SCN nests and was utilised overproportionally. Woodpecker hole was utilised in proportion to its availability, accounting for about 18% of SCN nests. Other bird-induced hole was used underproportionally, which may be partly related to the fact that such cavities occurred mostly in snags.

As woodpecker hole was not preferred and support less than one fifth of the SCNs, the generally accepted doctrine of woodpeckers as keystone species (ANGELSTAM 1990) was not supported by this study (more detailed discussion in Section 5.7.2). Instead, branch hole is a more important resource for SCNs in West Khentey. This utilisation proportion of cavity types is similar to that found in natural forests in Sweden: 65% and 22% of SCN nests in branch holes and woodpecker holes, respectively (CARLSON et al. 1998). Therefore this might to certain extent represent the general pattern in boreal Eurasia, at least in deciduous dominated forests.

5.5   Nest Site selection of Individual Species

5.5.1   Nest site selection of PCN species

Aspen, poplar and birch were important nest tree species for the three PCN species studied. The relative preference for *Populus* species over birch was *D. major*, *D. minor* and *P. montanus* in descending order. *Populus spp.* are susceptible to heartrot, which provides a soft substrate for excavation, while retains a firm sapwood shell, that gives stability for the cavity, and are thus well documented for their importance for woodpeckers (CONNER et al. 1976, WESOLOWSKI & TOMIALOJC 1986, STENBERG 1996, HART & HART 2001). However, the nests of *P. montanus* were rarely found in aspen. This might be partly due to the difference in their territory size and the patchy distribution of aspen in the study area. *D. major* and *D. minor* usually utilised any suitable aspen in their birch-dominated territory, while the small territory of *P. montanus* would limit its acquisition to this scarce resource. The firm sapwood of *Populus* might also cause higher burden to the smaller *D. minor* and *P. montanus*. The high preference for *Populus* of *D. major* could also be related to its larger body size. *Populus* have much larger mean diameter than birch in the study area (Table 5.2), which could support the spacious nest cavity of *D. major*.

All three PCN species studied preferred large trees, and the association to large trees formed again the descending order of *D. major*, *D. minor* and *P. montanus*. Large trees have higher structural stability, and it is possible to nest higher in larger trees. However, suitable large trees might be rare. *D. major* utilised largest trees and never nested in trees of DBH less than 25cm, reflecting its needs of building more spacious cavities because of its larger body size. *P. montanus* used smaller trees than other two species, which might be due to the scarcity of suitable large trees in its small territory.

The same constraints were also reflected in the nest substrate diameter, thus *D. major* excavated in the thickest substrate and *P. montanus* utilised the thinnest. By nesting in thinner part of trees, nests could be placed higher, but there might be a disadvantage of reduced thermal isolation due to thinner walls. Building in thinner substrate may also reduce the effort of excavating through thick bark and cambium. The nests of *P. montanus* were placed in thinner substrates when the nest cavity was

excavated by itself, and in thicker parts when it utilised branch holes. This was partly due to that such cavities usually occurred in older, and thus thicker, part of trees.

Living trees were used underproportionally by all PCNs. *D. major* preferred fresh dead trees overproportional to their availability, which offered a compromise between structural stability and the burden of excavation (STENBERG 1996). As less strong excavators, *D. minor* and *P. montanus* highly preferred broken snags. The condition of nest substrate also revealed the difference of excavating ability. About 40% of *D. major* excavated in living part of trees, with the cost of heavier excavation burden and the benefit of lower predation rate and stable microclimate. *D. minor* excavated only in dead substrates. *P. montanus*, when behaving as an excavator, also used dead substrates exclusively.

The nest cavities of these three PCN species showed no difference in their height above ground. And their nests were in general higher than that of SCNs, which is usually explained as an adaptation against nest predation. Nest predation rate was found to decrease with cavity height (NILSSON 1984b, LI & MARTIN 1991). Higher nests are less likely to be found by predators from ground, and have an increased energy cost for predators to reach them. Higher nests also raise the ability of parents to detect and deter potential predators (MARTIN & LI 1992). But predation might not be the only explanation. Excavating low in a tall snag would largely reduce the structural stability of the tree and lead to a high risk of tree break at the cavity location. The downward decay due to fungi invasion from the broken top may also make excavating close to broken top energetically profitable (JACKSON & JACKSON 2004).

PCNs usually build their cavity opening as small as possible, just fitting to their own body size. This could decrease the detection and access by predators as well as minimise the energy cost of excavation. The opening shape was close to round, which is the most efficient shape. The cavity opening dimensions of *D. major* and *D. minor* had very small intraspecific variances. *P. montanus*, as a less skilful excavator, had less standardised cavity openings, which were usually not perfectly round and had less smooth edge.

In the present study, 16% of *P. montanus* didn't excavate nest cavities by themselves. This option eliminated the burden of excavation and provided the advantages of nesting in living substrates and earlier fledging. However, it might encounter the competition with SCNs, and these usually lower holes could increase the predation risk.

In summary, these three PCN species had some adaptations in common, i.e. cavities high in the tree with opening shape close to round and minimised opening dimension. While they also showed different adaptations in nest tree and nest substrate selection, which were shaped by their different excavation ability, body size and territory size.

5.5.2   Nest site selection of SCN species

S. europaea

In the study area, *S. europaea* showed highest preference for woodpecker holes compared to other SCN species, and utilised this resource overproportionally (Fig. 5.8). More than 80% of *S. europaea* nests were established in woodpecker holes. In Bialowieza National Park, Poland, *S. europaea* also showed relative preference for woodpecker holes, but the reported using rate was much lower than in this study, 32.8% in ash-alder stands and 41.4 % in oak-hornbeam stands (WESOLOWSKI 1989). This might be partially caused by the competition from the *S. vulgaris*. *S. vulgaris* was the main second user of woodpecker holes in Bialowieza, placing 56% of its nests in woodpecker holes. And the density of *S. vulgaris* was higher in ash-alder stands than in oak-hornbeam stands (WESOLOWSKI et al. 2002).

Since *S. europaea* highly preferred middle-sized woodpecker holes, which in the study area were mainly excavated by *D. major*, the nest site of *S. europaea* consequently resembled that of *D. major*. *S. europaea* used cavities in aspen overproportionally. This largely reflected the cavity availability of aspen-preferring *D. major*, instead of direct selection on tree species of *S. europaea*. It also used fresh dead trees overproportionally, placed its nest higher than all other SCNs, and bred in cavities with round opening shape with little variance in opening dimension, which were all characteristic for *D. major*. The only difference between *S. europaea* and *D. major* nest sites was that on average *S. europaea* nested in higher cavities than *D.*

major did. This was probably because that *S. europaea* selected higher ones from available old *D. major* holes, with the advantage of reduced predation of higher nests. In Europe, *S. europaea* was often reported as one of the SCNs which had highest nest sites (VAN BALEN et al. 1982, NILSSON 1984b, WESOLOWSKI 1989).

Fig. 5.8   Nests of *S. europaea* in a woodpecker hole (left) and in a branch hole (right).

F. albicilla

Similar to *S. europaea*, *F. albicilla* also nested mainly in excavated cavities. Of the two types of excavated cavities, *F. albicilla* used woodpecker holes and other bird-induced holes according to their abundance. But the abundance of the latter was about twice as many, thus most of *F. albicilla* nests were placed in other bird-induced holes, which were mainly excavated by *P. montanus* in the study area. As a consequence, the tree use and nest cavity characters of *F. albicilla* largely resembled those of *P. montanus*. Thus among the six SCN species studied, *F. albicilla* used the smallest trees, nested in cavities higher than all others except *S. europaea*, and its nest

cavities located mostly in dead substrate and had mainly round openings. On average, *F. albicilla* bred in higher cavities than *P. montanus* did, indicating that *F. albicilla* selected higher cavities from the available ones, possibly an adaptation against predation (NILSSON 1984b). The mean nest tree diameter of *F. albicilla* was larger than that of *P. montanus*, which was mainly because of some *F. albicilla* utilising woodpecker holes or branch holes.

Till few years ago, *F. albicilla* was considered as a subspecies of Red-breasted Flycatcher *F. parva*, with *F. p. parva* in west Palaearctic and *F. p. albicilla* in east Palaearctic. They were then separated into two species based on that the latter has different winter quarters (India instead of Africa), much lighter weight, almost unspotted white eggs, distinctly different song, and a more complete pre-breeding moult leading to the appearance of the orange patch in males at their first spring, and the patch never reaching the breast (BOURSKI, pers. com.).

These two closely related species also use completely different nest sites. In consistence with the present study, the studies in Central-Siberian Biosphere Reserve documented *F. albicilla* as an excavated cavity user. ROGACHEVA et al. (1991) reported that 9 out of 11 *F. albicilla* nests were arranged in *P. montanus* holes, and the others were in holes of *D. major* or *D. minor*. Recent 15 – 20 observations by the authors were basically in agreement, with some few nests found in branch holes (BOURSKI, pers. com.). In contrast, *F. parva* used mainly chimneys and half cavities, with relatively low nest height above ground (MIERA 1978, GLUTZ VON BLOTZHEIM & BAUER 1993, MITRUS & SOCKO 2004). Only 9 out of 49 nests near St. Petersburg were reported in "partially destroyed" woodpecker and *P. montanus* holes (MALCHEVSKI & PUKINSKI 1983).

What might be the selection force leading to such distinct nest site use of these two closely related species? The availability of excavated cavities may play an important role. *P. montanus* is numerous in Siberia, and almost no other species competes with *F. albicilla* to be a secondary user (BOURSKI, pers. com.). However, though *P. montanus* is less numerous in Europe, its distribution covers almost all the breeding range of *F. parva*, and the density is still in general higher than the latter. Several European SCN species have been observed using *P. montanus* cavities, but mostly as accidental cases (GLUTZ VON BLOTZHEIM & BAUER 1993). Thus it is not yet clear if

the availabilities of *P. montanus* cavities for *F. albicilla* and for *F. parva* differ to a great extent.

P. ater and P. major

Opposite to above two species, *P. ater* and *P. major* behaved as branch hole specialists (Fig. 5.9). They were not selective with respect to tree species or tree diameter, as they frequently use deciduous trees and large trees, following the higher availability of holes in such trees. However, they showed high preference for cavities in living trees and in living substrates. Tit species breeding almost exclusively in living trees was also reported in Europe (WESOLOWSKI 1989, 1996, GÜNTHER & HELLMANN 1995). As described above (Section 5.4.3), the structural stability of living trees is higher, and cavities in living substrates had less predation risk and more favourable microclimate. Another factor could be that many cavities in dead substrates might have been too heavily decomposed and become unsuitable. Thus cavities with suitable inner conditions in dead trees should have been overestimated.

As branch hole specialists, the nest cavity characters of *P. ater* and *P. major* followed the appearance of such cavities. Such cavities usually occurred lower in thicker parts

Fig. 5.9 *P. ater* **prefers nesting in branch holes in living trees.**

of trees, which had undergone a longer time enough for cavities to develop. Such cavities also mostly had slit-like opening shape, due to the nature of branch fall and wood texture, as well as the mechanism of frost crack. Such nest site characters of non-excavating tit species were frequently documented in Europe (VAN BALEN et al. 1982, WESOLOWSKI 1989, 1996, SANDSTRÖM 1992). In the study of the Marsh Tit *Parus palustris* in Poland, such patterns of nest-site use were suggested as anti-predator adaptations (WESOLOWSKI 2002).

C. familiaris

Distinct from all others, *C. familiaris* specialised on slit-like cavities, and most of its tree use could be explained by the availability of such cavities. It preferred larch in comparison with other CNB species, and used cavities in larch overproportionally. This mainly reflected the fact that long crevices mostly occurred behind the thick bark of larch. It nested in larger trees than other SCNs except *S. europaea*, since bark crevices occurred mainly in old trees, and old larch trees could develop very large diameters. When slits were formed in smaller trees, as encountered in this study due to fire fissure and shear force when snags broke, it utilised small trees as well. It accepted a very wide range of cavity opening length, while the cavity opening width was generally very small.

P. auroreus

P. auroreus behaved as a generalist in many aspects. It utilised tree species, tree DBH and tree condition according to cavity availability, indicating that it was not selective to these tree attributes. It was the only SCN species having no specific preference for certain cavity type, even one nest was found in a ground hole at the river bank. *P. auroreus* also used cavities of most variable opening dimensions and opening shape. The Common Redstart *Phoenicurus phoenicurus* in Europe appeared less selective in nest sites as well (VAN BALEN et al. 1982, GLUTZ VON BLOTZHEIM & BAUER 1993). Using diverse nest sites could be more likely to develop in such later breeding migrants.

In summary, though overlap existed, the preferences were still distinct between most of these SCN species. As demonstrated by the discriminant function analysis, nest cavity type was the most important variable for distinguishing species. The inner

dimensions of cavities, which was suggested to be an important factor of cavity occupancy and often differs among species (van Balen et al. 1982, Johnsson et al. 1993, Carlson et al. 1998), were not measured in this study. Different types of natural cavities could reflect differences in inner dimensions to certain extent. Except *P. auroreus*, all SCNs had specific preference for a certain cavity type, and their nest tree use and nest site characters reflected mainly the occurrence of such cavities. This emphasised that the attributes of natural cavities are usually diverse and correlated, very different from nest boxes, which tend to be uniform.

5.5.3   Niche overlap and role of competition

Among the three PCN species, *D. major* had larger niche breadth, in terms of its ability of excavating in diverse tree species and substrate of different condition. However, it was confined to using substrates above certain diameter and thus needed larger trees. The two smaller PCNs, *D. minor* and *P. montanus*, were not likely to suffer from competition with *D. major*, since their preferred nest sites were distinct. As dead wood specialists, the nest sites of *D. minor* and *P. montanus* were similar to some extent. However, on average *P. montanus* used smaller trees and excavated in thinner substrate. It also appeared to associate with more heavily decayed wood than *D. minor*. Thus competition for nest sites between these two species was not observed in the study period. Snag availability was not likely to be a limiting factor for these two species. In the young birch-larch forest, where birch snags were abundant, the density of both species was not higher than that in the mature birch-larch forest and the riparian forest. Territoriality, predation or food supply were possible factors limiting their populations.

Among SCNs, *C. familiaris* bred earliest, and it utilised unique niche, thus it was basically free from inter-specific nest site competition. *S. europaea*, also as an early breeder, encountered little nest site competition from other species as well. Its nest-site, mostly in living or freshly dead large trees, placed high up with the cavity opening minimised by itself, seemed an optimum in terms of both reduced predation and favourable microclimate. From preliminary observations, *S. europaea* appeared to have higher breeding success than *P. montanus*, *F. albicilla* and *P. auroreus*.

The specialisation on branch holes of *P. ater* and *P. major* did not appear to be forced by the competition of *S. europaea*. There were always some usable woodpecker holes left for the later-coming *P. auroreus* and *F. albicilla*. Moreover, in fact, without the ability of minimising cavity opening, middle-sized woodpecker holes were not likely to be a good breeding place. In Bialowieza, some *P. palustris* bred in woodpecker holes, and such nests were depredated more often than the nests in branch holes (WESOLOWSKI 2002). It is interesting that both *P. ater* and *P. major* were never found using the old nests of *P. montanus*, which were a plentiful resource and located high with small opening. *P. ater* and *P. major* had to make the choice of nesting low but in living or at least more intact substrates, or nesting high in decayed wood. And they gave the priority to the former. PERRINS (1979) explained low nesting height of *P. major* by preferred foraging sites in the breeding season. However, this didn't fit to *P. ater*, which usually foraged high in thin twigs (GLUTZ VON BLOTZHEIM & BAUER 1993).

Competition was most likely to occur between theses two species. Though on average *P. ater* used cavities of smaller opening than that of *P. major*, certain overlap existed. Competition for nest sites between them were observed a few times during the study. The dominant competitor, *P. major*, had relatively low density in most of the study area. In fragmented West European stands where nest boxes were supplemented, its density frequently reached 35 pairs/10 ha (DHONDT & SCHILLEMANS 1983, VAN BALEN 1984, WESOLOWSKI et al. 1987). While in the birch-larch forests of the study area, its density was lower than 2 pairs/10 ha. In Bialowieza, a similar low density of 2 – 3.5 pairs/10 ha was also reported (TOMIALOJC et al. 1984, WESOLOWSKI et al. 1987). The low density of this dominant competitor should not be due to cavity availability, since many usable nest sites were left for *P. ater*. And for *P. ater*, the constraint on nest site acquisition was more likely due to intraspecific territoriality rather than interspecific competition.

F. albicilla, facing the same choice of nesting in branch holes or excavated holes, gave the priority to the latter. It was possible that, for this latest-breeding migrant, most of the favourable branch holes were already occupied by *P. ater* and *P. major*. However, this pattern might be more likely to reflect the different trade-offs of different species. As a canopy fly-catcher, nesting high would be advantageous for

reduced exposure of adult birds and nest sites to predators. Since branch holes were rare in higher parts of trees, *F. albicilla* used more woodpecker holes and *P. montanus* holes. Despite the distinct nest site use of *F. parva* in Europe, other two European *Ficedula* species, *F. albicollis* and *F. hypoleuca*, also often nest high above ground when they use natural cavities (SACHSLEHNER 1995, CZESZCZEWIK & WALANKIEWICZ 2003; but NILSSON 1984b). In Bialowieza, where cavities were abundant, *F. hypoleuca* still nested higher than Parus species (CZESZCZEWIK & WALANKIEWICZ 2003).

P. auroreus, being a nest site generalist, had certain extent of overlap with most of other SCN species, as indicated by the confounding results of discriminant function analysis. The nest-site selection of this species was most likely to be shaped by interspecific competition, as it often utilised cavities with unnecessarily large openings. Nevertheless, its density might not be limited by the availability of cavities, since many cavities occupied by the later-coming *F. albicilla* could be usable for *P. auroreus* as well. Its density was low in most of the study area, mainly due to its association with open area and shrubs. Experimental manipulation would be necessary to investigate whether its nest site use was shaped by ongoing competition, or being less selective in nest site had become an adaptation of this migrant.

In general, the role of interspecific competition in shaping nest-site selection and limiting population density appeared much less important than that reported in other studies. Many of such results could arise from impoverished nest site availability in managed forests (Brawn & Balda 1988). Moreover, most of the superior competitors in other studies were edge species or introduced species, with the association of human activities. In the Netherlands, competition of *S. vulgaris* shaped nest-site use and population size of *P. major* (VAN BALEN et al. 1982). In Sweden, the dominance of Jackdaws *Corvus monedula* forced other users of *D. martius* holes to use shallower and lower cavities, and made Stock Doves *Columba oenas* used cavities deeper in forest (JOHNSSON et al. 1993). In United States, the nest niche of introduced *S. vulgaris* and House Sparrow *Passer domesticus* overlapped with Bluebirds *Sialia spp.*, and caused great decline of *Salia* populations (ERSKINE & MCLAREN 1976, POGUE & SCHNELL 1994, SEDGWICK 1997). The competition with *S. vulgaris* also limited Tree Swallows *Tachycineta bicolour* to smaller cavities and nest sites farther

from woodland edges (PETERSON & GAUTHIER 1985, RENDELL & ROBERTSON 1989, DOBKIN et al. 1995). The aggressiveness of *S. vulgaris* could exert selection on other CNBs to shift their nesting phenology and behaviour (KOENIG 2003). In Bialowieza, WESOLOWSKI (1989) also suggested that interspecific competition, though playing some role in cavity selection (sequential use of the same cavity, interspecific fight), could be less important than in managed forest.

5.6 Sequential Cavity Use

Cavity reuse was often studied by observing the sequential use of the cavities of specific woodpecker species (e.g. KÜHLKE 1985, JOHNSSON et al. 1993, BONAR 2000, MEYER & MEYER 2001, WIESNER 2001, KOTAKA & MATSUOKA 2002), while only very few have considered the reuse pattern of the whole CNB community. The overall reuse rate in the present study was 37%, very similar to the few available documented values: 36% in pine-Douglas fir forest (SAAB et al. 2004), 37% in boreal pine-Douglas fir forest (AITKEN et al. 2002), and 38% – 56% in cottonwood bottomland (SEDGWICK 1997). The comparison was influenced slightly by whether the authors included unusable cavities in the analysis, but the proportion of unusable cavities was usually less than 5%. The reuse rates reported by all studies should be considered as the minimum of the reality, since the use by nocturnal species were generally underestimated, and the nesting attempts failed at an early stage could be difficult to detect.

5.6.1 Reuse at guild level

The rate of reuse old nest cavities presumably depends on costs and benefits of using old cavities and on availability of suitable excavating substrates or cavities (SEDGWICK 1997, AITKEN et al. 2002). Cavities not occupied in the previous year may have fewer parasites or debris (SHORT 1979, RENDELL& VERBEEK 1996). These cavities may also be less susceptible to predation, since some predators may learn the location of old nest sites and revisit them (SONERUD 1985, NILSSON et al. 1991). Therefore, it might be advantageous to use cavities not occupied in the previous year. However, most previously unoccupied cavities may indicate a lower quality of inner

dimension or surroundings, and competition for the few qualified and previously unoccupied ones may be strong. For PCNs, reusing old cavities has further benefit in saving considerable time and energy for excavation that could be allocated to reproduction. However, cavity excavation is suggested to be an integral component of courtship, functioning in pair bond formation and maintenance (LAWRENCE 1967), thus many PCNs excavate one or even more new cavities each year. The reuse of WPCNs may be shaped by both the availability of suitable excavating substrate and the competition with SCNs.

Since the costs and benefits of reuse differ among guilds, the reuse pattern of each guilds may be different. The reuse rate of each guild, however, appeared discordant among studies (Table 5.3). In West Khentey, cavities previously used by SCNs had the highest reuse rate, previous WPCN cavities were seldom reused, and previous PCN cavities were reused to an intermediate extent. This pattern was most similar to another boreal study site (AITKEN et al. 2002). But in other two study sites, on the contrary, previous WPCN cavities had highest reuse rate (SEDGWICK 1997, SAAB et al. 2004).

Table 5.3   Guild level cavity reuse pattern in the literature.

Location	Original occupant	Cavity reuse (%)		
		by different species	by same species	not reused
West Khentey, Mongolia (this study)	PCN	19	13	69
	WPCN	16	0	84
	SCN	1	45	54
Colorado, USA (SEDGWICK 1997) [1]	PCN	33	23	44
	WPCN	58	8	34
	SCN	18	35	47
British Columbia, Canada (AITKEN et al. 2002)	PCN	21	7	72
	WPCN	6	11	83
	SCN	18	30	53
Idaho, USA (SAAB et al. 2004) [2]	PCN	22	2	76
	WPCN	9	47	45
	SCN	16	22	62

[1] Only the reuse of 1985 cavities in 1986 was presented, since the data of between year reuse of 1986 and 1987 were not presented (Table 1 in SEDGWICK 1997). Black-capped Chickadee *Poecile atricapillus* was grouped as WPCN according to AITKEN et al. 2002.

[2] Two mammal species were included in SCNs.

The reuse pattern also differed among studies, again with most disagreement in WPCNs. AITKEN et al. (2002) suggested that, WPCN cavities were generally more shallow and with entrances too small for some SCNs, thus they were not favoured by SCNs. WPCNs might be less able to compete with the larger SCNs, thus they reuse their own cavities. Therefore the reuse of WPCN cavities should be low and mainly by the same species. However, this could not be generalised to different sites. In West Khentey, reuse of WPCN cavities was low, but all were used by SCNs. This might be owing to enough suitable snags for excavation, thus almost all WPCNs constructed new cavities. And the smaller cavities of WPCNs were still usable by small SCN species. In the study of SEDGWICK (1997), reuse rate of WPCN cavities was high, and they were mostly reused by SCNs. This was resulted from that the smallest SCN species House Wren *Troglodytes aeddon* frequently used the smaller cavities of the only WPCN Black-capped Chickadee *Poecile atricapillus*. The competition for cavities was considered strong in that study site (SEDGWICK & KNOPF 1992), and strong competition often leads to small species using smaller cavities to reduce the chance of eviction by a larger competitor (PETERSON & GAUTHIER 1985, RENDELL & ROBERTSON 1989). In the study of SAAB et al. (2004), WPCN cavities had high reuse rate, and were mostly reused by the same species. This was the consequence of that the WPCN Lewis's Woodpecker *Melanerpes lewis* frequently occupied a nest cavity over several years. The authors explained this with its very poor excavator morphology.

It was corresponding among the four studies, that the reuse of previous PCN cavities were mainly by other species, while the reuse of previous SCN cavities were mainly by the same species (Table 5.3). In Europe, WESOLOWSKI (1989) reported that woodpeckers hardly ever reused their own cavities, while SCNs often bred in cavities previously utilised by their own species. VAN BALEN et al. (1982) observed that woodpecker holes were always used by another species in the year after excavation, which indicated the high cavity demand in this Dutch study site with highest cavity occupancy ever documented (see Section 5.3.4). The constancy of the ten SCN species there averaged 64%, also higher than reported in other studies (Table 5.3).

The reuse of SCN cavities by different species may indicate the extent of nest niche overlap. Then the very low interspecific cavity reuse of SCNs in West Khentey

compared to other studies might imply more distinct niche partition and less competition among SCN species. The reuse of PCN or WPCN cavities by different species shows the excavator-secondary user relationships, while under some circumstances it may imply competition as well. The most often documented case was that, in North America, the aggressive invader *S. vulgaris* overtook the nest cavities of woodpeckers and forced the latter to excavate new ones or reuse the older ones (TROETSCHLER 1976, INGOLD 1989, 1996). The snatch of PCN or WPCN nest cavities by SCN species has not been observed in West Khentey.

5.6.2   Reuse at species level

Capability of excavation, ability for nest site competition or quality and abundance of preferred cavity type also differ among species, thus the tendency for reuse of each species may differ as well. In the present study, the interpretation of reuse at species level was largely limited by the sample size of each species. Among PCNs, *D. major* appeared to reuse its nest cavities more often. Excavator species vary in their propensity to excavate. The ultimate factor is often supposed to be their difference in morphology. Species with weak skull and bill morphology are considered to have higher propensity to use existing cavities. They depend on particular soft substrate for excavation. If soft wood is not available, then existing cavities are used (MARTIN & LI 1992, MARTIN 1993, SAAB et al. 2004). This was not supported by the present study. *D. leucotos* and *D. minor*, which had weak excavation morphology (MEYER et al. 1993) and depended highly on soft substrate, did not use existing cavities. This could be explained by the abundance of snags in the study area and the limited number of observations, therefore reuse was not observed. However, throughout the literature, these species rarely use existing cavities (WESOLOWSKI & TOMIALOJC 1986, AULÉN 1988, GLUTZ VON BLOTZHEIM & BAUER 1993, WINKLER et al. 1995). When soft substrate is not available, they decline in numbers or disappear from the habitat, instead of using existing cavities (AULÉN 1988, BLUME 1990, PECHACEK 1995, MIKUSINSKI & ANGELSTAM 1997, CARLSON 2000).

The proximate causes to the extent of reuse may include habitat factors and inter- and intraspecific interactions. AITKEN et al. (2002) found that, among PCNs, the reuse by the same species was highest for the most abundant woodpecker species Northern Flicker *Colaptes auratus*. And the authors pointed out that intraspecific competition

and availability of suitable excavating substrates might be part of the explanations. For *D. major*, VAN BALEN et al. (1982) found no use of existing cavities in the four observations. WESOLOWSKI & TOMIALOJC (1986) documented 3.8% of its breeding attempts in existing cavities. In Japan, KOTAKA & MATSUOKA (2002) reported no reuse of *D. major* cavity by itself in urban area (n = 24), and a 20% reuse rate in suburban area (n = 12). In Germany, 14 – 70% of *D. major* were found to nest in old cavities instead of building new ones (BLUME 1977, WITT 2004). Due to the limited sample size in the present and other studies, as well as very few information about habitat and local CNB community in the literature, it was difficult to generalise the factors influencing the rate *D. major* using old cavities.

The cavities of *D. major* were often occupied by *S. europaea*, in consistence with other studies (WESOLOWSKI 1989, GÜNTHER & HELLMANN 1997, KOTAKA & MATSUOKA 2002). In Europe, *S. vulgaris* appeared to have the priority to *D. major* cavities over *S. europaea*. In areas where the competition of *S. vulgaris* was strong, *S. vulgaris* usually accessed the cavities in the following year of *D. major* nesting, and *S. europaea* used the cavities after the occupation of *S. vulgaris* (VAN BALEN et al. 1982).

P. montanus never reused its own old cavities, and its cavities were sometimes reused by *F. albicilla*. The reuse rate of *P. montanus* cavities was lower than that of *D. major* cavities. This might be partially explained by the smaller opening size and inner dimension of *P. montanus* cavities, limiting the species able to use them. Most of these cavities were located in heavily decayed substrates, thus might deteriorate rapidly and became unsuitable for breeding in the following year.

Among SCNs, despite of those with too few data, the cavities of *S. europaea* and *P. ater* were reused by the same species most frequently, while cavities previously occupied by *F. albicilla* were never reused. This might be partly explained by the quality and the abundance of their preferred nest sites. *S. europaea* nested high and seldom in snags, *P. ater* nested in living trees and mostly in sound substrates, both might be advantageous in having less predation rate, higher structural stability and steadier microclimate. Therefore the high reuse rate might be related to the high cavity quality, as nest site fidelity developed after successful breeding attempts have been reported for several CNB species and other birds (KORPIMAKI 1993, HAAS

1998). Beside quality, these cavities in sound wood also had longer usability over years.

In contrary, *F. albicilla* nests were located mainly in decayed substrates, which could result in lower breeding success and reduce the propensity to reuse. Such cavities might also undergo too rapid decay, the quality decreasing with time, and soon become unsuitable. While in the same time *P. montanus*, which was at least twice as abundant as *F. albicilla* in the study area, supplied newer cavities each year. *F. albicilla* pairs usually visited several cavities before choosing one for breeding, and the abundant newer cavities were more likely to be used. The study with nest boxes also suggested that nest site fidelity of Eastern Bluebird *Sialia sialis* depended on the quality of alternative resources (STANBACK & ROCKWELL 2003).

Observing the pattern of sequential cavity use is also another way to study the interspecific similarity of preference for certain cavities (VAN BALEN et al. 1982). Sequential use of cavities between different species may indicate niche overlap and the potential for competition. In the study area, no interspecific reuse between SCNs was observed in the study period, even between *P. ater* and *P. major*, which had very similar nest sites (Section 5.5). This might be owing to the very low density of *P. major* in most of the study area. Or there might be some nest site variables not measured in the present study, e.g. cavity inner dimension, which distinguished the nest sites of these two species. In the 33 observations of *P. major* nest cavities by VAN BALEN et al. (1982), one was previously used by *P. ater*. *P. major* and *S. europaea* were found reusing previous cavities of each other (WESOLOWSKI 1989), which was also not observed during the period of this study. One interesting reuse case was that a branch hole nested by *S. europaea* in 2002 was used by the WPCN *P. montanus* in the following year. And one *P. montanus* nest in 2002 was placed in a middle-sized woodpecker hole, the entrance of which showed apparent modification by *S. europaea*. In both cases, the original cavity opening sizes were too large and might not be preferred by *P. montanus*. Presumably the previous occupation and cavity opening minimisation by *S. europaea* had made these cavities profitable for *P. montanus*, and in the same time limited the usability of these cavities by larger species.

5.6.3   Characters of reused cavities

In the study area, cavities in living substrates were more frequently reused than those in dead substrates, and branch holes and woodpecker holes were reused more frequently than other bird-induced holes. This to a certain extent reflected the nest site preference of *S. europaea* and *P. ater* (Section 5.5.2), which were abundant and had high propensity to reuse. In the study of the reuse of *D. major* holes in Germany, GÜNTHER & HELLMANN (1997) also found cavities in living trees were more attractive to SCNs.

In Canada, AITKEN et al. (2002) found higher reuse of cavities with large opening and inner dimension. Cavities in aspen and cavities near forest edge were also reused more often. This pattern was mainly generated by the nesting preferences of dominant PCN Northern Flicker *Colaptes auratus* and dominant SCN *S. vulgaris*. Both species had comparatively larger size and strongly preferred edges. The higher reuse of cavities in aspen was mainly because aspen was an edge-associated tree species (AITKEN et al. 2002).

In the study of *D. martius* holes in Sweden, cavity height above ground was important to cavity reuse (JOHNSSON et al. 1993). Higher cavities were used more often, and the dominant species Jackdaw *Corvus monedula* used the highest ones. The high abundance of edge-associated *C. monedula* also resulted in higher reuse rate of cavities at forest edge.

Cavities with high reuse rate may indicate good qualities and/or more limited availability of such cavities. The "good qualities" include not only the characteristics of the cavity or cavity tree itself, but also surrounding habitat or landscape attributes such as the proximity to other resources. Thus what are the "good qualities" may differ from species to species. And the reuse pattern of the whole CNB community is further shaped by its characteristic species composition and the distribution of available cavities. Therefore, the characters of highly reused cavities showed inconsistency among studies.

Since cavities in more decayed wood had higher maximum temperatures and greater daily temperature fluctuations (WIEB 2001), nesting in sound substrate might be especially profitable in West Khentey, where temperature fluctuation was extreme,

compared to other sites. Higher reuse of cavities in living wood might also indicate that, in this area, main predation pressure was from predators which foraged by chewing or ripping open cavities. However, it could also be possible that the higher reuse of cavities in living substrates was simply because they were physically longer usable, compared to those in dead substrates. Since cavities in living trees had higher occupancy than those in dead trees (Section 4.5.3), and branch holes had higher occupancy than other bird-induced holes (Section 4.5.6), the frequent reuse of cavities in living trees and branch holes could also be explained by that there were less free alternatives. Further detailed information about breeding success, predation rate and the quality and abundance of alternative cavities is necessary to clarify the factors shaping reuse patterns.

5.7   Nest Web

5.7.1   Structure of the nest web in West Khentey

Based on the characteristics of the resource (cavities), the nest web of the CNB community in the study area could be divided into two subwebs: the excavated cavity subweb and the non-excavated cavity subweb. The former could be further split up into three chains: the large-sized, the middle-sized and small-sized excavated cavity chains. *D. martius* was the centre of the large-sized excavated cavity chain. As for the tree species involved, the active *D. martius* nests were only observed in aspen and Scots pine in the study period. But unoccupied old cavities were also found in poplar and larch, indicating the tree species that might develop to diameters large enough could be used. *B. clangula* was the only secondary user recorded. But the observations of such cavities were few, and more cryptic users, such as Strigidae and Anatidae, might be overlooked. *D. major*, *D. leucotos* and *P. canus* were the excavating species in the middle-sized excavated cavity chain, and potentially *P. tridactylus* should also be included. *D. major* produced larger effects than the others, as it was more numerous in the study area and constructed most of this resource. Both birch and aspen were important in this chain. While aspen had an overproportional importance relative to its abundance, due to the preference of *D. major*. Six secondary users were involved in this chain. The excavators in small-sized excavated cavity chain were *D. minor* and *P. montanus*, and the latter accounted for most of the

resource in this chain, due to its high abundance. The key tree species was birch. Three SCN species were involved in this chain.

The non-excavated cavity subweb was comprised of branch hole chain and other distinct and rare cavity types. The branch hole chain was largely based on birch, and was used by up to seven species. Other special cavity types were mostly provided by larch, and involved three SCN species.

Nest cavity characters and reuse patterns discussed in previous sections could be incorporated with the nest web. The nest sites of the members of excavated chains located higher and had round cavity openings, while the nest sites of the members of non-excavated chains located lower and had slit-like cavity openings. For the small-sized excavated cavity chain, the cavities were mostly in dead substrates, and the reuse rate was generally low. This chain also had higher turnover rate, in terms of higher cavity recruitment (higher excavator density and mostly constructing new nest cavities) and higher cavity loss (frequent nest tree/substrate fall and rapid deterioration). For the other two excavated chains and the branch hole chain, cavities were placed in sounder wood, and the reuse rate was high. The turnover rate of middle-sized excavated cavity chain should be moderate, due to moderated excavator density, frequent construction of new cavities, and a moderate rate of cavity loss. Large-sized excavated cavity chain and branch hole chain should have lowest turnover, as the result of relatively lower recruitment (low density of *D. martius* and slow formation of non-excavated cavities) and lower cavity loss (usually in living and large trees).

Beside West Khentey, the only nest web studied was in British Columbia, Canada (MARTIN & EADIE 1999, MARTIN et al. 2004). Trembling aspen *Populus tremuloides* was the key tree species for the nest web in British Columbia, as it was the main deciduous species in the system. Another distinct difference was that, in British Columbia, only about 7.5% of the nests were located in non-excavated cavities. There was no bird species specialised on non-excavated cavities, and only one species preferred non-excavated cavities over excavated ones. Two woodpecker species, the Red-naped Sapsucker *Sphyrapicus nuchalis* and the Northern Flicker *Colaptes auratus*, created about 74% of all utilised cavities. This differed greatly from the

significant role of non-excavated cavities in West Khentey, where 44% of all observed nests were located in non-excavated cavities.

5.7.2   The role of woodpeckers

Based on the simulations with nest web, the widely accepted idea that woodpeckers are keystone species for CNB communities (ANGELSTAM 1990) was not generally supported in this study. Cavities of *D. martius* might be a highly valuable resource, because large non-excavated cavities were very rare. In the boreal forest in Canada, BONAR (2000) searched the cavities with size comparable to that of the Pileated Woodpecker *Dryocopus pileatus*, which was similar to that of *D. martius*. Only less than 2% of such cavities were not excavated, while others were constructed by *D. pileatus*. This underlined the importance of large woodpecker species. In the present study, only *B. clangula* was observed nesting in *D. martius* cavities. The rare and cryptic users, such as owls and ducks, were not adequately sampled, therefore the importance of *D. martius* might be underestimated. Nevertheless, several large owl and duck species in the study area are not obligate cavity nesters (Appendix; GLUTZ VON BLOTZHEIM & BAUER 1993). Therefore, *D. martius* may be crucial to *B. clangula* and the Goosander *Mergus merganser*, but it doesn't exhibit far-reaching influence over the structure and function of the CNB community. *D. martius* is often referred as a keystone species in Europe (KÜHLKE 1985, JOHNSSON 1993, ROLSTAD et al. 2000). Several large and obligate European CNB species, e.g. Jackdaw *Corvus monedula*, Stock Dove *Columba oenas* and Tawny Owl *Strix aluco*, were not recorded in the study area. Thus *D. martius* might play a more important role in the CNB community in Europe than in that in West Khentey.

Middle-sized woodpecker species did not play key roles in the CNB community. No SCN depended exclusively on the resource they supplied. Only *S. europaea* utilised it to a higher extent, and this species could well adapt to branch holes. It also breeds earlier than most of other SCNs and has the special behaviour of minimising the nest cavity opening, which reduced its suffering from the competition for branch holes with other SCNs. And the abundance of branch holes was able to accommodate such nest use shifts. The usability of *D. minor* holes was limited by its opening dimension. And its importance in the nest web was largely diluted by *P. montanus*, which supplied similar resource in larger amount.

In Europe, several studies also considered that the importance of woodpeckers in general as keystone species in producing holes for CNBs should be re-evaluated. In Germany, it was suggested that the value of *D. major* holes might be overestimated, as they only supported a minor proportion and species diversity of SCNs (GÜNTHER & HELLMANN 1997, 2001). In Bialowieza, Poland, all SCN species except *S. vulgaris* placed the majority of their nests in branch holes, and in average only about 16% of SCN nest cavities were made by woodpeckers (WESOLOWSKI 1989). In Sweden, branch holes rather than woodpecker holes were considered as an important resource for SCNs (SANDSTRÖM 1992, CARLSON et al. 1998).

The studies in North America, instead, often indicated highly significant role of woodpeckers. In Canada, more than 90% of CNB nests were located in excavated cavities (MARTIN & EADIE 1999). In United States, STAUFFER & BEST (1982) found 70 – 80% of SCN nests in excavated cavities. DOBKIN et al. (1995) documented that almost all cavities showed some signs of excavation or substantial modification by woodpeckers. Thus woodpeckers are more likely to act as keystone species in these systems. As studies covering the whole CNB community were few, it is not yet clear if such difference is general between the two biogeographic regions.

Some studies used the positive association between woodpecker abundance and SCN abundance to demonstrate woodpeckers as nest providers for SCNs (e.g. DOBKIN & WILCOX 1986, MARTIN & EADIE 1999). In the present study, such positive correlation also existed, but it probably indicated common habitat preference rather than nest site relationship. Thus woodpeckers appeared as indicators of habitat quality and SCN abundance instead of as keystone species.

5.7.3   The role of birch

The simulation with nest web revealed a widespread effect in the CNB community after the removal of birch. This was the consequence of both the high cavity-holding rate of birch and its high abundance in the study area. A keystone species has to act on the system with effects much larger than would be predicted from its relative abundance (KREBS 2001). In the study area, this was more likely true for birch in the spruce-fir forest. But the present data did not allow the analysis for each habitat separately.

Though birch could not be asserted as a keystone species for the CNB community, the nest web analysis outlined the far-reaching influence when birch was replaced by conifers. And that was what has happened in large areas of boreal and hemiboreal forests (SANDSTRÖM 1992, ANGELSTAM & MIKUSINSKI 1994, HAUSNER et al. 2003). Due to the transformation of deciduous forests into coniferous plantations, or through the suppress of fire in managed forest which inhibited the natural regeneration of secondary deciduous forest, the abundance of birch was decreasing in Scandinavia till 1980s. Afterwards it started to increase as the result of increasing demand of pulp industry. But it was usually felled at DBH about 20 – 25 cm, before it could become useful to CNBs (SANDSTRÖM 1992).

Though birch is interconnected with most of the CNB species, it rarely reaches the size large enough for *D. martius* to nest, and thus can not support the large-sized excavated cavity chain. It also rarely holds suitable crevices for *C. familiaris*. Thus the admixture of large trees and thick bark conifers was important to sustain a diversified CNB community.

It was contended that there are several advantages of a nest web perspective. First, a nest web analysis reveals the kind of links that might exist among all the species in the community. It allows a broader community focus instead of the common attention which is usually paid only to single or several species in the community. Secondly, it outlines the direct and indirect interactions which are critical to predict the response of the community to perturbations or change. Thirdly, it may help to identify keystone species or keystone interactions. Finally, some existing ecological theory on food webs might be applied to predict the structure, stability and resilience of CNB communities, or, in another way round, the analysis of nest webs might be used to test the food web theory in a new and perhaps more tractable system (MARTIN & EADIE 1999). However, it should be noticed that such simulations were simply based on one dimension, i.e. nest site, of the requirements of CNBs. The change of tree species composition would also alter the food items and abundance, as well as habitat structure. The removal of a bird species might not only influence the nest site availability of others, but also change the extent of food competition and predation pressure. Such interactions are beyond the analysis scope of nest web.

SUMMARY

Cavity-nesting birds (CNBs) comprise a major component of many forest bird communities. For their close association with trees and cavities, they are highly sensitive to the alteration of forest structure. Therefore they are considered as indicators of several forest qualities and forest bird diversity, and many CNB species have declined due to modern forestry and anthropogenic landscape alterations.

Though CNBs have been intensively studied, most information was gathered with nest boxes and in managed forests, which might not represent the natural conditions. Forest structure and cavity availability, which are critical in investigating the nest-site selection of and competition among CNBs, were seldom sufficiently quantified. And most studies focused only on single species. Community-level approaches were few, and the interspecific relationships were largely ignored. Therefore the objectives of this study were to investigate cavity abundance in different types of natural boreal forest and the characteristics of cavity trees, to survey CNB composition and the characteristics of trees and cavities utilised by CNBs, to study the nest-site selection of individual bird species, and to investigate interspecific interactions through the pattern of sequential cavity use and the nest web analysis.

The study site was Khan Khentey Strictly Protected Area (48-49°N, 107-110°E), northeast Mongolia. It is situated in the transition zone of Siberian taiga and Central Asian steppe. The environment is characterised by undulating terrains, harsh continental climates and mosaic land covers of forest and steppe. The field work was carried out in four different habitats: the mature birch-larch forest, the young birch-larch forest, the riparian mixed forest and the spruce-fir coniferous forest.

In each habitat, five 1 ha plots (50 m×200 m) were established. Two points in each plot were taken systematically for taking habitat measurements. At each point, standing stems (= 5 cm diameter at breast height (DBH)) were sampled by plotless method. For each sampled tree, tree species, DBH, tree condition and if the tree carried fire scars and fungi conks were recorded. Each sampled stem was also searched for cavities. Cavities were classified into woodpecker hole, other bird-induced hole, branch hole or bark crevice. Nests of all CNB species were searched in 2002 and 2003. A nest cavity was defined when an adult bird was observed bringing

in nesting material or food. In the quantitative plots, nest search was confirmed with territory mapping, in order to locate all the nest cavities in the plots. Nest cavities found outside the plots were also recorded. For each nest, the species, DBH, condition and the presence of fire scars and fungi conks of the nest tree were recorded, as well as nest cavity type, cavity height above ground, substrate diameter, substrate condition and cavity opening length and width.

The cavity abundance in the study area averaged 30 cavities/ha. The spruce-fir forest had lowest cavity density (18 cavities/ha), due to less branch holes in this habitat. Cavity occurrence was related to tree species, tree DBH, tree condition and the occurrence of fire scars and fungi conks. Over 50% of the cavities were found in birch, while poplar was the most cavity-rich tree species related to its abundance. Cavity holding rate rose with ascending DBH. Cavities, especially excavated ones, occurred overproportionally in tall snags. Both the occurrence of fire scars and fungi conks showed positive association with the occurrence of cavities.

The density of CNBs in the study area averaged 2.4 nests/ha, lower in the spruce-fir forest than in other three deciduous-dominated forest. The overall cavity occupancy in the study area was approximately 5%. CNB density was positively correlated with the proportion of deciduous stems and shrub coverage in the stand. Deciduous trees, larger trees, dead trees and trees with fire scars and fungi conks were preferred by primary cavity nesters (PCNs). Secondary cavity nesters (SCNs) also used such trees overproportionally, which mostly in accordance with cavity availability in these trees.

For individual species, the nest sites of *D. minor*, *P. montanus* and *F. albicilla* had high similarity, as they nested in excavated cavities with small and round openings located high in thin and broken snags. The nest sites of *D. major* and *S. europaea* were similar in that they both bred in cavities with round openings of diameter 4-5 cm located high in large and living or intact dead trees. Both *P. ater* and *P. major* preferred branch holes with slit-like openings, located low in living trees. *P. auroreus* utilised a wide range of cavities, while *C. familiaris* was distinct from others in specialising on long slits.

The observation of sequential cavity use showed that the cavities previously occupied by *D. major* and *P. montanus* were frequently used by *S. europaea* and *F. parva*,

respectively, in the following year. Previous *S. europaea* and *P. ater* cavities were frequently reused by the same species. Cavities in living substrates were reused more often than those in dead ones. Nest web analysis suggested that no SCN species was completely dependent on middle- or small-sized woodpecker holes. They could switch to branch holes when woodpecker holes were lacking. The removal of birch would, however, strongly influence the structure of CNB community.

The cavity abundance in the study area was high compared to literature. The cavity holding rates were very similar to related species in Sweden, which might represent characteristic values in boreal Eurasia. The naturalness of the study area, in terms of both natural forest structure with abundant deciduous, old and decayed trees and natural process of fire dynamic and fungi decay, presumably led to the high cavity abundance. The CNB density in the study area corresponded well to the documented values, which resulted in a low cavity occupancy compared to documented values.

The nest sites of PCN species showed some attributes in common, i.e. cavities high in the tree with round opening shape and minimised opening dimension, as possible adaptations against predation and minimising excavation burdens. While they also showed differences in nest tree and nest substrate selection, shaped by their different excavation ability, body size and territory size. Most SCNs had a preferred cavity type, and their nest tree use and nest site characters reflected mainly the occurrence such cavities. The extent of interspecific competition shaping nest-site selection and limiting population density appeared less intense than that reported in other studies.

Higher reuse rate of cavities in living substrates might reflect cavity usability and quality. Such cavities had more favourable microclimates and were safer from predation. Woodpeckers in general as keystone species for CNB communities was not supported in this study. Only *D. martius* might have irreplaceable function in producing large cavities. Birch had fundamental importance in the study area, as the consequence of both its high cavity-holding rate and its high abundance. And the nest web analysis outlined what might happen, and has happened in large areas of boreal and hemiboreal forests, when birch forests were transformed into coniferous plantations.

ZUSAMMENFASSUNG

Höhlenbrütende Vogelarten stellen einen bedeutenden Anteil vieler Waldvogelgemeinschaften. Wegen ihrer engen Bindung an entsprechende Habitatstrukturen sind sie sehr empfindlich gegenüber Veränderungen der Waldstruktur. Daher werden sie als Indikatoren für Habitatqualitäten und Vogeldiversität aufgefasst und viele höhlenbrütende Vogelarten haben infolge moderner Forstwirtschaft und anthropogener Landschaftsveränderung im Bestand abgenommen.

Obwohl höhlenbrütende Vögel sehr intensiv untersucht wurden, basieren die meisten Erkenntnisse auf Untersuchungen mittels Nistkästen und in bewirtschafteten Wäldern. Die Verhältnisse unter natürlichen Bedingungen könnten sich jedoch anders darstellen.

Die Waldstruktur und Verfügbarkeit von Baumhöhlen, welche entscheidend für die Untersuchung der Brutplatzwahl und Konkurrenz unter Höhlenbrütern sind, wurden selten ausreichend quantifiziert. Und die meisten Studien betrachteten nur eine einzelne Art. Ansätze zur Untersuchung der entsprechenden Artengemeinschaften und ihrer interspezifischen Beziehungen wurden meist vernachlässigt. Daher war die Zielsetzung dieser Studie die Baumhöhlenabundanz verschiedener, borealer Naturwaldtypen und die Beschaffenheit der Baumhöhlen zu untersuchen, die Zusammensetzung der Artengemeinschaften von höhlenbrütenden Vogelarten sowie die Charakteristiken genutzter Bäume und Baumhöhlen zu erfassen und die interspezifischen Interaktionen über Muster der Folgenutzung und nest web Analyse zu bestimmen.

Das Untersuchungsgebiet war das streng geschützte Reservat Kahn Khentey im Nordosten der Mongolei (49-49°N, 107-110°O). Es liegt in der Übergangszone der Sibirischen Taiga und der zentralasiatischen Steppe. Die Landschaft ist durch hügeliges Terrain, raues, kontinentales Klima und ein Mosaik aus Wald und Steppe charakterisiert. Die Untersuchungen wurden in vier verschiedenen Habitaten durchgeführt: alter Birken-Lärchen-Wald, junger Birken-Lärchen-Wald, Aumischwald und Fichten-Tannen-Wald.

In jedem Habitat wurden fünf ein Hektar große (50mx200m) Untersuchungsflächen eingerichtet. In zwei systematisch ausgewählten Punkten in jeder Untersuchungsfläche wurden systematisch Habitatparameter erfasst. An jedem Punkt wurden stehende Baumstämme ($\geq$ 5 cm Brusthöhendurchmesser (BHD)) mittels Winkelzählprobe ausgewählt. Für jeden ausgewählten Stamm wurden Baumart, BHD, Vitalität und das Vorhandensein von Feuernarben, Pilzkonsolen und Baumhöhlen aufgenommen. Die Höhlen wurden klassifiziert in Spechthöhlen, durch andere Vogelarten aktiv angelegte Höhlen, Astlöcher oder Rindenspalten. Nester aller höhlenbrütenden Vogelarten wurden in 2002 und 2003 gesucht. Ein Brutnachweis wurde angenommen, wenn adulte Vögel Nestmaterial oder Futter eintrugen. In den fünf quantitativen Untersuchungsflächen wurde unterstützend eine Revierkartierung vorgenommen um eine vollständige Erfassung der Bruthöhlen zu gewährleisten. Hinsichtlich ihrer qualitativen Merkmale wurden auch wurden außerhalb der Untersuchungsflächen gelegene Bruthöhlen aufgenommen. Für jeden Baumstamm mit Bruthöhle wurden Baumart, BHD, Vitalität und das Vorhandensein von Feuerschäden und Pilzkonsolen erfasst. Ebenso wurden Höhlentyp, Höhe der Bruthöhle über dem Boden, Substratdurchmesser, Substratzustand und Höhe und Weite der Höhlenöffnung erfasst.

Die durchschnittliche Baumhöhlenabundanz belief sich auf 30 Höhlen je Hektar. Die Höhlenabundanz war im Fichten-Tannen-Wald am geringsten (18 Höhlen/ha) infolge des geringeren Vorkommens von Astlöchern in diesem Habitat. Das Vorhandensein von Baumhöhlen stand in Relation zu Baumart, BHD, Baumzustand und dem Vorhandensein von Feuernarben und Pilzkonsolen. Über 50% der Höhlen befanden sich in Birken, während Pappel in Relation zu ihrer Abundanz die höhlenreichste Baumart darstellte. Die prozentuale Verteilung der Baumhöhlen stieg mit zunehmendem BHD. Baumhöhlen, insbesondere die aktiv angelegten, waren überproportional häufig in hohen Baumstümpfen. Das Vorhandensein von Baumhöhlen stand sowohl mit dem Vorhandensein von Feuernarben als auch dem von Pilzkonsolen in Zusammenhang.

Die Dichte höhlenbrütender Vögel betrug im Mittel 2,4 Brutpaare je ha und war geringer im Fichten-Tannen-Wald als in den anderen drei Habitaten mit höherem Laubholzanteil. Insgesamt betrug die Höhlennutzungsrate im Untersuchungsgebiet

ungefähr 5%. Die Dichte höhlenbrütender Vögel war positiv korreliert mit dem Anteil an Laubholzstämmen und der Deckung der Strauchschicht in dem Waldbestand. Laubholzarten, größere Bäume, tote Bäume und Bäume mit Feuernarben und Pilzkonsolen wurden von primären Höhlennutzern bevorzugt. Sekundäre Höhlennutzer nutzen solche Bäume ebenfalls überproportional, meistens in Übereinstimmung mit der Höhlenverfügbarkeit in diesen Bäumen.

In bezug auf einzelne Arten zeigte die Brutplatzwahl von D. minor, P. montanus und F. albicilla hohe Similarität. Diese Arten nisteten in aktiv angelegten Höhlen mit kleinen, runden Öffnungen, die sich hoch in dünnen und gebrochenen Baumstümpfen befanden. Die Nistplätze von D. major und S. europaea waren einander ähnlich, da beide Arten in Höhlen mit runden Öffnungen von etwa 4-5 cm Durchmesser brüteten, die sich hoch in großen und lebenden Bäumen oder intakten Stämmen toter Bäume befanden. Sowohl P. ater als auch P. major bevorzugten Astlöcher mit schlitzartigen Öffnungen, die sich in geringer Höhe in lebenden Bäumen befanden. P. auroreus nutzte eine breite Palette unterschiedlich beschaffener Höhlen, während C. familiaris sich von den anderen Arten durch die Spezialisierung auf lange Schlitze unterschied.

Die Beobachtung der Folgenutzungen zeigte, dass Höhlen, die zuvor von D. major und P. montanus benutzt wurden, häufig jeweils von S. europaea und F. parva im Folgejahr genutzt wurden. Vormals von S. europaea und P. ater besetzte Höhlen wurden häufig von denselben Arten wiederbesetzt. Höhlen in lebendem Substrat wurden häufiger wiederbesetzt als solche in toten Bäumen. Anhand der Ergebnisse der nest web Analyse konnte für keine Art der Gruppe der sekundären Höhlenutzer ein vollständige Abhängigkeit von mittelgroßen oder kleinen Spechthöhlen angenommen werden. Diese Arten konnten Astlöcher nutzen, wenn Spechthöhlen fehlten. Das Entfernen der Birke würde hingegen die Struktur der Artengemeinschaft höhlenbrütender Vögel deutlich beeinflussen.

Die Baumhöhlenabundanz in dem Untersuchungsgebiet war im Vergleich zu Literaturangaben hoch. Die prozentuale Verteilung der Höhlen nach Baumarten war vergleichbar mit denen verwandter Arten in Schweden. Dies könnte eine charakteristische Eigenart der borealen Wälder in Eurasien sein. Die hohe Baumhöhlenabundnaz dieses Untersuchungsgebiets lag vermutlich in seiner Natürlichkeit, sowohl hinsichtlich der Naturwaldstrukturen mit hohen Abundanzen

von Laubhölzern, alten und zerfallenden Bäumen als auch der natürlichen Prozesse von Feuerdynamik und Pilzbefall, begründet. Die Siedlungsdichte der untersuchten Vogelartengemeinschaft korrespondierte deutlich mit diesen Eigenschaften, woraus eine im Vergleich zu berichteten Werten geringe Höhlenbesetzungsrate resultierte.

Die Nistplätze der primären Höhlennutzer zeigte einige Gemeinsamkeiten, wie z.B. die Anlage von Baumhöhlen hoch über dem Boden mit runden Öffnungen und minimierter Öffnungsweite, als mögliche Adaptationen gegenüber Prädation und Aufwandsminimierung bei der Höhlenanlage. Ebenso zeigten diese Arten Unterschiede bei der Wahl von Baumart und Substrat, bedingt durch die unterschiedlichen körperlichen Fähigkeiten zur Höhlenanlage, Körpergröße und Reviergröße. Die meisten sekundären Höhlennutzer zeigten Präferenz für einen bestimmten Höhlentyp und in der Nistbaumnutzung und Höhlensubstratnutzung spiegelte sich hauptsächlich die Häufigkeit solcher Höhlen wieder. Das Ausmaß einer die Nistplatzwahl und Populationsdichte bestimmenden interspezifischen Konkurrenz erschien geringer als in anderen Studien berichtet.

Die höhere Folgenutzungsrate von Höhlen in lebendem Substrat könnte die Qualität und Nutzbarkeit dieser wiederspiegeln. Solche Höhlen wiesen ein günstigeres Mikroklima auf und waren sicherer vor Prädation. Die Annahme, Spechte seien generell Schlüsselarten für die Artengemeinschaften höhlenbrütender Vögel, konnte in dieser Studie nicht belegt werden. Lediglich D. martius könnte eine unersetzbare Funktion in der Anlage großer Höhlen spielen. Die Birke hatte eine fundamentale Bedeutung in dem Untersuchungsgebiet als Konsequenz sowohl ihrer hohen Höhlenbürtigkeitsrate als auch ihrer hohen Abundanz. Und die nest web Analyse stellte heraus, welche Folgen eintreten könnten und in großen Flächen borealer und hemiborealer Wälder eingetreten sind, wenn Birken-(Misch)wälder in Nadelholzplantagen umgewandelt würden.

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ABBREVIATIONS

CNB   Cavity Nesting Bird

DBH   Diameter at Breast Height

GEF   Global Environment Facility

KKSPA   Khan Khentey Strictly Protected Area

MNE   Ministry for Nature and the Environment of Mongolia

PCN   Primary Cavity Nester

SCN   Secondary Cavity Nester

UNDP   United Nations Development Programme

WWF   World Wildlife Fund

APPENDIX

List of cavity nesting birds in West Khentey, Mongolia

Latin name	English name	
Tadorna ferruginea	Ruddy Shelduck	
Anas platyrhynchos	Mallard	*
Bucephala clangula	Common Goldeneye	
Mergus merganser	Common Merganser	
Surnia ulula	Northern Hawk-Owl	*
Glaucidium passerinum	Eurasian Pygmy-Owl	
Strix uralensis	Ural Owl	*
S. nebulosa	Great Gray Owl	*
Hirundapus caudacutus	White-throated Needletail	
Apus pacificus	Pacific Swift	
Upupa epops	Hoopoe	
Jynx torquilla	Wryneck	
Picus canus	Gray-headed Woodpecker	
Dryocopus martius	Black Woodpecker	
Dendrocopus major	Great spotted Woodpecker	
D. minor	Lesser spotted Woodpecker	
D. leucotos	White-backed Woodpecker	
Picoides tridactylus	Northern Three-toed Woodpecker	
Motacilla alba	White Wagtail	
Tarsiger cyanurus	Red-flanked Bluetail	
Phoenicurus phoenicurus	Eurasian Redstart	
P. auroreus	Daurian Redstart	
Turdus ruficollis	Dark-throated Thrush	*
Ficedula albicilla	Red-throated Flycatcher	
F. mugimaki	Mugimaki Flycatcher	
Parus montanus	Willow Tit	
P. ater	Coal Tit	
P. major	Great Tit	
P. cinctus	Siberian Tit	
Sitta europaea	Nuthatch	
Certhia familiaris	Northern Treecreeper	

* non-obligatory cavity nesters.

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