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Heart rot as a key factor for cavity tree selection in the black woodpecker

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ABSTRACT

Cavity nesting birds invest considerable time and effort into the construction of nests. The investment can be particularly high for species such as the black woodpecker (*Dryocopus martius*) that selects living trees as nest substrates. However, the investment may be reduced if fungal rot is present to help soften the wood. We used Resistograph drills to objectively assess fungal decay and tested whether black woodpeckers preferred trees with heart rot as sites for cavity starts. In doing so we also examined the distribution of fungal decay across the tree radius, analysed location of cavity starts with respect to proximity to heart rot, and evaluated wood condition at fresh and old cavity starts. Heart rot was significantly more common in beeches (*Fagus sylvatica*) with cavity starts than in random reference beeches. Fungal decay was not evenly distributed across the tree radius, but was more prevalent both in the central and outer thirds than in the middle third. Distance to heart rot was smaller from cavity starts than from random drills, suggesting a preference to initiate cavities close to heart rot. Wood density at fresh cavity starts was significantly higher than at old cavity starts. Collectively, these findings imply that black woodpeckers prefer to excavate cavity starts in beeches with heart rot, which the woodpeckers can detect based on cues unavailable to humans. The decay is reducing the energy expenditure of the black woodpecker and is a part of the long time excavation strategy. The cavity starts are an important factor in the process of excavating the large black woodpecker cavities in beech that enhance biodiversity in managed forests. Future studies should attempt to uncover the mechanisms woodpeckers use in selecting the locations of cavity starts.

1. Introduction

The selection of an appropriate nest site is an important determinant of fitness in many species, putting considerable efforts into the selection and the construction of a nest. For example, many cup-nesting birds incur high nest loss rates due to predation, implying strong selection for well-concealed nest sites (Martin, 1995; Weidinger, 2002; Pasinelli and Schiegg, 2006). Species nesting in cavities generally show reduced nest predation and species excavating their own nest cavity (i.e. primary cavity nesters) enjoy increased nest survival compared to species using existing cavities or holes (i.e. secondary cavity nesters) (Martin, 1995). The construction of an elaborate nest may be important in sexual selection (Alcock, 2001), while the construction of a well-insulated nest in environments with large variability in weather conditions during the period of offspring rearing may affect nestling survival both directly or indirectly via carry-over effects during later life stages. In both contexts of sexual and natural selection, individuals investing more time and energy in nest-site selection and nest building may gain fitness benefits compared to individuals spending less effort in these endeavours.

Fungi softening the wood prior to excavation would decrease energy expenditure for tree cavity excavators, but might increase the risk of tree breakage. Tree cavity excavation thus involves compromises between energy costs during the building stage, short-term stability of the tree trunk to guarantee nestling survival and the possibility of re-using the nesting site over years. While many woodpecker species prefer to excavate nest cavities in wood showing clear signs of decay (e.g. Jackson and Jackson, 2004; Pasinelli, 2006), other species have been suggested to use sound wood. A particularly striking apparent example among the latter species is the black woodpecker (*Dryocopus martius*), the largest woodpecker species in the Palearctic. Excavation in the black woodpecker usually begins with a cavity start that may not be finished the same year (Glutz von Blotzheim and Bauer, 1980; Meyer and Meyer, 2001; Gorman, 2011). Trees as well as the immediate substrate at black woodpecker cavities look healthy from outside. However, whether the black woodpecker excavates cavities in sound wood or prefers fungus-infected trees for cavity construction has remained a subject of controversy for decades (Jamnicky, 1994; Meyer and Meyer, 2001; Mueller, 2004).

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In this study we evaluated four hypotheses related to cavity tree selection and cavity excavation behaviour in the black woodpecker. First, we tested whether the black woodpecker selected trees with fungal rot (i.e. heart rot) by comparing trees with cavity starts to reference trees without cavity starts. If the black woodpecker selects trees with fungal rot for cavity excavation, we expected trees with cavity starts to have lower wood resistance compared to trees without cavity starts. Wood resistance as an indicator of fungal rot was measured with a Resistograph (Rinn et al., 1996; Schepps et al., 1999).

Second, in cavity start trees with signs of fungal decay, we additionally examined whether fungal rot was evenly distributed across the tree radius. Because trees with black woodpecker cavity starts and cavities, respectively, look uninfected from outside (see above), we expected fungal decay to be more prevalent in the inner than in the outer parts of the tree radius. Third, we tested whether the black woodpecker initiated cavities at sections of a tree located near heart rot. If it did, we predicted that the distance to heart rot would be less from cavity starts than from random locations. Finally, we evaluated whether wood condition at fresh and old cavity starts differed. We expected wood at fresh cavity starts to be harder than wood at old cavity starts, owing to the softening effects of fungal decay over time at the latter.

2. Methods

2.1. Study sites

The study was conducted in the continental zone of central Europe in two woodland areas of southern Germany in 2009. Elevation of the woodland areas studied ranged from 200–600 m a.s.l. Fieldwork took part in Lower Bavaria, Germany (Kelheim, Hienheimer Forst, 48°54′N, 11°48′E), where 1246 ha were surveyed, and in the biosphere reserve Swabian Jura (Baden-Wuerttemberg (48°24′N, 09°36′E) with 6600 ha. European Beech (*Fagus sylvaticus* L.) and Norway Spruce (*Picea abies* (L.) Karst.) dominated the forests. The proportion of beech ranged from 70% in the Hienheimer Forst to 80% in the biosphere reserve of Swabian Jura.

2.2. Study trees

We focused on old beech stands (100 years and older), because the black woodpecker needs large trees for cavity excavation (tree diameter at the cavity entrance >38 cm, Glutz von Blotzheim and Bauer, 1980), and beech is the most important cavity tree species in our study areas (unpublished data). In these old beech stands, we systematically searched for black woodpecker cavity starts and cavities. For this study, we restricted our analyses to trees having only cavity starts. We focused on cavity starts to examine the wood conditions that are encountered by black woodpeckers when they begin excavating. Cavity starts were defined as rounded injuries of the bark, reaching into the wood and situated at the tree trunk with signs of beak strokes visible. None of the other woodpecker species occurring in our study forests builds cavities in large beeches lacking visual evidence of fungal decay (e.g. conks) at the height of the cavity, so we could safely assume that cavity starts considered in this study were initiated by the black woodpecker.

For each tree, we recorded the following measures: tree species, social classes proposed by Kraft 1884 (cited in Burschel and Huss (1987): 1 = tree is predominant, 2 = dominant, 3 = subdominant, 4 = suppressed, 5 = understory) in the stand, diameter at breast height (dbh), diameter at the cavity start, nearest distance of the cavity start to the next branch, exposition of the cavity (main compass directions), and age of cavity starts (fresh or old). Age of cavity start was distinguished based on wood colour, which at fresh cavity starts is much lighter than at older cavity starts.

2.3. Tree drills

We examined 30 beech trees with cavity starts. These trees were climbed and wood density at the cavity starts was recorded with a special drill (IML Resistograph). A needle of 40-cm length and 4-mm diameter was horizontally drilled into the tree. Three brad points on the head of the drilling device create a triangle with the fine needle in its centre. This anchors the drill in the bark and ensures a radial motion of the needle. The average deviation of the needle from the radial direction hardly influences the measuring results (Rinn et al., 1996).

The Resistograph measures the wood resistance at the tip of the needle. Wood-decaying fungi break down lignin and cellulose. This process softens the wood, making it less resistant to the drill and resulting in a change of power consumption which is measured electronically (Rinn et al., 1996; Schepps et al., 1999). This reflects wood resistance and is plotted against drilling depth. The resulting graph resembles an ECG (electrocardiogram). We refer to this graph as drilling profile, which allows quantification of extent of decay.

Wood resistance was recorded both electronically and on a drilling profile printout, representing the whole radius to the pith of the trunk. To make sure that we had drilled into the heart of the trunk, we inspected the pattern of annual growth rings on the printout (see Fig. 1a). On the printout, wood resistance is plotted as a curve, with low values indicating weak resistance and hence decayed wood. The method provides a reliable quantitative measure of rot (e.g. Rinn et al., 1996; Schepps et al., 1999; Gruber, 2001).

Four drills were made per tree. First, we drilled into the centre of the cavity start (hereafter referred to as HCD = horizontal cavity drill). A second and third drill was made to the left and to the right, respectively, but at the same level as the cavity start (HLD = horizontal left drill and HRD = horizontal right drill). Both HLD and HRD were directed from the trunk surface to the tree heart, with the drill direction having an angle of 45° to the HCD. A fourth drill was taken 30 cm underneath the cavity start (HUD = horizontal underneath drill). These latter three reference drills were compared with the drill through the cavity start to find out if the cavity start had been placed near heart rot. For each drill, distance to heart rot was measured on the drilling profile. We defined distance to heart rot (cm) as the distance from one centimetre after the needle had left the drilling machine to heart rot, indicated by fungal decay on the drilling profile. Heart rot in this study is defined as fungal decay in the inner layers of the tree, but not in the sapwood. The tree thus resembles a tube-like structure consisting of a softened centre surrounded by a hard zone of sound wood.

If there were multiple cavity starts in one tree, we took the largest for the HCD.

2.4. Reference trees

Within 15–20 m of each beech tree with a cavity start, another beech without cavity start (or cavity) was selected, hereafter referred to as a reference tree. We recorded social class, dbh and age class for each reference tree. Each reference tree was climbed and the same four drills as for the corresponding tree with cavity start were taken with the Resistograph at a comparable height and exposition.

2.5. Statistical analyses

The graphs of the drilling profiles from the Resistograph were visually inspected and ranked by professional arborists. If a fungus had softened the wood, the wood density in the graph dropped or the peaks flattened (Fig. 1). In such cases, the tree was considered to be infected by fungi and the wood correspondingly decayed. The relation between fungal wood decay (yes/no) and tree type (tree with cavity start/reference tree) was assessed with a Chi-square test. In addition, wood resistance values of cavity start trees and reference trees were compared with a Wilcoxon signed-rank test.

To evaluate whether fungal infections were evenly distributed across the tree radius, the graph of the horizontal cavity drilling profile over the tree radius was divided into three sections of equal size. For each section, we determined whether fungal decay was present or not. We then compared the occurrence/absence of fungal decay between sections with McNemar tests (Eliasziw and Donner, 1991).

Distance to heart rot was measured on the drilling profiles. For each tree, we assessed the distance of the cavity start and of one reference drill, respectively, to the nearest visible decay in centimetres (see above). The reference drill was randomly chosen among the HLD, HRD and HUD (see above). Distances to heart rot were compared with a Wilcoxon signed-rank test.

To examine whether wood resistance at fresh and old cavity starts differed, the outermost 9 cm of the trunk at each cavity start were divided into three parts: (1) 1–2.9 cm, (2) 3–5.9 cm, (3) 6–9 cm. For each part, wood density was compared between fresh cavity starts and old ones with Mann–Whitney *U*-tests. All analyses were done in SPSS Statistics 18.

3. Results

3.1. Comparison of trees with cavity starts to reference trees

The 30 trees with cavity starts and the 30 reference trees did not significantly differ in dbh (mean ± SD, cavity start trees = 59.8 ± 8.8 cm, reference trees = 58.9 ± 9.2 cm; paired *t*-test, $t = -0.887$, $df = 29$, $p = 0.382$), age class (Wilcoxon signed rank test, $Z = 0.00$, $p = 1$) and social position (Wilcoxon signed rank test, $Z = -1$, $p = 1$).

3.2. Condition of trees with and without cavity starts

Based on the horizontal cavity drill (HCD), 94% of the 30 trees with cavity starts showed evidence of heart rot in the visually inspected graphs of the resistogram (Figs. 1 and 2). Heart rot was significantly more often found in trees with cavity starts than in reference trees (Chi square test: $\chi^2 = 32.06$, $df = 1$, $N = 30$, $p = 0.001$). Only in two cases had black woodpeckers selected trees without signs of heart rot at the level of the cavity start for initiating excavation of the cavity.

Wood density significantly differed between matched pairs of trees with cavity starts and reference trees (Wilcoxon signed-rank test: $z = 0.196$, one-sided, $N = 30$, $p = 0.025$). Trees with cavity starts generally showed reduced wood density compared to reference trees. In seven cases, also the reference trees showed signs of wood decay.

3.3. Distribution of fungal decay

Fungal decay was unevenly distributed across the tree radius (Fig. 3). [McNemar-test: two-sided exact significance, $p = 0.005$, $N = 30$]. More specifically, the central and the outer sections, respectively, were more strongly decayed than the middle section [McNemar-test: one-sided exact significance, $N = 30$, (middle-centre-section) $p = 0.002$, (middle-outer section) $p = 0.011$)]. However,

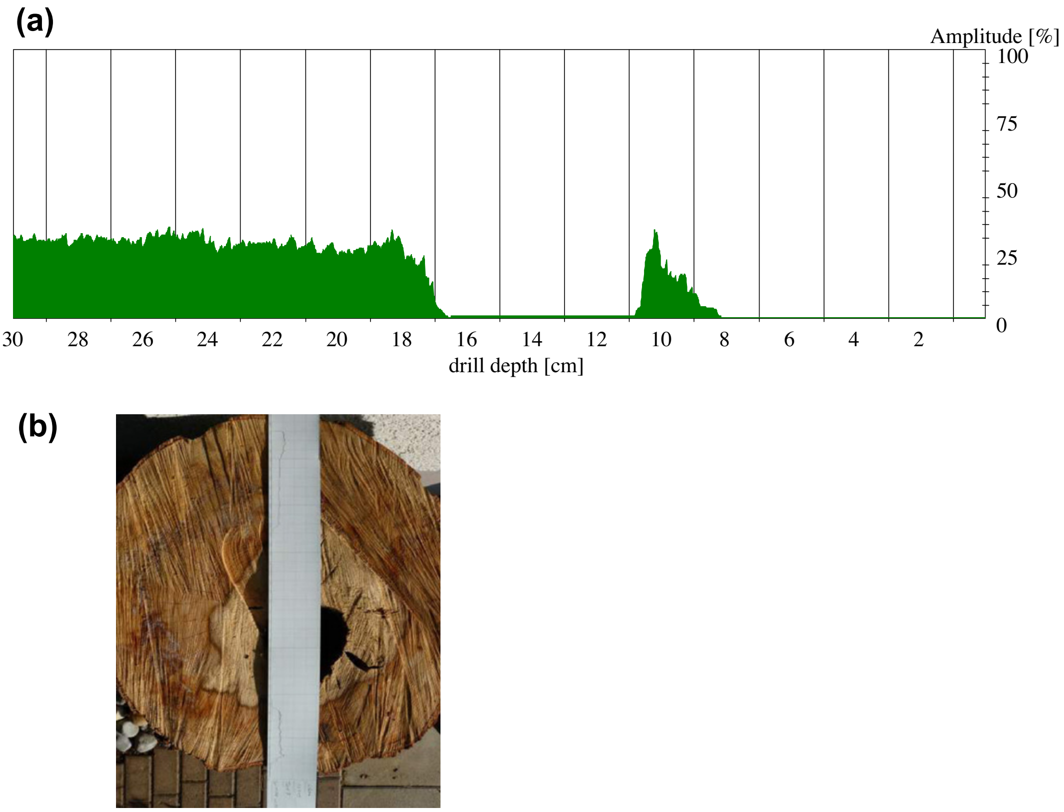

Fig. 1. Resistograph drilling profile (a) and beech section overlaid with the corresponding drilling profile (b). In panel a the drilling profile starts at 1 cm in the sapwood and ends in the tree centre, here 29 cm from the tree surface. The amplitude in percent indicates the wood resistance, i.e. wood density in relative values. The regular zigzag pattern from 18 to 30 cm is caused by variation of wood density in the tree ring mainly at the tree ring boundaries, with wood grown during spring having lower density than wood grown at other times of the year. The entrance of the cavity start extends from 1 to 8 cm. Density of the sapwood increases from 8 to 10 cm, indicating sound wood, while fungal decay has considerably softened the wood from 10 to 17 cm. In panel b, heart rot shows in light colour, making it distinguishable from the surrounding wood.

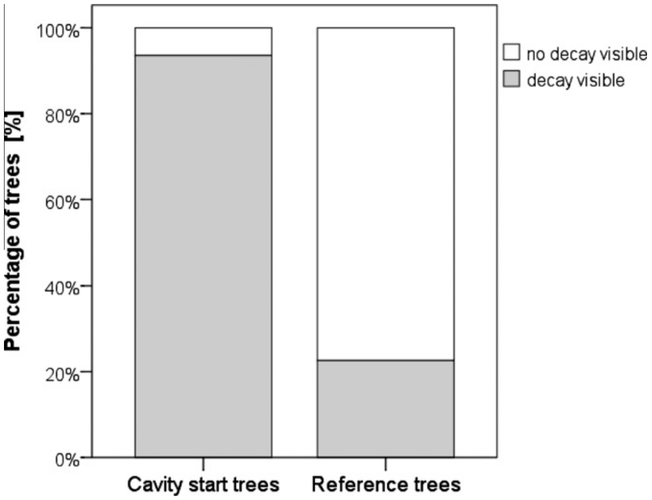

Fig. 2. Occurrence of heart rot in beeches with cavity starts ($N = 30$) and without cavity starts (reference trees, $N = 30$). Shaded = trees with heart rot, unshaded = without heart rot.

there was no significant difference between the central and outer sections ($p = 0.387$).

3.4. Distance to heart rot

Distance from cavity starts to heart rot was significantly smaller than the distance from reference locations on the same tree to heart rot (Wilcoxon test: $z = -4470$, two sided, $N = 30$, $p = 0.0001$ (Fig. 4).

3.5. Wood condition at fresh and old cavity starts

At the outermost part 1, wood density at fresh cavity starts ($N = 8$) was significantly higher than at old cavity starts ($N = 22$) (Mann–Whitney *U*-test: $U = 153$, one-sided $p = 0.03$, Fig. 5). No differences between fresh and old cavity starts were found for part 2 ($U = 133$, $p = 0.194$) and for part 3 ($U = 129$, $p = 0.254$), respectively.

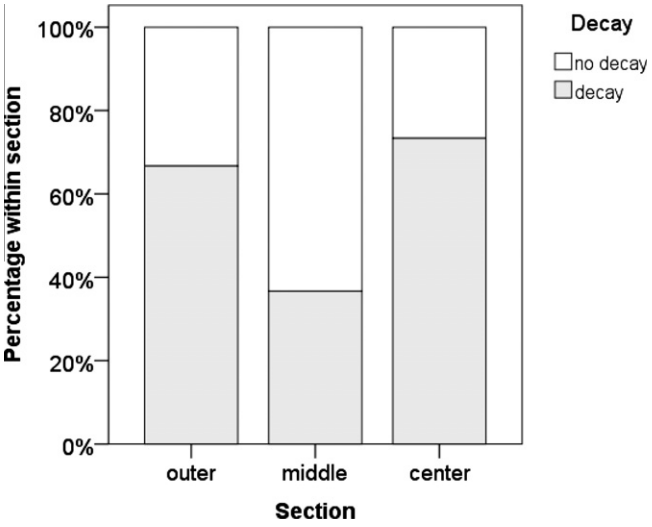

Fig. 3. Distribution of fungal decay across the tree radius at the level of the cavity starts. Percentage of trees with and without fungal decay, respectively, are shown for each of three sections. See text for explanations of the sections. Shaded = fungal decay present, white = no fungal decay. $N = 30$ trees per section.

Fig. 4. Distance to heart rot from drills at cavity starts and at reference locations on the same trees. One of the three reference drills per tree (i.e. HLD, HRD, HUD) was randomly chosen for comparison. $N = 30$. The horizontal lines show the medians, boxes depict the 25% and 75% quartiles and the vertical lines indicate the range of the data.

4. Discussion

Our study showed that heart rot was significantly more common in beeches with cavity starts than in random reference beeches (hypothesis 1). At the level of the cavity start, fungal decay was not evenly distributed across the tree radius (hypothesis 2, Fig. 3). However, our expectation of stronger decay of the inner than outer tree sections was only partly supported, because there was a difference between the inner and middle thirds of the tree radius, but no significant difference between the inner and outer thirds. The black woodpecker initiated cavities adjacent to heart rot (distance to heart rot was smaller from cavity starts than from reference locations; hypothesis 3). Wood resistance at fresh cavity starts was significantly higher than at old cavity starts (hypothesis

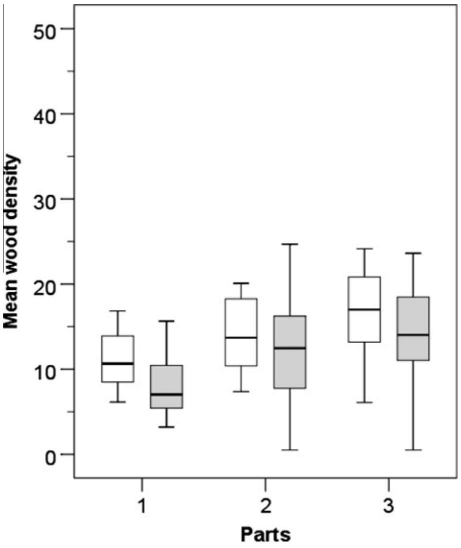

Fig. 5. Wood density at the outermost 9 cm of a tree in relation to age of cavity starts. Part 1 = 1–2.9 cm, part 2 = 3–5.9 cm, part 3 = 6–9 cm. White boxes = fresh cavity starts ($n = 8$), shaded boxes = old cavity starts ($n = 22$). The horizontal lines show the medians, boxes depict the 25% and 75% quartiles and the vertical lines indicate the range of the data.

4), but only for the 3 cm immediately inward from the start. Collectively, these findings imply that black woodpeckers prefer to excavate starts in beeches with heart rot and that cavity starts are preferentially placed in the immediate vicinity to heart rot.

4.1. Condition of trees with and without cavity starts

Most Holarctic woodpecker species have been shown to select trees softened by fungi for cavity construction (e.g. Utschick, 1991; Jackson and Jackson, 2004; Gorman, 2004; Pasinelli, 2006). In the black woodpecker, the largest Holarctic woodpecker species, the association of cavities and trees infected by fungi has been discussed controversially. Jamnicky (1994), examining woodchips of three black woodpecker cavities in beech, found evidence for decayed wood in two cases and sound wood in the other. Studies, which included cavity inspections, also regularly reported of cavities infected with heart rot (Meyer and Meyer, 2001; Sikora, 2007). Others, neither testing for wood decay itself nor including cavity inspections, found no visual evidence for decay, because nest trees appeared to be vital and healthy (Utschick, 1991; Müller, 2005). However, a systematic study comparing wood conditions at cavity starts with conditions at comparable positions in available trees has not been carried out so far.

In our study, black woodpecker significantly preferred trees with heart rot to start excavating a cavity, as 94% of all beech trees ($n = 30$) showed evidence of internal fungal decay at the level of the cavity starts. Heart rot occurred almost five times more often in cavity start trees than in reference trees. The woodpeckers thus seemed to have been able to detect trees with heart rot in the presence of sections of sound sapwood surrounding the heart rot. It is possible that woodpeckers are able to acoustically detect internal fungal decay by tapping on the tree with their bill or just “feel” the difference in wood resistance. Alternatively, trees with heart rot may also show fungal decay on the stem surface, which the woodpeckers may use as cues for the internal tree status. In fact, fungal decay was more pronounced at the outer than at the middle sections of the tree radius.

Whatever the mechanisms responsible for cavity tree selection are, our results strongly suggest that a beech selected by the black woodpecker for cavity excavation is usually already infected by wood-decaying fungi, even when the tree looks healthy from outside. The two cavity starts found in trees without evidence of fungal decay were possibly initiated by inexperienced individuals. However, it is currently unknown whether cavity excavation behaviour is subject to learning during a woodpecker’s life.

4.2. Location of cavity starts in relation to heart rot

Black woodpeckers initiated cavity starts at sections of a tree located near heart rot, since distances to heart rot were significantly less from cavity starts than from locations close-by. This indicates that woodpeckers select those locations with the relatively smallest amount of sound sapwood between the tree surface and the decayed wood. Again, we currently do not understand how the black woodpecker finds these places, but the possible explanations given above (tapping, enhanced fungal decay on the stem surface) also apply here. Nevertheless, on some trees, small cavity starts existed close to large ones, suggesting that trial-and-error may be part of the tactic, at least in some individuals.

4.3. Wood condition at fresh and old cavity starts

In our study, wood density of the outermost 3 cm of the tree was significantly lower at old cavity starts than at fresh ones (Fig. 5). These results suggest that injuries of the bark made by the black woodpecker enhanced fungal colonisation and subsequent decay of the sapwood. Woodpeckers are occasionally discussed as vectors of fungi (e.g. Jackson and Jackson, 2004; Farris et al., 2004). Whether woodpeckers were carriers of wood-inhabiting fungi in our study is unknown. Farris et al. (2004) reported that wood-inhabiting fungi were recovered in significantly greater frequencies from the bill of woodpeckers than from the bill of non-cavity-nesting species, suggesting that woodpeckers may indeed act as vectors of fungi. Such dispersal of fungal spores or hyphae is likely to contribute to the process of decay. Woodpeckers may also support the wood-decaying action of fungi by the mechanical degradation of wood through their foraging and excavation activities.

4.4. How do fungi enter the tree?

Fungi can enter the tree centre through old broken limbs, enabling heart rot fungi to bypass the tree’s sapwood defences (Conner et al., 1976; Butin, 1983; Jackson and Jackson, 2004; Schweingruber, 2007). Injuries not associated with branches are unlikely to result in heart rot (Jackson and Jackson, 2004). The sapwood’s parenchyma seals the site of a wound and is most active in setting up biochemical and physical barriers in the outer section of the trunk (M. Walter, personal communication). Because of these barriers, it is easier for fungi to infect the centre of the tree over the branches than from the outer wood sections of the stem. A woodpecker opening the wood body in the sapwood section is softening the wood, too, but this activity enhances very different fungus species, which are less destructive for the wood body than heart rot fungi (Butin, 1983). Thus, there is fungal decay from two sides: strong decay spreading from inside of the tree by fungi entering over dead branches or old injuries and weak decay at the outside of a tree initiated by the activity of woodpeckers, followed by fungal infections.

From an internal pocket of decay, the infection grows up- and downward. In an attempt to isolate the decay, the tree builds a compartmentalised transition zone where the decay is stopped. The isolation includes physical and chemical barriers (toxic phenols) (Butin, 1983; Jackson and Jackson, 2004). A cavity in a well-compartmentalised pocket of decay in a living tree is easier to excavate than in sound wood and still can last for decades. Over a 25-years-period, only about 1% of all black woodpecker cavities in beeches were lost by storm and 4.6% by harvesting (Meyer and Meyer, 2001).

Not all fungal decay equally facilitates woodpecker excavation. The important fungi for woodpeckers are heart rot fungi (brown rot and white rot). Root rots or butt rots also soften the wood, but do so close to the ground. Woodpeckers avoid excavating cavities close to the ground, likely due to the associated increased predation risk (Jackson and Jackson, 2004).

4.5. Dynamics of cavity excavation

For most woodpecker species, cavity excavation is often done only 2–6 weeks before nesting – and often takes only 2–3 weeks. Excavation in the black woodpecker usually begins with a cavity start that is not always finished the same year. Instead, the black woodpecker frequently re-uses cavities over several years (Gorman, 2011). On average, black woodpeckers return within 5–6 years and finish a cavity (Glutz von Blotzheim and Bauer, 1980; Meyer and Meyer, 2001). However, cavities can be at times excavated much faster, in softwood (*Populus* sp., *Salix* sp.) within 2 weeks and in beech within 3–4 weeks (Glutz von Blotzheim and Bauer, 1980; Meyer and Meyer, 2001; Gorman, 2011). Not all cavity starts will eventually be completely excavated. Gorman, (2004) reported that when a new pair takes over a territory, it always excavates a new cavity. The annual number of new cavities is about 0.1/100 ha or 1/100 ha in 10 years (Meyer and Meyer, 2001). On average, an adult black woodpecker finishes just one or two cavities in its life.

In our study areas, starts (*n* = 30) were much rarer than excavated cavities and ranged from 1.1% (Swabian Jura, *n* = 119) to 25.6% (Kelheim, *n* = 55) of all cavity trees. Meyer and Meyer (2001) studied 570 black woodpecker cavity trees for over 24 years in Thuringia, Germany. About 14% of all cavities were cavity starts, about 59% were intact nest sites, 12% were in poor condition (roosting sites), and almost 15% were no longer suitable for woodpeckers. In contrast, Günther, (2005) recorded 74% cavity starts, 9.5% nest sites and 16.5% unsuitable cavities (*n* = 1020) in mixed beech (73%) and pine (26%) forests. These studies indicate cavity starts are a part of the excavation process in the black woodpecker. Opportunities for fungi to intrude a bole increase with forest age (Niedermann-Meier et al., 2010). We hypothesise that in old forests increasingly more trees with heart rot are available for cavity excavation and that variation in the number of cavity starts across studies may be related to (past) forestry practise and forest age in the respective study areas.

5. Conclusions

Forestry is moving toward production of beech timber in 100 years and less (Knoke and Schulz-Wenderoth, 2001), and this may not provide the older trees needed by woodpeckers. The infection of wood with fungi is a question of tree vitality and age. A lack of infected trees and black woodpecker cavities, which play a core role for forest biodiversity in managed forests (Meyer and Meyer, 2001; Gorman, 2011), will put many other forest species under pressure.

Forestry (timber production) and the black woodpecker seem to focus on the same beech trees with strong boles without branches for 10 m or more. Our study shows that the black woodpecker prefers to excavate cavity starts in trees with heart rot which is invisible to humans. Nowadays, forest management plans in many countries protect woodpecker trees (Wimmer and Zahner, 2010), which are of limited economic value. However, protection of trees with cavity starts should be considered as well because these trees are an essential component in the longterm genesis of large cavities.

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