Foraging behaviour of the Eurasian Three-toed Woodpecker Picoides tridactylus in its peak abundance after wildfire

Versluijs, Martijn

2022-02-02

Versluijs , M , Mikusinski , G & Roberge , J-M 2022 , ' Foraging behaviour of the Eurasian Three-toed Woodpecker Picoides tridactylus in its peak abundance after wildfire ' , Ardea , vol. 110 , no. 1 , pp. 75-88 . https://doi.org/10.5253/arde.v110i1.a2

http://hdl.handle.net/10138/353815
https://doi.org/10.5253/arde.v110i1.a2

Ardea110_1536765_Versluijs

Versluijs *et al.*: FORAGING BEHAVIOUR OF EURASIAN THREE-TOED WOODPECKER AFTER WILDFIRE

Foraging behaviour of the Eurasian Three-toed Woodpecker *Picoides tridactylus* in its peak abundance after wildfire

Martijn Versluijs[1, 2*], Grzegorz Mikusiński[3, 4], Jean-Michel Roberge[2, 5]

Versluijs M., Mikusiński G. & Roberge J.-M. 2022. Foraging behaviour of the Eurasian Three-toed Woodpecker Picoides tridactylus in its peak abundance after wildfire. Ardea 110: ###–###. doi:10.5253/arde.v110i1.a2

In the boreal biome, forest fires are the most important natural disturbance influencing tree substrate availability and quality for a range of specialized species. This includes the Eurasian Three-toed Woodpecker *Picoides tridactylus*, which is known to promptly utilize burned forest habitats. However, there are no studies addressing the foraging behaviour of this woodpecker in forests affected by wildfire. Such knowledge could assist the development of efficient post-fire management strategies which are in line with biodiversity conservation objectives. This study describes the foraging behaviour of the Eurasian Three-toed Woodpecker during the breeding season in a forest area of 13,100 ha in south-central Sweden affected by a major wildfire in 2014. During the second breeding season after fire, we used instantaneous sampling where we observed the foraging behaviour of 28 individuals during a total of 1681 observation minutes. Our results suggest that Norway Spruce *Picea abies* and larger diameter trees (DBH > 25 cm) are important foraging substrates. However, data on time spent foraging on the different substrates suggest that Scots Pines *Pinus sylvestris* also are important. In particular, we identified the importance of the root collars, where excavation into sapwood was the main foraging method. Our study was performed during a clearly visible peak of Eurasian Three-toed Woodpecker abundance and this may suggest that the level of food resources available was very high which led to observed foraging patterns not necessarily observed in other types of habitats.

Key words: Fennoscandia, fire, foraging observations, habitat use, root collars

[1] The Helsinki Lab of Ornithology (HelLO), Finnish Museum of Natural History, University of Helsinki, FI-00014 Helsinki, Finland;

[2] Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences (SLU), SE-901 83 Umeå, Sweden;

[3] School for Forest Management, Swedish University of Agricultural Sciences, Box 43, SE-739 21 Skinnskatteberg, Sweden;

[4]Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-730 91 Riddarhyttan, Sweden;

[5]Swedish Forest Agency, Box 284, SE-901 06 Umeå, Sweden;

[*]corresponding author (martijnversluijs@hotmail.com)

The Eurasian Three-toed Woodpecker *Picoides tridactylus* (Three-toed Woodpecker from hereon) is often classified as an old-growth forest specialist (Pakkala *et al.* 2002, Pechacek & d'Oleire-Oltmanns 2004, Wesołowski *et al.* 2005, Stachura-Skierczyńska *et al.* 2009). However, several studies have shown that this species benefits from large-scale natural disturbances such as fire (Fayt 2003, Versluijs *et al.* 2017). In south-central Sweden, Gustafsson *et al.* (2019) demonstrated a dramatic, but short-lasting increase in local abundance of Three-toed Woodpeckers two years after a large wildfire. In the boreal biome, forest fires are an important natural disturbance, shaping complex habitats (Hunter 1993, Esseen *et al.* 1997, Angelstam 1998, Kuuluvainen 2002) and fundamentally affecting forest biodiversity (Lowe *et al.* 2012, Hekkala *et al.* 2014, Hjältén *et al.* 2017). It is expected that fire influences tree substrate availability and quality (Stokland *et al.* 2012, Hjältén *et al.* 2017, 2018), which may result in changes in both the abundance and assemblage composition of saproxylic insects, the main food source of Three-toed Woodpeckers (Hyvärinen *et al.* 2009, Hekkala *et al.* 2014, Kärvemo *et al.* 2017). Currently, due to modern forestry practices and fire suppression, large wildfires have largely disappeared from the European boreal forest and when fires occur, salvage logging is frequently conducted within two years to reduce economic loss, allow faster regeneration of desired tree species and prevent the spread of insect pests (Müller *et al.* 2019). However, salvage logging is recognized as an important threat for many organisms associated with burned forest (Thorn *et al.* 2020). Żmihorski *et al.* (2019) have shown that the Three-toed Woodpecker occurred significantly less frequently in salvage-logged forest in comparison with burned but not salvaged forests. Yet, the relation between Three-toed Woodpeckers and burned habitat is poorly understood and therefore more studies addressing their ecology, including foraging behaviour, in forests affected by wildfire are required.

A study by Versluijs *et al.* (2020) performed in forest stands subjected to prescribed burning in northern Sweden showed that Three-toed Woodpeckers preferred foraging substrates that can generally be described as freshly dead trees with a diameter at breast height (DBH) of more than 15 cm. Norway Spruce *Picea abie* and birch *Betula* spp. were the preferred tree species. Additionally, it was observed that bark scaling was the main foraging method. In a study performed in Finland, Scots Pines *Pinus sylvestris* damaged by prescribed burning were intensively used for sap drinking during the first weeks after fire (Pakkala *et al.* 2017). Similar foraging strategies have been reported in the American Three-toed Woodpecker *Picoides dorsalis* and Black-backed Woodpecker *Picoides arcticus,* two species closely related to the Eurasian Three-toed Woodpecker (Murphy & Lehnhausen 1998, Nappi & Drapeau 2011, Nappi *et al.* 2015).

The Eurasian Three-toed Woodpecker is included in annex I of the EU Birds Directive and red-listed as ‘near threatened’ in Sweden. Furthermore it is considered a model species for biodiversity conservation and management in boreal and high-altitude forests (Robles & Pasinelli 2014). This is due to its potential importance as an indicator species of forest structural complexity and species diversity (Mikusiński *et al.* 2001, Roberge & Angelstam 2006, Versluijs *et al.* 2019). The woodpecker’s habitat requirements have also been used to provide quantitative targets for the amount of deadwood in managed forests (Bütler *et al.* 2004). Additionally, Three-toed Woodpeckers fulfil an important keystone role by providing cavities for a variety of secondary cavity users among mammals, birds and invertebrates (Pakkala *et al.* 2018b). This is of particular importance in boreal forests, where decay-formed tree cavities are rare (Andersson *et al.* 2018). Knowledge about the foraging behaviour of the Three-toed Woodpecker after wildfire is needed in order to assess the effect of an expected increase in fire frequency in Northern Europe (Lehtonen *et al.* 2016), which warrants development of efficient post-fire management strategies that are in line with biodiversity conservation objectives.

The objective of this study was to describe the foraging behaviour of the Three-toed Woodpecker during the breeding season in forest recently affected by wildfire. It was performed in an area of 13,100 ha in south-central Sweden impacted by a major wildfire in 2014. This wildfire was the largest in Sweden for at least a century. Our study is based on field observations conducted in 2016, i.e. during the peak of the species' post-fire abundance (Gustafsson *et al.* 2019). We studied the selection of individual foraging substrates by the woodpecker and the allocation of foraging time among substrates with different characteristics.

METHOD

Study area

The study area was located in the province of Västmanland in south-central Sweden (59.8°N, 16.1°E; Figure 1). Before the fire, the area was highly forested (85%) and represented typically managed south-boreal forest landscapes with even-aged stands spanning from recently logged to mature forests. Low-productive Scots Pine forests dominated (53%), with 22% of mixed coniferous forests (i.e. Pine and Norway Spruce *Picea abies*), 18% of stands dominated by Norway Spruce and very few stands rich in deciduous trees (Gustafsson *et al.* 2019). Analysis of aerial photos taken in 2014 before the wildfire estimated that about 14% of the forest area was covered by young stands or was recently logged (tree height < 7 m), 70% by middle-age stands (tree height 7–20 m) and 16% by older stands (tree height > 20 m; Nilsson *et al.* 2014). The fire started 31 July 2014, and within a few days spread across 13,100 ha (Gustafsson *et al.* 2019). Fire severity was generally high (highest in the northern part of the fire area) and caused extensive tree mortality (Nilsson *et al.* 2014, Gustafsson *et al.* 2019). After the fire had been extinguished, a large salvage logging operation was implemented in parts of the area, approximately 15% of the burned area was left as post-fire retention on and around the cutting blocks (mostly on unproductive sites like pine swamp stands, dry pine forests on shallow soil and border zones to mires). Salvage logging was mostly concentrated in the northern parts of the burnt landscape, whereas in the south approximately 7600 ha were left untouched.

The impact of the fire on forest ecosystems has been followed in 2062 circular plots with radius of 10 m distributed in a regular grid with 300 m between the plots' central points (Nilsson *et al.* 2014). This monitoring was based on an analysis of high-resolution aerial photographs taken before the fire (spring 2014), directly after the fire (autumn 2014), as well as a series of such photographs taken annually since 2015 (Björn Nilsson, unpubl. data). We used those data to characterize the areas where observations of the foraging behaviour of the Eurasian Three-toed Woodpecker were made (see below).

Focal observations

The entire study area was divided into systematically distributed 1 × 1 km (100 ha) plots, from which 17 were selected. The selection of four initial plots was based on observation of the species in parallel bird counts performed in the burned area. Then, additional observation plots were selected using the rule of at least 1 km spatial separation between the plots, presence of unlogged forest stands and securing good access for the observer (Figure 1). Territory sizes of Three-toed Woodpeckers typically range between 60–340 ha (Pakkala *et al.* 2002, Pechacek 2004, Pechacek & d'Oleire-Oltmanns 2004), thus this spatial separation of the plots led to the assumption that repeated observations from the same quadratic plots belonged to individuals from the same territory, while individuals observed in different plots are unlikely to be the same. According to the sampling of high-resolution aerial photographs in spring 2014 (9–12 circular plots in each of the 1 × 1 km plots included in this study), Scots Pine was the most numerous tree species with an average canopy cover of 69% (range: 36–93%). According to annual follow-up, on average, only 7.5% of all trees were healthy and undamaged in 2016, while damaged trees and standing dead trees represented 9.7% and 43.8% of the initial cover of living trees. Of the living trees observed before fire, on average some 18.3% were estimated to be downed (logs) in 2016. More detailed description of the 1 × 1 km study plots based on the sampling is presented Table S1.

We used the same observation protocol as in Versluijs *et al.* (2020). However, the present study was performed in another region located several hundred kilometres farther to the south, the types of fires differ (small controlled prescribed fires in Versluijs *et al.* 2020 vs. a large wildfire in the present study) and the study designs differ. From the end of April to the end of June in 2016, the 17 plots were surveyed multiple times for the presence of Three-toed Woodpeckers. The woodpeckers were located by walking slowly through selected study plots. Both auditory (drumming, pecking sounds of foraging woodpeckers and calls) and visual cues were used to detect the birds. Once a bird was found, it was observed until it flew out of sight (this is hereafter referred to as an ‘observation session’). Observation distance was more than ten meters from the bird to avoid disturbances. Instantaneous sampling (i.e. fixed interval time point; Martin and Bateson 1993) was used: we recorded every minute if the individual was foraging or not. When the woodpecker was foraging, the following variables were recorded: estimated foraging height, foraging location (trunk, branch or root collars; see Figure S1 for example of root collars) and substrate diameter at foraging height (estimate using the woodpecker’s body length, i.e. 20–24 cm, del Hoyo *et al.* 2020, as a reference). Foraging height was divided into four classes, 1 (0–2 m), 2 (2–5 m), 3 (5–10 m) and 4 (>10 m). Three foraging techniques were distinguished (Villard 1994, Murphy & Lehnhausen 1998): (1) bark scaling accompanied by surface pecking, (2) excavation into sapwood and (3) sap-feeding. For each substrate selected by a Three-toed Woodpecker, the following variables were recorded: tree species (Scots Pine, Norway Spruce, birch, Aspen *Populus tremula* and other deciduous trees), diameter at breast height (DBH) in 10 cm classes: (1) 5–15 cm, (2) 15–25 cm, (3) 25–35 cm, (4) 35–45 cm, tree health status (hereafter ‘decay stage’ for conciseness) based on four classes (Thomas *et al.* 1979): (1) healthy living tree, (2) dying tree which is still alive, (3) recently dead tree with 100% bark attached, (4) dead tree with <100% bark attached. To determine the availability of substrates in the immediate vicinity of the selected trees, all variables pertaining to substrate characteristics were recorded also for the nearest tree (living or dead) with a DBH > 5 cm (hereafter ‘nearest available tree’).

Statistical analysis

SELECTION OF FORAGING SUBSTRATES WITH DIFFERENT CHARACTERISTICS

To analyse selection for different foraging substrates as a function of their characteristics, a conditional logistic regression was used with the clogit function from the ‘survival’ package in R (Therneau & Lumley 2009). Conditional logistic regression is a type of logistic regression model based on matched case-control pairs. Here, each used tree was matched with the nearest available tree, hence allowing the model to control for local habitat differences regarding substrate availability. Unfortunately, our sample size is not large enough to allow random factors in the models, i.e. in mclogit (mixed model conditional logistic). Therefore, to account for differences in the number of trees used by an individual, we statistically weighted the data according to the number of trees used. Thus, each woodpecker individual contributed only one degree of freedom in the model regardless of its number of observations (Desrochers 1992). This approach allowed us to use all observations while avoiding pseudo-replication (Machlis *et al.* 1985). Tree species, DBH and decay stage were included as independent variables. Backward elimination was used to select the best model.

Manly selection ratios (Manly *et al.* 2002) were computed for each substrate characteristic found to be the best predictor according to the conditional logistic regression models. Selection ratios are based on the ratio between the use of a given substrate by the woodpecker and its availability (i.e. the nearest available tree). The substrate type is considered ‘preferred’ when the 95% confidence interval (CI) of its selection ratio is >1, as ‘avoided’ when the 95% CI < 1 and as used proportionally to its availability when the 95% CI includes 1 (Manly *et al.* 2002).

FORAGING BEHAVIOUR AS MEASURED THROUGH FORAGING TIME

To determine the allocation of foraging time among foraging substrates, we analysed time spent foraging on a specific substrate (number of foraging minutes per observation session) in relation to substrate characteristics. Because we collected foraging behaviour at one-minute intervals, time spent foraging in relation to tree species, DBH and decay stages were analysed using a generalized linear mixed model (GLMM) with Poisson distribution and random effects. We included the interaction with the bird’s sex in the model whenever significant to control for intersexual differences. Additionally, plot and observation session were included as random variables, and the logarithm of total observation time per session as an offset. Furthermore, the foraging position on the tree in terms of foraging height and substrate diameter at foraging height was modelled. Foraging height was collected as categorical data (see above ‘Focal observations’ section), therefore we used the same GLMM model structure as previous described. A linear mixed model (LMM) was used to determine the importance of substrate diameter at foraging height. In all models we used backward elimination to select the best model. All foraging sessions longer than five minutes were included in the analyses pertaining to foraging time. Due to the variation in the length of observation sessions, the total observed foraging time on a given substrate per observation session could not be used directly in the presentation of the results. Instead, we plotted the predicted model outcomes where we corrected for observation session length.

RESULTS

Three-toed Woodpeckers were found in 16 of the 17 surveyed plots. In total, we collected 1681 minutes of observations from 28 different individuals (13 females and 15 males), based on the assumption that woodpeckers in different plots are different individuals. For the 13 females we collected data based on 827 minutes of observations. For the 15 males, we collected data based on 854 observation minutes. In total, 466 utilized trees formed the basis for assessing foraging substrate selection and foraging time (Table 1). See Table S1 for a detailed overview of utilized trees belonging to tree species and decay stages.

Selection of foraging substrates with different characteristics

Tree species ($P < 0.001$), decay stage ($\chi^2_1 = 6.8$, $P < 0.001$) and DBH ($\chi^2_1 = 13.02$, $P < 0.001$) predicted foraging substrate characteristics (Table 2). Sex was not significant in the model, nor was any interaction. Three-toed Woodpeckers were less likely to be found foraging on Pine and birch than on Spruce. Pine was used less than proportionally to its availability while Spruce was used more than proportionally to its availability (Figure 2A). Dying trees (decay stage 2) were avoided, dead trees with <100% bark attached (decay stage 4) were near-significantly preferred, while living trees (decay stage 1) and recently dead trees (decay stage 3) were used proportionally to their availability (Figure 2B). Additionally, trees of DBH ≥ 25 cm (i.e. belonging to the categories 25–35 and 35–45 cm) were preferred (Figure 2C).

Foraging behaviour as measured through foraging time

Bark scaling was the most common foraging method, accounting for 93.6% of the foraging time (Figure 3A). The remaining 6.4% of the foraging time was dedicated to excavating; sap-feeding was not observed. The trunk was the most common foraging location, representing 79% of the foraging time (Figure 3A). Furthermore, approximately 17% of the foraging time was spent on root collars of standing trees (Figure 3A). The root collars of Pines were more important for Three-toed Woodpeckers than root collars of other trees species: of the total foraging time on root collars, 99% was recorded on Pines (Figure 3B). When foraging on root collars, excavating into sapwood was the main foraging technique (Figure 3B). Only one male was found foraging on a fallen tree: a freshly dead Pine. However, this foraging time (20 minutes during one single observation session) was not enough to be considered in the analysis. Average diameter of the foraging substrate at foraging height was 17.3 cm and this did not differ between sexes ($\chi^2_1 = 0.16$, $P = 0.677$). Preferred foraging height did differ significantly between sexes ($\chi^2_3 = 10.5$, $P = 0.014$). Both male and female spent more foraging time in the higher part of the tree (>10 m) compared with the other individual height categories (0.2, 2–5 and 5–10 m, respectively), but males spent substantially longer time than females on the lower part (<2 m) of the trees (Figure 4).

The observed foraging time on different tree species and trees belonging to different decay stages also differed between sexes (interaction of sex with tree species: $\chi^2_2 = 21.25$, $P < 0.001$, decay stage: $\chi^2_3 = 12.4$, $P = 0.006$). Both females and males spent more foraging time on Pine compared with birch and Spruce (Figure 5A). Moreover, males spent more of their foraging time on birch compared with females. For both females and males, decay stage 3 had the highest mean predicted foraging time (Figure 5B). Males spent more of their foraging time on recently dead trees (decay stage 2) compared with females. Foraging time differed significantly among DBH classes ($\chi^2_3 = 25.07$, $P < 0.001$), a pattern which was consistent between sexes. The woodpeckers spent most time on trees with DBH of 5–35 cm (i.e. categories 5–15, 15–25 and 25–35 cm).

DISCUSSION

To our knowledge, this is the first study quantifying the foraging behaviour of the Eurasian Three-toed Woodpeckers in forests affected by wildfire. The study, performed in boreal Fennoscandia, used simultaneous measures of the selection of foraging substrates with different characteristics and foraging behaviour measured through foraging time. Our results stress that important foraging substrates are spruce, dead trees, as well as trees with a DBH larger than 25 cm. The preference of Norway Spruce as foraging substrate in forests dominated by Scots Pine is in line with other studies showing that Spruce is the preferred tree species (Fayt 1999, Zhu *et al.* 2012, Versluijs *et al.* 2020). However, though Pines were selected less than based on their availability, the time Three-toed Woodpeckers foraged on Pine trees during observation sessions was found to be higher than for birch and Spruce (Figure 5A). The latter suggests that the woodpeckers spend more foraging time per selected Pine tree. Indeed, when calculating the average foraging time per tree, our data shows that the Three-toed Woodpeckers forage on average 3.2 ± 3.24 min (±SD) on birch, 3.8 ± 1.75 min on Pines and 2.8 ± 2.4 min on Spruce. Nevertheless, when splitting up the average foraging time spent on a Pine tree between foraging locations, we can see that the average foraging time when foraging on the trunk is 2.7 ± 1.2 min and 4.8 ± 2.3 min when foraging on root collars. Thus, our results indicate that longer foraging durations on Pines may be because of the importance of root collars of Pines as foraging substrate for Three-toed Woodpeckers. Furthermore, approximately 17% of the total foraging time was spent on the root collars of this species. The main foraging technique when foraging on root collars was excavating into sapwood, which probably explains the relatively long foraging time of woodpeckers on Pines. Pechacek (2006) found that pecking (that together with digging best corresponds to excavating in our study) was the most time-consuming foraging behaviour of another subspecies of Eurasian Three-toed Woodpecker *P. t. alpinus* in the German mountains. However, to our knowledge no other studies have described the importance of root collars for Three-toed Woodpeckers. Neither was this behaviour observed in woodpeckers foraging in areas being subject to prescribed burnings in northern Sweden (Versluijs *et al.* 2020). We suspect that a high abundance of wood-boring arthropods, most likely beetle larvae from the family Buprestidae or Cerambycidae, attracts Three-toed Woodpeckers to forage on the root collars even if access to this resource means higher energetic effort. Pines are fire resistant (Fernandes *et al.* 2008), which results in lower mortality and more lightly charred trees. Lightly charred snags could harbour a higher abundance of wood-boring beetle larvae; Nappi *et al.* (2010) found higher numbers of Cerambycidae in lightly vs. severely charred snags. Colonization of fire-affected trees by the beetles is expected to happen based on changes in the chemical composition of trees. It has been found that trees which experience higher stress had significant higher ethanol concentrations and this resulted in higher abundance of wood-boring arthropods (Kelsey & Joseph 2003, Kelsey & Westlind 2017). Additionally, the root collars of the more fire-resistant Pine are usually thicker than those of Spruce and as such, less susceptible to rapid desiccation that prevents colonization by wood-living arthropods.

In the present study, bark scaling was the most common foraging method accounting for 93.6% of the foraging time, which corroborates previous research suggesting that the Three-toed Woodpecker is a specialist closely associated with bark beetles (Curculionidae, Scolytinae) as main prey (Fayt 1999). Sap-feeding was not observed in this study. This could possibly be explained by the fact that the utilization of sap is more common in the pre-nesting period (Pakkala *et al.* 2018a). However, our observation period (April until the end of June) overlaps with the pre-nesting period. It also overlaps with the observation periods used in Versluijs *et al.* (2020) and Pakkala *et al.* (2018a). In those studies, it was shown that Three-toed Woodpeckers use up to 14.7% of their foraging time in forests being subject to prescribed burnings (Versluijs *et al.* 2020) and between 18–33% in mature forests (Pakkala *et al.* 2018a, Versluijs *et al.* 2020) for sap-feeding. It could be that a higher tree mortality after wildfire (62.1 ± 13.8% (±SD); Table S1) compared to prescribed burning (33.1 ± 11.7%; Versluijs *et al.* 2017, 2020) resulted in a lower availability of living trees for sap-feeding.

The average diameter of the foraging substrate at foraging height was 17.3 cm, which is comparable with results obtained in forests subjected to prescribed burning and unburned forest (Versluijs *et al.* 2020). In our current study, males spent more time on the lower part of the tree than females, which is in accordance with what was found in other forests (Hogstad 1977, 1991, Pechacek 2006, Zhu *et al.* 2012, Versluijs *et al.* 2020). These findings confirm that intersexual niche-partitioning is consistent over a large geographical range and within different forest habitats. As proposed by Pechacek (2006), males have larger bills than females and thus they are better equipped to cope with both thicker bark and deeply entrenched energy-rich wood-boring cerambycid larvae in the lower parts of trees. Females, however, may avoid these difficult substrates and forage higher in trees and even on branches with thinner bark. These areas of the tree tend to harbour mostly small spiders and bark beetles (Jakuš 1998, Foit 2010). Furthermore, the woodpeckers seemed to avoid dying trees. Trees dead for a longer time (decay stage 4) were near-significantly used more than proportionally to their availability. Recently dead trees (decay stage 3) were neither selected nor avoided, however, mean foraging time suggests that Three-toed Woodpeckers did spend most of their foraging time on these trees. This latter observation is in line with earlier studies reporting that Three-toed Woodpeckers prefer such fresh snags (Hogstad 1991, Pechacek 2006, Versluijs *et al.* 2020). The above-mentioned suggestion of a trend for a preference for trees in decay stage 4 could be due to limitations of the decay-stage classification that we used. Bark status (100% bark attached for stage 3 and <100% for stage 4) may not be a reliable indicator of decay stage after wildfire, where many newly killed trees lose patches of bark very quickly due to the extreme heat during the fire (pers. obs. D. Graszka-Petrykowski). Moreover, due to very high tree mortality caused by fire in our study area, the proportions of living, dying and dead trees available for foraging differs greatly from those in unburnt forests and this limits the opportunity for direct comparisons of their selection. Therefore, our results regarding decay stage should be interpreted with caution.

With respect to the DBH of the foraging substrate, our results show that Three-toed Woodpeckers in burned habitat select trees with a DBH above 25 cm. This is in line with what was found for the Eurasian and American Three-toed Woodpeckers and the Black-backed Woodpecker, who were shown to select larger snags (>15 cm) for foraging (Murphy & Lehnhausen 1998, Nappi *et al.* 2015, Versluijs *et al.* 2020). However, our results suggest that Eurasian Three-toed Woodpeckers may also spend considerable time utilizing smaller diameter trees in the range of 5–35 cm and thus overall they did not spend much time on very large trees. A possible explanation for this could be that there are only a few large trees in the forest or that larger trees provide more prey items (Saint-Germain *et al.* 2004) or they offer highly rewarding prey items (e.g. larger insect larvae) that are relatively rare (Zhang *et al.* 1993, Foit 2010) compared to smaller trees. Hence, due to lower prey availability on smaller trees, searching time will likely increase, thus resulting in the woodpeckers being detected on smaller trees more often.

It needs to be emphasized that our study encompasses a short window of foraging opportunity two years after wildfire and that there is a lack of studies that focus just on the foraging of Three-toed Woodpeckers in such settings. As recently pointed out by Hammond & Theimer (2020) in their review of tree-scale foraging ecology of woodpeckers in North America, while there is a consistent positive relationship between the presence of woodpecker prey and woodpecker tree use, there is a clear gap in our knowledge linking tree use by prey to tree use by woodpeckers.

This study was performed during a clearly visible peak of Three-toed Woodpecker abundance in the second breeding season after the fire (Gustafsson *et al.* 2019). This may suggest that the level of food resources available to Three-toed Woodpecker was very high during the study year, possibly leading to foraging patterns not necessarily observed in other types of habitats, as exemplified by foraging on pines killed by fire and the complete lack of observations on sap-feeding. It appears that the high abundance of Three-toed Woodpeckers in our study corresponds well to the dynamics of post-fire wood-dependent beetle communities (Fayt 2003, Fredriksson *et al.* 2020). Importantly for Three-toed Woodpeckers, the years following fire show high abundance of Spruce bark beetles (the main insect prey for the woodpecker in autumn-spring) and longhorn beetles (the main food supply for the nestlings; Fayt 2003). These patterns of high abundance of spruce bark beetles and longhorn beetles match well with the Three-toed Woodpeckers selection preference of spruce and importance of the root collars of pines found in this study.

In forests affected by wildfire, the Three-toed Woodpecker preferred to select larger size dead trees (DBH > 25 cm), mostly Spruce as foraging substrates. Additionally, we identified the importance of the root collars of Pines as an important foraging substrate. These identified foraging attributes may be used in developing post-fire management policies and in selecting areas for retention that would support Three-toed Woodpeckers.

ACKNOWLEDGMENT

We are grateful to Dariusz Graszka-Petrykowski for help with the fieldwork. We also thank Håkan Olsson and Björn Nilsson for making their unpublished data on forest development available to us. Funding was provided by the Faculty of Forest Sciences, Swedish University of Agricultural Sciences SLU.

REFERENCES

Andersson J., Domingo Gomez E., Michon S. & Roberge J.-M. 2018. Tree cavity densities and characteristics in managed and unmanaged Swedish boreal forest. Scand. J. For. Res. 33: 233–244.

Angelstam P.K. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. J. Veg. Sci. 9: 593–602.

Bütler R., Angelstam P., Ekelund P. & Schlaepfer R. 2004. Dead wood threshold values for the Three-toed Woodpecker presence in boreal and sub-Alpine forest. Biol. Conserv. 119: 305–318.

del Hoyo J., Collar N. & Christie D.A. 2020. Eurasian Three-toed Woodpecker (*Picoides tridactylus*), v. 1.0. In: Billerman S.M., Keeney B.K., Rodewald P.G. & Schulenberg T.S. (eds) Birds of the world. Cornell Lab of Ornithology, Ithaca, NY, USA.

Desrochers A. 1992. Age and foraging success in European Blackbirds: variation between and with individuals. Anim. Behav. 43: 885–894.

Esseen P.-A., Ehnström B., Ericson L. & Sjöberg K. 1997. Boreal forests. Ecol. Bull. 46: 16–47.

Fayt P. 1999. Available insect prey in bark patches selected by the Three-toed Woodpecker (*Picoides tridactylus*) prior to reproduction. Ornis. Fenn. 76: 135–140.

Fayt P. 2003. Insect prey population changes in habitats with declining vs. stable Three-toed Woodpecker (*Picoides tridactylus*) populations. Ornis. Fenn. 80: 182–192.

Fernandes P.M., Vega J.A., Jiménez E. & Rigolot E. 2008. Fire resistance of European pines. For. Ecol. Manage. 256: 246–255.

Foit J. 2010. Distribution of early-arriving saproxylic beetles on standing dead Scots pine trees. Agric. For. Entomol. 12: 133–141.

Fredriksson E., Mugerwa Pettersson R., Naalisvaara J. & Löfroth T. 2020. Wildfire yields a distinct turnover of the beetle community in a semi-natural pine forest in northern Sweden. Ecological Processes. 9: 44.

Gustafsson L. *et al. &* Mikusiński G. 2019. Rapid ecological response and intensified knowledge accumulation following a north European mega-fire. Scand. J. For. Res. 34: 234–253.

Hammond R.L. & Theimer T.C. 2020. A review of tree-scale foraging ecology of insectivorous bark-foraging woodpeckers in North America. For. Ecol. Manage. 478: 118516.

Hekkala A.-M., Päätalo M.-L., Tarvainen O. & Tolvanen A. 2014. Restoration of young forests in eastern Finland: Benefits for saproxylic beetles (*Coleoptera*). Restor. Ecol. 22: 151–159.

Hjältén J., Hägglund R., Löfroth T., Roberge J.-M., Dynesius M. & Olsson J. 2017. Forest restoration by burning and gap cutting of voluntary set-asides yield distinct immediate effects on saproxylic beetles. Biodivers. Conserv. 26: 1623–1640.

Hjältén J., Dynesius M., Hekkala A.-M., Karlsson-Tiselius A., Löfroth T. & Mugerwa-Pettersson R. 2018. Saproxylic insects and fire. In: Ulyshen M. (ed.) Saproxylic insects. Springer-Verlag, Heidelberg.

Hogstad O. 1977. Seasonal change in intersexual niche differentiation of the Three-toed woodpecker (*Picoides tridactylus*). Ornis. Scand. 8: 101–111.

Hogstad O. 1991. The effect of social dominance on foraging by the Three-toed woodpecker (*Picoides tridactylus*). Ibis. 133: 271–276.

Hunter M.L. 1993. Natural fire regimes as spatial models for managing boreal forests. Biol. Conserv. 65: 115–120.

Hyvärinen E., Kouki J. & Martikainen P. 2009. Prescribed fires and retention trees help to conserve beetle diversity in managed boreal forests despite their transient negative effects on some beetle groups. Insect. Conserv. Diver. 2: 93–105.

Jakuš R. 1998. Patch level variation on bark beetle attack (Col., Scolytidae) on snapped and uprooted trees in Norway spruce primeval natural forest in endemic condition: effects of host and insolation. J. Appl. Entomol. 122: 409–421.

Kärvemo S., Björkman C., Johansson T., Weslien J. & Hjältén J. 2017. Forest restoration as a double-edged sword: the conflict between biodiversity conservation and pest control. J. Appl. Ecol. 54: 1658–1668.

Kelsey R.G. & Joseph G. 2003. Ethanol in ponderosa pine as an indicator of physiological injury from fire and its relationship to secondary beetles. Can. J. For. Res. 33: 870–884.

Kelsey R.G. & Westlind D.J. 2017. Ethanol and primary attraction of red turpentine beetle in fire stressed ponderosa pine. For. Ecol. Manage. 396: 44–54.

Kuuluvainen T. 2002. Disturbance dynamics in boreal forests: Defining the ecological basis of restoration and management of biodiversity. Silva. Fenn. 36: 5–11.

Lehtonen I., Venäläinen A., Kämäräinen M., Peltola H. & Gregow H. 2016. Risk of large-scale fires in boreal forests of Finland under changing climate. Nat. Hazard. Earth. Sys. 16: 239–253.

Lowe J., Pothier D., Rompré G. & Savard J.-P.L, 2012. Long-term changes in bird community in the unmanaged post-fire eastern Québec boreal forest. J. Ornithol. 153: 1113–1125.

Machlis L., Dodd P.W.D. & Fentress J.C. 1985. The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. Z. Tierpsychol. 68: 201–214.

Manly B.F.J., McDonald L.L., Thomas D.L., McDonald T.L. & Erickson W.P. 2002. Resource selection by animals: Statistical design and analysis for field studies. Kluwer Academic Publishers, Norwell, Mass.

Martin P. & Bateson P. 1993. Measuring Behavior: An introductory guide, 2nd ed. Cambridge University Press, Cambridge, United Kingdom.

Muotoiltu: ruotsi (Ruotsi)

Muotoiltu: ruotsi (Ruotsi)

Mikusiński G., Gromadzki M. & Chylarecki P. 2001. Woodpeckers as indicators of forest bird diversity. Conserv. Biol. 15: 208–217.

Müller J., Noss R.F., Thorn S., Bässler C., Leverkus A.B. & Lindenmayer D. 2019. Increasing disturbance demands new policies to conserve intact forest. Conserv. Lett. 12: e12449.

Murphy E.C. & Lehnhausen W.A. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. J. Wildl. Manage. 62: 1359–1372.

Nappi A., Drapeau P., Saint-Germain M. & Angers V.A. 2010. Effect of fire severity on long-term occupancy of burned boreal conifer forests by saproxylic insects and wood-foraging birds. Int. J. Wildland Fire 19: 500–511.

Nappi A. & Drapeau P. 2011. Pre-fire forest conditions and fire severity as determinants of the quality of burned forests for deadwood-dependent species: the case of the black-backed woodpecker. Can. J. For. Res. 41: 994–1003.

Nappi A., Drapeau P. & Leduc A. 2015. How important is dead wood for woodpeckers foraging in eastern North American boreal forests? For. Ecol. Manage. 346: 10–21.

Nilsson B., Tyboni M., Pettersson A., Granström A. & Olsson H. 2014. Punktgittertolkning av brandområdet i västmanland. Redovisning av uppdrag från Skogsstyrelsen. Arbetsrapport 433 2014. Umeå: Institutionen för skoglig resurshushållning. Sveriges lantbruksuniversitet.

Pakkala T., Hanski I. & Tomppo E. 2002. Spatial ecology of the three-toed woodpecker in managed forest landscapes. Silva. Fenn. 36: 279–288.

Pakkala T., Kouki J., Piha M. & Tiainen J. 2017. Phloem sap in fire-damaged Scots pine trees provides instant foraging opportunities for Three-toed Woodpeckers *Picoides tridactylus*. Ornis. Svec. 27: 144–149.

Pakkala T., Piiroinen J., Lakka J., Tiainen J., Piha M. & Kouki J. 2018a. Tree sap as an important seasonal food resource for woodpeckers: the case of the Eurasian three-toed Woodpecker (*Picoides tridactylus*) in southern Finland. Ann. Zool. Fenn. 55: 79–92.

Pakkala T., Tiainen J., Piha M. & Kouki J. 2018b. Three-toed Woodpecker cavities in trees: A keystone structural feature in forests shows decadal persistence but only short-term benefit for secondary cavity-breeders. For. Ecol. Manage. 413: 70–75.

Pechacek P. 2004. Spacing behaviour of Eurasian Three-toed Woodpecker (*Picoides tridactylus*) during the breeding season in Germany. Auk. 121: 58–67.

Pechacek P. 2006. Foraging behaviour of Eurasian Three-toed Woodpeckers (*Picoides tridactylus alpinus*) in relation to sex and season in Germany. Auk. 123: 235–246.

Pechacek P. & d'Oleire-Oltmanns W. 2004. Habitat use of the three-toed woodpecker in central Europe during the breeding period. Biol. Conserv. 116: 333–341.

Roberge J.-M. & Angelstam P. 2006. Indicator species among resident forest birds – A cross-regional evaluation in northern Europe. Biol. Conserv. 130: 134–147.

Robles H. & Pasinelli G. 2014. Woodpeckers as model organisms in a changing world. Foreword to the 7th International Woodpecker Conference Proceedings. Acta Ornithol. 49: 203–206.

Saint-Germain M., Drapeau P. & Hébert C. 2004. Xylophagous insect species composition and patterns of substratum use on fire-killed black spruce in central Quebec. Can. J. For. Res. 34: 677–685.

Muotoiltu: ruotsi (Ruotsi)

Stachura-Skierczyńska K., Tumiel T. & Skierczyński M. 2009. Habitat prediction model for three-toed woodpecker and its implications for the conservation of biologically valuable forests. For. Ecol. Manage. 258: 697–703.

Stokland J., Siitonen J. & Jonsson B.G. 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge, UK.

Therneau T. & Lumley T. 2009. Survival: Survival analysis, including penalized likelihood. R Package v. 2.42-3. http://cran.r-project.org/package=survival

Thomas J.W., Anderson R.G., Maser C. & Bull E.L. 1979. Snags. Ch. 5 in: Thomas J.W. (ed.) Wildlife habitat in managed forest the Blue Mountain of Oregon and Washington. U.S. Forest Service, Wildlife Management Institute, U.S. Dept. of Interior, Bureau of Land Management, Washington, D.C., USA.

Thorn S. *et al.* & Leverkus A.B. 2020. Estimating retention benchmarks for salvage logging to protect biodiversity. Nat. Commun. 11: 4762.

Versluijs M., Eggers S., Hjältén J., Löfroth T. & Roberge J.-M. 2017. Ecological restoration in boreal forest modifies the structure of bird assemblages. For. Ecol. Manage. 401: 75–88.

Versluijs M., Hjältén J. & Roberge J.-M. 2019. Ecological restoration modifies the value of biodiversity indicators in resident boreal forest birds. Ecol. Indic. 98: 104–111.

Versluijs M., Eggers S., Mikusiński G., Roberge J.-M. & Hjältén J. 2020. Foraging behavior of the Eurasian Three-toed Woodpecker (*Picoides tridactylus*) and its implications for ecological restoration and sustainable boreal forest management. Avian Conserv. Ecol. 15(1):6.

Villard P. 1994. Foraging behavior of Black-backed and Three-toed Woodpeckers during spring and summer in a Canadian boreal forest. Can. J. Zool. 72: 1957–1959.

Wesołowski T., Czeszczewik D. & Rowiński P. 2005. Effects of forest management on Three-toed Woodpecker (*Picoides tridactylus*) distribution in the Białowieża Forest (NE Poland): conservation implications. Acta Ornithol. 40: 53–60, 58.

Zhang Q.-H., Byers J.A. & Zhang X.-D. 1993. Influence of bark thickness, trunk diameter and height on reproduction of the longhorned beetle, *Monochamus sutor* (Col., Cerambycidae) in burned larch and pine. J. Appl. Entomol. 115: 145–154.

Zhu Y., Lü N., Pechacek P., Li J. & Sun Y.-H. 2012. Foraging behavior of the Eurasian Three-toed Woodpecker subspecies *Picoides tridactylus funebris* in southern Gansu, China. Birds China 3: 60–66.

Żmihorski M., Hebda G., Eggers S., Månsson J., Abrahamsson T., Czeszczewik D., Walankiewicz W. & Mikusiński G. 2019. Early post-fire bird community in European boreal forest: Comparing salvage-logged with non-intervention areas. Global. Ecol. Conser. 18. e00636.

SAMENVATTING

In boreale bossen behoren bosbranden tot de meest belangrijke natuurlijke verstoringen die de beschikbaarheid en kwaliteit van het hout beïnvloeden. De door brand aangetaste bomen zijn een belangrijke habitat voor een groep gespecialiseerde vogelsoorten. De Drieteenspecht *Picoides tridactylus* is een van deze soorten. Het is bekend dat de soort onmiddellijk gebruikmaakt van het

verbrand bos om er te foerageren en in te broeden. Er zijn echter geen onderzoeken die het foerageergedrag van Drieteenspechten beschrijven in bossen na een natuurbrand. Dergelijke kennis zou een bijdrage kunnen leveren bij de ontwikkeling van efficiënte beheerstrategieën na bosbranden die in overeenstemming zijn met de doelstellingen voor het behoud van de biodiversiteit. Het hier beschreven onderzoek beschrijft het foerageergedrag van Drieteenspechten in een bosgebied van 13.100 ha gelegen in zuid-centraal Zweden, dat in 2014 getroffen werd door een grote natuurbrand. Tijdens het tweede broedseizoen na de brand hebben wij het foerageergedrag van 28 individuen gedurende 1681 minuten geobserveerd, Onze resultaten laten zien dat Drieteenspechten een voorkeur hebben om in Fijnsparren *Picea abies* te foerageren, vooral inbomen met grotere diameters (DBH > 25 cm). Echter, als wij kijken naar de tijdsbesteding van foeragerende Drieteenspechten in de verschillende soorten bomen dan blijkt dat Grove Dennen *Pinus sylvestris* ook erg belangrijk zijn. Hier gebruiken ze voornamelijk de wortelhalzen, wat nog niet eerder bij Drieteenspechten is waargenomen. Deze studie werd uitgevoerd tijdens een piek met grote aantallen Drieteenspechten. Dit kan erop wijzen dat de beschikbaarheid van voedsel erg hoog was. Mogelijk heeft dit geleid tot de waargenomen patronen in het foerageergedrag van Drieteenspechten die niet werden waargenomen in andere tijdsperiodes of leefgebieden.

Corresponding editor: Rienk Fokkema

Received 7 April 2021; accepted 31 October 2021

PHOTOS

An adult male Eurasian Three-toed Woodpecker foraging on a fire affected pine tree (photo Dariusz Graszka-Petrykowski, Västmanland, Sweden, June 2016).

A managed south-boreal forest area recently affected by wildfire; a typical habitat occupied by Eurasian Three-toed Woodpeckers (photo Dariusz Graszka-Petrykowsk, Västmanland, Sweden, May 2016).

TABLES

Table 1. Total observation time (min), total foraging time (min), number of used trees and mean observation session length (±SE, min) divided between sex, *n* = number of woodpecker individuals.

Sex	*n*	Observation time	Foraging time	Used trees	Observation session length (mean ± SE)
Female	13	827	505	215	37.3 ± 7.2
Male	15	854	503	251	29.2 ± 4.6

Table 2. Parameter estimates and odds ratios for conditional logistic regression models describing characteristics of trees used by foraging Three-toed Woodpecker. Sex and interaction terms were excluded as they were not significant in the models.

Parameter	Estimate	SE	*T*	*P*	Odds ratio (95% CI)
Tree species (birch vs. Nordic Spruce)	–0.41	0.13	–3.16	0.002	0.66 (0.52–0.86)
Tree species (Pine vs. Nordic Spruce)	–0.53	0.06	–8.47	<0.001	0.58 (0.51–0.66)
Tree species (Scots Pine vs. birch)	–0.13	0.11	–1.11	0.265	0.87 (0.70–1.10)
Decay stage	0.33	0.05	6.81	<0.001	1.39 (1.26–1.53)
DBH	0.04	0.01	13.02	<0.001	1.04 (1.03–1.05)

FIGURES

Figure 1. Location of the study area, with the outline of the burned area (in red) and the squares (in black) which were surveyed for the presence of Three-toed Woodpeckers. The plot numbers refer to the habitat data presented in Table S1.

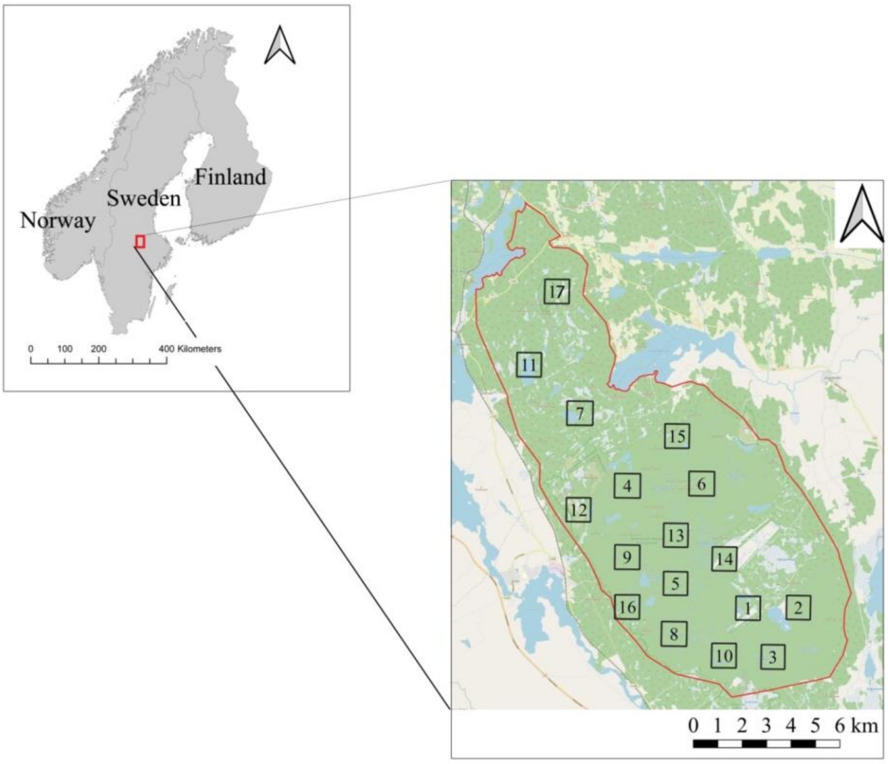


Figure 2. Manly selection ratios with 95% confidence intervals for (A) tree species, (B) decay stage and (C) DBH (diameter at breast height). Selection ratios are based on the ratio between substrate selected by Three-toed Woodpecker and availability (measured as the nearest tree). Values above 1 indicate preference whereas values below 1 indicate avoidance.

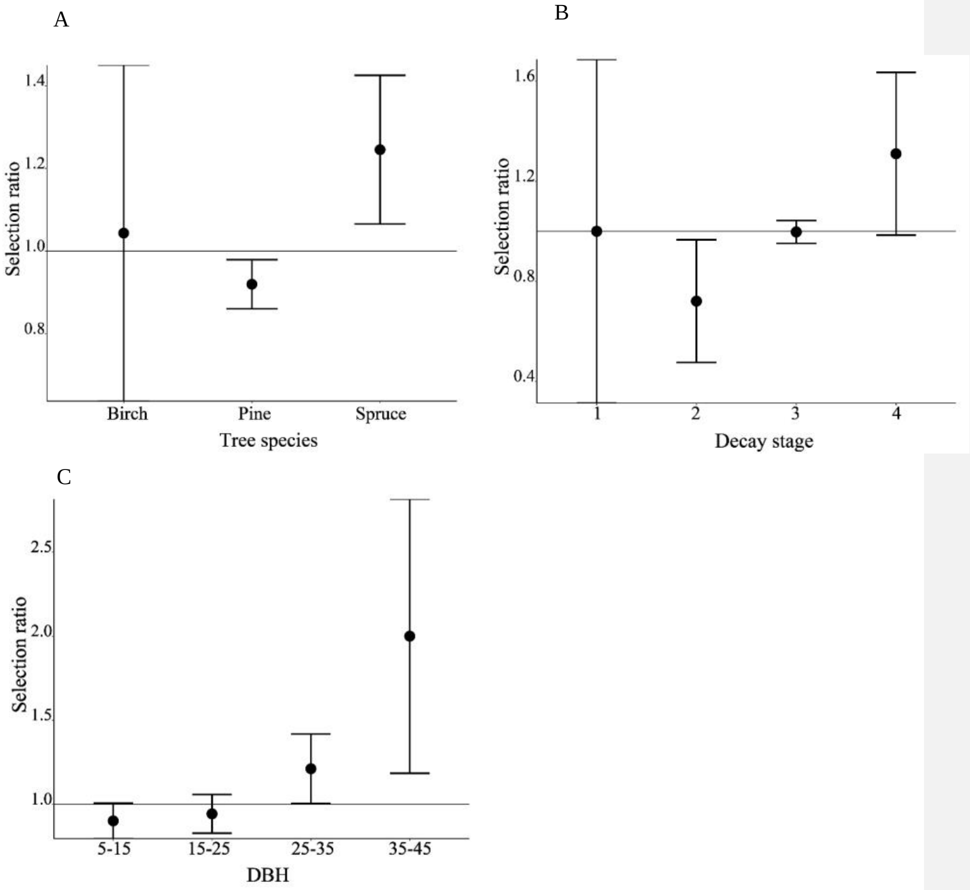


Figure 3. Proportion of foraging time spent (A) using different foraging methods and locations and (B) using different foraging methods and tree species when foraging on root collars.

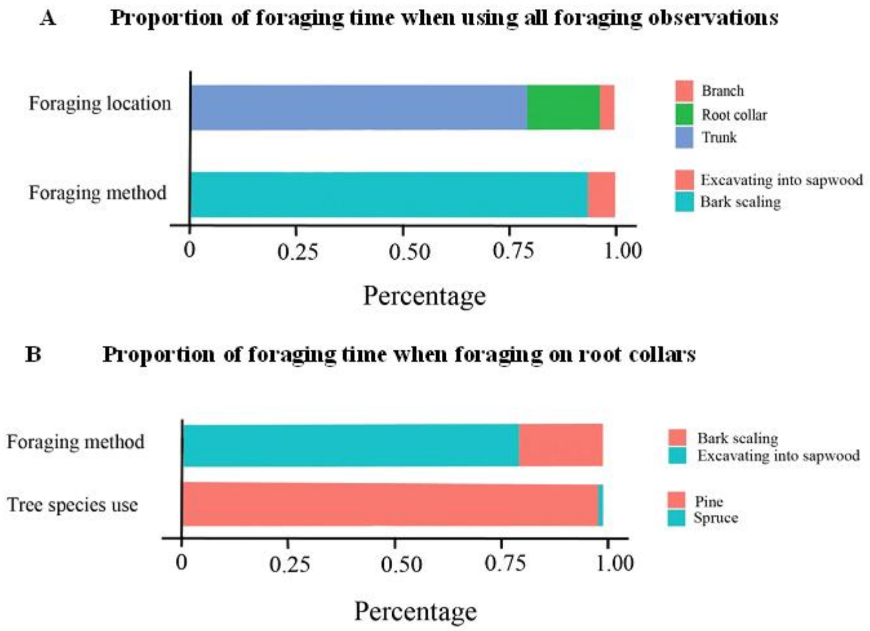


Figure 4. Predicted mean foraging time (min ± SE) per observation session of foraging height (m) in relation to sex. Results derived from GLMM models with Poisson distribution. Forest stand and observation session were included as random variables.

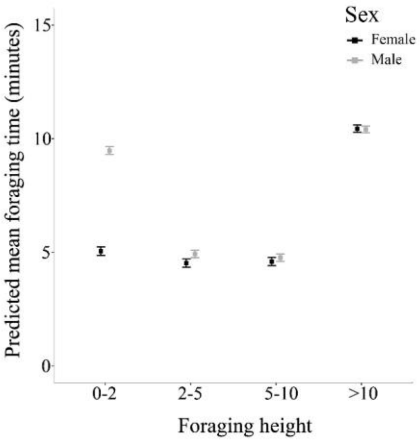
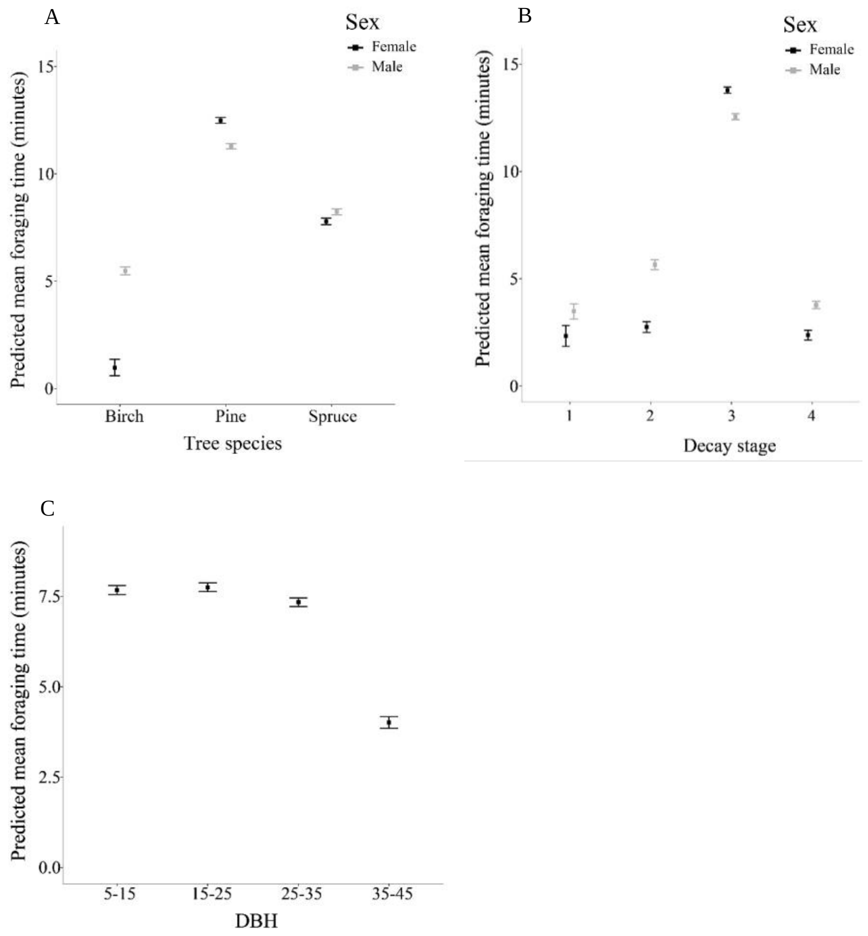


Figure 5. Predicted mean foraging time (min ± SE) per observation session for substrates belonging to different (A) tree species, (B) decay stages and (C) DBH (diameter at breast height) classes (sex was excluded). Results derived from GLMM models with Poisson distribution and forest stand and observation session were included as random variables. Sex was included when significant.



SUPPLEMENTARY MATERIAL

Figure S1. Example of root collars after wildfire in Västmanland, Sweden, 2016 (photo: Dariusz Graszka-Petrykowski)

Table S1. Characteristics of the 1x1 km study plots according to sampling in circular plots with radius of 10 m distributed in a regular grid with 300 m between plot's central points (Nilsson *et al.* 2014). Data concerning year 2016 is based on comparison with the number of living trees before the fire in 2014. Asterix after plot number indicates plots where foraging Three-toed Woodpeckers were not observed.

Plot number	Sample size (circular plots)	Average tree volume before fire (m^3)	Average pine (%)	Average spruce (%)	Average deciduous (%)	Average healthy trees in 2016 (%)	Average damaged trees in 2016 (%)	Average standing dead trees in 2016 (%)	Average downed dead trees in 2016 (%)
1	9	136.5	64.4	16.7	7.8	10	26.7	41.3	15.6
2	12	70.9	63.3	15.0	13.3	21.7	19.2	33.3	25.8
3	9	80.2	93.3	6.7	0	7.8	16.7	26.7	26.7
4	9	160.7	57.8	30	12.2	2.2	21.1	75.6	1.1
5	9	51.8	94.4	5.6	0	34.4	7.8	33.3	22.2
6	12	95.6	89.2	5.8	5.0	0	8.2	32.5	30
7	12	125	47.5	32.5	16.7	8.3	6.7	45.8	18.3
8	12	40.5	79.2	4.2	0	15	10.8	44.2	21.7
9	12	156.6	72.5	17.5	10.0	9.2	12.5	53.3	8.3
10	12	149.1	64.2	28.3	7.5	1.7	5	38.3	46.7
11	12	87.6	35.8	18.3	20.8	10	0.8	45.8	4.2
12*	12	111.5	47.5	20.8	23.3	0.8	7.5	65	10
13	12	82.6	80.8	5.0	5.8	0.8	13.3	61.7	24.2
14	12	73.3	71.7	9.2	2.5	4.2	6.7	37.5	18.3
15	12	65.8	81.7	5.8	4.2	0.8	0	12.5	15

16	12	113.4	48.3	25.8	17.5	0	0.8	39.2	16.6
17	12	125.9	73.3	18.3	8.3	0.8	0.8	59.2	5.8

Table S2. Number of trees used by the Eurasian Three-toed Woodpecker and number of available trees, by sex, decay stage and tree species.

Sex	Decay stage	Tree species used			Tree species available		
		birch	Scots Pine	Nordic Spruce	birch	Scots Pine	Nordic Spruce
Female	1	1	2	0	0	4	0
	2	0	11	0	0	15	0
	3	7	103	71	8	112	55
	4	0	12	8	0	11	10
Male	1	3	3	1	2	1	1
	2	0	19	0	1	27	0
	3	11	138	41	11	158	29
	4	3	21	11	1	9	11