Research Paper

Foraging behavior of the Eurasian Three-toed Woodpecker (*Picoides tridactylus*) and its implications for ecological restoration and sustainable boreal forest management

Martijn Versluijs[1], *Sönke Eggers*[2], *Grzegorz Mikusiński*[3,4], *Jean-Michel Roberge*[1,5] and *Joakim Hjältén*[1]

[1]Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences (SLU), Umeå, Sweden, [2]Department of Ecology, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden, [3]Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, Riddarhyttan, Sweden, [4]School for Forest Management, Swedish University of Agricultural Sciences, Skinnskatteberg, Sweden, [5]Swedish Forest Agency, Umeå, Sweden

ABSTRACT. Several studies have shown that the Three-toed Woodpecker (*Picoides tridactylus*) is strongly favored by large-scale disturbances, including forest fires. However, natural disturbances have largely disappeared from European boreal forests because of modern forestry practices and fire suppression. We currently lack knowledge on the foraging activity and resource use of the Eurasian Three-toed Woodpecker, especially in burned forests, and this restricts our ability to develop strategies for sustainable forest management and ecological restoration aiming at improving the situation of this woodpecker and associated species. In order to fill this knowledge gap, we studied the characteristics of selected foraging substrates and the foraging behavior of the Three-toed Woodpecker during the breeding season in unburned forests and forests that have been subjected to prescribed burning. We used instantaneous sampling during two consecutive springs (2016-2017), where we observed the woodpeckers' foraging behavior during a total of 977 minutes in burned forest and 962 minutes in unburned forests. The preferred foraging substrate for Three-toed Woodpeckers in both burned and unburned forests can be characterized as freshly dead trees with a DBH > 15 cm. However, data on time spent foraging on different substrates suggest that also substrates in the 5-15 DBH range and living trees are important. Additionally, prescribed burnings led to less pronounced selection of tree species, which suggest that fire may reduce differences in abundance of saproxylic insect prey between tree species. This information on substrate selection and foraging time provide complementary knowledge and thus should be used simultaneously when management strategies for improved woodpecker habitat are developed. Our results suggest that both prescribed burning and protecting forests with high density and diversity of dead wood provides habitat opportunities for Three-toed Woodpeckers and using both in management may maximize conservation outcome.

Comportement d'alimentation du Pic tridactyle (*Picoides tridactylus*) et ses implications pour la restauration écologique et les pratiques durables d'aménagement de la forêt boréale

RÉSUMÉ. Plusieurs études ont montré que le Pic tridactyle (*Picoides tridactylus*) profite des perturbations survenant sur de vastes étendues, dont les incendies de forêt. Toutefois, les perturbations naturelles n'existent presque plus dans les forêts boréales d'Europe en raison des pratiques forestières modernes et de la suppression des incendies de forêt. Le manque actuel de connaissances sur l'alimentation et l'utilisation des ressources par le Pic tridactyle, spécialement dans les forêts brûlées, restreint notre habilité à élaborer des stratégies d'aménagement durable des forêts et de restauration écologique visant à améliorer la situation de ce pic et d'autres espèces associées. Pour combler cette lacune, nous avons étudié les caractéristiques des substrats choisis pour l'alimentation et le comportement d'alimentation du Pic tridactyle durant la saison de nidification, dans des forêts non brûlées et des forêts ayant fait l'objet de brûlage dirigé. Nous avons échantillonné de façon instantanée durant deux printemps consécutifs (2016-2017), au cours desquels nous avons observé les pics s'alimenter durant 977 minutes en forêts brûlées et 962 minutes en forêts non brûlées. Le substrat favori des Pics tridactyles pour l'alimentation, tant en forêts brûlées que non brûlées, s'est révélé être des arbres fraîchement morts ayant un DHP > 15 cm. Cependant, selon le temps dédié par les pics pour s'alimenter sur les différents substrats, ceux compris dans la fourchette de DHP située entre 5 et 15, tout comme les arbres vivants, avaient aussi leur importance. De plus, dans le cas des feux dirigés, les pics ont été moins sélectifs dans leurs essences d'arbres, laissant croire que le feu pourrait réduire la variabilité de l'abondance des insectes saproxyliques qu'ils consomment entre les essences d'arbres. Ces résultats sur la sélection de substrats et le temps dédié à l'alimentation fournissent des connaissances complémentaires et devraient être considérés simultanément au moment d'élaborer des stratégies d'aménagement visant à améliorer l'habitat de ce pic. Nos résultats indiquent que le brûlage dirigé et la protection de forêts montrant une densité et une diversité élevées de bois mort fournissent de l'habitat pour les Pics tridactyles; l'utilisation de ces deux stratégies d'aménagement pourrait maximiser les retombées de conservation.

Key Words: *conservation; ecological restoration; prescribed burning; substrate selection; substrate use*

Address of Correspondent: Martijn Versluijs, Skogsmarksgränd 17, 90736 Umeå , Sweden, martijn.versluijs@slu.se

INTRODUCTION

As a consequence of human-induced habitat loss, fragmentation, and structural homogenization, many woodpecker species are threatened or have declining populations (Mikusiński 2006, Lammertink 2014, Vergara-Tabares et al. 2018). This especially concerns habitat specialists with strong affinity for old-growth forest or forest subjected to natural disturbances, e.g. windthrow, fire, and insect outbreaks. The occurrence and population dynamics of woodpeckers are strongly correlated with local habitat composition (Bütler et al. 2004a, Pechacek and d'Oleire-Oltmanns 2004, Roberge et al. 2008, Tremblay et al. 2009, Czeszczewik et al. 2013, Kajtoch et al. 2013, Kumar et al. 2014, Ojeda and Chazarreta 2014). At the local habitat level, woodpeckers need certain structures for foraging and breeding, such as large old trees and deadwood (Walters et al. 2002, Bütler et al. 2004a, Roberge et al. 2008).

The boreal biome is a dynamical system where wildfires belong to the most important natural disturbances shaping complex forest environments (Hunter 1993, Esseen et al. 1997, Angelstam 1998, Kuuluvainen 2002, Bergeron et al. 2004, Gauthier et al. 2015) and fundamentally affecting forest biodiversity (Lowe et al. 2012, Hekkala et al. 2014, Hjältén et al. 2017, Gustafsson et al. 2019). However, because of modern forestry practices and fire suppression, natural disturbances have largely disappeared from the European boreal forest and have been replaced by anthropogenic disturbances, including thinning, clearcutting, soil scarification, and planting of conifers (Esseen et al. 1997, Östlund et al. 1997, Linder and Östlund 1998, Wallenius 2011, Rolstad et al. 2017). Prescribed burning, as a form of ecological restoration, is assumed to be an efficient way to emulate wildfire and to create habitats for a range of different species including woodpeckers (Hjältén et al. 2017, Versluijs et al. 2017).

The Eurasian Three-toed Woodpecker (*Picoides tridactylus*), included in annex I of the EU Birds Directive and red-listed as "near threatened" in Sweden, is generally classified as an old-growth forest specialist (Pakkala et al. 2002, Pechacek and d'Oleire-Oltmanns 2004, Wesołowski et al. 2005, Stachura-Skierczyńska et al. 2009). However, several studies have shown that Three-toed Woodpeckers (including the American Three-toed Woodpecker *Picoides dorsalis*) are strongly favored by large-scale disturbances causing elevated mortality of trees, including forest fires (Murphy and Lehnhausen 1998, Hoyt and Hannon 2002, Fayt 2003, Nappi and Drapeau 2009, Edworthy et al. 2011, Versluijs et al. 2017). Fire induces profound changes in stand characteristics, which influence tree substrate availability and quality (Stokland et al. 2012, Hjältén et al. 2017, 2018). This may result in changes in both the abundance and assemblage composition of saproxylic insects, the main food source of Three-toed Woodpeckers (Saint-Germain et al. 2004a, b, 2008, Hyvärinen et al. 2009, Boucher et al. 2012, Hekkala et al. 2014, Kärvemo et al. 2017). It has been suggested that burning homogenizes the quality of tree species in terms of nutrients and structure, making them more equal for saproxylic insects and reduces differences in insect diversity among tree species (Wikars 2002, Toivanen and Kotiaho 2010). This, in turn, could result in woodpeckers being less likely to discriminate between tree species when foraging in burned forest.

Observational studies of Three-toed Woodpeckers in unburned forest in Norway and central Europe suggest that they spend most of their foraging time on dead standing, large diameter Norway spruces (*Picea abies*; > 10 cm) in an early decay stage (Hogstad 1977, 1991). The woodpecker's primary foraging method is bark-scaling on the trunk (Hogstad 1977, 1991, Pechacek 2006a). Similar foraging strategies have been reported in the American Three-toed Woodpecker, a species closely related to the Eurasian Three-toed Woodpecker. The American Three-toed Woodpecker tends to use larger diameter, recently dead (standing) conifer trees but living trees are important as well for sap licking (Imbeau and Desrochers 2002, Nappi et al. 2015). The use of recently dead conifer trees by the woodpecker may be explained by its specialization on bark beetles as a main prey. Nappi et al. (2015) found that trees used for foraging contained high abundance of Scolytinae beetles. In burned forests, the American Three-toed Woodpecker exhibits similar foraging preferences as in unburned forests (Murphy and Lehnhausen 1998). However, our knowledge on the foraging activity and resource use of Eurasian Three-toed Woodpecker is more limited, especially in burned forest. Understanding the foraging ecology of woodpeckers and their associations to tree characteristics is necessary for successful conservation work in managed forest landscapes. Thus, the lack of this knowledge restricts our ability to develop strategies for sustainable forest management and ecological restoration aiming at improving the situation of this woodpecker and associated species. This is particularly important in light of an expected increase in the frequency of wildfires in Northern Europe (Lehtonen et al. 2016), requiring development of efficient postfire management strategies that are in line with biodiversity conservation objectives. In this context, the Three-toed Woodpecker can be seen as a model species for biodiversity conservation, management, and ecological restoration in boreal and high-altitude forests. This is due to its sensitivity to habitat changes, potential importance as an indicator species for biodiversity (Mikusiński et al. 2001, Roberge and Angelstam 2006, Drever et al. 2008, Versluijs et al. 2019), and keystone role in providing cavities for secondary cavity-nesters (Pakkala et al. 2018a), a process of particular importance in boreal forests where decay-formed tree cavities are very rare (Andersson et al. 2018).

The objective of this study is to improve our understanding of the foraging ecology of Three-toed Woodpeckers and associated tree dynamics, necessary to develop strategies for sustainable forest management and ecological restoration. Therefore, the foraging substrate preferences of the Eurasian Three-toed Woodpecker was determined during the breeding season in unburned forests and forests that have been subjected to prescribed burning (5–6 years after treatment). We achieved this by studying (i) the selection of individual foraging substrates by the woodpecker and (ii) the allocation of foraging time among substrates with different characteristics. We expected tree species, decay stage, and tree diameter to be important characteristics determining the selection of foraging substrates. Furthermore, we predicted a difference in foraging behavior as measured through foraging time (regarding the use of different tree species, decay stages, tree diameter, and position on the substrates) between burned and unburned forest as substrate properties change because of fire.

METHOD

Study area

The study area is located in the middle and northern boreal zones (Ahti et al. 1968) of northern Sweden (63°23′N to 65°02′N and 16°80′E to 21°20′E). Data was collected in 30 forest stands of varying sizes, ranging from 3.5 to 25 hectares. The distance between neighboring study stands was ≥ 1 km. All stands were selected to be as similar as possible in terms of tree species composition and forest age. All stands were conifer-dominated, with a mixture of Scots pine (*Pinus sylvestris*) and Norway spruce and at least 10% deciduous trees. The most common deciduous tree species were silver birch (*Betula pendula*), downy birch (*Betula pubescens*), European aspen (*Populus tremula*), and goat willow (*Salix caprea*). Twenty stands were initially normal production stands, which were converted into voluntary set-asides and protected as part of Forest Stewardship Council (FSC) certification. All study stands were mature forest stands (> 80 years) that have never been clear-felled but historically subjected to selective felling. In 10 of the stands, prescribed burning was conducted in 2011. Before burning, 5–30% of the trees were harvested to improve local conditions for burning (by speeding up the drying out of the ground vegetation) and to cover the costs associated with the burning treatment. In addition to the extracted timber, approximately 2–5 m³/ha of the cut trees were left on the ground as fuel. Fire intensity (measured as the ratio between living and dead coniferous trees after fire) ranged from 0.23 to 1.00 in the prescribed burning stands. The remaining stands (10 voluntary set-asides and 10 stands located in formally protected nature reserves) are referred to as unburned forest stands. More detailed stand information regarding basal area and DBH of living and standing dead wood can be found in Table 1.

Focal observations

Fieldwork was carried out from the beginning of April to the end of June in 2016 and 2017. We located Three-toed Woodpecker individuals by walking slowly through the study stands, using both auditory (drumming and pecking sounds of foraging woodpeckers) and visual cues to detect the birds. Our study stands were smaller than the average territory size of the woodpecker (typically 60–340 ha; Pakkala et al. 2002, Pechacek 2004, Pechacek and d'Oleire-Oltmanns 2004). Studies of spacing behavior done in Germany demonstrated that the area used over the breeding season remain stable and home ranges of pairs (male and female) overlap with 66% (Pechacek 2004). Because it was not possible to distinguish individuals (the woodpeckers were not marked), repeated observation of a bird of a given sex in a given year in a study stand were treated as dependent units in the analyses. Pechacek (2006*b*) showed that although Three-toed Woodpeckers have a high breeding site fidelity between years, 60% of the observed woodpeckers found a new mate due to death or divorce. Because of this, we treated observations in the same stands but from two different years as independent observations.

Once a bird was found, it was observed until it flew out of sight. We kept an observation distance of > 10 m from the bird to avoid disturbances. We used instantaneous sampling, i.e., fixed interval time point (Martin and Bateson (1993), where we recorded for every minute if the individual was foraging or not. When the woodpecker was foraging, we recorded the following variables: foraging height, foraging site (trunk, branch, or exposed roots), and substrate diameter at foraging height (estimate at nearest cm using the Three-toed Woodpecker's body length [20–24 cm] as a reference). We recorded foraging height in four classes; 1 (0–2 m), 2 (2–5 m), 3 (5–10 m), and 4 (> 10 m). We distinguished three foraging techniques (Villard 1994, Murphy and Lehnhausen 1998, Imbeau and Desrochers 2002): (1) bark scaling accompanied by surface pecking, (2) excavation into sapwood, and (3) sap-licking. For each substrate selected by a Three-toed Woodpecker we recorded tree species (pine, spruce, birch, aspen, and other deciduous trees); DBH in 10 cm classes: (i) 5–15, (ii) 15–25, (iii) 25–35, (iv) 35–45; tree health status/decay stages (hereafter "decay stage" for conciseness) based on four classes (Thomas et al. 1979): (1) healthy living tree, (2) dying tree that 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, we also recorded data for all of the variables pertaining to substrate characteristics for the nearest available tree with a DBH > 5 cm.

Statistical analysis

Characteristics of selected foraging substrates

As a first step, we evaluated which of the different substrate variables most likely determined the potential of a tree to be used as foraging substrate. This was done by using each utilized substrate as the basic unit of observation, without accounting for the total observation time per individual substrate. We attributed a unique identification number with information about tree species, DBH, and decay stage to each individual tree used for foraging by Three-toed Woodpecker. We used conditional logistic regression with the clogit function from the "survival" package in R (Therneau and Lumley 2009) to analyze selection for different foraging substrates as a function of their characteristics. Conditional logistic regression is a type of logistic regression model based on matched case-control pairs. Here, we matched each used tree with the nearest available tree, hence allowing to control for local habitat differences regarding substrate availability. The total number of trees selected differed between woodpecker individuals. To account for these differences, we statistically weighted the number of trees used by an individual. For example, individual selection preference based on 100 used trees counted twice as much as one based on only 50 trees. Consequently, each woodpecker individual contributed only 1 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). We ran the models with tree species, DBH, and decay stage as independent variables and separately for burned and unburned forests, using backward elimination to select the best model.

Additionally, we used Manly selection ratios (Manly et al. 2002) 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 substrate used by Three-toed Woodpecker and its availability, i.e., the nearest tree 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 is < 1, and as used proportionally to its availability when the 95% CI includes 1 (Manly et al. 2002).

Table 1. Habitat structure of burned and unburned forest. Basal area and mean diameter at breast height (DBH; ± SE) are provided separately for four tree health statuses / decay stages and three tree species. Tree health status / decay stage is based on four classes: (1) healthy living tree, (2) dying tree that is still alive, (3) recently dead tree with 100% bark attached, (4) dead tree with < 100% bark attached.

Tree species	Tree health status / decay stage	Burned forest		Unburned forest	
		Basal area (m² ha⁻¹)	DBH (cm)	Basal area (m² ha⁻¹)	DBH (cm)
Scots pine	1	8.7 ± 1.7	23.9 ± 0.4	10.4 ± 1.8	26.1 ± 0.4
	2	0.1 ± 0.05	15.1 ± 2.5	0.03 ± 0.01	14.5 ± 4.2
	3	1.6 ± 0.3	17.8 ± 0.3	0.1 ± 0.03	13.7 ± 0.5
	4	1.3 ± 0.3	22.5 ± 0.4	0.5 ± 0.1	21.9 ± 0.4
Norway spruce	1	1.6 ± 0.5	15.3 ± 0.5	15.1 ± 1.1	15.3 ± 0.1
	2	-	-	0.04 ± 0.03	18.5 ± 4.9
	3	3.2 ± 0.5	13.6 ± 0.1	0.5 ± 0.1	15.1 ± 0.2
	4	0.2 ± 0.05	14.8 ± 0.4	0.1 ± 0.04	16.2 ± 0.4
Birch	1	0.9 ± 0.3	17.6 ± 0.4	2.5 ± 0.3	14.2 ± 0.1
	2	0.02 ± < 0.01	16.5 ± 1.8	0.05 ± 0.02	14.2 ± 0.7
	3	1.7 ± 0.3	12.5 ± 0.1	0.3 ± 0.05	13.0 ± 0.2
	4	0.1 ± 0.05	13.5 ± 0.5	-	-

Foraging behavior as measured through foraging time

To determine how substrate characteristics influenced foraging time, we analyzed time spent foraging on a specific substrate (number of foraging minutes per observation session) in relation to substrate characteristics. We analyzed time spent foraging with tree species, DBH, and decay stages in interaction with forest type, i.e., unburned or burned forest, as factors using a generalized linear mixed model (GLMM) with Poisson distribution. We included the bird's sex in the model whenever significant to control for intersexual differences in foraging behavior. We included forest stand and year as random variables, and the logarithm of total observation time per session as an offset. Furthermore, the foraging position on the tree regarding foraging height and diameter of foraging substrate was modeled. Foraging height was collected as categorical data; therefore we used the same model structure as in the previous analysis. 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 5 min were included in the analyses pertaining to foraging time. For graphical representation, we plotted the predicted model outcomes.

RESULTS

In 2016, we collected 638 minutes of observations from 14 different woodpecker individuals (Table 2). In total, we observed six individuals (three males and three females) in burned stands and eight individuals (four males and four females) in unburned stands. In 2017, we collected 1301 minutes of observations from 12 different individuals. We observed six of these individuals in burned stands (three males and three females) and six individuals (three males and three females) in unburned stands. In total, 203 utilized trees in burned forest and 94 utilized trees in unburned forest formed the basis for assessing foraging substrate selection and foraging time spent by woodpeckers (Table 2).

Characteristics of selected foraging substrates

Tree species (p < 0.001), decay stage (burned: $X^2_{Decay\ stage}$ = 11.3, p < 0.001, unburned: $X^2_{Decay\ stage}$ = 16.7, p < 0.001) and DBH (burned: X^2_{DBH} = 17.4, p < 0.001, unburned: X^2_{DBH} = 15.1, p < 0.001) predicted characteristics of foraging substrate in both burned and unburned forest stands (Table 3). In burned stands, Three-toed Woodpeckers were less likely to be found foraging on pine than on spruce and birch. Even though pine was avoided in burned forest, birch and spruce were not used more than proportionally to their availability (Fig. 1A). Hence, none of the latter two species was significantly preferred. Decay stage influenced substrate selection: healthy living trees (decay stage 1) were avoided and recently dead trees (decay stage 3) were preferred (Fig. 1B). Additionally, trees in the category of DBH 15–25 cm and 35–45 cm were preferred whereas trees with a DBH in the category of 5–15 were avoided (Fig. 1C).

In unburned stands, spruce was significantly preferred over birch and pine, additionally birch was preferred over pine (Table 3). This was supported by the selection ratios, which showed that spruce was preferred and pine was avoided (Fig. 1A). Three-toed Woodpeckers preferred dying trees (decay stage 2), recently dead trees (decay stage 3), and trees dead for a longer time (decay stage 4). They also preferred trees with a DBH of 15–25 cm (Fig. 1B and C). Trees with DBH in the category of 5–15 and living trees were avoided (Fig. 1B and C).

Foraging behavior as measured through foraging time

Bark scaling was the most common foraging method, accounting for 85.3% of the foraging time in burned forest and 80.1% in unburned forest. The second most common foraging method was sap licking, with 14.7% of the foraging time in burned forest and 19.9% in unburned forest. Three-toed Woodpecker prefer larger DBH trees for sap licking; all observations were collected on trees

Table 2. Total observation time (minutes), total foraging time (minutes), number of used trees, and mean sampling intervals (± SE) divided between sex and given over the two study years. n = number of woodpecker individuals.

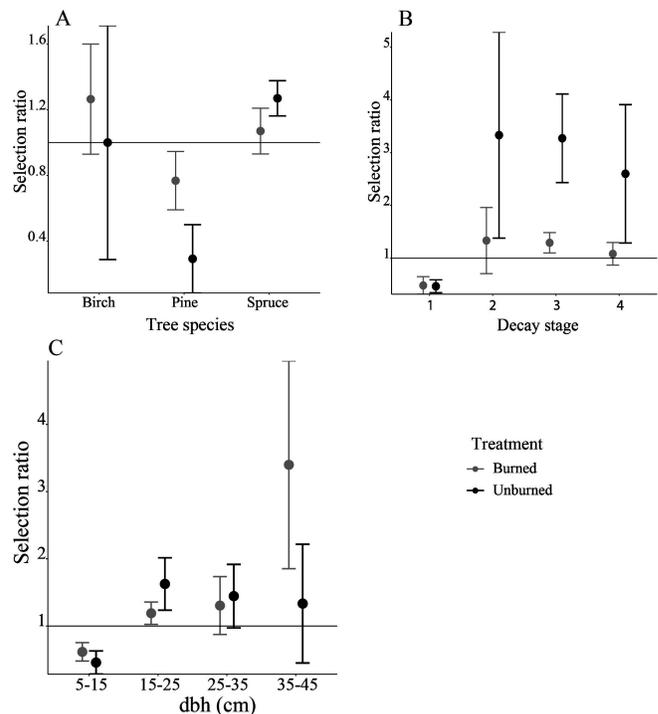| Year	Sex	Burned forest				Unburned forest			
		n	Observation time	Foraging time	Used trees	Sampling intervals (mean ± SE)	n	Observation time	Foraging time	Used trees	Sampling intervals (mean ± SE)
2016	M	3	162	151	73	27.3 ± 4.9	4	93	82	17	17.6 ± 4.5
2016	F	3	221	176	51	24.2 ± 4.1	4	162	129	16	29.2 ± 11.0
2017	M	3	273	95	47	53.2 ±21.2	3	443	204	39	44.0 ± 9.0
2017	F	3	321	134	32	26.0 ± 4.2	3	264	185	22	23.3 ± 4.1

Table 3. Parameter estimates and odds ratios for conditional logistic regression models describing characteristics of trees used by foraging Three-toed Woodpeckers (*Picoides tridactylus*) in burned and unburned forest. Models were run separately for the two forest types. Sex was excluded because it was not significant in the models. DBH, diameter at breast height.

Model Parameter	Estimate	SE	T	P	Odds ratio (95% CI)
A. Burned forest					
Tree species (birch vs. spruce)	0.07	0.09	-0.79	0.430	1.07 (0.89-1.28)
Tree species (pine vs. spruce)	-1.11	0.09	-12.01	< 0.001	0.32 (0.27-0.39)
Tree species (pine vs. birch)	-1.18	0.11	-10.12	< 0.001	0.30 (0.24-0.38)
Decay stage	0.45	0.04	11.34	< 0.001	1.63 (1.49-1.77)
DBH	0.08	0.01	17.35	< 0.001	1.08 (1.07-1.09)
B. Unburned forest					
Tree species (birch vs. spruce)	-1.14	0.20	-5.58	< 0.001	0.32 (0.21-0.48)
Tree species (pine vs. spruce)	-3.73	0.25	-14.56	< 0.001	0.02 (0.01-0.04)
Tree species (pine vs. birch)	-2.59	0.27	-9.57	< 0.001	0.07 (0.04-0.12)
Decay stage	1.13	0.06	16.67	< 0.001	3.09 (2.71-3.53)
DBH	0.13	0.01	15.1	< 0.001	1.15 (1.13-1.17)

Fig. 1. Manly selection ratios with 95% confidence intervals for tree species, decay stage, and diameter at breast height (dbh). Selection ratios are based on the ratio between substrate selected by Three-toed Woodpeckers (*Picoides tridactylus*) and availability (measured as the nearest tree). Values above 1 (horizontal line) indicate preference, and values below 1 indicate avoidance.

with a DHB larger than 15 cm, with 54% on trees with a DBH between 15–25 cm. Excavation into sapwood was neither observed in burned forest nor in unburned forest. In both forest types, the trunk was the most common foraging location, representing 96.8% of the foraging time in burned forest and 95.8% in unburned forest. We did not recorded any observation of Three-toed Woodpeckers using lying dead trees as a foraging substrate, in spite of the presence of substantial amounts of it in some of the study stands. The average foraging time per used tree did not differ between burned and unburned forest ($X^2 = 1.6$, df = 1, p = 0.209).

Substrate diameter at foraging height did not differ between burned and unburned forest ($X^2 = 0.03$, df = 1, p = 0.854) or between sexes ($X^2 = 1.76$, df = 1, p = 0.183) and was on average 18.2 cm in burned forest and 17.1 cm in unburned forest. Males spent significantly more time foraging on the lower part (< 2 m) of trees compared to females ($X^2 = 115.6$, df = 3, p < 0.001, Fig. 2A). Moreover, independent of sex, Three-toed Woodpeckers in burned areas spent significantly more time foraging below 2 m than at higher heights ($X^2 = 83.5$, df = 4, p < 0.001, Fig. 2B). In

contrast, Three-toed Woodpeckers in unburned forests foraged less often below 2 m than at higher heights.

The distribution of the observed foraging time among different tree species, trees belonging to different decay stages, and DBH were influenced by forest type (tree species: $X^2 = 25.2$, df = 2, p < 0.001; decay stage: $X^2 = 26.5$, df = 3, p < 0.001; DBH: $X^2 = 46.1$, df = 3, p < 0.001). In burned forest, Three-toed Woodpeckers spend slightly more foraging time on birch and spruce compared to pine (Fig. 3A). In unburned forest, differences in foraging time among tree species were larger than in burned forest: Three-toed Woodpeckers spend most of their foraging time on spruce and

Fig. 2. Predicted mean foraging time (minutes) per observation session with standard error (SE) of foraging height in relation to (A) sex, (B) treatment. Results derived from GLMM models with Poisson distribution. Forest stand and year were included as random variables.
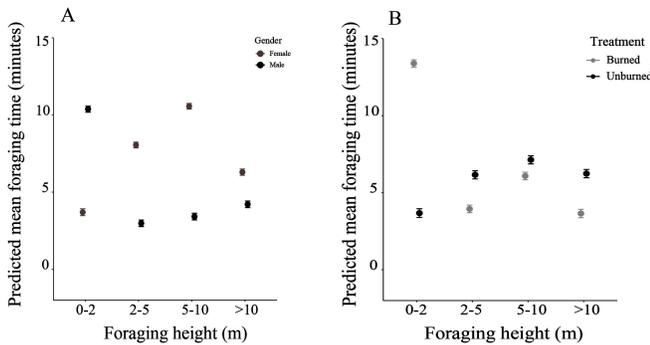

Fig. 3. Predicted mean foraging time (minutes) per observation session with standard error (SE) for substrates belonging to different (A) tree species, (B) decay stages, and (C) diameter at breast height (dbh) classes. Results derived from GLMM models with Poisson distribution and corrected for differences between sex, forest stand, and year were included as random variables.
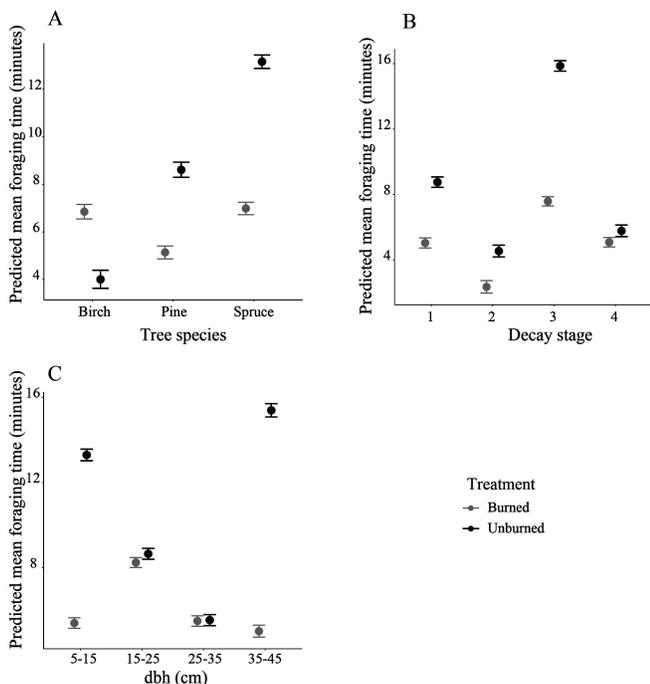
least time on birch (Fig. 3A). In both forest types, decay stage 3 had the highest mean predicted foraging time (Fig. 3B). Furthermore, a considerable amount of foraging time was spent on healthy living trees (decay stage 1). In burned forest, Three-toed Woodpeckers, spent the most time foraging on trees with a

DBH between 15–25 cm. In contrast, in unburned forest they spent on average most time on trees with a DBH of 5–15 and 35–45 cm (Fig 3C).

DISCUSSION

This study is among the first to quantify the foraging requirements of the Eurasian Three-toed Woodpecker in burned forest and to compare foraging behavior between burned and unburned forests. By determining simultaneously the characteristics of selected foraging substrates and foraging behavior as measured through foraging time, this study provides a comprehensive overview of the foraging ecology of the Eurasian Three-toed Woodpecker in boreal forests. The two methods provided complementary knowledge and thus using them simultaneously helps to improve our understanding of the woodpecker's foraging behavior (Imbeau and Desrochers 2002, Nappi et al. 2015). Knowledge from this study is important for the development of strategies for forest management and ecological restoration based on the relation between tree dynamics and the foraging ecology of woodpeckers.

Based on tree selection analyses, our results demonstrate that in both unburned and burned boreal forest, tree species, decay stage, and DBH are important factors influencing foraging substrate selection by the Eurasian Three-toed Woodpecker. In addition, patterns of substrate use as measured through foraging time differed substantially between burned and unburned forest. In burned forest, we found less pronounced importance of tree species (especially based on foraging time). Healthy living trees seem to be more important in terms of foraging time than suggested by the analysis of the characteristics of selected substrates that does not account for time. This may be an indication of the importance of tree sap from living trees as a food source for the woodpecker. However, bark scaling was the main foraging technique, which corroborates previous knowledge suggesting that the Three-toed Woodpecker is a specialist closely associated with bark beetles (Curculionidae; Scolytinae) as a main prey (Fayt 1999, Nappi et al. 2015).

Characteristics of selected foraging substrates

Our results suggest that in burned forest stands, typical foraging substrates for Three-toed Woodpeckers are spruce or birch, recently dead trees (decay stage 3), and trees with a DBH in the categories 15–25 cm and 35–45 cm. Our results are in line with those obtained from burned forests of Northern America, where the American Three-toed Woodpecker and Black-backed Woodpecker (*Picoides arcticus*) have been shown to select larger snags (> 15 cm) for foraging (Murphy and Lehnhausen 1998, Nappi and Drapeau 2011).

In unburned forests, the Three-toed Woodpecker showed a clear preference for Norway spruce. One possible explanation for this is that their main prey, bark beetles, are relatively more abundant in spruce than in the other tree species in unburned forest compared to burned forest. A study preformed in the same study system in 2013 (Hägglund and Hjältén 2018) provides support for this, although it is unclear whether this pattern for bark beetle distribution persisted until this study was performed (2017). Furthermore, Three-toed Woodpeckers preferred dying trees

(decay stage 2), recently dead trees (decay stage 3), and trees dead for a longer time (decay stage 4), as well as trees with a DBH of 15–25 cm. Healthy living trees and trees with a DBH in the category of 5–15 were avoided according to the substrate selection analyses. These results are in line with knowledge pertaining to American Three-toed Woodpeckers in unburned forest (Imbeau and Desrochers 2002, Nappi et al. 2015), which showed a stronger preference for fresh larger diameter snags over living trees. Nappi et al. (2015) found that the main prey item of American Three-toed Woodpecker, i.e., Scolytinae, were found in high abundance in trees selected for foraging.

Foraging behavior as measured through foraging time

The prediction that time spent on a selected foraging substrate should differ between burned and unburned forest because of changes in substrate properties caused by fire was partly supported. We found such differences in terms of tree species, decay stage, and DBH. In unburned forests, Three-toed Woodpeckers clearly spent most of their foraging time on spruce. This is in line with other studies that reported that Three-toed Woodpeckers primarily forage on spruce (*Picea* spp.; Hogstad 1991, Villard 1994, Imbeau and Desrochers 2002, Pechacek 2006*a*, Nappi et al. 2015). Nevertheless, such a clear difference in foraging time between tree species was not found in burned forests. Even though most time was spent on spruce and birch, a considerable amount of time was also spent on pine. This in contrast to other studies that show that two years after wildfire in mixed burned forest stands, Three-toed Woodpeckers mainly forage on spruce trees (Murphy and Lehnhausen 1998, Fayt 1999). The time elapsed since fire and fire severity are two important factors that should be taken into account when comparing studies regarding fire and woodpecker behavior. High abundance of insects is generally limited to the first few years after fire (Saint-Germain et al. 2004*b*, Boulanger and Sirois 2007), which is also found for woodpecker abundance (Murphy and Lehnhausen 1998, Fayt 2003, Gustafsson et al. 2019). However, low fire severity can prolong the availability of appropriate host trees for saproxylic insects and thus enhance food availability over a longer time period (Nappi et al. 2010). An important portion of our burned study stands were characterized by low to moderate fire severity that resulted in mixture of live, declining, and dead trees, which may explain some of the differences with other studies. In addition, one other potential explanation for woodpecker use of both pine and spruce in this study may be that after prescribed burning, saproxylic beetle distribution becomes more homogenized between tree species (Wikars 2002, Nappi et al. 2010, Toivanen and Kotiaho 2010, Hägglund and Hjältén 2018), making woodpeckers more likely to spend time foraging on several different tree species. For example, Nappi et al. (2010), found no significant differences between mean densities of wood-boring Cerambycidae larvae in bole segments of lightly burned pine vs. spruce trees. Still, we did not measure prey availability in this study and can therefore only speculate regarding explanations behind the observed foraging patterns. More studies combining measures on foraging preferences and prey distribution and abundance are therefore needed.

In both burned and unburned forest, Three-toed Woodpeckers on average spent most of their foraging time on recently dead

trees (decay stage 3). This is in line with results from earlier studies reporting that Three-toed Woodpeckers prefer fresh snags (Hogstad 1991, Pechacek 2006*a*, Nappi et al. 2015). However, we found that Three-toed Woodpeckers also spent a considerable amount of time on living trees, in spite of the fact that living trees were avoided in terms of substrate selection. On healthy living trees, the woodpecker spent on average 55% of their time licking sap. These results may indicate that the woodpeckers dedicate a disproportionally larger amount of time to sap licking, i.e., healthy living trees form a small proportion of the trees used by the woodpecker, but the woodpeckers spend a substantial amount of time on these trees. Hence, sap from living trees may be an important food source for both the Eurasian and American Three-toed Woodpecker (Nappi et al. 2015, Pakkala et al. 2018*b*). Overall, we found that Three-toed Woodpeckers spent up to 19.9% of their total foraging time sap-licking in unburned and 14.7% in burned forest. This is similar to what Nappi et al. (2015) reported in mature coniferous forest by American Three-toed Woodpecker. They demonstrated that they spent up to 20% of their foraging time in sap-licking on healthy trees. Additionally, for the Eurasian Three-toed Woodpecker it has been shown that up to 33% of their foraging time was spent sap-licking (Pakkala et al. 2018*b*). In this study, Three-toed Woodpeckers in burned forest spent the most time foraging on trees with a DBH between 15–25 cm while in unburned forest they spent on average the most time on trees with a DBH of 5–15 and 35–45. These results are partly in line with studies from unburned forest, where it has been shown that Three-toed Woodpeckers mainly forage on trees with a DBH > 10 cm (Hogstad 1977, 1991, Pechacek and d'Oleire-Oltmanns 2004, Zhu et al. 2012). However, this study suggests that, once selected, woodpeckers may spend considerable time utilizing smaller diameter trees in the range of 5–15 cm in unburned forest. We have shown that trees in this range were not used for sap licking and thus the most likely explanation is that natural self-thinning in the studied old forest stands leads to the slow death of small-diameter spruce, which are abundantly colonized by bark beetles such as *Pityogenes chalcographus* (Fayt 1999).

We confirmed that in unburned forest the primary foraging method of Three-toed Woodpeckers is bark-scaling and that their main foraging location is on the trunk (Hogstad 1977, 1991, Pechacek 2006*a*). Moreover, we found that Three-toed Woodpeckers behaved similarly in burned forests. Average diameter of foraging substrate did not differ between forest types; these results are similar to what was found by Zhu et al. (2012) and Pechacek (2006*a*) in unburned forests. Our data did support our prediction that foraging height, measured through foraging time, would differ between burned and unburned forest. However, the differences found between sexes were not influenced by treatment, but treatment had, independently of sex, an effect on foraging height. Our results show that Three-toed Woodpeckers in burned forest spent more foraging time on the lower part of the trunk (0–2 m). With regard to sex, our results are in line with the literature showing that male Three-toed Woodpeckers generally forage lower on the trunk than females (Hogstad 1977, 1991, Pechacek 2006*a*, Zhu et al. 2012). However, these results may suggest that the spatial distribution of prey species changes after prescribed burning. Prescribed burning usually results in higher fire impact on the lower part of the trees. It is suggested

that shading, bark thickness, and burn severity are important factors affecting the spatial distribution of bark beetles on trees (Jakuš 1998, Fayt 1999, Foit 2010). Similar to our results, Nappi et al. (2003) and Nappi and Drapeau (2011) found that Black-backed Woodpeckers in burned forests foraged mainly on the lower part of the tree and related this to high prey availability after fire in the lower five meters of the trunk. Within this study we did not measure food availability but it will be of importance to investigate the consequences of fire on the spatial distribution of prey species. Sampling saproxylic arthropods would be a logical next step to fill this knowledge gap.

CONCLUSIONS

In this study we found that in both burned and unburned forests, typical foraging substrates can be characterized as freshly dead trees with a DBH of more than 15 cm. Additionally, data on time spent foraging on the different substrates suggest that also substrates in the 5–15 DBH range and living trees are important. Living trees are probably important for sap licking.

This study was performed 5–6 years after fire and still the burned sites offered foraging substrate for Three-toed Woodpeckers. This is in contrast to wildfires, where it has been found that Three-toed Woodpecker densities often drop after 2–4 years (Fayt 2003, Gustafsson et al. 2019). Still, Nappi et al. (2010)'s study of the Black-backed Woodpecker showed a similar pattern in wildfires that burned with variable severity as in our study: the woodpecker still occurred at high densities 6–8 years after wildfire. One possible explanation for this variation is that under low intensity fires (as is usually the case in prescribed burning), mortality of the different trees in the forest can occur more gradually over several years. It can take several years for partially burned trees to die from fire stress or beetle attack (McHugh and Kolb 2003). Therefore, bark beetle abundance may remain elevated across the forest stand a longer time after fire. This suggests that the use of prescribed burning can be an efficient way for rapid and apparently long-lasting enrichment of important forest structures for woodpeckers.

In unburned forests, quantity and quality of dead wood is critical for the occurrence of Three-toed Woodpeckers and other dead wood associated species (Bütler et al. 2004*b*, Roberge et al. 2008). Even though dead wood quantities in Swedish forests have increased by 25% since 1994, (Jonsson et al. 2016), the levels are still only about 10% of those found in old growth forest and heterogeneity of dead wood types is low in terms of tree species, DBH, and decay stages. Additionally, Hedwall and Mikusiński (2015) demonstrated very low levels and slow increase of dead wood in Swedish protected areas. Therefore, we suggest that the best conservation strategy for the Three-toed Woodpecker is to conserve remaining old-growth forests and create more fresh dying trees and dead wood of different tree species and DBH classes in managed and protected forests to continuously provide sufficient quantities of recently dead or dying trees at the landscape level.

Overall, the results from this study support earlier recommendations by Drapeau et al. (2009) that a better understanding of the foraging ecology of woodpeckers and their association to deadwood is necessary for successful conservation work in managed forest landscapes. Rather than solely focusing on snag numbers for nesting and roosting purposes, a broader consideration of decaying and dead trees dynamics relating to the foraging ecology of woodpeckers and relationships between tree decay, insect abundance, and woodpeckers foraging should be considered in forest conservation and management.

Responses to this article can be read online at:
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