

Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest

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Abstract

Predicting species' responses to habitat loss is a significant challenge facing conservation biologists. We examined the response of both European three-toed woodpecker subspecies *Picoides tridactylus tridactylus* and *P. tr. alpinus* to different amounts of dead wood in a boreal and a sub-Alpine coniferous forest landscape in central Sweden and Switzerland, respectively. Habitat variables were measured by fieldwork in forests with breeding woodpeckers ($n = 10 + 12$) and in control forests without breeding woodpeckers ($n = 10 + 12$) in the same landscape. Logistic regression analyses revealed steep thresholds for the amount of dead standing trees and the probability of three-toed woodpecker presence in both Sweden and Switzerland. The probability of the presence of three-toed woodpeckers increased from 0.10 to 0.95 when snag basal area increased from 0.6 to 1.3 m² ha⁻¹ in Switzerland and from 0.3 to 0.5 m² ha⁻¹ in central Sweden. In Switzerland, a high road network density was negatively correlated to the presence of woodpeckers ($r = -0.65$, $p = 0.0007$). The higher volumes of dead wood in Switzerland, where population trends are more positive, than in central Sweden, where the population is declining, would suggest that the volumes of dead wood in managed forests in Sweden are too low to sustain three-toed woodpeckers in the long-term. In terms of management implications, we suggest a quantitative target of at least 5% of standing trees in older forests being dead over at least 100 ha large forest areas. This corresponds about to ≥ 1.3 m² ha⁻¹ (basal area) or ≥ 15 m³ ha⁻¹ (volume), still depending on site productivity.
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1. Introduction

Loss of habitat is the major reason for local extirpation and, ultimately, the extinction of species. While habitat loss is often a continuous change in the process of habitat fragmentation in ecological systems, the response of different components of ecosystem integrity to habitat loss may be non-linear (Fahrig, 2001; Muradian, 2001). Both models and empirical studies have demonstrated the existence of ecological thresholds of habitat proportions for different species at the landscape scale (e.g., Andren, 1994; With and Crist, 1995; Jansson and Angelstam, 1999; Fahrig, 2001). Thus, an answer to the

question “How much habitat is enough?”, or in other words knowledge of ecological thresholds for the amount of habitat area or habitat features required at different ecological scales, is necessary to prevent further local and regional loss of species (Fahrig, 2001). Consequently, ecological thresholds are a key feature that should be taken into consideration (Simberloff, 1995; With and Crist, 1995; Muradian, 2001) in the context of forest biodiversity maintenance, both by nature conservation per se, and by sustainable forest management and forest certification processes.

The usefulness of keystone species (Paine, 1966) and umbrella species (Fleishman et al., 2000; Fleishman et al., 2001) for biodiversity conservation is gaining increasing acceptance among ecologists and conservation biologists (Simberloff, 1999; Roberge and Angelstam, in

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press). Among vertebrates, woodpecker species are a particularly interesting group to be studied with respect to non-linear responses to habitat loss. They are of special importance due to their key-stone role in supplying forests with tree-cavities, that serve secondary users as nesting or roosting holes (Saari and Mikusinski, 1996). Moreover, among area-demanding species specialised in natural forest components such as old trees, dead wood and structural diversity (Angelstam, 1990; Angelstam and Mikusinski, 1994; Mikusinski and Angelstam, 1997), they are also considered to be the most demanding guild in terms of their ecological requirements. Furthermore, a positive relationship has been reported between woodpecker species richness and the number of other forest species (Martikainen et al., 1998; Mikusinski et al., 2001).

In the case of conifer-dominated forests, the three-toed woodpecker is a potential umbrella species for which habitat threshold values could be developed (Angelstam, 1998; Mikusinski et al., 2001; Nilsson et al., 2001; Angelstam et al., 2003). Moreover, Imbeau (2001) considered the three-toed woodpecker as a possible keystone species (*sensu* Thompson and Angelstam, 1999). In addition to its qualities as a potential umbrella and keystone species, other reasons justify its suitability as an important candidate for the development of habitat threshold values for the purpose of forest biodiversity management. It is the only woodpecker occurring in both the New and the Old Worlds (Winkler et al., 1995), thus showing a large geographic distribution. Consequently, habitat threshold values translated into management recommendations could be applied over a wide geographic area. Moreover, Alpine populations are also sedentary in winter (Winkler et al., 1995), and Swedish populations mostly sedentary (Svensson et al., 1999). Local reasons, such as forest management practices, must, therefore, be considered to explain population fluctuations. For example, the ongoing decline of populations in Fennoscandia is directly related to the modern forestry practice of removing old and dead trees (Nilsson, 1992; Angelstam and Mikusinski, 1994; Tucker and Heath, 1994). Finally, three-toed woodpeckers are important predators of insects that are prone to outbreaks. Examples of these insects include *Polygraphus* and *Ips* in Eurasia and spruce bark beetle *Dendroctonus obesus* in America. Thanks to their ability to concentrate locally in burned sites or windfall areas (Koplin, 1969; Murphy and Lehnhausen, 1998), three-toed woodpeckers can be considered as natural agents against insect plagues (Bütler and Schlaepfer, 2003).

Three-toed woodpeckers mainly feed on the larvae of scolytid beetles and other insects found in dying and dead trees (Pechacek and Kristin, 1993; Murphy and Lehnhausen, 1998; Fayt, 1999) and, in spring, they occasionally lick sap from tree trunks in which they make small holes (Glutz von Blotzheim, 1994; Pechacek,

1995). Consequently, recently dead trees are one of the most important habitat features for foraging (Hogstad, 1970; Hess, 1983; Pechacek, 1995; Murphy and Lehnhausen, 1998; Ruge et al., 1999; Imbeau and Desrochers, 2002). Dead wood amounts in woodpecker habitats, however, have rarely been quantified (Derleth et al., 2000), and the existence of a dead wood threshold value for this species has never been tested using dead wood as a resource (but see Pakkala et al., 2002).

The aims of this study were to search for possible dead wood threshold values playing an important role in the local continued presence of three-toed woodpeckers in boreal and mountain forests, and to derive quantitative targets for management implications. We chose an original approach replicated in two different landscapes and with two palearctic subspecies *Picoides tridactylus tridactylus* (in Northern Europe) and *P.t.alpinus* (in the mountains of Central, Southern and South-East Europe).

2. Material and methods

2.1. Study areas

We conducted our study in two coniferous forest regions, one located in central Sweden (SE) and one in Switzerland (CH) (Fig. 1). Whereas Norway spruce (*Picea abies*) is the main tree species in the Swiss sub-Alpine mountain forest landscape, the Swedish forest landscape is characterised by boreal forests dominated by a mixture of Scots pine (*P. sylvestris*) and Norway spruce. In order to take into account the heterogeneity arising from the topography of Swiss mountain regions, data was collected in three areas (Fig. 1) situated in the eastern/central and the western Lower Alps and in the Jura Mountains. In 1993 a small population of three-toed woodpeckers was detected the first time in the Swiss Jura (Chabloz and Wegmüller, 1994), where the species was not present before. As the Swiss three-toed woodpecker population is obviously in expansion (Schmid et al., 1998), it seemed interesting to us to include such a newly colonised area. In contrast, boreal forests in central Sweden are homogenous and population trends are generally negative (BirdLife, 2000). For this reason, there was no sub-division into different areas.

2.2. Study design

In each region pair-wise sampling units of 1 km² were studied (10 + 10 units in Sweden and 12 + 12 in Switzerland). Each pair consisted of 1 km² where the three-toed woodpecker had been breeding (called “presence”) in the years of bird surveys (1998–2000 in Sweden and 1993–2001 in Switzerland) and one randomly selected

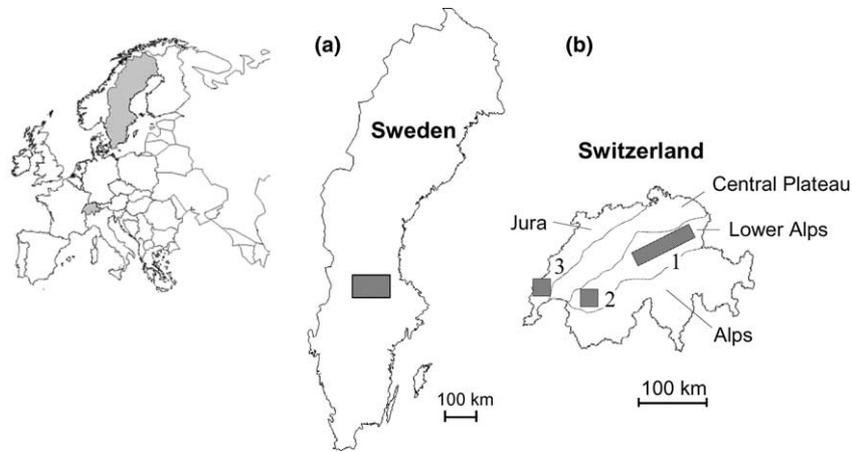


Fig. 1. Study sites: (a) a boreal landscape located in central Sweden and (b) a Swiss sub-Alpine landscape, sub-divided into three areas, situated in the eastern/central (1) and western Lower Alps (2) and in the Jura Mountains (3).

unit, within an area of 30 km², where it was not observed (called “absence”). Presence was indicated where nests were found or birds observed, according to the criteria of probable breeding as defined in the International Ornithological Atlases (Sharrock, 1973). The selection of presence/absence 1 km² was based on data provided by an Atlas project of the Swiss ornithological station of Sempach (cf. Schmid et al., 1998), regional bird associations and local amateur ornithologists in Switzerland and Sweden, and was subject to the following criteria: (a) Norway spruce or Scots pine tree dominated forests; (b) the majority of the forest stands more than 100 years old, i.e. mature to over-mature, the stand age preferred by three-toed woodpeckers; (c) between 1200 and 1700 m a.s.l. in Switzerland, where the probability of three-toed woodpecker occurrence is highest (cf. Schmid et al., 1998) and between 100 and 300 m a.s.l. in Sweden; (d) forest cover within each sampled 1 km² \geq 70%. The mean forest covers in Switzerland were 80% (presence) and 84% (absence) and in Sweden 90% (presence) and 90% (absence).

2.3. Data gathering

In each 1 km² sampling unit 4 × 4 systematically placed sampling plots were used to sample the amount of dead wood. The distance between sampling plots was 250 m (Fig. 2). Systematic sampling plots located in a non-forested area (e.g. pasture, wet area) were moved to the closest forest area. Four types of variables were defined (Table 1). Measurements of the basal area of trees were made using a relascope. A snag was defined as any standing dead tree with a minimal height of 1.7 m. The minimal diameter for recording snags, logs (laying dead trees) and living trees was 10 cm dbh, and the measurement unit was stand basal area (m² ha⁻¹). Since three-toed woodpeckers prefer recently dead trees as foraging substrate, we introduced four variables de-

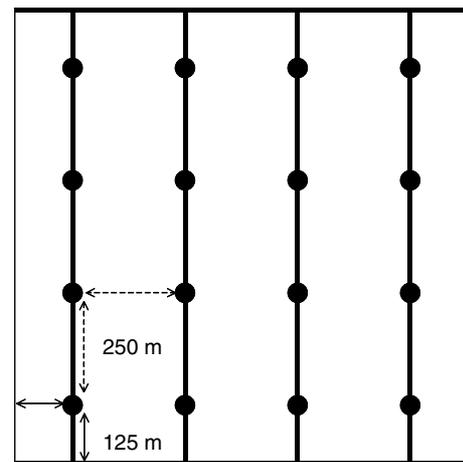


Fig. 2. Data gathering in a 1 km² sampling unit with systematic sampling plots and transect lines.

scribing the decomposition stage of dead trees: snags with/without bark and hard/soft logs (Table 1). Slope and aspect were measured in degrees. Road/track density was the total length of roads and tracks in the 1 km² accessible by a tractor. Roads and tracks were measured using topographical maps. Harvesting intensity was defined as the density of tree stumps within the plot (30 m of diameter). It was classified in two categories: \leq 3 stumps per plot (extensive harvesting) and \geq 10 (intensive harvesting). Harvesting time was also a dichotomous variable used to date the harvesting period into recent (tree stumps are hard, uncovered by mosses or vegetation) or past (tree stumps are soft or decomposed and/or covered by mosses or vegetation). A plot could, therefore, present both recent and past harvesting.

Ringed trees are trees having small holes made in the bark by woodpeckers (and in particular by three-toed woodpeckers), typically distributed as horizontal lines on the trunk (Ruge, 1968; Scherzinger, 1982; Glutz von Blotzheim, 1994). The total number of ringed trees in the

Table 1

Measured variables in 1 × 1 km sampling units ($n = 12 + 12$ in Switzerland (CH) and $n = 10 + 10$ in central Sweden (SE)), in which the three-toed woodpecker was present and absent, respectively

Type	Variable	Unit	Type of measure	Level	Landscape
Habitat features	Snags	m ² ha ⁻¹	Relascope	Plot	CH/SE
	Logs	m ² ha ⁻¹	Relascope	Plot	CH/SE
	Living trees	m ² ha ⁻¹	Relascope	Plot	CH/SE
	Spruce trees	% of living trees	Relascope	Plot	CH/SE
	Pine trees	% of living trees	Relascope	Plot	SE
	Deciduous trees	% of living trees	Relascope	Plot	SE
	Tree height	m	Heightmeter	Plot	CH/SE
Topography	Slope	degrees	Clinometer	Plot	CH
	Aspect	degrees (0–360°)	Compass	Plot	CH
Management	Road/track density	km km ⁻²	Topographical maps	Field unit	CH/SE
	Intensive harvesting	% of occurrence	Visual appreciation	Field unit	CH/SE
	Extensive harvesting	% of occurrence	Visual appreciation	Field unit	CH/SE
	Recent harvesting	% of occurrence	Visual appreciation	Field unit	CH/SE
	Past harvesting	% of occurrence	Visual appreciation	Field unit	CH/SE
Continuity	Snags with bark	% of occurrence	Visual appreciation	Field unit	CH/SE
	Snags without bark	% of occurrence	Visual appreciation	Field unit	CH/SE
	Hard logs	% of occurrence	Visual appreciation	Field unit	CH/SE
	Soft logs	% of occurrence	Visual appreciation	Field unit	CH/SE
	Ringed trees	Number, age	Visual appreciation	Field unit	CH/SE

Each sampling unit contained 16 systematic sampling plots.

1 km² was counted by walking on transect lines between the plots (total distance 6 km per sampling unit; Fig. 2), and their approximate age determined using the following categories: (i) fresh signs (transparent, sticky and flowing resin in the holes); (ii) quite fresh signs (white or yellow resin not flowing any more); (iii) old signs (no resin, only small holes); (iv) signs of long use (the tree has formed bulges). We estimated the basal area measurement reproducibility, since two different persons measured the habitat variables in Switzerland and Sweden, respectively. This estimation was based on data from 209 plots, measured twice separately by two different persons. Differences of less than 10% have been found between the two sets of basal area measurement results.

2.4. Statistical analyses

For the statistical analyses we used STATISTICA 6.0[®] statistical software. The analyses were carried out separately for Switzerland and Sweden. For dichotomous variables (i.e. intensive/extensive harvesting, recent/past harvesting, snags with/without bark, hard/soft logs; cf. Table 1), we calculated the proportion of sampling plots per 1 km² where the observed characteristic occurred. For each 1 km², we calculated mean values for all variables measured in the sampling plots. The 1 km² were then separated into two groups (woodpecker forests and control forests, i.e. without woodpeckers), and group means and ranges were calculated for all variables. The continuous variable aspect was transformed into a categorical variable (eight categories of 45° from 0° to 360°), and a Chi-square goodness-of-fit test was

conducted on plot data frequency distribution ($n = 192$ for presence and $n = 192$ for absence plots) to test for differences between groups (Zar, 1999).

Because of the binary nature of the response variable for the three-toed woodpecker (“presence” and “absence”, coded as 1 and 0), logistic regression (Hosmer and Lemeshow, 1989) was chosen as the appropriate method to evaluate the existence of dead wood threshold values. Following Hosmer and Lemeshow (1989), the potential predictor variables were first assessed for significance in a univariate analysis by a pair-wise two-sample *t*-test. Thus, variables in percentages (cf. Table 2) were arcsine square-root transformed in order to normalise the data distribution (Zar, 1999).

A correlation matrix was calculated between all independent variables to examine possible co-linearity. After this we calculated univariate logistic regression models. The resulting models were assessed using goodness-of-fit based on maximum likelihood estimates, and the overall rate of correct classification of the response variable (“presence” and “absence”). For the regression models for snag basal area, we calculated the first derivative function to compare the steepness of the slopes between the models for Sweden and Switzerland. The *x*-values of the inflexion points of the two models were tested for statistical difference at a level of $\alpha = 0.01$ by calculating its standard errors.

To enable comparison with other studies reporting dead wood amounts in forest stands, which are usually expressed as volume per hectare (m³ ha⁻¹), we also calculated the dead wood volumes (*V*) by a formula: $V = \text{basal area} * \text{tree height} * \text{shape index (correction factor)}$

Table 2
Variable means and ranges for the 1 × 1 km sampling units in which the three-toed woodpecker was present and absent, respectively

Variable	Presence		Absence		t- Statistics		t-Statistics		
	Mean (range) <i>n</i> = 12	Mean (range) <i>n</i> = 12	<i>t</i>	<i>p</i>	Mean (range) <i>n</i> = 10	Mean (range) <i>n</i> = 10	<i>t</i>	<i>p</i>	
<i>Habitat features [unit]</i>		Switzerland				Sweden			
Snags [m ² ha ⁻¹]	2.3 (0.6–6.0)	0.4 (0.0–0.8)	4.78	0.0006***	0.8 (0.4–1.0)	0.2 (0.1–0.4)	7.07	0.0001***	
Logs [m ² ha ⁻¹]	2.2 (0.9–4.1)	0.6 (0.2–1.2)	6.23	0.0001***	1.8 (0.9–2.9)	0.8 (0.4–1.1)	5.59	0.0003***	
Living trees [m ² ha ⁻¹]	25.6 (17–38)	30.4 (19–39)	-2.54	0.0273**	15.0 (11–18)	12.1 (7–16)	2.42	0.0386**	
Spruce [%]	91 (81–95)	86 (78–95)	2.02	0.0683*	45 (30–67)	34 (14–59)	1.97	0.0805*	
Pine [%]	n.d.	n.d.	n.d.	n.d.	45 (30–65)	59 (29–86)	-2.68	0.0252**	
Deciduous [%]	n.d.	n.d.	n.d.	n.d.	11 (4–36)	7 (0–21)	1.38	0.2169	
Tree height [m]	23 (19–26)	23 (19–27)	-0.24	0.8115	17 (14–23)	14 (10–16)	3.66	0.0053***	
<i>Topography</i>									
Slope [°]	21 (8–36)	13 (4–30)	2.45	0.0322**	n.d.	n.d.	n.d.	–	
<i>Management</i>									
Road/track density [km/km ⁻²]	1.8 (0.0–3.6)	5.3 (2.9–7.3)	-7.32	0.0000***	1.1 (0.0–2.1)	1.2 (0.0–2.9)	-0.46	0.6569	
Intensive harvesting [%]	27 (0–50)	54 (13–94)	-2.42	0.0342**	19 (0–44)	35 (19–50)	-2.61	0.0282**	
Extensive harvesting [%]	28 (6–63)	3 (0–13)	5.08	0.0004***	69 (56–88)	68 (56–100)	-0.26	0.7975	
Recent harvesting [%]	46 (19–88)	52 (19–81)	-0.58	0.5742	13 (0–31)	30 (0–56)	-2.17	0.0583*	
Past harvesting [%]	84 (56–100)	90 (69–100)	0.01	0.9908	75 (50–88)	78 (56–100)	-0.99	0.3472	
<i>Continuity</i>									
Snags with bark [%]	69 (44–80)	30 (0–50)	6.25	0.0001***	19 (0–38)	11 (0–19)	1.74	0.1164	
Snags without bark [%]	23 (13–31)	7 (0–19)	5.55	0.0002***	19 (0–31)	7 (0–19)	3.00	0.0149**	
Hard logs [%]	79 (56–94)	47 (19–69)	6.85	0.0000***	53 (31–75)	26 (0–44)	3.61	0.0057***	
Soft logs [%]	37 (6–60)	15 (6–25)	5.19	0.0003***	36 (25–50)	23 (13–38)	3.46	0.0071***	
Ringed trees [<i>n</i>]	9 (0–35)	1 (0–4)	2.36	0.0377**	4 (0–16)	0 (0–0)	2.33	0.0450**	

n.d.: no data collected.

* Significant at the 0.10 level.

** Significant at the 0.05 level.

*** Significant at the 0.01 level.

Table 3
 Linear correlations between the measured variables (Pearson r) in Swiss sub-Alpine spruce forests ($n = 24$) and Swedish boreal forests ($n = 20$)

	Snags	Logs	Living trees	Spruce	Pine	Deciduous	Tree height	Slope	Road-track density	Intensive harvesting	Extensive harvesting	Recent harvesting	Past harvesting	Snags with bark	Snags without bark	Hard logs	Soft logs	Ringed trees	
Snags	–	<i>0.80*</i>	<i>0.69*</i>	<i>0.61*</i>	<i>-0.54*</i>	<i>0.22</i>	<i>0.79*</i>	<i>0.15</i>	<i>-0.47*</i>	<i>-0.10</i>	<i>-0.48*</i>	<i>-0.24</i>	<i>0.59*</i>	<i>0.56*</i>	<i>0.67*</i>	<i>0.44</i>	<i>0.72*</i>		
Logs	0.86*	–	<i>0.49*</i>	<i>0.41</i>	<i>-0.41</i>	<i>0.27</i>	<i>0.45</i>	<i>-0.03</i>	<i>-0.37</i>	<i>-0.04</i>	<i>-0.33</i>	<i>-0.21</i>	<i>0.39</i>	<i>0.37</i>	<i>0.81*</i>	<i>0.54*</i>	<i>0.68*</i>		
Living trees	0.08	-0.08	–	<i>0.53*</i>	<i>-0.37</i>	<i>-0.18</i>	<i>0.74*</i>	<i>0.20</i>	<i>-0.36</i>	<i>0.13</i>	<i>-0.38</i>	<i>0.09</i>	<i>0.62*</i>	<i>0.36</i>	<i>0.61*</i>	<i>0.18</i>	<i>0.55*</i>		
Spruce	0.51*	0.16	0.19	–	<i>-0.64*</i>	<i>0.08</i>	<i>0.73*</i>	<i>0.34</i>	<i>0.03</i>	<i>-0.10</i>	<i>-0.23</i>	<i>-0.02</i>	<i>0.42</i>	<i>0.58*</i>	<i>0.28</i>	<i>0.26</i>	<i>0.23</i>		
Pine					–	<i>-0.63*</i>	<i>-0.48*</i>	<i>-0.30</i>	<i>0.09</i>	<i>-0.06</i>	<i>0.36</i>	<i>-0.20</i>	<i>-0.17</i>	<i>-0.25</i>	<i>-0.28</i>	<i>-0.28</i>	<i>-0.22</i>		
Deciduous						–	<i>0.06</i>	<i>0.07</i>	<i>-0.28</i>	<i>0.28</i>	<i>-0.32</i>	<i>0.26</i>	<i>-0.08</i>	<i>-0.24</i>	<i>-0.02</i>	<i>0.36</i>	<i>0.05</i>		
Tree height	0.03	0.36	0.31	-0.50*			–	<i>0.39</i>	<i>-0.23</i>	<i>0.10</i>	<i>-0.24</i>	<i>-0.01</i>	<i>0.68*</i>	<i>0.49*</i>	<i>0.36</i>	<i>0.22</i>	<i>0.40</i>		
Slope	0.06	0.41	0.24	0.09				0.23	–										
Road/track density	-0.64*	-0.53*	0.20	-0.42				0.20	0.19	–	<i>0.43</i>	<i>-0.11</i>	<i>0.20</i>	<i>0.18</i>	<i>0.47*</i>	<i>0.05</i>	<i>0.00</i>	<i>-0.26</i>	<i>-0.14</i>
Intensive harvesting	-0.47*	-0.30	0.45*	-0.09				0.06	-0.10	0.42	–	<i>-0.42</i>	<i>0.70*</i>	<i>-0.02</i>	<i>-0.02</i>	<i>-0.06</i>	<i>-0.19</i>	<i>-0.49*</i>	<i>-0.49*</i>
Extensive harvesting	0.64*	0.48*	-0.20	0.39				-0.14	-0.13	-0.74*	-0.73*	–	<i>-0.07</i>	<i>0.68*</i>	<i>-0.16</i>	<i>-0.31</i>	<i>-0.20</i>	<i>0.32</i>	<i>-0.16</i>
Recent harvesting	-0.36	0.16	-0.24	-0.56*				0.44	0.33	0.45*	0.09	-0.39	–	<i>-0.23</i>	<i>-0.17</i>	<i>-0.28</i>	<i>-0.31</i>	<i>-0.33</i>	<i>-0.36</i>
Past harvesting	-0.24	-0.56*	-0.07	-0.06				-0.33	-0.62*	-0.02	0.02	-0.03	-0.51*	–	<i>-0.08</i>	<i>-0.24</i>	<i>-0.16</i>	<i>0.00</i>	<i>-0.33</i>
Snags with bark	0.78*	0.70*	0.07	0.45*				0.16	0.27	-0.71*	-0.47*	0.63*	-0.28	-0.41	–	<i>0.16</i>	<i>0.43</i>	<i>0.26</i>	<i>0.26</i>
Snags without bark	0.77*	0.69*	-0.19	0.39				-0.01	0.03	-0.76*	-0.39	0.72*	-0.15	-0.44	0.79*	–	<i>0.42</i>	<i>0.00</i>	<i>0.39</i>
Hard logs	0.68*	0.77*	-0.22	0.14				0.37	0.22	-0.39	-0.44	0.55*	0.32	-0.49*	0.61*	0.70*	–	<i>0.25</i>	<i>0.55*</i>
Soft logs	0.27	0.51*	-0.24	0.05				0.09	-0.12	-0.47*	-0.28	0.34	-0.08	-0.19	0.56*	0.60*	0.52*	–	<i>0.11</i>
Ringed trees	0.70*	0.53*	0.11	0.35				-0.01	-0.04	-0.52*	-0.28	0.48*	-0.19	-0.01	0.41	0.30	0.32	0.22	–

In bold: Switzerland; in italics: Sweden.

* Significant at $p < 0.05$.

for tree shape of trees estimated as the ratio between the actual volume of the cone-shaped tree and an assumed cylinder with constant diameter corresponding to the basal area at breast-height) (Anonymous, 1982, p. 213). While shape indices range from 0.55 to 0.75 in well-managed forests, to be conservative, we used a shape index of 0.5. This means that our volume estimates are in the low range.

3. Results

3.1. Characteristics of the woodpecker and control forests

3.1.1. In Switzerland

A strong positive linear relationship existed between the amounts of logs and snags ($r = 0.86$, $t = 8.01$, $p = 0.0000$, $n = 24$; Table 3). The basal area of snags was more than five times higher in woodpecker forests than in control forests, whereas the basal area of logs was more than three times higher (Table 2). The proportion of snags compared to all standing trunks was significantly higher in woodpecker forests (presence: $8.3 \pm 1.5\%$; absence: $1.3 \pm 0.2\%$; mean \pm SE; Fig. 3). Tree height and the percentage of spruce trees did not differ in the two groups at the $p < 0.05$ level. The basal area of living trees was lower in woodpecker forests.

The topographical situation was not identical in both groups. In woodpecker forests, the slope was steeper than in control forests (Table 2). Woodpecker forests were more SE oriented than control forests, where the most frequent orientation was NW–NE ($\chi^2 = 82.30$, $df = 7$, $p < 0.000$).

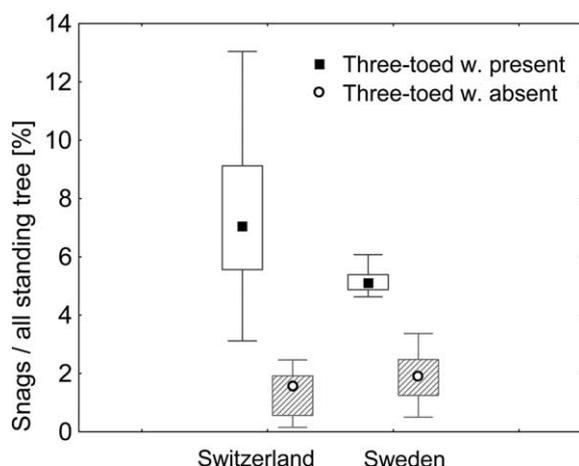


Fig. 3. Box-plots for the basal area proportion of snags compared to all standing (living and dead) trunks, shown separately for forests with three-toed woodpeckers vs. forests without this bird species. Box-plots represent median, 25, 75 percentiles, non-outlier min, non-outlier max. The two boxes on the left present data from Switzerland (distribution of mean values for sampling units of 1 km^2 ; $n = 12$ each, presence and absence) and the two boxes on the right present data from central Sweden ($n = 10$).

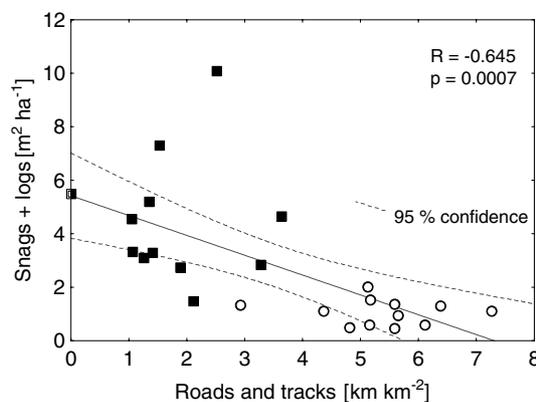


Fig. 4. Negative linear correlation between dead wood amount and road network density for Switzerland. On the x-axis, the total length per km^2 of roads and tracks suitable for trucks or tractors to convey harvested wood. On the y-axis the basal area of all standing and lying dead wood (minimal dbh 10 cm). Black squares: units with breeding three-toed woodpeckers; white circles: units without three-toed woodpeckers.

Extensive harvesting was significantly more frequent in woodpecker than in control forests (Table 2). The road/track density was three times higher in control forests than in the woodpecker forests. It negatively affected the amount of standing and lying dead wood (Fig. 4). A positive linear relationship existed between the variables extensive harvesting and snags ($r = 0.64$, $t = 3.93$, $p = 0.0007$, $n = 24$) and a negative relationship between road/track density and snags ($r = -0.64$, $t = 3.95$, $p = 0.0007$, $n = 24$; Table 3). There was no difference in management history (i.e. recent/past harvesting) between the two groups.

Snags with or without bark and hard or soft logs (i.e. variables measuring the continuity over time of food resources) occurred more frequently in woodpecker forests than control forests (Table 2). These variables were positively correlated with the two quantitative variables snag and log basal area, as they described the stage of decay of dead wood (Table 3).

Road/track density negatively affected three-toed woodpecker presence in Switzerland. We found a non-linear relationship indicating a threshold between 2.6 and 3.5 km/km^2 (x -values at $p = 0.9$ and 0.5 ; Table 4). Woodpecker forests had more ringed trees than control forests (Table 2). The number of ringed trees exhibited a significant non-linear relationship with the probability of woodpecker presence in Switzerland (Table 4). In several woodpecker forests we found ringed trees with signs of very long use (i.e. bulges).

3.1.2. In Sweden

In accordance with the results for Switzerland, snag and log basal area showed the most significant between-group differences for all measured habitat variables (Table 2). A strong positive linear relationship existed

Table 4
Model statistics for all variables (df = 1)

Variable	β (SE)	χ^2	p	Odds ratio	CC (%)	β (SE)	χ^2	p	Odds ratio	CC (%)
		Switzerland					Sweden			
Snags	7.03 (3.44)	25.04	0.000	–	95.8	23.28 (15.04)	21.93	0.000	81.0	90.0
Logs	7.85 (3.86)	25.11	0.000	121.0	91.7	9.60 (6.83)	18.68	0.000	–	90.0
Living trees	–0.12 (0.07)	3.29	0.070	4.0	66.7	0.41 (0.21)	5.26	0.022	3.5	65.0
Spruce	0.13 (0.09)	2.59	0.107	5.0	70.0	0.08 (0.04)	3.71	0.054	3.5	65.0
Pine	–	–	–	–	–	–0.07 (0.04)	4.40	0.036	5.4	70.0
Deciduous	–	–	–	–	–	0.07 (0.07)	1.24	0.266	1.6	55.0
Tree height	–0.07 (0.18)	0.16	0.687	–	60.0	0.69 (0.35)	9.35	0.002	9.3	75.0
Slope	0.07 (0.05)	2.34	0.126	1.4	54.2	–	–	–	–	–
Road/track density	–2.49 (1.19)	26.64	0.000	121.0	91.7	–0.22 (0.58)	0.14	0.706	0.7	45.0
Intensive harvesting	–0.05 (0.03)	7.36	0.007	10.0	75.0	–0.08 (0.04)	5.57	0.018	3.5	65.0
Extensive harvesting	0.23 (0.10)	18.06	0.000	15.0	79.2	0.01 (0.03)	0.45	0.832	1.6	65.0
Recent harvesting	–0.01 (0.02)	0.30	0.582	1.4	54.2	–0.09 (0.04)	6.32	0.012	16.0	80.0
Past harvesting	–0.02 (0.04)	0.24	0.623	1.4	54.2	–0.02 (0.03)	0.36	0.548	1.0	50.0
Snags with bark	0.26 (0.13)	25.51	0.000	–	95.8	0.07 (0.05)	2.86	0.091	4.0	65.0
Snags without bark	0.48 (0.21)	24.06	0.000	121.0	91.7	0.14 (0.06)	7.09	0.008	9.3	75.0
Hard logs	0.21 (0.09)	21.02	0.000	55.0	87.5	0.14 (0.06)	12.74	0.000	9.3	75.0
Soft logs	0.18 (0.07)	16.09	0.000	33.0	83.3	0.14 (0.07)	7.42	0.006	3.5	65.0

β = parameter estimate, SE = standard error, CC = correct classification.

between log and snag basal area ($r = 0.80$, $t = 5.58$, $p = 0.0000$, $n = 20$; Table 3). The basal area of snags was four times higher in woodpecker forests compared to control forests, and the basal area of logs twice as high. Between-group differences for snags and logs were less marked than in Swiss forests. In Sweden, snag amounts in woodpecker forests were smaller than in Switzerland ($0.8 \pm 0.1 \text{ m}^2 \text{ ha}^{-1}$ and $2.3 \pm 0.4 \text{ m}^2 \text{ ha}^{-1}$; mean \pm SE), whereas this was not the case for logs ($1.8 \pm 0.2 \text{ m}^2 \text{ ha}^{-1}$ and $2.2 \pm 0.3 \text{ m}^2 \text{ ha}^{-1}$). As in Switzerland, the proportion of snags compared to all standing trunks was significantly higher in woodpecker forests (presence: $4.8 \pm 0.3\%$; absence: $1.9 \pm 0.3\%$; mean \pm SE; Fig. 3). In contrast to Switzerland, the basal area of living trees was significantly higher in woodpecker forests as compared to control forests (Table 2). The percentage of pine trees was smaller in woodpecker forests, whereas the proportion of spruce trees, even if slightly higher in woodpecker forests, did not differ significantly between groups at the $p < 0.05$ level. There was no difference between the groups for deciduous trees.

Intensive harvesting occurred more frequently in control forests as compared with woodpecker forests (Table 2). The road/track density between groups was not different, and no correlation was found between dead wood amounts and road/track density (snags: $r = 0.15$, $t = 0.65$, $p = 0.5231$, $n = 20$; logs: $r = -0.03$, $t = -0.13$, $p = 0.9006$, $n = 20$; Table 3). As was the case for Switzerland, there was no between-group difference for management history at the $p < 0.05$ level (i.e. recent/past harvesting; Table 2).

Both hard and soft logs occurred more frequently in woodpecker forests than control forests (Table 2). Snags

without bark occurred more often in woodpecker forests, whereas snags with bark did not exhibit any difference between the groups. As for Switzerland, these variables describing dead wood decay stages were positively correlated to the basal areas of snags and logs (Table 3).

As in Switzerland, woodpecker forests had more ringed trees than control forests (Table 2). In contrast, no ringed trees with signs of very long use (i.e. bulges) have been found.

3.2. Critical dead wood threshold values for the three-toed woodpecker

Several variables associated with snag amounts were highly inter-correlated (in Switzerland: basal area of snags vs. snags with bark, road/track density, logs, hard logs, soft logs, harvesting intensity; always $r > 0.60$, $p < 0.001$, $n = 24$; in Sweden: snags vs. living trees, tree height, logs and hard logs; always $r > 0.65$, $p < 0.002$, $n = 20$; Table 3). Univariate logistic regression models for snags reached a good fit and high accuracy, both for Sweden and Switzerland (Table 4).

Critical values, expressed as a minimal amount of snags ($\text{m}^2 \text{ ha}^{-1}$), below which the probability of three-toed woodpecker presence drops quickly, were not identical for Switzerland and Sweden (Fig. 5(a)). The means and standard errors of the independent values for the inflexion points of the logistic regression function (at $p = 0.5$) were $0.91 \pm 0.14 \text{ m}^2 \text{ ha}^{-1}$ (Switzerland) and $0.42 \pm 0.05 \text{ m}^2 \text{ ha}^{-1}$ (Sweden). These means differed significantly at a level of $\alpha = 0.01$. The estimated between-person difference for the measurement of snag basal area (1 km^2 mean $\pm 9.6\%$) was too small to in-

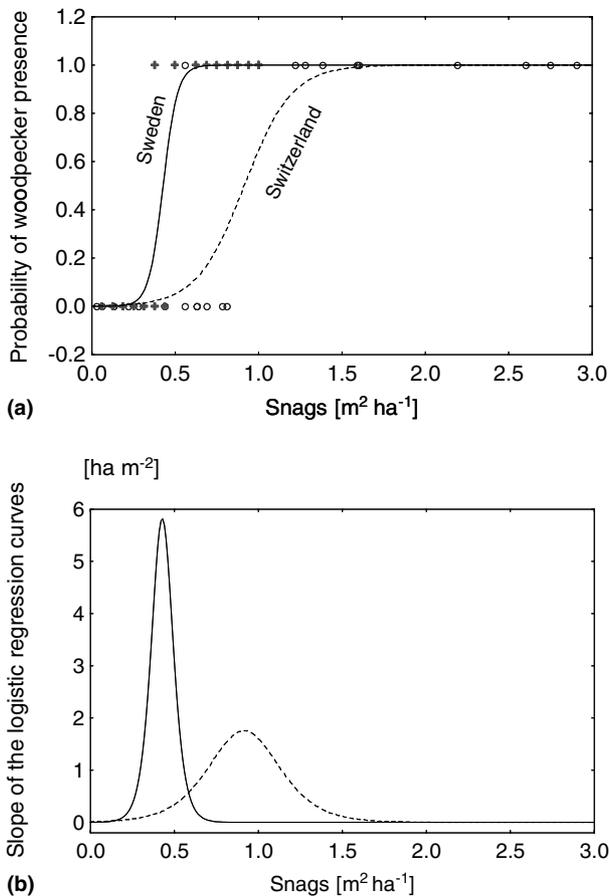


Fig. 5. (a) Univariate logistic regression models for Switzerland (broken line) and Sweden (whole line) showing significant relationships between the amounts of snags and the probability of three-toed woodpecker presence. For the inflexion points ($p = 0.5$) the x -values are $0.91 \pm 0.14 \text{ m}^2 \text{ ha}^{-1}$ (mean \pm SE) for Switzerland and $0.42 \pm 0.05 \text{ m}^2 \text{ ha}^{-1}$ for Sweden. Crosses: Swedish sample units ($n = 20$); circles: Swiss sample units ($n = 24$). (b) First derivative function of these two regression curves.

validate this result. This also applies to the propagated error for the proportion snags/all standing trees (1 km^2 mean \pm 11%). The first derivative function of the regression model resulted in a narrow and high peak for Sweden and a larger and lower peak for Switzerland (Fig. 5(b)), indicating the existence of an abrupt threshold with a steep slope for Swedish forests. In the model, the probability of three-toed woodpecker presence increased from 0.10 to 0.95 when snag basal area increased from 0.6 to 1.3 $\text{m}^2 \text{ ha}^{-1}$ for Switzerland and from 0.3 to 0.5 $\text{m}^2 \text{ ha}^{-1}$ for central Sweden.

4. Discussion

4.1. Critical dead wood threshold

Several authors have demonstrated that three-toed woodpeckers forage on dying and dead trees, and, in

particular, on recently dead standing spruce trees (Hogstad, 1970; Hess, 1983; Pechacek, 1995; Murphy and Lehnhausen, 1998; Ruge et al., 1999; Imbeau and Desrochers, 2002). Accordingly, in our study the basal area of snags, which was highly correlated with the basal area of logs, was the best predictor of three-toed woodpecker presence in both Switzerland and Sweden. The probability of presence exhibited a significant non-linear response to different amounts of dead wood, thus indicating that below a critical minimal amount, breeding woodpeckers may disappear from the habitat.

Our results suggest that the amount of standing dead trees related to a given probability of woodpecker presence is smaller in Sweden than in Switzerland (Figs. 3 and 5). Does this mean that Alpine three-toed woodpeckers need a higher density of snags than boreal birds? We think not. Instead, the figures should be put into the context of woodpecker population trends in the two study areas. The Swiss three-toed woodpecker population is stable or even increasing (Schmid et al., 1998), possibly due to an under-exploitation of marginal mountain forests since World War II (Derleth et al., 2000), a factor that is related to a rapid increase of wood harvesting costs (Brassel and Brändli, 1999). Under such conditions, the amounts of dead trees and the availability of food resources are likely to increase. By contrast, the Swedish population is decreasing (BirdLife, 2000), due to the loss of suitable habitat and the decline in the quality of the remaining habitat caused by forest management. Considering that the occurrence of a species is expected to track environmental changes with a time delay (“extinction debt” Tilman et al., 1994), the current situation in central Sweden may already be below the landscape threshold for the woodpecker meta-population capacity (Hanski and Ovaskainen, 2000). It is possible that the central Swedish population is a sink population whose survival hinges on migration from source populations further to the north where more naturally dynamic forests remain.

Results from extinction models and some empirical data for vertebrates indicate that regional species extinction starts to accelerate when the suitable habitat area drops below 20–30% of the original suitable habitat area (cf. Andren, 1994; Jansson and Angelstam, 1999; Carlson, 2000). Thus, Nilsson et al. (2001) suggested that at least 20% of original densities of large dead trees are needed at the landscape level for biodiversity preservation. Central Swedish dead wood amounts in three-toed woodpecker habitats may be close to or below 20% of the amounts found in naturally dynamic forests (cf. Table 5). In addition, our data suggest a higher sensitivity to changes in dead wood amounts for boreal three-toed woodpeckers than their sub-Alpine counterparts; i.e. the peak of logistic regression model is narrow and the slope sharper (Fig. 5(b)), which means, for example, that a small decrease in dead wood amounts

Table 5
Dead wood amounts in European sub-Alpine and boreal conifer forests

Country	Site selection type	Stand age [years]	Logs [m ³ ha ⁻¹] mean (range)	Snags [m ³ ha ⁻¹] mean (range)	Snag proportion of stems [%]	Total dead wood [m ³ ha ⁻¹] mean (range)	Authors
<i>European sub-Alpine spruce forests</i>							
Switzerland	Managed		3.9–21.6	0.0–4.2		3.9–25.8	Guby and Dobbertin (1996)
Switzerland	Managed	>100	7	12	7	19	Derleth et al. (2000)
Germany	Unmanaged	140–260	~ ^a 56	~28		84 (10–180)	Rauh and Schmitt (1991)
Germany	Unmanaged	Old			5–10	20–60	Utschick (1991)
Switzerland	Unmanaged	>100	31	32	20	63	Derleth et al. (2000)
Poland	Unmanaged	All age classes	73	59	~14	131	Holeksa (2001)
Slovakia	Unmanaged	All age classes				80–273	Korpel (1995)
Slovakia	Unmanaged	All age classes				42	Korpel (1995)
Slovakia	Unmanaged	All age classes			~9	80–220	Korpel (1995)
Switzerland	With <i>Picoides trid.</i>	>100	21 (10–43)	19 (6–34)	8 (3–22)	40 (16–65)	This study
Switzerland	Without <i>Picoides trid.</i>	>100	7 (2–16)	5 (0–10)	1 (0–3)	12 (5–26)	This study
<i>European boreal conifer forests</i>							
Southern Finland	Managed	Mature				14 (2–28)	Siitonen et al. (2000)
Southern Finland	Managed	Overmature				22 (7–38)	Siitonen et al. (2000)
Central Sweden	Managed	All age classes	2.8	1.2		4.0	Fridman and Walheim (2000)
Central Sweden	Managed	101–140				7.2	Fridman and Walheim (2000)
Central Sweden	Managed	>140				11.7	Fridman and Walheim (2000)
Southern Finland	Unmanaged	Old-growth	~78	~33		111 (70–184)	Siitonen et al. (2000)
Central and northern Sweden	Unmanaged	88–270			~30	89 (27–201)	Linder et al. (1997)
Northern Sweden	Unmanaged	Old-growth	17–65	0.5–13			Jonsson (2000)
Northern Finland	Unmanaged (pine)	Old-growth	~11–13	~6–8	~19	19	Sippola et al. (1998)
Northern Finland	Unmanaged (spruce)	Old-growth	~36–42	~8–24	~19–27	60	Sippola et al. (1998)
Central Sweden	With <i>Picoides trid.</i>	Mature	16 (7–28)	7 (3–10)	5 (3–6)	23 (10–37)	This study
Central Sweden	Without <i>Picoides trid.</i>	Mature	5 (3–8)	2 (0–3)	2 (0–3)	7 (3–11)	This study

^a ~ calculated by the authors of this study.

results in a quick drop of the probability of woodpecker presence.

For the purpose of the precautionary principle, we suggest, therefore, that forest management recommendations be based on a strategy maximising the probability of woodpecker presence. For example, to achieve a level of probability of $p = 0.95$, our model predicted necessary snag amounts of $1.3 \text{ m}^2 \text{ ha}^{-1}$ for Switzerland and $0.5 \text{ m}^2 \text{ ha}^{-1}$ for Sweden (Fig. 5(a)). For the studied sub-Alpine forests, a basal area of $\geq 1.3 \text{ m}^2 \text{ ha}^{-1}$ corresponds to a volume of $\geq 15 \text{ m}^3 \text{ ha}^{-1}$ or $\geq 5\%$ of the standing basal area being dead trees. Both basal area and volume depend on the site productivity, which is probably lower in boreal forests than in sub-Alpine forests. Thus, consideration of the ratio of dead trunks to the total number of trunks, independently of the site productivity, is a better way of providing general recommendations. With the aim of reversing the negative population trends in central Sweden, we would suggest aiming for $\geq 5\%$ of standing dead trunks in older forests, as is the case in Switzerland. This corresponds approximately to a mean volume of $15 \text{ m}^3 \text{ ha}^{-1}$, still depending on site productivity, over at least 100 ha large forest areas.

Whereas many studies on dead wood requirements of different woodpecker species have been conducted in North America (e.g., Samuelsson et al., 1994; Bull et al., 1997; Keisker, 2000), few literature data are available for Northern Europe, and even fewer for European sub-Alpine forests. The critical value of at least 5% dead trunks in older forests that we determined for three-toed woodpecker requirements lies within the range of 5–10% recommended by Utschick (1991) as an optimal snag proportion for forest birds.

The comparison with other studies shows that for both studied landscapes, dead wood amounts measured in forests without three-toed woodpeckers correspond well to the amounts that have been found in other managed forests by different methods (Table 5). Fridman and Walheim (2000) report around $2\text{--}3 \text{ m}^3 \text{ ha}^{-1}$ dead wood in the lowland part of central Sweden where our study was carried out. It should be noted that the differences in the amount of dead wood within our study areas are small compared with the difference between naturally dynamic forests and our study areas, especially for central Sweden (Table 5). Siitonen (2001) reviewed publications of the amount of dead wood in unmanaged boreal forests and found it to vary from 18% to 37% of the total wood volume. Nilsson et al. (2002) reported for old-growth boreal and temperate forests that around 10% of all standing trunks are dead. The dead wood volume in recently disturbed forest is often considerably larger. In general, the amount of dead wood in managed boreal forests is 2–5% of the amount found in naturally dynamic forests (Siitonen, 2001; Angelstam, unpublished data). When considering that remaining unman-

aged reference areas where dead wood can be studied generally are located on sites with poorer than average productivity (e.g. Yaroshenko et al., 2001), and that dead wood should be divided into different categories of diameter and decay stage (Stokland, 2001), it is likely that the decline in certain types of dead wood (e.g. large and decayed) from natural to managed landscapes is even greater.

To recommend the critical dead wood thresholds for three-toed woodpeckers as a practical management target, however, it is necessary to evaluate the umbrella value of this woodpecker species for other taxa in conifer-dominated boreal and mountain forest (Angelstam et al., 2003; Roberge and Angelstam, 2004). Several links with biodiversity and habitat quality have previously been demonstrated. Mikusinski et al. (2001) found that the number of forest bird species is correlated positively with woodpecker species richness and, in particular, with the presence of the three-toed woodpecker. Suter et al. (2002) demonstrated that the Capercaillie (*Tetrao urogallus*), co-occurring with the three-toed woodpecker, is an umbrella for red-listed mountain birds. Pakkala et al. (2002) found a positive correlation between the occurrence of breeding three-toed woodpeckers and territory and landscape quality. In addition to these findings, it would be important to analyse systematically the umbrella value of this species in different landscapes.

4.2. Ringed trees as indicators of breeding continuity?

We observed more ringed trees in Switzerland than in Sweden. Given that sap licking is a general habit of European three-toed woodpeckers (Ruge, 1968; Scherzinger, 1982; Glutz von Blotzheim, 1994; Pechacek, 1995), which has also been observed in eastern North America (Imbeau and Desrochers, 2002), a longer presence of this bird species in the same habitat would result in a higher number of ringed trees. Also, the estimated age of ringed trees does not refute this hypothesis. Indeed, we found no signs of very long use (i.e. the tree has formed bulges) in Sweden, whereas in several breeding forests in Switzerland such trees have been observed. Based on these findings, we therefore expect a longer breeding continuity in Swiss forests as compared to Swedish forests. This hypothesis may be explained by the different forest management regimes in Alpine and boreal forests. In Switzerland, selective tree cutting creates a dynamics of small gaps within stands, which retains favourable habitat features for the woodpecker over time. Hence, the three-toed woodpecker's presence in the same habitat may be continuous over a very long time and many and very old signs can be found. By contrast, in Sweden clear-cutting has been the general harvesting type since the late 19th and the rotation time of around 80 years for Norway spruce and 100 years for

Scots pine is relatively short. Three-toed woodpeckers need forests with dead wood, either in old-growth stands or in stands subject to stand-replacing disturbance by fire or wind (Angelstam and Mikusinski, 1994). Consequently, in managed forests in Sweden they would not be expected to stay longer than about 10–30 years in the same old forest patch, a too short a time to create numerous signs or signs of long use. The introduction of variable retention in forestry (Angelstam and Pettersson, 1997) is likely to increase the time with sufficient amount of dead wood during a rotation by about 10 years at the beginning of the succession. Our findings are corroborated by Nilsson and Ericson (1997) who expect species in temperate forests to be more dependent on spatial and temporal forest continuity than species in boreal forests, due to the different disturbance regimes.

4.3. Influence of management intensity and accessibility

In managed forests, dead wood amounts are closely related to the intensity of forest management, which is also linked to the accessibility of harvesting areas, as demonstrated in this study. Because of Switzerland's difficult terrain, in about 80% of the area, trees are felled by hand using chainsaws and then they are transported by tractors or cable cranes to the nearest forest road. In addition to regular selective tree cutting, diseased and dead trees are removed by salvage cutting (Guby and Dobbertin, 1996). In our study, the road network density negatively affected dead wood amounts, and, indirectly, the spatial distribution of three-toed woodpeckers in Switzerland (Fig. 4).

In Switzerland, the network of forest roads grew by about 10% or 2.5 m ha^{-1} over the past 10 years (Brassel and Brändli, 1999). Thus, the forest in the Alps and Lower Alps has become more accessible, whereas accessibility in the Central Plateau has only improved slightly. If this trend in forest road growth in mountain areas continues, and if the management goals do not change in favour of more dead wood in the forests, we can expect a negative influence on woodpecker populations. The predicted threshold value, beyond which road density has a strong negative impact on three-toed woodpecker presence, was between 2.6 and 3.5 km/km^2 . Assuming that the current growth of the forest road network of 10% per decade continues, the critical threshold of 2.6 km/km^2 could be reached in about 30 years (based on the current mean value of road density in three-toed woodpecker forests of 1.8 km/km^2).

In Sweden the road network density was generally lower than in Switzerland and did not explain the presence or absence of three-toed woodpeckers. Indeed, for the range of road network density found in Sweden (i.e. 0– 2.9 km/km^2 ; cf. Table 2), we found no significant correlation between dead wood amounts and road/track density in Switzerland either (cf. Fig. 4). In Sweden the

presence of a dense road and track network has been easy to establish due to the flat topography. It was variation in the intensity of forest owner's management practices rather than variation in road density that determined the amount of dead wood in Sweden.

4.4. Perspectives

Based on the observed differences between the Swedish and Swiss study areas, we suspect that three-toed woodpeckers in central Sweden have to move around considerably in the search for adequate forest patch islands within a generally intensively managed forest landscape. In contrast, three-toed woodpeckers in Switzerland are likely to be more sedentary, often located in areas on steep slopes and difficult to access (Bütler and Schlaepfer, 1999), i.e. where the road network is poorly developed. Two important management consequences follow from this hypothesis: in Sweden clear-cut patch design (directly affecting the amount of residual dead wood and indirectly affecting the local density of old forest patches), and stand rotation time are likely to be closely related to the trend in the three-toed woodpecker population; and in Switzerland, the level of road network development that facilitates forest management intensification and salvage cutting, whereby declining and dying trees are removed, is likely to affect three-toed woodpecker populations. Our study demonstrated the existence of dead wood thresholds for the local presence of three-toed woodpeckers. We expect that the spatial arrangement and density of dead-wood rich forest patches (i.e. old-growth or stands subjected to stand-replacing disturbance by fire or wind) on the landscape scale would explain regional woodpecker breeding densities.

The accuracy of the recommended targets for dead tree volumes and basal areas should be verified in other sub-Alpine and boreal forests with various site productivity conditions and forest management types. Some further work has to be done in order to account for the large scale succession, for example assessment of the usefulness of snag retention in clear-cuts for the three-toed woodpecker.

5. Conclusion

We demonstrated the dependence between three-toed woodpecker presence and high dead wood amounts, in particular standing dead trees, both in Switzerland and central Sweden. Thresholds related to snag amounts existed for both the nominate *P.t. tridactylus* and *P.t. alpinus* subspecies of this bird. In Switzerland the high road network density, a measure for the good accessibility of the forest stands for harvesting, negatively affected the woodpecker's presence. We suggest that a

quantitative target for three-toed woodpeckers is at least 5% standing dead trees in forest stands over about 100 ha. This proportion corresponds to about $\geq 1.3 \text{ m}^2 \text{ ha}^{-1}$ (basal area) or $\geq 15 \text{ m}^3 \text{ ha}^{-1}$ (volume), still depending on site productivity. Because of its dead wood dependence, the three-toed woodpecker may also be considered as an indicator species for sites with a high value for other specialised species dependent on dead wood, many of which are red list species.

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