

Insect prey population changes in habitats with declining vs. stable Three-toed Woodpecker *Picoides tridactylus* populations

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The effect of food supply on the Three-toed Woodpecker *Picoides tridactylus* breeding density and productivity was investigated by comparing the pattern of annual changes in prey abundance in habitats with declining vs. stable woodpecker populations. In a burnt area of eastern Finland, where the woodpecker breeding population has been continuously diminishing, following a major increase the first year after fire, only the abundance of spruce bark beetles (Col., Scolytidae) (the woodpecker autumn-spring main insect prey) decreased through the years. Conversely, the abundance of longhorn beetles (Col., Cerambycidae) (the nestling main food supply) increased dramatically. On the other hand, in neighbouring old-growth patches where one pair was breeding annually, abundance of spruce bark and longhorn beetles did not change significantly between years, although the abundance level of the bark beetles differed among patches. Hence, my results suggest the woodpecker breeding population to be limited by food supply available outside the breeding season, as shown for other forest bird species. The finding, however, that woodpeckers breeding 6–7 years after the fire reared larger broods than earlier pairs, while brood size did not change annually under old-growth conditions, suggests longhorn beetle availability to be critical to reproductive success.

1. Introduction

The understanding of factors limiting bird populations has always been a challenging and exciting field of interest among population biologists. Its difficulty arises from the multiplicity of factors and scales that influence key parameters of population dynamics: survival, dispersal, and reproduction (Newton 1998). Results from thoroughly studied bird populations suggest change in breeding populations to be unrelated to the number of young produced in the previous year

(Lack 1964, Perrins 1965, Wiktander 1998). Instead, survival and recruitment of juveniles into populations appear to be a critical factor affecting subsequent breeding densities (Perrins 1965, Dhondt & Eyckerman 1980). Further investigations under naturally or experimentally fluctuating food conditions indicate that the recruitment of juveniles and thereby population density would be regulated by food supply available outside the breeding season, in autumn-winter (Gibb 1960, Perrins 1966, Van Balen 1980, Drent 1984, Nilsson 1987, Hannon *et al.* 1987). Clutch size,

on the other hand, is largely determined by the amount of food available to nestlings (e.g., Siikamäki 1994).

Occasional observations of local aggregations in forest areas recently disturbed by fire (Sorvari 1994, Murphy & Lehnhausen 1998, Imbeau *et al.* 1999), water (Yeager 1955), wind (Virkkala *et al.* 1991), and/or infested by phytophagous insects (Baldwin 1960, Koplín 1972, Crockett & Hansley 1978) suggest the population size of the Three-toed Woodpecker *Picoides tridactylus* to be limited by habitat/food resources hardly found under conventional forest management (Imbeau *et al.* 1999). Accordingly, results from analyses of stomach contents show that they prey the whole year upon insects that colonise dying and recently dead trees. From late summer to early spring, they prey almost exclusively upon conifer bark beetles (Coleoptera, Scolytidae), with a marked preference for the species that colonise spruce trees (Hogstad 1970, Koplín & Baldwin 1970, Koplín 1972, Massey & Wygant 1973, Pechacek & Krištín 1993, Fayt 1999). During the summer months, however, wood-boring beetle larvae, and especially longhorn beetle larvae (Coleoptera, Cerambycidae), contribute significantly to the diet of individuals, including nestlings (Hogstad 1970, Pechacek & Krištín 1996, P. Pechacek & A. Krištín, pers. comm.). Such a seasonal variation in diet preferences coincides with seasonal changes in habitat use for prey searching. While wintering individuals preferentially forage in pure spruce stands, late spring-summer birds select stands with a larger deciduous component and forage on more decayed trees (Wesołowski & Tomiałojć 1986, Hogstad 1991, Pechacek & Krištín 1996, D. Nowak, pers. comm.). Nevertheless, although changes in the woodpecker abundance after disturbance has been found related to extra food resources available in the dying and dead trees (Koplín 1972), proximate factors controlling for the observed population changes, and in particular the roles played by bark and wood-boring beetles, are still unclear.

In this four year study, I examine the effect of food supply on Three-toed Woodpecker populations by comparing the pattern of annual changes in prey abundance between forest habitats (burnt vs. old-growth) differing in disturbance history (accidental fire vs. regular small-scale gap dynam-

ics created by wind and tree-scale biotic interactions) and woodpecker numerical responses to habitat change (decreasing vs. stable). The following hypotheses derived from the previous studies of factors limiting forest bird populations in the temperate zone were tested: (1) the woodpecker breeding density varies in parallel with the abundance of its main autumn-winter insect prey, the spruce bark beetles, and (2) the woodpecker brood size changes accordingly to the nestling food supply, the longhorn beetle larvae.

2. Material and methods

2.1. The study species

The Three-toed Woodpecker is the only woodpecker to be found in both the Old and New Worlds (Winkler *et al.* 1995) (although recent molecular investigations suggest that a separate species exists on each continent; Zink *et al.* 2002), with a circumpolar range of distribution that closely coincides with that of spruce trees *Picea spp.* (Baldwin 1968, Bock & Bock 1974). In European forest landscapes, the woodpecker abundance is positively correlated with the proportion of spruce-dominated forests over 100 years old, the proportion of trees with a trunk diameter of 20–50 cm, and the amount of dead wood (Hess 1983, Virkkala *et al.* 1994, Amcoff & Eriksson 1996). In the Alps, Three-toed Woodpeckers inhabit altitude forests with an average dead wood volume of 63 m³/ha (Derleth *et al.* 2000). This makes the Three-toed Woodpecker a species susceptible to forest management (Rassi 2000). The woodpecker main insect prey (the bark beetles and longhorn beetles) share similar life-histories: they both attack recently dead trees, they both benefit from thick, moist phloem (a thin layer of living tree tissue found between the outer bark and sapwood), and they both emerge as adults from brood trees for only a brief period (Powell 2000).

2.2. The study area and woodpecker populations

This study was carried out between 1996 and 1999 in North Karelia, easternmost Finland (63°N, 31°E).

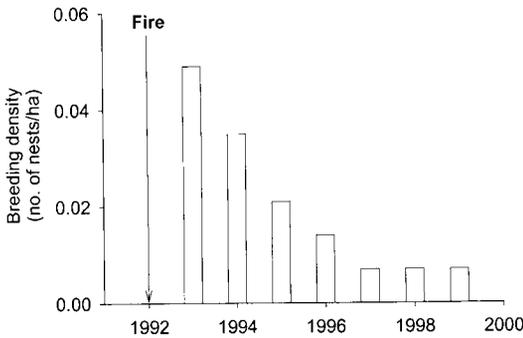


Fig. 1. Changes in Three-toed Woodpecker breeding density after fire, Eastern Finland (1993–1999).

Data on insect prey abundance were collected in Kitsi, a mostly pine-dominated *Pinus sylvestris* forest area burnt in 1992, and seven neighbouring (up to 66 km from the burnt area) spruce-dominated old-growth forest patches. The forest area of Kitsi burnt as fire escaped from an originally planned prescribed fire plot of 10 ha. The total burned area was 143 ha but with considerable variation in severity, due to prevailing wind and heterogeneous soil conditions. In co-operation with the Finnish Forest and Park Service (the owner of the land), it was decided to set apart the burnt area from conventional management plans. Burned trees remained in the area to allow for natural development of the vegetation. In the year after fire, Sorvari (1994) found a total of 7 nests of Three-toed Woodpeckers in a 70 ha part of the burnt area, corresponding to a 7-fold increase (0.028–0.2 ind./ha) in the woodpecker breeding density relative to densities normally found in nearby old-growth spruce forests. Five of those 7 nests were found in a dry heath forest plot of 17 ha. During the following years, the decline of the woodpecker population was apparent (Sorvari 1994, this study) (Fig. 1). In 1996, at the start of the study, two breeding pairs were present. From 1997–1999, a single and same (colour-ringed) pair was left breeding in the periphery of the burnt area. The fate of the population after 1999 is unknown. By contrast, in the studied old-growth patches (65–90 ha), one pair of woodpeckers was found annually breeding.

Similarly to Sorvari (1994), in this study, woodpecker density was estimated from March to June, based on early morning drumming activities of territorial individuals followed by active nest search-

ing. Nests were annually located by nest-excavation noises in early morning, by accidental discovery, usually after the discovery of fresh wood chips on the ground floor, and by the noisy vocalisations of offspring. Determining the woodpecker brood size required climbing the nest tree and using a small mirror and flashlight to investigate the cavity. In case the nestling count was uncertain, the tree cavities were revisited during the following days.

2.3. Insect sampling

Window flight traps, a reliable sampling device for bark beetles (Martikainen *et al.* 1996, 1999), were used as the sampling method to estimate local food abundance within patches. The traps were made of two perpendicular intercepting 20 × 40 cm transparent plastic planes, and a plastic funnel leading into a container attached below the panes. A solution of water, salt and detergent was used in the container to preserve the insects. A sampling effort of 1 trap per 7 ha was assumed to allow (i) a representative sampling of the patchily distributed forest beetles, and (ii) to consider traps as independent observations. Accordingly, woodpecker habitats were divided into 7 ha plots (200 × 350 m) on maps with scales of 1:10 000 to 1:20 000. Within each plot, 1 tree was chosen to which 1 trap was hung close by the trunk to a solid branch 1.5 m above the ground, measured from the lower margin of the panes. Traps were located after choosing from random number combinations their direction and distance from the centre of each plot. The yearly sampling period was 1 May–20 July, covering the main flying season for the beetles. Overall, ten traps were distributed all over each woodpecker habitat patch; they were annually located on the same trees and emptied twice during the summer. In Kitsi, insects were sampled during the 4-year study period with traps distributed over half of the burnt area (70 ha), covering the area where the different woodpeckers (two pairs in 1996 and one in 1997–1999) were confined during reproduction. Under old-growth conditions, forest beetles were collected in 1, 4, and 6 patches in 1996, 1997, and 1998–1999, respectively. Among those, the same four old-growth patches were yearly sampled from 1997–1999. However, due to trap damages caused

at some point by accidental tree/branch fallings or encounters with moose (*Alces alces*), the information collected from 5 out of the 40 traps used annually could not be included in the final analysis.

In this study, estimates of prey abundance included the number of bark beetles (Bb), spruce bark beetles (Sbb), wood-boring beetles (Wbb) and, in particular, longhorn beetles (Lhb), and individual beetles (Total). It also included the number of bark (Bbsp) and longhorn (Lhbsp) beetle species. Among wood-boring beetles, I counted the number of individuals belonging to families known to develop large larvae (i.e., Elateridae, Anobiidae, Oedemeridae, Cerambycidae and Curculionidae). Bark beetles were classified as species living on spruce according to the species assemblage previously found from the bark of spruce trees selected by foraging Three-toed Woodpeckers (Fayt 1999, 2003).

2.4. Statistical analyses

Data were analysed using SPSS 11.0 for Windows. All variables were examined for the distribution of the data using a one-sample Kolmogorov-Smirnov test. None of them required standard transformations to fulfil the demands of parametric analyses. Pearson correlations were used to analyse trends after fire in population levels of the woodpecker and of its insect prey. A sequential Bonferroni correction was performed to control the error rate from multiple correlative tests. A GLM repeated measures ANOVA procedure was performed to test for effects of year (1997–1999) and territory (4) on abundance patterns and species richness of saproxylic beetles as well as brood size of woodpeckers living in old-growth forests. The sphericity of the variance-covariance matrix was tested with Mauchly's test of sphericity. In case the test gave significant P value, the degrees of freedom within subject tests were corrected with Greenhouse-Geisser epsilon.

3. Results

Insect catches from window traps yielded altogether 19 251 individual beetles, which included

14 262 bark beetles (74.1%) from 31 species. Richness in bark beetles captured in the breeding habitats of the Three-toed Woodpecker ranged between 15 and 22 species.

In Kitsi burnt forest, where the breeding density of Three-toed Woodpeckers has been declining from 1993–1999 ($r = -0.923$, $n = 7$, $P = 0.003$) (Fig. 1), neither the total number of individual beetles, the number of individual bark- and wood-boring beetles, nor the number of bark and longhorn beetle species showed significant trends for the period 1996–1999 (Table 1, Fig. 2). In contrast, the abundance of the bark beetles that specifically live on spruce trees decreased while longhorn beetle availability increased significantly (Table 1, Fig. 2). However, when adjusting P-values with a Bonferroni correction, none of the insect variables changed significantly after fire.

When looking at between-year variations in beetle supply among the same four old-growth patches (1997–1999), only the abundance of bark beetles changed annually, but did not differ among patches (Table 2, Fig. 2). Interestingly, among bark beetles, the population level of the spruce beetles was found patch-specific, without variation between years.

The woodpecker mean brood size increased several years after fire, although the overall pattern was not significant ($r = 0.753$, $n = 5$, $P = 0.141$). While 3 nests checked in 1993, 2 in 1996 and 1 in 1997 contained each 3 nestlings, the pair breeding in 1998 and 1999 produced 4 fledglings consecutively (Hannu Huuskonen & Juha Miettinen, pers. comm.; this study). Under old-growth conditions (4 patches, 3 years), brood size did not change between years (GLM repeated measures ANOVA: $df = 2$, $MS = 0.750$, $F = 2.455$, $P = 0.166$).

4. Discussion

The main objective of this study was to clarify factors underlying variability in the breeding density of Three-toed Woodpeckers. Comparing abundance patterns of selected bark- and wood-living arthropods after fire for the period 1996–1999, only bark beetles living on spruce (the woodpecker autumn-spring food supply) and longhorn beetles (whose larvae account for the

woodpecker nestling main food supply) showed significant population changes. Contrary to spruce bark beetles, whose abundance declined through the years in parallel to the woodpecker breeding population, the abundance of longhorn beetles increased significantly. After sequential Bonferroni correction, however, none of the seven food estimates showed significant trends after fire. Nevertheless, given that spruce bark and longhorn beetles would still show significant responses if they were the only tested variables, I suggest the observed population changes of the beetles to follow realistic dynamics. Accordingly, earlier entomological surveys carried out among burnt plots of the neighbourhood have emphasised a general increase in numbers of scolytids immediately after fire, although densities of several species, including spruce bark beetles, were already declining in the second year after fire (Rutanen 1994, Muona & Rutanen 1994).

In neighbouring old-growth patches, on the other hand, where one pair of woodpeckers was

breeding annually, abundance of longhorn and spruce bark beetles did not change significantly between years, although the abundance level of the bark beetles differed among patches. Thus, my results would support the prediction that food supply outside the breeding season control for the subsequent breeding density of the Three-toed Woodpecker, as demonstrated in other forest bird populations (Perrins 1965, 1966, Van Balen 1980, Hannon *et al.* 1987, Nilsson 1987).

Interestingly, I found longhorn beetles, the woodpecker nestling main food supply, to increase sharply in density several years after fire, at times when the woodpecker and spruce bark beetle populations have already collapsed. Given the positive effect of food available to nestlings on bird clutch size in general (Siikamäki 1994), my results would thus suggest that a patch suitable for a reproducing Three-toed Woodpecker would not be necessarily suitable for a wintering individual, and vice versa. In agreement with this suggestion, in Kitsi, I found the woodpecker pair breeding 6 and 7 years after

Table 1. Pearson's correlation table showing trends after fire (1996–1999) in number of individuals (Total¹⁾, Wbb²⁾, Bb³⁾, Sbb⁴⁾, Lhb⁵⁾) and species (Bbsp⁶⁾, Lhbbsp⁷⁾) of selected forest beetles. Correlation coefficients between variables are added. Significant (*: $P < 0.05$) values in bold face.

	Year	Total	Wbb	Bb	Sbb	Lhb	Bbsp	Lhbbsp
Year (n = 4)	1							
Total (n = 2739)	-0.450	1						
Wbb (n = 401)	0.430	0.856	1					
Bb (n = 1687)	-0.758	0.852	-0.577	1				
Sbb (n = 632)	-0.978*	0.416	-0.235	0.661	1			
Lhb (n = 147)	0.989*	-0.565	0.477	-0.847	-0.949	1		
Bbsp (n = 25)	-0.603	0.981*	-0.153	0.890	0.583	-0.699	1	
Lhbbsp (n = 7)	0.753	-0.365	-0.269	0.381	-0.872	0.705	-0.522	1

¹⁾No. of individual beetles of all the families

²⁾No. of individual wood-boring beetles of the families Elateridae, Anobidae, Oedemeridae, Cerambycidae, Curculionidae

³⁾No. of individual bark beetles of all the species

⁴⁾No. of individual bark beetles of the species that specifically live on spruce

⁵⁾No. of individual longhorn beetles of all the species

⁶⁾No. of bark beetle species

⁷⁾No. of longhorn beetle species

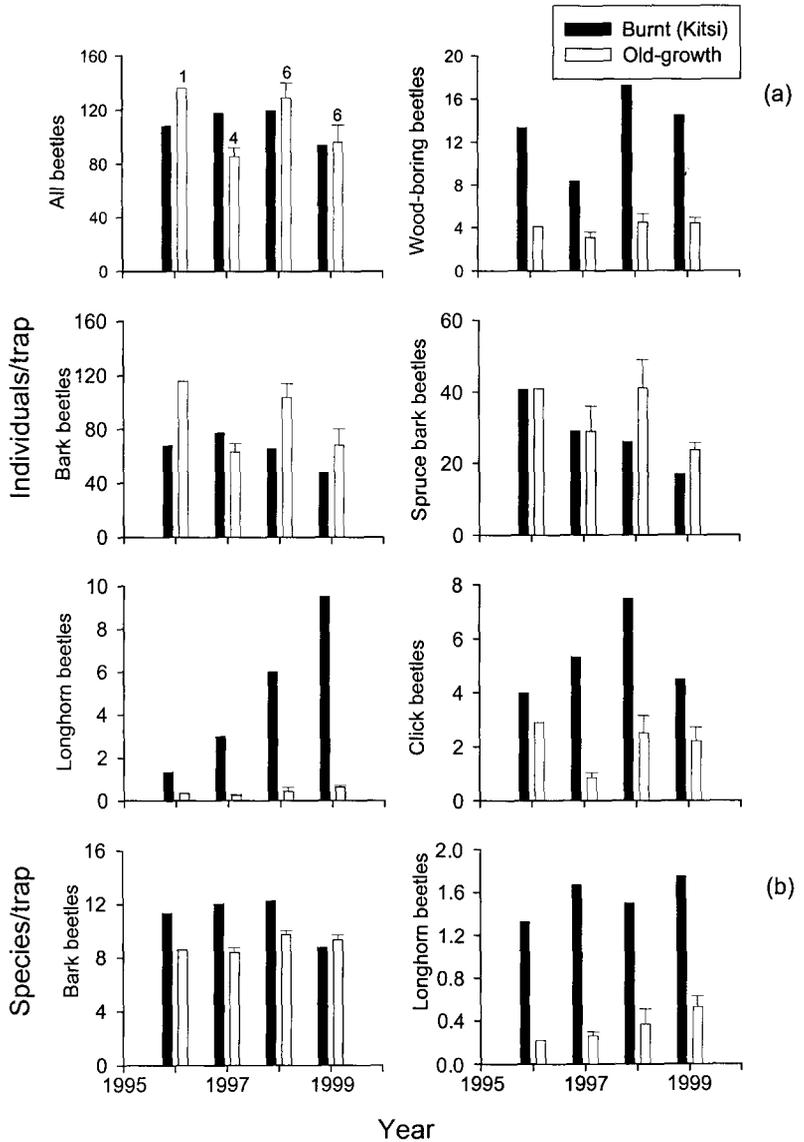


Fig. 2. Annual number per trap of individuals (a) and species (b) of selected conifer forest beetles in burnt vs. old-growth habitat types (1996–1999). Mean numbers annually collected in old-growth habitats are plotted with standard errors and patch sample size.

fire to rear larger broods than earlier pairs. Under old-growth conditions on the other hand, where the abundance of the woodpeckers and its winter and summer prey were found relatively stable through the years, mean brood size did not change significantly for the period 1997–1999.

Based on the above discussion, a general figure is proposed that emphasises the importance of the disturbance history of a forest patch on population responses of its saproxylic beetles, with implications for the habitat selection of the predatory Three-toed Woodpecker (Fig. 3). A stand-

replacing disturbance (such as a forest fire) can transform most of the living stand into coarse woody debris (Siitonen 2001). The trees killed decay progressively, but the lack of new dead wood production in the regenerating stand limits the long-term persistence of associated beetle fauna. After a few years, changes in bark and wood properties induce changes in the abundance of spruce bark beetles and of longhorn beetles. Prey responses, in turn, affect differently the suitability of the patch for a Three-toed Woodpecker, depending on the time of the year. In old-growth

habitats, on the other hand, the continuous production of heterogeneity in forest structure allows the coexistence of multiple stages of decay of woody debris and stable woodpecker-prey relationships, driven by small-scale gap-dynamics and stand development (Kuuluvainen 2002).

Alternatively, one may suggest the parallel increase in longhorn beetle availability and the

woodpecker reproductive output to be an artefact, due to possible change in the age structure of the bird population (Sæther 1990). In the first year after fire, the area may have been colonised by inexperienced young individuals while, later on, an increase in the mean age of the population would account for the observed positive trend in brood size. Also, a progressive increase in pair-

Table 2. GLM repeated measures ANOVA table for the effects of year (1997, 1998, or 1999) and territory (4) on (A) abundance and (B) species richness of bark-living and wood-boring beetles living in old-growth forest patches inhabited by the Three-toed Woodpecker. Significant values in bold face. Superscript indices quote the Greenhouse-Geisser epsilon (ϵ) value used in correction of degrees of freedom when needed (see text for details).

	Source of variance	df	MS	F	P
A) Number of individuals					
All beetles (Total)	Year ¹	1.648	10008.135	3.310	0.053
	Year × Territory ¹	4.945	1797.301	0.594	0.702
	Error ¹ (Within)	51.100	3023.328		
	Territory	3	3258.936	2.235	0.104
	Error (Between)	31	1458.041		
Wood-boring beetles (Wbb)	Year	2	6.862	1.126	0.331
	Year × Territory	6	4.312	0.708	0.645
	Error (Within)	62	6.094		
	Territory	3	13.012	1.619	0.205
	Error (Between)	31	8.037		
Bark beetles (Bb)	Year ²	1.609	12462.384	4.976	0.016
	Year × Territory ²	4.828	1347.062	0.538	0.741
	Error ² (Within)	49.889	2504.420		
	Territory	3	2112.541	1.765	0.174
	Error (Between)	31	1197.098		
Spruce bark beetles (Sbb)	Year ³	1.476	2227.318	2.590	0.100
	Year × Territory ³	4.429	510.885	0.594	0.685
	Error ³ (Within)	45.769	860.109		
	Territory	3	2164.110	5.762	0.003
	Error (Between)	31	376.243		
Longhorn beetles (Lhb)	Year	2	0.931	1.379	0.259
	Year × Territory	6	0.588	0.871	0.522
	Error (Within)	62	0.675		
	Territory	3	0.202	0.423	0.738
	Error (Between)	31	0.478		
B) Number of species					
Bark beetles (Bbsp)	Year	2	6.667	2.409	0.098
	Year × Territory	6	1.197	0.432	0.855
	Error (Within)	62	2.768		
	Territory	3	10.288	2.632	0.067
	Error (Between)	31	3.909		
Longhorn beetles (Lhbsp)	Year	2	0.443	0.940	0.396
	Year × Territory	6	0.324	0.686	0.661
	Error (Within)	62	0.472		
	Territory	3	0.325	0.974	0.417
	Error (Between)	31	0.334		

¹ $\epsilon = 0.824$, ² $\epsilon = 0.805$, ³ $\epsilon = 0.738$

bond duration under declining density conditions may promote early breeding and thereby larger clutch size, as shown for the Lesser spotted Woodpecker *Dendrocopos minor* (Wiktander 1998). In Kitsi, where the same pair (ringed in 1997 as second calendar year individuals) was breeding from 1997–1999, fledging date shifted from 09.07 in 1997, 25.06 in 1998 to 21.06 in 1999.

Some forest management implications can be drawn from my results. First, because the bird diet change seasonally, with bark-living and wood-boring insect prey that respond differently to changes in structural heterogeneity, this study underlines the necessity to take both winter and summer food components into account when securing habitats for the woodpecker. Presumably, a woodpecker should be more likely to survive the winter and reproduce subsequently in a habitat patch showing marked seasonal variation in food supply (e.g., a several years old burnt area) if that particular patch is part of a landscape mosaic where patch-specific disturbance dynamics would ensure overall stable food conditions. In case of seasonal food shortage, the woodpecker may adjust its home-range accordingly into adjacent forest patches. In the case of Kitsi, the burnt area was part of a larger old-growth network. The additional finding that the abundance of spruce bark beetles in a forest patch would limit its woodpecker breeding density is important, given earlier results showing a lower spruce beetle abundance at the edges of old-growth remnants in drained managed forest landscapes compared to patches embedded in a swampy untouched environment (Fayt 2004). Such results predict a negative impact of landscape-level forest drainage on local consumer-resource dynamics and, in turn, the proportion of habitats required in a forest landscape for the maintenance of the species.

Although the study is based on a relatively large insect sample size and covered several years, I suggest however my results from burnt forests to be treated cautiously, given a lack of replicates of Three-toed Woodpeckers breeding in burnt areas. This is because burnt areas of several tens of hectares with significant tree mortality are extremely rare nowadays in Fennoscandia, due to efficient salvage logging and systematic fire suppression during the past century, enforced by law (Zackrisson 1977, Parviainen 1996, Östlund *et al.*

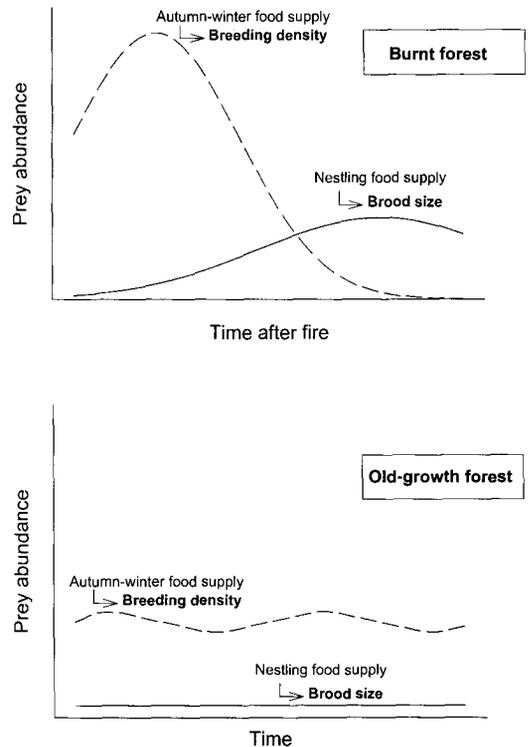


Fig. 3. Diagram illustrating annual changes in autumn-winter (spruce bark beetles) and summer (longhorn beetle larvae) food supply of Three-toed Woodpeckers in burnt vs. old-growth patches, with implications for the woodpecker breeding density and reproductive output.

1997). Also, the ecological effects of fire are clearly scale-dependent, influenced by local factors as fire behaviour, vegetation type, amount, distribution and quality of fuels, climate, hydrology, topography, and pre- and post-burn weather (McCullough *et al.* 1998). All in all, this study stresses how little we actually know about organism responses to changing heterogeneity in a forest environment where disturbances used to play a key role in determining its multi-scale structure, age class, and composition.

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Selostus: Pohjantikan populaatiokokoa säätelevistä tekijöistä

Pohjantikka suosii elinympäristönään metsäpalon, veden, tuulen tai kasveja syövien hyönteisten vahingoittamia alueita. Ravintoanalyysit osoittavat pohjantikan käyttävän ravinnokseen hyönteisiä, jotka kolonisoivat lahoavia puita. Pohjantikan populaatiokokoa rajoittavatkin sellaiset elinympäristö- ja ravintoresurssit, joita enää harvoin löytyy talousmetsistä. Lisäksi pohjantikka suosii eri vuodenaikoina eri hyönteislajeja ja tämä näkyy linnun habitaatinvalinnassa. Artikkelin kirjoittaja tutki Pohjois-Karjalassa tarjolla olevan ravinnon vaikutusta pohjantikkapopulaatioihin. Tutkimuksessa tarkasteltiin pohjantikan ravintokohteiden vuosivaihtelua ja sen heijastumista pohjantikkamääriin erilaisissa elinympäristöissä (palanut metsä vs. vanha metsä), jotka erosivat myös häiriöhistorialtaan toistaan. Tutkimusalueita olivat Kitsin paloalue (paloi vuonna 1992, 143 ha) sekä seitsemän läheistä kuusivaltaista vanhan metsän aluetta. Tutkimusalueilla seurattiin pohjantikkamääriä ja lajin pesimämenestystä sekä kerättiin ikkunapyydyksillä hyönteisaineistoa. Kitsin paloalueella pohjantikkokojen määrät ovat vähentyneet huomattavasti vuosien 1993–1999 aikana (Kuva 1). Kitsin alueella ei havaittu merkittäviä muutoksia kovakuoriaisten kokonaismäärässä, puuainesta ravinnokseen käyttävien kovakuoriaisten kokonaismäärässä ja kaarnakuoriaisten eikä myöskään sarvijäärien määrissä. Pohjantikan ravintokohteista kuusissa elävien kaarnakuoriaisten (pohjantikan syys-kevätaikaista ravintoa) määrän havaittiin vähenevän ja sarvijäärien (sarvijäärien toukat ovat pohjantikan poikasajan pääravintoa) määrän kasvaneen vuosina 1996–1999. Vanhoissa metsissä pohjantikkamäärissä ei havaittu muutoksia. Tarkasteltaessa hyönteismääriä neljällä vanhan metsän alueella vuosina 1997–1999, havaittiin ainoastaan kaarnakuoriaisten määrissä vuosien välistä vaihtelua. Kuusissa elävien kaarnakuoriaisten määrissä havaittiin

vaihtelua vanhojen metsäalueiden välillä, mutta vuosien välistä vaihtelua ei todettu. Pohjantikan pesyekoko kasvoi, joskaan ei merkitsevästi, paloalueella useita vuosia palon jälkeen. Vanhoissa metsissä lajin pesyekoko ei muuttunut. Tulokset viittaavat siihen, että pesimäkauden ulkopuolisen ajan ravinnon määrä vaikuttaa seuraavan pesimäkauden pohjantikkatiheyteen. Lisäksi havaittiin, ettei pohjantikalle sopiva pesimähabitaatti välttämättä ole kelvollinen talvihabitaatti tai päinvastoin. Artikkelin kirjoittaja esittää mallin (Kuva 3), joka kuvaa kuinka pohjantikan syystalvisen ravintokohteen (kuusia hyödyntävien kaarnakuoriaiset) ja kesän ravintokohteen (sarvijääret) määrien vaihtelu vaikuttaa pohjantikan pesimäaikaiseen tiheyteen sekä pesyekokoon paloalueilla ja vanhoissa metsissä. Metsänhoitotoimenpiteitä suunniteltaessa tulisi artikkelin kirjoittajan mukaan huomiota sekä pohjantikan pesimäaikaiset että pesimäkauden ulkopuoliset ruokailualueet ja -tottumukset.

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