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Population ecology  
of the Three-toed Woodpecker  
under varying food supplies

by  
Philippe Fayt



Joensuu  
2003



*The ancient Forest. All that lives here, lives not next to each other, but rather with each other. In this community everything submits to influence, and imposes its influence on the environment. A splendid, harmonised symphony of power, health and immortality.*

Jan Walencik (2000)

Front cover drawing:  
The star of the book (© Philippe Fayt)

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**Keywords:** Breeding density, body size, brood size, heterogeneity, Fennoscandia, food supply, natal dispersal, *Picoides tridactylus*, parental care, population dynamics, predatory impact, resource phenology, scale

In this study, ecological factors underlying multi-scale variability in the productivity and abundance of the Three-toed Woodpecker *Picoides tridactylus* were studied in Fennoscandia from 1996-1999. Patch suitability for a resident woodpecker was estimated in relation to seasonal and inter-annual changes in prey availability and profitability. The methods used to clarify dietary preferences and sample prey populations included bark sampling and insect trapping with window-flight traps. The information on dispersal patterns comes from ringing data records. The results suggest that food supply, determined by the annual timing of prey development and prey abundance, and its variability in time and space are key factors in understanding individual responses and population processes in the woodpecker.

In agreement with previous studies of factors limiting forest bird populations, I found the woodpecker breeding density and success to depend on different food resources. While annual variation in breeding density paralleled variation in the bird's autumn-winter food supply, the spruce bark beetles (Col., Scolytidae), brood size was related to the amount of profitable longhorn beetle larvae (Col., Cerambycidae), the nestling's main food. Different patterns of annual changes in the abundance of the woodpecker's autumn-winter and summer food supply between burnt and old-growth patches emphasised the importance of patch disturbance history for its suitability as a woodpecker habitat.

The management level of a forest landscape was found to influence the spatial distribution of bark beetle species diversity and abundance within its inclusive old-growth habitat units, depending on whether a patch was surrounded by ditched clear-cuts or untouched peatlands. In particular, with a lower spruce bark beetle abundance at the edges of old forest remnants in drained managed landscapes compared to patches in swampy environment, my results provide explanation for the importance of swamp forests for the woodpecker winter survival and subsequent breeding density.

In Finland, juvenile woodpeckers dispersed from their natal habitats at times of sudden changes in the spatial distribution of insect prey as part of their development, leading to a local decline in prey availability. The results suggest that prey availability, whose timing is mediated by the timing of prey development, has a proximate effect on the propensity of the juveniles to disperse, although a causal relationship was not found.

Although a speculative conclusion, annual trends in natal dispersal rate in relation to spring temperature incline me to propose that the yearly number of dispersers from a population depends on its productivity, which, in turn, depends on how closely reproducing individuals are able to match breeding time with annual pattern of food supply. The importance of the juveniles for the population dynamics of conifer bark beetles is acknowledged, depending on the numbers of woodpeckers dispersing over the landscape when beetle larvae reach a profitable size. The possibility that the juveniles might disperse at different times from regions with contrasting temperature conditions is discussed, as a result of spatial heterogeneity in resource phenology.

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## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles, referred to in the text by their Roman numerals **I-VII**:

- I** Fayt, P. 1999. Available insect prey in bark patches selected by the Three-toed Woodpecker *Picoides tridactylus* prior to reproduction. *Ornis Fennica* 76: 135-140.
- II** Fayt, P. 2003. Time of natal dispersal and reproductive decisions of the Three-toed Woodpecker under varying food conditions. – In: Pechacek, P. and d'Oleire-Oltmanns, W. (eds.), International Woodpecker Symposium. Forschungsbericht 48. Nationalparkverwaltung Berchtesgaden, pp. 35-48.
- III** Fayt, P. Brood size determinants of the Three-toed Woodpecker *Picoides tridactylus* in boreal forests. *Manuscript (submitted)*.
- IV** Fayt, P. Dispersal patterns of Three-toed Woodpeckers in relation to food availability: consequences for the population dynamics of the woodpecker at the scale of Fennoscandia. *Manuscript*.
- V** Fayt, P., Machmer, M.M. and Steeger, C. Regulation of conifer bark beetles by woodpeckers - a literature review. *Manuscript (submitted)*.
- VI** Fayt, P. 2003. Insect population changes in habitats with declining vs. stable Three-toed Woodpecker populations. *Ornis Fennica* 80 (*in press*).
- VII** Fayt, P. 2003. Old-growth boreal forests, three-toed woodpeckers and saproxylic beetles – the importance of landscape management history on local consumer-resource dynamics. *Ecological Bulletins* 51 (*in press*).

Some unpublished results are also presented.

## 1. INTRODUCTION

Understanding of the 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 the key parameters of population dynamics: survival, dispersal, and reproduction. Its implications are crucial, since only a thorough understanding of variability in individual numbers is likely to provide meaningful guidelines for population management (Marzluff et al. 2000).

Main factors related to changes in bird numbers and distribution include food-supply, inter- and intra-specific competition, predation, and parasitism (Newton 1998). Among these, food has an overwhelming influence on the major life history traits of individuals and population processes, and it controls directly or indirectly the effects of other factors (Newton 1980, Martin 1987). For example, it has been shown that food availability in autumn and winter-time determines local variations in subsequent breeding density by influencing the survival and recruitment of juveniles into populations (Perrins 1966, Van Balen 1980, Hannon et al. 1987, Nilsson 1987). In spring, food supply affects laying date and thereby clutch size in those species in which there is a seasonal decline in clutch size, as demonstrated by food supplementation experiments (Martin 1987, Daan et al. 1988). Laying time, in turn, determines fledging success (Smith 1993, Verboven and Visser 1998), and environmental conditions experienced during ontogeny affect fitness-related traits such as clutch size (Haywood and Perrins 1992) and body size (Sedinger et al. 1995) of the surviving individuals. In migrating species, the pre-breeding nutritional condition of the parents affects reproductive success (Sandberg and Moore 1996). Spatial distribution and abundance of food resources, on the other hand, influence the

outcome of social interactions within and between species (Henderson and Hart 1995, Sutherland 1996). Partially reduced food supplies explain interference between foraging individuals (Dolman 1995, Cresswell 1998), which promotes the dispersal of juveniles as a result of adjustments in dominance hierarchies (Lundberg 1985, Hannon et al. 1987). Food supply influences indirectly the predation rate, for example at nest sites, depending on alternative prey availability, the landscape context and the predator community (Schmiegelow and Mönkkönen 2002). Food level and general habitat quality also affects the magnitude of critical trade-offs in birds, for example between reproductive effort and health condition (Wiehn 1997), mate choice (Alatalo et al. 1986), parental care (Hakkarainen and Korpimäki 1994) and the evolution of reproductive strategies (e.g., Korpimäki 1988).

As a general pattern, food is a fluctuating resource, changing in space and time in a predictable or unpredictable way (Dempster and Pollard 1981). In the Northern Hemisphere, food supply changes annually in parallel to predictable variation in photoperiod and ambient temperature. The most spectacular consequence of this is probably the evolution of bird migration over continents (Gauthreaux 1985). Nevertheless, on smaller spatial scales, variation in food distribution, quality, abundance, and profitability is also a reality, although not as obvious.

Heterogeneity is a natural and multi-scale feature of forested habitats (Kuuluvainen 2002). It involves the fact that forest habitats are spatially variable in terms of resources available for a living bird, whether heterogeneity is viewed at branch, tree, or stand level. For instance, it is now well established that the nutritional properties of host plants may differ tremendously among and within tree species (Tikkanen 2000). This has direct implications for the fitness, abundance,

and population dynamics of herbivorous insects but also of their associated predators, parasites, and pathogens (Van Balen 1973, Sipura 1999). Similarly, lichen mass show a strong positive relationship to mass, diameter and age of branches (Esseen et al. 1996). Lichen abundance, on the other hand, determines the number and biomass of invertebrates and spiders, which in turn make up the main food source of numerous foliage gleaning passerine birds (Pettersson et al. 1995, Pettersson 1996). Below ground level, heterogeneity in soil properties may also contribute to forest structure, for example by predisposing trees to pathogen infestations on root tips, subsequent beetle attacks and early mortality (Hertert et al. 1975, Fraedrich and Tainter 1989).

Although such tree-scale biotic interactions (so called bottom-up control; Lertzman and Fall 1998) are clearly seen as a source of multi-scale ecological patterns, forest structural features are, however, also to a large extent determined by factors operating and interacting on larger scales, namely abiotic environmental and allogenic disturbances (or top-down control) (Kuuluvainen 2002). Landscape characteristics such as topography, soil, hydrology, climate, or land use determine the composition and physiognomy (i.e., the spatial arrangement) of its inclusive habitat patches (Dunning et al. 1992). Variation in the structure and abiotic conditions of forest landscapes, for their part, set the limits of microclimatic variability among patches and determine their likelihood of being disturbed at regular intervals by physical agents. The importance of multi-scale interactions in determining forest structure is furthermore emphasised by the possibility of disturbance propagation and amplification from tree to landscape levels, for example during insect outbreaks (Rykiel et al. 1988). Thus, when studying various effects of food supply on forest bird populations, careful attention should be paid to relating individual responses and

population processes to habitat heterogeneity at local level, but also on larger scales.

## 2. THE STUDY

### 2.1. Aims

In this thesis, my aim is to study the ecological factors underlying variability in the seasonal and inter-annual abundance of the Three-toed Woodpecker *Picoides tridactylus* at patch, landscape, and regional levels in Fennoscandia. More specifically, I investigate whether **(1)** food supply, in terms of both availability and profitability, determines the breeding density, reproductive output, population dynamics, and predatory impact of the woodpecker **(I-V)**, and **(2)** how patch and landscape silvicultural history may influence the outcome of the predator-prey relationships **(VI-VII)**. The information is then combined to develop forest management guidelines that take into account the preservation of the species.

First **(I)**, I clarify the diet preferences of the bird prior to reproduction, after taking bark samples from recent foraging trees. Then **(II, III, IV)**, I relate seasonal and inter-annual variation in prey development timing and availability among patches to the reproductive output and dispersal patterns of the woodpecker. In particular, I test for the hypothesis that prey life cycle induces changes in food profitability, which, together with prey abundance, serves as a predictable cue for assessing the benefits of investment in reproduction, and explains the onset of the woodpecker's natal dispersal. In the next paper **(V)**, a literature review allows me to test for the idea that predatory woodpeckers, and especially Three-toed Woodpeckers, can contribute to the natural regulation of their prey. In the sixth paper **(VI)**, I compare the short-term effects of fire vs. gap-dynamics on woodpecker abundance and its food supply. Finally **(VII)**, I study whether the conservation value of forest patches for a

resident woodpecker is landscape specific by relating prey distribution to edge proximity in old-growth patches with natural (unditched peatland) vs. managed (ditched clear-cuts) surroundings.

The thesis is based on circumstantial evidence that food availability limits woodpecker numbers, leading to testable hypotheses. The available evidence falls into two categories: (a) patch differences in food correlated with patch differences in bird numbers (II, III, V); and (b) seasonal and annual differences in food correlated with seasonal and annual differences in bird numbers (II, IV, VI). For convenience, in this study, a patch is defined as a focal unit of a forest landscape that is set off from surrounding habitats by an ecologically meaningful edge (Fagan et al. 1999). Prey availability is an attribute of the habitat and refers to the absolute amount of food available to a foraging woodpecker. Prey profitability takes into account the temperature-dependent timing of prey development in relation to the woodpecker breeding cycle.

## 2.2. Predictions

On the basis of the literature, sets of predictions are generated across the different papers, linking food supply to woodpecker individual and population responses. These predictions can be summarised as follows:

1. The autumn-winter food supply should control woodpecker breeding density.
2. Both the availability and profitability of nestling food supply should explain breeding time and thereby brood size among reproducing individuals.
3. Mean brood size should be larger in years with a warmer spring if laying date is related to the time of prey development.
4. The reproductive output of a population should determine the number of dispersing juveniles.

5. Local prey availability should decline at the time when young woodpeckers disperse across landscapes.

6. Earlier-dispersing juveniles should be larger than later-dispersing birds, as a result of higher food supply availability among early broods.

7. Juvenile woodpeckers should disperse first from warmer areas.

8. The Three-toed Woodpecker should have a stabilising effect on the population dynamics of its prey.

## 2.3. Why?

There are multiple reasons for choosing the Three-toed Woodpecker as a study species and woodpeckers in general as a group of interest.

1. The year-round diet preferences of the species are well known, and sampling of the insect prey is relatively easy. This allows for testing hypotheses relative to the importance of food supply on bird population dynamics.

2. The Three-toed Woodpecker is a prey specialist, depending the whole year round on insect preys that colonise dying and recently dead trees. This makes the woodpecker a species particularly sensitive to forest management and the consequent removal of dead trees. Accordingly, the Three-toed Woodpecker is a declining species over most of its range, in parallel to fragmentation and loss of naturally dynamic forest habitats (Rassi 2000). In Finland, the Three-toed Woodpecker is included in the list of the Wild Birds Directive of the European Union (i.e., a list of species for which every effort should be made to avoid reducing their population size or range due to human-related activities). It is also classified as a Finnish responsibility species of European Conservation Concern, since >10% of its European population breeds in the country (Rajasärkkä 1997). Yet, although the negative impact of forest management practices on saproxylic invertebrate communities has been increasingly studied

(Siitonen 2001), its potential cascading effects on the reproduction, survival and recruitment of predatory woodpeckers are poorly understood.

3. Because of its highly specialised requirements for properties characterising naturally dynamic forest patches and landscapes, the Three-toed Woodpecker is an appropriate indicator of forest habitat quality (Angelstam 1998, Nilsson et al. 2001). In addition, the role of woodpeckers in general as umbrella species and key actors in forest animal communities by providing cavities for secondary cavity-nesters is increasingly acknowledged (Martikainen et al. 1998, Martin and Eadie 1999, Mikusinski et al. 2001).

4. From a behavioural perspective, woodpeckers share unique features among birds. In contrast to most altricial bird species, the males generally take a larger share in parental care than the females (Winkler et al. 1995). Besides their peculiar habits of excavating cavities both for reproduction and for roosting, the males incubate and brood by night and part of the day, which seems to preclude multi-nest polygynous mating and under some circumstances promote the rare multi-nest polyandry (Willimont et al. 1991, Wiktander et al. 2000). Additional observations of co-operative breeding in some of the species confirm the adaptive and puzzling nature of their sex-specific reproductive strategies (Stacey and Bock 1978, Stacey and Koenig 1984).

### 3. MATERIAL AND METHODS

#### 3.1. Study species

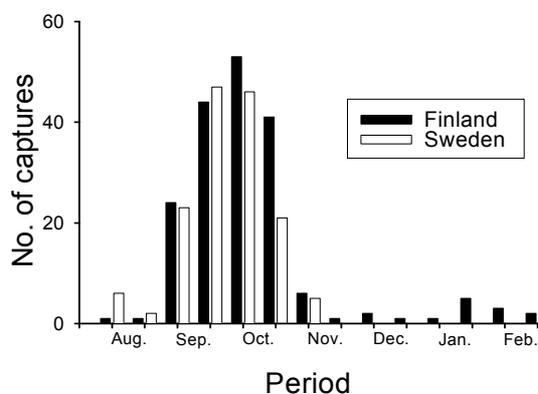
The Three-toed Woodpecker is the only woodpecker to be found in both the Old and New Worlds (Winkler et al. 1995) (although recent molecular investigations suggest that a separate species exists on each continent; Zink et al. 2002). As its name suggests, and together with the north american Black-backed Woodpecker *Picoides arcticus*, the Three-toed

Woodpecker has a reduced hallux instead of a distinct fourth zygodactyl toe as in *Dendrocopos* species. Typically, it inhabits mature boreal or montane coniferous forests, with a distribution that coincides with that of spruce tree species *Picea* spp. (Baldwin 1968, Bock and Bock 1974). In the whole Eurasian region, the total number of subspecies is five (*P. t. albidior*, *alpinus*, *crissoleucus*, *funnebris*, *tridactylus*). In Europe, the Three-toed Woodpecker population is subdivided into two subspecies. While the nominal form *P. t. tridactylus* is limited to the boreal forest of Fennoscandia and Western Russia, the sub-species *P. t. alpinus* is found in the mountainous areas of Central, Eastern and South-East Europe, mainly the Czech Republic, France, Germany, Greece, Poland, Slovakia, and Switzerland (Winkler et al. 1995). In North America, three different subspecies are described, namely *P. t. bacatus*, *P. t. dorsalis*, and *P. t. fasciatus*. Based the supposition on mitochondrial gene tree from world-wide the representatives of the genus, the New World *Picoides* may have evolved from several Eurasian invasions (Weibel and Moore 2002).

The Three-toed Woodpecker is everywhere a rare species (Goggans et al. 1989, Tucker and Heath 1994). Occasional observations of local aggregations in forest areas recently disturbed by fire (Sorvari 1994, Murphy and 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 and Hansley 1978) suggest that its population size is 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 round on insects that colonise dying and recently dead trees (i.e., with firm bark coverage). From late summer to early spring, they prey almost exclusively on conifer bark beetles (Coleoptera, Scolytidae), with a

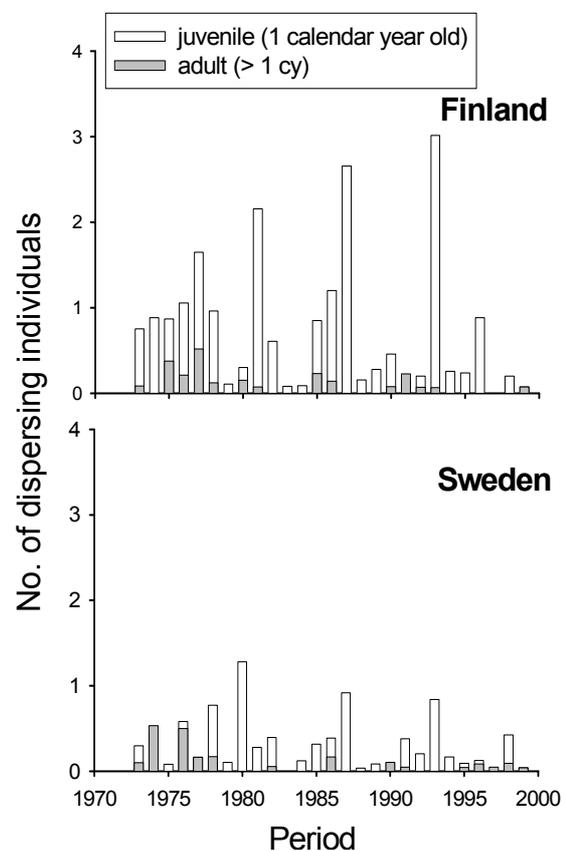
marked preferences for the species that colonise spruce trees (Hutchison 1951, Dement'ev 1966, Hogstad 1970, Koplín and Baldwin 1970, Koplín 1972, Massey and Wygant 1973, Pechacek and Krištín 1993). Three-toed woodpeckers, on the other hand, have been shown to ignore very small spruce bark beetle larvae, younger than  $3^{1/2}$  to 4 months of age (Koplín and Baldwin 1970). 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 (Dement'ev 1966, Hogstad 1970, Pechacek and Krištín 1996, P. Pechacek and 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 (Wesolowski & Tomialojc 1986, Hogstad 1991, Pechacek and Krištín 1996, D. Nowak, pers. comm.).

The Three-toed Woodpecker starts reproducing the first year following birth (i.e., in its second calendar year) (P. Fayt, pers. obs.). It lays between 2 and 6 eggs in May-June in a newly excavated cavity (Dement'ev 1966, Wesolowski and Tomialojc 1986).



**Figure 1.** Natal dispersal period of the Three-toed Woodpecker in Finland and Sweden (1973-2000).

In this study carried out in Finland, clutch size varied between 2 and 5 eggs ( $3.35 \pm 0.94$ ,  $n = 26$ ). The fledglings leave the nest in June-July; they start to disperse from their natal habitats mainly from August to November (Fig. 1). Like most woodpeckers, the Three-toed Woodpecker is primarily a resident species throughout its breeding range (Burdett and Niemi 2002). Nevertheless, evidence for large-scale irruptions exist on both continents (Yunick 1985; Fig. 2). As is the case for other irruptive bird species, the majority of the dispersing individuals are juveniles (e.g., Perrins 1966, Hildén 1982; Fig. 2).



**Figure 2.** Number of juveniles and adults dispersing in Finland and Sweden (1973-2000). The annual number of dispersers was related to the total number of fully-grown birds ringed each year in each country and expressed as the number of woodpeckers per 10,000 birds ringed.

The woodpecker's 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). Bark and wood-boring beetles undergo complete metamorphosis, developing successively into larvae (an early soft-bodied form without wing pads), pupae (a quiescent soft form with wing pads), and adults (hard-bodied with an external exoskeleton; Stark, 1982). Their life cycle includes three phases (Stark 1982). The first is the process of colonisation in early to mid-summer, when beetles invade trees before they start to reproduce. The second is a reproduction phase, which includes mating, oviposition, and brood development up to the time of emergence. The third is a natal dispersal phase. As for other ectothermic organisms, ambient temperature has a major influence upon the duration and timing of the different phases of development of the insect prey (Annala 1969, Salonen 1973, Post 1984). Beetle emergence or timing of natal dispersal depends on the time of reproduction (Annala 1969). In addition, the length of the life cycle depends on the species of beetle and factors such as moisture content of tree tissues and density of conspecifics (Post 1984).

Several traits, however, distinguish bark and longhorn beetles. Bark beetles are small (< 6 mm in length) but very numerous, and densely aggregated in the phloem (Powell 2000). Conifer bark beetles do not enter the sapwood of the tree and remain inside the bark, where they go through their development. Emerging beetles then leave their brood trees from August to November, prior to hibernation (e.g., Annala 1969). By contrast, the wood-boring beetles can be much larger (up to 50 mm) but less numerous and less clumped than bark beetles (Powell 2000). Longhorn beetles, whether shallow (e.g., *Tetropium* sp., *Rhagium* sp.) or deep (e.g.,

*Monochamus* sp.) borers, spend a part of their larval stage inside the sapwood (xylem) after a first period spent in the phloem (Post 1984, Bílý and Mehl 1989). Such wood-boring activity of larvae into the sapwood prior to pupation does not begin before late August-September of the beetle's first season (Rose 1957, Post 1984, Bílý and Mehl 1989).

During this study, the main difficulties encountered in the field were: (1) the rarity of the species and its low breeding density in apparently "optimal" habitats (1pair/about 70 ha of old-growth conifer forest), (2) the low detectability of the species outside the normal periods of drumming activities, and (3) the limited prospection capabilities under spring snow conditions.

### 3.2. Study areas

The data on woodpecker breeding parameters and food supply presented in this thesis were collected between 1996 and 1999 in North Karelia, easternmost Finland (63°N, 31°E). The study area consisted of a patchwork of eight Norway spruce-dominated old-growth stands and one Scots pine-dominated *Pinus sylvestris* stand burnt over in 1992. Among the eight old-growth habitat patches, five were surrounded by ditched clear-cuts and three were surrounded by untouched peatlands. As a result, the patches were spatially isolated from the others. The shortest distance between two patches was 500 m, and the longest 66 km. Each patch (65-90 ha) was annually inhabited by a single pair of Three-toed Woodpeckers, except in 1996 when a second pair was found breeding just outside the burnt area, while using it as a foraging area.

The information on dispersal patterns of Three-toed Woodpeckers originates from bird ringing activities carried out between 1973 and 2000 in Finland and Sweden.

### 3.3. General methods

### 3.3.1. The woodpecker data

#### 3.3.1.1. Reproduction

Fast drumming is used as a long-range territorial signal early in the morning. It is performed by both sexes during the spring, mainly from March to May, but also in late summer-early autumn (P. Fayt, unpubl.). Patch occupancy was annually checked by listening for drumming activities under natural conditions (without playback induction). Nests were then actively sought from early May onwards all over the woodpecker habitats. They were annually located by nest-excavation noises in early morning, by accidental discovery, usually after the discovery of fresh wood chips on the forest floor, and by the noisy vocalisations of the offspring.

Breeding time was estimated from the fledging date instead of from the laying date, by backward calculation from the date of fledging, to control for between-pair variation in the length of the incubation and rearing periods. Fledging date corresponded to the number of days from the 1st of June to the fledging day. Nests were visited daily once a nestling was seen extending its head from the cavity to beg for food; fledging was considered to have taken place when the first nestling had left the nest (II, III).

To determine the brood size of the woodpeckers it was necessary to climb the nest tree with metal shoes and use a small mirror and flashlight to investigate the cavity. If the nestling count was uncertain, the tree cavities were revisited during the following days. To avoid repeated brood size measurements from the same females, woodpeckers were individually colour-ringed whenever it was possible. A total of 10 breeding females and 12 breeding males were trapped and colour-ringed. The birds were captured after they entered the nest cavity to feed the offspring by placing a plastic tunnel prolonged by a hoop net in front of the nest hole. In addition, males and females that could not be trapped were

identified as different birds when they were observed in forest stands a year before the capture of the second calendar year individuals, or after the occurrence of colour-ringed residents (II, III, VI).

Based on 6 hours per nest (with 2 consecutive hours' observation per day during the two last weeks of the rearing period), parental effort was estimated from the feeding frequency per hour and per nestling. Attention was paid to counting the number of wood-boring beetle larvae delivered (e.g., longhorn beetle). The diet of the offspring was identified and quantified by using spotting scopes (II).

In order to relate local woodpecker reproductive output to ambient temperature conditions, mean brood size was measured annually from the same five habitat patches and related to the mean air temperature recorded during the preceding winter (November-March) and spring (April-May). Winter and spring temperatures in the study area were estimated by taking an average of the monthly mean temperatures measured from the nearby weather station of Lieksa Lampela (63°19'N, 30°03'E) (III).

To see whether interspecific pressure may contribute to explain a significant part of the variation in the reproductive performances of resident Three-toed Woodpeckers, I measured the breeding density and mean brood size of Great spotted Woodpeckers *Picoides major* reproducing in the same habitat patch as a pair of Three-toed Woodpeckers. The methods of finding nests and counting nestlings were the same as those used for Three-toed Woodpeckers (III).

#### 3.3.1.2. Dispersal patterns

Higher numbers of juvenile woodpeckers would be expected to disperse in autumns following warmer springs in the case that temperature-dependent profitability of insect prey is a factor explaining fitness variation among individuals (IV). Accordingly, spring temperature (April-

May) in Finland was annually related to the following autumn number of dispersing juveniles and to the winter population density of the woodpecker (1973-1999). The spring temperature throughout the country was estimated by taking an average of the monthly mean temperatures measured from six weather stations; two stations were situated in southern Finland (61°N, 22°-28°E), two in central Finland (63°N, 23°-30°E) and two in northern Finland (65°N, 26°-29°E). The yearly spring air temperature was calculated by taking an average of the monthly mean temperatures recorded from the six weather stations. The annual number of dispersing woodpeckers was estimated from the ringing data records of the Finnish Museum of Natural History. Importantly, juveniles were only considered as dispersing individuals when they were captured in localities known not to be breeding grounds of the woodpecker. Because the number of woodpeckers captured every autumn might be connected with the ringing activity effort, counts were made comparable by relating them to the total number of fully grown birds ringed each year and expressed as the number of woodpeckers per 10,000 birds ringed. Winter density was estimated by dividing the yearly number of individuals observed during the early- (01. – 14.11), mid- (25.12 – 07.01) and late- (21.02 – 06.03) census periods of the national winter bird count (1975-99) with the total length of census routes and transformed into a population index.

To investigate whether juveniles dispersed earlier from regions with an earlier prey development, the capture coordinates of dispersing juveniles were related to isotherms connecting points where a mean temperature of 5°C is measured at different times in spring (i.e., the temperature threshold when the woodpecker prey start moving and developing again after hibernation).

Patterns of woodpecker dispersal in space and time were compared between

Finland and Sweden, on the basis of additional information available from the ringing records of the Swedish Museum of Natural History. Together with capture coordinates and biometry, the yearly number of birds dispersing in Sweden was compared to the yearly number of dispersers in Finland. Woodpecker counts in Sweden were related to the total number of fully-grown birds ringed each year, as in Finland.

### 3.3.2. The insect prey data

In this thesis, habitat suitability for a Three-toed Woodpecker was defined as a function of available food supply, in terms of abundance throughout the year and profitability in relation to reproductive activities.

#### 3.3.2.1. Prey abundance

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. A sampling effort of 1 trap per 7 ha was assumed to allow a representative sampling of the patchily distributed forest beetles. Traps were located after choosing their direction and distance from the centre of sample plots from random number combinations. 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 emptied twice during the summer. During the whole study period, insect populations were sampled in about 1,590 ha of naturally dynamic forest habitats. Catches from window traps yielded altogether 19,251 individual beetles, which included 14,262 bark beetles (74.1%) from 31 species (**III**, **VI**, **VII**). Estimates of prey abundance included the number of individual beetles of all the families, the number of bark beetles, the number of individual bark

beetles of the species that specifically live on spruce, the number of individual wood-boring beetles (including the families Elateridae, Anobidae, Oedemeridae, Cerambycidae, Curculionidae), the number of longhorn beetles, and the number of bark and longhorn beetle species. Scolytids were classified as species living on spruce according to the species assemblage found from the bark of spruce trees selected by the woodpecker (I, II, VI). In paper VII, bark beetle species were categorised according to whether they live preferentially on standing dead trees or on logs, roots and stumps, as indicators of spatial variation in the distribution of suitable woody microhabitats.

### 3.3.2.2. Prey profitability

To clarify the diet preferences of the woodpecker, to link prey profitability to reproductive decisions, and to relate prey availability to natal dispersal, bark samples from spruce trees bearing recent Three-toed Woodpecker foraging tracks were collected during the pre-reproduction, reproduction, post-reproduction, and natal dispersal periods of the bird (I, II, III). The first period coincided with late winter and ended with the start of nest excavation; the subsequent reproduction period lasted until fledging. The natal-dispersal period was defined on the basis of information provided by ringing records (the dispersal time of young woodpeckers at the habitat level was thus inferred from information gathered at the landscape level). The post-reproduction period was then considered to be the time between fledging and natal dispersal. In order to minimise the multiple effects of tree host conditions on the spatial distribution of beetle communities on trunks, the samples (10x15 cm) were collected exclusively from standing trees, at breast height.

A total of 355 bark samples were collected, yielding 10,343 individual bark beetles (3,768 larvae, 950 pupae, and 5,625 adults (including juveniles and sub-

adults)). On the basis of the sequential order of the beetles' development stages (egg-larva-pupa-adult), an index of development for the spruce bark beetle community was built up by dividing the number of adult beetles of the different species by the number of larvae collected during the reproduction, post-reproduction, and natal dispersal periods of the woodpecker. Accordingly, it was assumed that the earlier and/or faster the prey community reproduction and/or development is, the more adults and fewer bark beetle larvae should be collected and the higher the index should be. This method also assumed that the development time of the bark beetle community should reflect the timing of development and thereby the size-dependent profitability of alternative prey, such as longhorn beetle larvae (II, III).

## 4. RESULTS AND DISCUSSION

### 4.1. Diet preferences

In paper I, I looked at the insect content of the bark of trees selected by foraging Three-toed Woodpeckers. Bark samples were taken from March to May, although most samples were collected in the first two months. In agreement with earlier results from the Northern Hemisphere, whether from stomach or dropping analyses, I found the predatory woodpecker to have particularly narrow dietary requirements outside the breeding season. Some 89% of the samples originated from spruce trees, and 96.9% of the insect prey collected were bark beetles. Interestingly, 78.5% of the adult bark beetles belonged to species previously found to respond negatively to forest edge proximity by withdrawing into the interior parts of forest stands. This led me to suppose that Three-toed Woodpeckers may suffer from lower winter foraging efficiency in a fragmented mature spruce forest landscape, if the proportion of interior forest decreases.

## 4.2. Breeding density

In paper VI, the hypothesis that the autumn-winter food supply of the woodpecker (the spruce bark beetles) control the subsequent woodpecker breeding density was examined 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 dynamics created by wind and tree-scale biotic interactions) and the woodpeckers' numerical responses to habitat change (decreasing vs. stable). In a forest patch burnt in 1992, where the burned trees remained in the area to allow for natural development of the vegetation, a decline in the woodpecker breeding population paralleled a progressive reduction in spruce bark beetle availability. 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 after fire. In neighbouring old-growth patches, on the other hand, where one pair of woodpeckers bred annually, the abundance of spruce bark beetles did not change significantly between years, although it differed among patches. My results suggest that the woodpecker breeding population is limited by the level of food available outside the breeding season, as shown for other forest bird populations (Perrins 1966, Van Balen 1980, Hannon et al. 1987, Nilsson 1987).

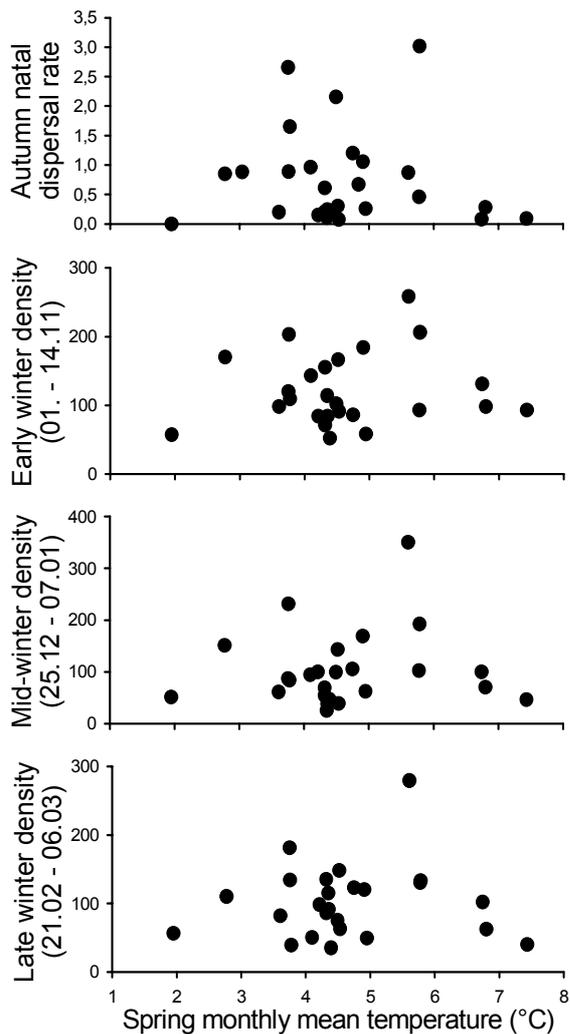
## 4.3. Breeding performance

In papers II and III, I studied the effect of prey profitability (based on the timing of their development) on reproductive decisions in Three-toed Woodpeckers, without taking into account and with taking into account the potential effects of confounding factors such as breeding time, food abundance and level of interspecific pressure for available food resources, respectively.

In paper II, I found that woodpecker starting breeding earlier in habitats with fewer bark beetle larvae and with more adult beetles sampled throughout the season. In accordance with the above assumption, it is suggested that woodpeckers nested earlier in forest habitats where the beetles reproduced earlier and/or development was faster, and the beetles emerged earlier. Brood size, in turn, was inversely related to the number of spruce bark beetle larvae and pupae. Or, conversely, brood size was larger in forest patches with more adult beetles. Thus, because the woodpecker bred earlier in habitats with more adults and fewer beetle larvae, a seasonal decline was observed in woodpecker brood size, as is found in other woodpecker species and single-brooded birds in general (e.g., Wiklander 1998).

In paper III, besides the effect of breeding time, I found patch-level variation in the woodpecker brood size to be explained by the timing of bark beetle development and the number of bark and longhorn beetle species, which were inter-correlated. Numbers of both beetle species, in turn, were strongly positively correlated with the abundance of longhorn beetles. The breeding density and success of coexisting Great spotted Woodpeckers did not influence the Three-toed Woodpecker productivity. Neither were they correlated with various estimates of animal food supply.

Thus, Three-toed Woodpeckers were found to lay clutches earlier and to rear larger broods in patches where the spruce bark beetles developed earlier, where the bark and longhorn beetle communities were more diverse, and where longhorn beetles were more abundant. Assuming a higher size-dependent profitability of longhorn beetle larvae in patches with early bark beetle development, it is proposed that brood size in the Three-toed Woodpecker depends on both abundance and phenology of Cerambycid beetle larvae in relation to the bird breeding



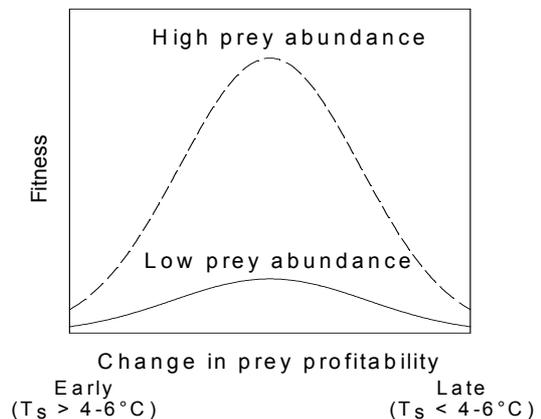
**Figure 3.** Rate of natal dispersal (1973-1999) and winter population size (1975-1999) of the Three-toed Woodpecker in Finland as a function of monthly mean temperature of the preceding spring (April-May).

cycle. This conclusion is in line with earlier findings, that productivity in birds is largely determined by the amount of food available to nestlings (e.g., Siikamäki 1995).

Like other woodpecker species that feed on bark- and wood-living arthropods (Hogstad and Stenberg 1997, Pasinelli 1999), the mean brood size of the Three-toed Woodpecker increased with spring ambient temperature. Although the study

covered a relatively short period of time (4 years), the results would provide additional evidence for the key impact of prey profitability at the time of egg laying on the bird's reproductive decisions. The results led to the prediction that the number of dispersing juvenile woodpeckers should increase with the mean temperature of the preceding spring (IV). In Finland, however, autumn captures of juvenile woodpeckers and the subsequent winter population size did not increase with the spring temperature conditions. Instead, woodpecker numbers seemed to reach a maximum following springs with a monthly mean temperature of 4-6°C, although a considerable inter-annual variation was apparent (Fig. 3).

Although this is a speculative proposal, I suggest that this pattern is a result of the decisions of breeding individuals to adjust their heritable breeding date to the development time of their prey, with special reference to longhorn beetle larvae, in an attempt to match breeding time and nestling food profitability under variable food abundance level.



**Figure 4.** Predicted fitness variation in breeding Three-toed Woodpeckers with changing prey profitability (development time) under contrasting prey abundance.  $T_s$  is the spring monthly mean  $T^\circ$ .

Only with a monthly temperature of 4-6° in spring (April-May) (i.e., the temperature

threshold when bark-living saproxylic beetles such as bark beetles restart moving and developing after hibernation) would the parents be able to match breeding time with food supply and to maximise their lifetime reproductive success. Even in the case of optimal timing of prey development, however, food supply would also depend on prey abundance, accounting for between-year variation in reproductive output and dispersal rate (Fig. 4).

#### 4.4. Parental care

In paper II, nestlings from earlier/larger broods were found to receive more wood-boring beetle larvae than those from later/smaller broods. Since the feeding rate did not change with breeding time and brood size, I suggest that, in line with previous results, a seasonal decline in wood-boring larva delivery rate is rather caused by habitat-related differences in the supply of the beetle larvae at the time of brood rearing than by differential adjustment in parental effort between early and late breeders. Similarly, Hogstad and Stenberg (1997) found White-backed Woodpeckers *Picoides leucotos* to breed earlier, lay larger clutches and produce heavier fledglings in years and places with warmer winter and early spring temperatures (and thus with the earliest prey development). They also found that pairs breeding in warmer places (with a shorter winter period) brought more wood-boring larvae for their young compared to pairs from colder places, despite similar feeding rates between the pairs from both areas. As a result, fledglings were found to be the heaviest in the warmest habitats in spring. The heaviest fledglings were also the most likely to be recruited subsequently into the local population, a finding in agreement with the previously found association between body size and survival among juvenile birds (e.g., van der Jeugd and Larsson 1988, Brinkhof et al. 1997).

#### 4.5. Natal dispersal

In paper II, I investigated whether the onset of natal dispersal in the Three-toed Woodpecker is related to change in prey availability. To do so, I compared the abundance of bark beetles living in spruce trees in relation to the woodpecker breeding cycle, after taking bark samples. The dispersal period was inferred from information gathered at landscape level, from ringing data files.

Besides a synchronous development of the different beetle species, I found young woodpeckers to disperse in Finland and Sweden at the time when the abundance of the bark beetles in my study area (Eastern Finland) was lower than during the preceding spring, in the reproductive and post-reproductive periods. Since a similar number of adult beetles was present in the bark during the post-reproductive and the dispersal periods of the bird, despite a peak in the number of juveniles and sub-adults among the different species of beetles during the former period, this apparent reduction in food level seemed to result from the dispersal of synchronously-developed beetle species within the habitat. This is consistent with earlier results from studies dealing with the population ecology of bark beetles under boreal conditions, showing that the newly-formed beetles leave their brood trees from late August to November, prior to hibernation (Chararas 1962, Annala 1969). In addition, a review of the existing literature on the ecology of longhorn beetle larvae revealed simultaneous changes in their availability, due to gallery excavation deeper inside the wood from the phloem, before pupation.

These findings would suggest that a sudden change in the spatial distribution of insect prey, whose timing is mediated by the timing of the prey development, may temporarily lower their availability for foraging woodpeckers and promote the dispersal of young individuals. The dispersal time of juvenile birds, on the other hand, is known to affect their own

lifetime reproductive success and, therefore, also that of their parents (Verboven and Visser 1998, Visser and Verboven 1999). This prompts me to propose that, by using the profitability of prey at the time of egg-laying for the fine-tuning of their reproductive decisions, female Three-toed Woodpeckers behave in a way that allows them to optimise their inclusive fitness.

Nevertheless, although my data emphasised coincidence between change in the spatial distribution of insect prey and the assumed onset of woodpecker natal dispersal, this study suffered from the absence of statistical verification that these two phenomena are causally related. This was due to the lack of direct field observations that young woodpeckers effectively dispersed at times of changes in prey availability. My results are therefore non-conclusive.

#### **4.6. Body size and dispersal patterns**

In altricial birds, there is evidence that fledgling size is related to hatch date (e.g., Alatalo and Lundberg 1986, Brinkhof et al. 1997), and that late-hatched individuals in a population disperse and search for vacant habitats later than do birds from early broods (Pinowsky 1965). This explains the general finding that early dispersers are larger than late-dispersing juveniles (Nilsson and Smith 1985, Hogstad 1990, Lens and Dhondt 1994). In paper IV, I examined the prediction that earlier-dispersing juvenile Three-toed Woodpeckers from a population should be larger than later-dispersing ones, presumably as a result of higher delivery rate of wood-boring larvae in earlier broods. In addition, if change in food availability promotes dispersal among juveniles, and if such a change is related to the life cycle of the prey, woodpeckers would be expected to disperse first from warmer areas (i.e., regions with earlier dates for the 5°C isotherm in spring). Thus, individuals dispersing from colder habitats

or regions should be, on average, smaller than those coming from warmer habitats, as shown with White-backed Woodpeckers (Hogstad and Stenberg 1997).

In Finland, earlier-dispersing juvenile males and females were, on average, longer-winged than their later-dispersing counterparts. Wing length, in turn, is positively correlated with bill length (Hogstad 1983). Body weight, on the other hand, did not follow any linear seasonal trends, although an existing inter-correlation between weight and wing length of male and female nestlings (P. Fayt, unpubl.) suggested that this discrepancy is a result of the limited sample size. In Sweden however, contrary to the prediction, the body size of the dispersers did not decrease with capture date. Instead, some of the juvenile males and females were found to be the heaviest and have the longest wings in the middle of September, while earlier- and later-dispersing individuals were smaller. One explanation for this could be the arrival in mid-September of larger individuals originating from Finland, as is suggested by the dispersal patterns of juveniles on both sides of the Baltic Sea.

Regarding the dispersal patterns of juveniles in relation to capture date, most individuals dispersing during the first half of the dispersal period (August-September) were captured at the northernmost ringing stations in Finland and Sweden (63-65°N) while, from early October onwards, juveniles were mostly captured in the southern parts of the countries (58-60°N). Such a pattern would contradict the earlier stated prediction, that juveniles from warmer regions should disperse before those originating from colder northern regions.

Alternatively, one would expect early birds from warmer regions preferentially to follow a northern direction, in order to benefit from the still available developing bark and wood-boring beetles hatched a year before. Only then would the later dispersers from colder regions fly

southwards, to profit from the newly growing bark beetle larvae. This is because spruce bark beetle larvae younger than 3<sup>1/2</sup> to 4 months of age are ignored by foraging Three-toed Woodpeckers (Koplin and Baldwin 1970), presumably being too small to be profitable. A consequence of this would be the capture of the earlier-dispersing individuals in northern Fennoscandia, despite their southern origin, from warmer regions.

Interestingly, the finding that seasonal variation in capture location coincided with simultaneous increases in the woodpecker average body size suggest the possible occurrence of several somewhat partially differentiated populations in Fennoscandia. As discussed elsewhere (Dhondt et al. 1990, Blondel et al. 1993, Blondel et al. 1999, Thomas et al. 2001), predictable climatic variability across landscapes and presumed limited dispersal (and thus gene flow) are pointed out as potential factors in promoting the evolution of those populations, by local adaptations of breeding adults to their environment. For comparison, in Finland, genetic diversity of isolated small populations of the Siberian Jay, another old-growth coniferous taiga forest dweller, has recently been found to be lower than that of populations in continuous distribution areas (Uimaniemi et al. 2000). This was apparently attributable to low intrinsic natal dispersal capabilities in fragmented forest landscapes.

#### 4.7. Predatory impact

In paper V, a literature review of case studies from the northern hemisphere revealed that, among woodpeckers preying on conifer bark beetles, the Three-toed Woodpecker was the most responsive to prey population changes. In comparison to other guild members (namely the Downy *Picoides pubescens*, the Black-backed, *P. arcticus* and the Hairy Woodpeckers *P. villosus*), the Three-toed Woodpecker was found to show the greatest numerical

response to prey density, with population densities increasing up to 44.8-fold during infestations, relative to those supported at endemic beetle levels. Furthermore, comparison of beetle mortality inside and outside woodpecker exclosures demonstrated the potential of woodpeckers to reduce up to 98% of spruce bark beetles populations, depending on prey density and whether a study took the indirect effects of predator feeding (desiccation, parasitism, predation) into consideration.

The review highlights several ecological factors that are associated with the predatory impact of the woodpeckers and its variability. The population response of woodpeckers to prey density and predatory impact was a function of (1) the woodpecker natal dispersal rate and success, (2) the size-mediated profitability of the bark beetle larvae at the time the bird is dispersing through the infestation, (3) limitations imposed by territoriality at the highest prey densities, (4) seasonal variation in the caloric content of insect prey and the metabolic rate and consequent food requirements of woodpecker species, and (5) stand-level factors that are related to site-specific silvicultural practices.

This allows me to propose a general mechanistic framework that accounts for variation in the predatory impact of woodpeckers on spruce bark beetles. Overall, it stresses the close relationship between the multi-scale heterogeneity of forested habitat, driven by succession and disturbance patterns in space and time, predator-prey population processes operating at landscape levels, and local consumer-resource dynamics.

Interestingly, in habitat patches where Three-toed Woodpeckers were continuously present, the abundance level of spruce bark beetles did not change significantly between years (VI). Conversely, the number of bark beetles of the species on which the woodpecker does not prey (i.e., mainly *Hylastes* and *Trypodendron* spp.) showed significant annual fluctuations. This result, although

preliminary, suggests a stabilising role of the woodpeckers on the population dynamics of their prey. In accordance with this supposition, lower beetle populations with more stable dynamics are expected in forest patches where the predatory woodpeckers are regular or year-round visitors than in patches where the woodpeckers are rarely seen.

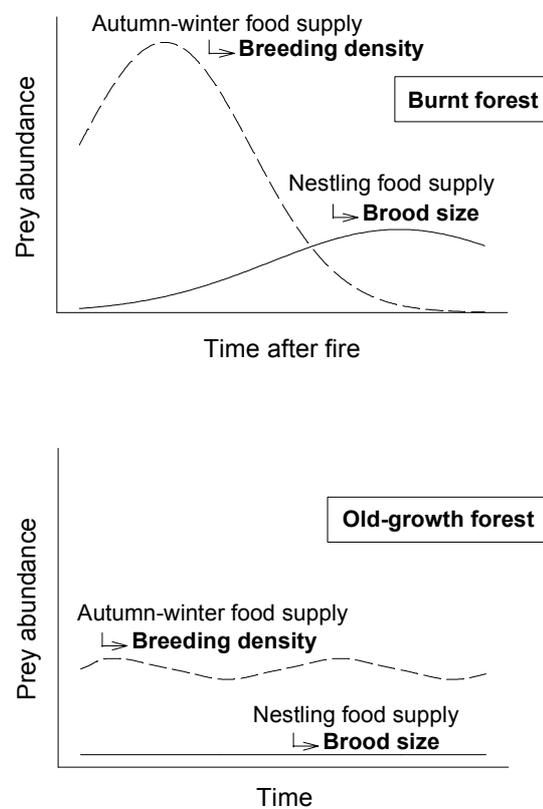
#### 4.8. Habitat suitability

In papers VI and VII, I studied bark and wood-boring beetle population responses to patch- and landscape-level management history, as a prerequisite for developing meaningful management plans for the Three-toed Woodpecker.

In paper VI, I compared the short-term effects of accidental fire vs. regular small gap-dynamics on the woodpecker's abundance and its food supply. After fire, unlike the case of spruce bark beetles (the autumn-winter prey whose abundance declined through the years in parallel to the woodpecker breeding population), the abundance of longhorn beetles (the nestling food supply) increased progressively in parallel to the bird's reproductive output. By contrast, in old-growth habitats, the continuous production of heterogeneity in forest structure allowed stable woodpecker-prey relationships, both in summer and in wintertime (Fig. 5).

Hence, this study shows that a patch suitable for a wintering Three-toed Woodpecker is not necessarily suitable for a reproducing individual, and vice versa. This is because the bird's dietary requirements change seasonally, with autumn-winter and summer prey responding differently to changing heterogeneity. Alternatively, basing suppositions on the preceding results connecting the population dynamics of conifer bark beetles with that of their avian predators (V), it may be suggested that the contrasting population trends of bark and wood-boring beetles after fire result from different mortality patterns in space and

time, due to differences in vulnerability (location, length of exposure) to predation under high woodpecker density.



**Figure 5.** Illustrated 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 woodpecker breeding density and reproductive output.

In paper VII, I found the management history of a forest landscape to influence the spatial distribution of bark beetles within its inclusive old-growth habitat units. Spruce bark beetle abundance was found to be lower at the edges of old-growth remnants in drained managed forest landscapes compared to patches embedded in a swampy untouched environment. Also, while the number of bark beetle species did not change with distance from the edge in swamp forests, the number did increase from the edge into the interior part of remnants surrounded by ditched clear-cuts. Comparing the

distribution patterns of the different bark beetle species, however, only the species assemblage in the case of standing trees responded to edge proximity.

In this thesis, I found the number of bark beetle species in a forest patch to affect positively the woodpecker brood size (III), being positively correlated with the abundance of longhorn beetles. Spruce bark beetles, on the other hand, made up its main winter-early spring food supply (I), and their availability underlay variation in its breeding density (VI). Thus, my results emphasise the importance of old-growth swamp forests in the boreal landscape as they lower the threshold in the proportion of original habitats that is required to ensure the reproduction and secure the winter food supply of a viable Three-toed Woodpecker population.

## 5. CONCLUDING REMARKS

### 5.1. Food supply and population ecology

Although the boreal forest, the dominant biome in Fennoscandia (Esseen et al. 1997), is relatively homogeneous in structure due to low tree species diversity, its latitudinal (56°N-69°N) and altitudinal extensions mean that it offers varying living conditions for associated organisms, both spatially and temporally. This has major implications for ecosystem productivity, resource phenology, the evolution of phenotypic plasticity, and the general structuration of natural communities (Stearns 1989, Hunter and Price 1992). In this thesis I have studied how spatial and temporal heterogeneity in food supply influence the abundance patterns of Three-toed Woodpeckers at patch, landscape, and regional levels.

Consistent with my original predictions, I found that:

1. the woodpecker breeding density varied in parallel to the abundance level of its autumn-winter main insect prey, the spruce bark beetles.

2. patch-level variation in the nestling food supply, the longhorn beetle larvae, accounted for individual variation in brood size and offspring feeding behaviour. Food supply, in turn, was a function of both prey abundance and phenology in relation to the bird breeding cycle.

3. the woodpecker mean brood size increased with the monthly mean temperature in spring (April-May), in line with predictions linking prey development time and reproductive decisions.

5. young woodpeckers dispersed across landscapes at times of lower local prey availability, due to changes in prey spatial distribution, whose timing is mediated by the timing of their development. The results, however, were not conclusive, as a causal relationship was missing.

6. there was a seasonal decline in the size of the dispersing juveniles, though this relationship holds good only for those dispersing over Finland.

8. year-to-year populations of spruce bark and longhorn beetles were stable in old-growth habitats where the woodpecker is continuously present, contrarily to populations of the bark beetle species on which the woodpecker does not prey.

In apparent contradiction with two of my predictions, I also found that:

4. the yearly number of dispersing juveniles did not increase linearly with ambient temperature of the preceding spring. Nevertheless, though these conclusions are speculative, I suggest this lack of positive relationships to result of how closely reproducing individuals are able to match breeding time to annual pattern of food supply. In other words, the yearly number of dispersing juveniles from a population would depend on its productivity, as initially predicted. Juveniles, on the other hand, may contribute significantly to controlling local infestations of conifer bark beetles, depending on their abundance when they disperse over the landscapes as the beetle larvae reach a profitable size.

7. most juveniles dispersing before October were captured on the northern shoreline of the Bothnian Bay, while most of the later dispersers were ringed on the southern coasts of Finland and Sweden. This pattern would emphasise an early dispersal from individuals originating from colder regions. However, I also suggest an alternative scenario, where early and late dispersers would adjust their dispersal directions differently, as a result of asynchronous changes in food supply across landscapes due to climatic variability and the consequent spatial heterogeneity in resource phenology. Early and late dispersers, from warmer and colder regions, would follow northwards and southwards directions to cope with this heterogeneity, respectively.

This raises the possibility whether contrasting patterns of insect prey phenology across Fennoscandia and presumed limited dispersal may have promoted the differentiation of several Three-toed Woodpecker populations, by local adaptations of breeding adults with their environment. Those populations would then differ from each other in their breeding timing, natal dispersal time and dispersal directions as adaptive responses to asynchronous and spatial changes in food supply. Some of the individuals, however, may occasionally disperse over large distances, for example, between Finland and Sweden. This hypothesis could explain results that are apparently contradictory to my earlier predictions, such as a lack of linear decline in the body size of dispersing juveniles in Sweden or the capture of the early-dispersing juveniles in northern Fennoscandia.

In line with this hypothesis, in Finland, the available evidence suggests that the number of dispersing Three-toed woodpecker has declined since ringing data have been available (adult:  $r_s = -0.398$ ,  $n = 27$ ,  $P = 0.040$ ; juvenile:  $r_s = -0.399$ ,  $n = 27$ ,  $P = 0.039$ ). This, in turn, may reinforce local adaptations to resource phenology but promote maladaptive

reaction norms in the face of global environmental stochasticity.

Accordingly, the results of this thesis suggest that food supply, determined by the annual timing of prey development and prey abundance, together with its variability in time and space, is a key factor in understanding individual responses (density, productivity, parental care, predatory impact) and population processes (timing, rate and patterns of dispersal) in the Three-toed Woodpecker.

## 5.2. Management implications

My results present several implications for the conservation of the Three-toed Woodpecker and the general management of the boreal forest. They support the proposal of forest management guidelines that consider the occurrence of the species in forested landscapes as closely dependent on the distribution patterns and population dynamics of its insect prey, and not merely on the supply of potential nesting trees, as was the case in the past (Imbeau and Desrochers 2002).

1. With brood size in a forest patch positively correlating with the number of bark and longhorn beetle species (III), my results suggest reproductive success in Three-toed Woodpeckers to be a reliable indicator of local saproxylic beetle diversity. Thus, the simultaneous measurement of the woodpecker brood size among patches may be a particularly useful method when attempting to rank forest areas with the highest conservation value in a minimum period of time and with limited effort.

2. In Finland, the numbers of bark and longhorn beetle species are known to increase with decreasing latitude (Lekander et al. 1977, Väisänen and Heliövaara 1994), together with a warmer climate and earlier prey development. Moreover, the number of bark beetle species has been shown to increase with the age of the forest and the amount and also the diversity of decaying wood

available (Martikainen et al. 1996, Martikainen et al. 1999). This underlines the importance of naturally dynamic forest habitats such as old-growth stands, and in particular those in the southern parts of the country, for the productivity of its woodpecker population and the diversity of its saproxylic insect communities. In the Alps, Three-toed Woodpeckers are typically found in forest habitats with an average dead wood volume of 63 m<sup>3</sup>/ha (i.e., 70 standing dead trees/ha) (Derleth et al., 2000). In the course of this study, in Finland, I collected between 15 and 22 species of bark beetles in the woodpecker breeding habitats, while Martikainen et al. (1999) estimated an average dead wood volume of 62.7 m<sup>3</sup>/ha from structurally similar sites with at least 15 species of bark beetles observed (P. Martikainen, pers. comm.). Estimated home range sizes for three radio-tagged individual Three-toed Woodpeckers during an epidemic mountain pine beetle outbreak in Canada were 304, 142 and 53 ha (Goggans et al. 1989). In the Alps, Pechacek (in press) found breeding pairs to have an average home-range size of 86.4 ± 23.4 ha, although with considerable variation between pairs (33.9 – 287.4 ha). Prior to nesting and during the post-nesting period, both sexes used seemingly larger home ranges than during nesting (up to 381.7 ha). In my study area of Eastern Finland, pairs were found breeding in old-growth patches between 65-90 ha (with 1 pair per patch).

3. The conservation value of an old-growth forest patch for a resident woodpecker is shown to be landscape-specific, with edge-related biotic conditions influenced by the soil properties and hydrology of the surrounding matrix (VII). Showing a lower amount of spruce bark beetles at the edge of old-growth remnants in drained landscapes than in swampy environments, this study confirms the important role of swamp forests for the woodpecker winter survival and subsequent breeding density (Wesolowski

and Tomialojc 1986). In southern Finland, Pakkala et al. (2002) found most Three-toed Woodpecker breeding territories located in mature spruce-dominated forests, often connected to spruce bogs. This finding has major practical consequences for the total proportion of original habitats that would be required in a forest landscape to maintain the species, making threshold values dependent on the landscape context.

4. Although both spruce bark and longhorn beetles readily colonise dying and recently dead trees, the present results suggest that the woodpecker insect prey respond differently to naturally changing heterogeneity in structure and abiotic conditions, depending on the origin of the process (fire vs. gap dynamics) (VI). The bark and longhorn beetle populations may also be differently affected by woodpecker predation, due to differences in vulnerability under snowy boreal conditions. This would emphasise the importance of patch disturbance history and living conditions on its long-term suitability for a resident woodpecker. In case of seasonal food shortages, however (for example several years after a fire), the woodpecker should be more likely to persist in the area if the patch is part of a landscape mosaic where patch-specific disturbance dynamics would ensure overall stable food conditions. Accordingly, Pakkala et al. (2002) found the probability of territory occupancy by the woodpecker and its persistence on a larger scale to increase both with the quality of a territory and with the quality of its surrounding, in terms of tree stem volume, age and composition (importance of spruce and broad-leaved trees) as well as the degree of connectivity to other potential territories.

5. The finding that predatory woodpeckers, especially Three-toed Woodpeckers, may cause considerable mortality in conifer bark beetle populations is important. It means that the woodpecker might contribute significantly to the natural regulation of the major “pest”

scolytids of managed forests, at least at the endemic or epidemic phase. Presumably, the Three-toed Woodpecker will have a far greater impact if it reaches the plot at the start of an infestation, before explosion of the beetle population. Thus, establishing regional networks of old-growth forests where the woodpecker is present might help to delay and/or lessen beetle outbreaks, and thus reduce the damage caused by economically important bark beetles in managed forests. During this study, in my Three-toed Woodpecker habitats, the proportion of primary bark beetles (namely *Ips typographus*, *Dendroctonus micans*, *Pityogenes chalcographus* and *Tomicus piniperda*) accounted altogether for only 1.14% of the total catch, despite significant dead wood volume.

6. Linking spatial heterogeneity in prey phenology across landscapes and dispersal patterns of juvenile woodpeckers in Fennoscandia, I suggest that dispersal movements from southern Finland might contribute to the presence of the species further north and vice versa. Also, information from bird ringing activities suggest occasional cross-border movements, for example between Finland and Sweden. This would emphasise the real and urgent need for a representative network of large old-growth forest reserves in both northern and southern Fennoscandia, in order to ensure the long-term persistence of the species in modern managed forest landscapes.

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## REFERENCES

- Alatalo, R.V. and Lundberg, A. 1986. Heritability and selection on tarsus length in the Pied Flycatcher (*Ficedula hypoleuca*). *Evolution* 40: 574-583.
- Alatalo, R.V., Lundberg, A. and Glynn, C. 1986. Female pied flycatchers choose territory quality and not male characteristics. *Nature* 323: 152-153.
- Angelstam, P. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *J. Veg. Sci.* 9: 593-602.
- Annala, E. 1969. Influence of temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). *Ann. Zool. Fennici* 6: 161-207.
- Baldwin, P.H. 1960. Overwintering of woodpeckers in bark-beetle infested spruce-fir forests in Colorado. 12<sup>th</sup> Int. Ornithol. Congr. Proc., Helsinki: 71-84.
- Baldwin, P.H. 1968. Predator-prey relationships of birds and spruce beetles. *Proc. North Central Branch – E.S.A.* 23: 90-99.
- Balen, J.H. van. 1973. A comparative study of the breeding ecology of the Great Tit, *Parus major* in different habitats. *Ardea* 61: 1-93.
- Balen, J.H. van. 1980. Population fluctuations of the Great Tit and feeding conditions in winter. *Ardea* 68: 143-164.
- Bílý, S. and Mehl, O. 1989. Longhorn Beetles (Coleoptera, Cerambycidae) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* 22, E.J. Brill/Scandinavian Science Press, Denmark.
- Blondel, J., Dias, P.C., Maistre, M. and Perret, P. 1993. Habitat heterogeneity and life-history variation of mediterranean blue tits (*Parus caeruleus*). *Auk* 110: 511-520.
- Blondel, J., Dias, P.C., Perret, P., Maistre, M. and Lambrechts, M. M. 1999. Selection-based biodiversity at a small spatial scale in a low-dispersing insular bird. *Science* 285: 1399-1402.
- Bock, C.E. and Bock, J.H. 1974. On the geographical ecology and evolution of the Three-toed Woodpeckers, *Picoides tridactylus* and *P. arcticus*. *Am. Midl. Nat.* 108: 397-405.
- Brinkhof, M.W.G., Cavé, A.J. and Perdeck, A.C. 1997. The seasonal decline in the first-year survival of juvenile coots: an experimental approach. *J. Anim. Ecol.* 66: 73-82.
- Burdett, C.L. and Niemi, G.J. 2002. Conservation Assessment for Three-toed woodpecker (*Picoides tridactylus*). USDA Forest Service, Eastern Region.
- Chararas, C. 1962. Étude biologique des Scolytides des conifères. Paul Lechevalier, Paris.
- Cresswell, W. 1998. Variation in the strength of interference competition with resource density in Blackbirds, *Turdus merula*. *Oikos* 81: 152-160.
- Crockett, A.B. and Hansley, P.L. 1978. Apparent response of *Picoides* woodpeckers to outbreaks of the pine bark beetle. *West. Birds* 9: 67-70.
- Daan, S., Dijkstra, C., Drent, R. and Meijer, T. 1988. Food Supply and the Annual Timing of Avian Reproduction. *Proc. Int. Ornithol. Congr., XIX*: 392-407.
- Dement'ev, G.P. 1966. Northern Three-toed Woodpecker. In: Dement'ev, G.P. and Gladkov, N.A. (eds.). *Birds of the Soviet Union. Volume 1.* Israel Program for Scientific Translations, Jerusalem, pp. 624-627.
- Dempster, J.P. and Pollard, E. 1981. Fluctuations in resource availability and insect populations. *Oecologia* 50: 412-416.
- Derleth, P., Bütler, R. and Schlaepfer, R. 2000. The Three-toed Woodpecker (*Picoides tridactylus*): an indicator of ecological quality in the forest ecosystem of the Pays-d'Enhaut region (Swiss Prealps). *Schweiz. Z. Forstwes.* 151: 282-289 (in French with English summary).

- Dhondt, A.A., Adriaensen, F., Matthysen, E. and Kempenaers, B. 1990. Nonadaptive clutch sizes in tits. *Nature* 348: 723-725.
- Dolman, P.M. 1995. The intensity of interference varies with resource density – evidence from a field-study with snow buntings, *Plectrophenax nivalis*. *Oecologia* 102: 511-514.
- Dunning, J.B., Danielson, B.J. and Pulliam, H.R. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65: 169-175.
- Esseen, P.-A., Renhorn, K.-E. and Pettersson, R.B. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. *Ecol. Appl.* 6: 228- 238.
- Esseen, P.-A., Ehnström, B., Ericson, L. and Sjöberg, K. 1997. Boreal forests. *Ecol. Bull.* 46: 16-47.
- Fagan, W.F., Cantrell, R.S. and Cosner, C. 1999. How habitat edges change species interactions. *Am. Nat.* 153: 165-182.
- Fraedrich, S.W. and Tainter, F.H. 1989. Effects of dissolved oxygen concentration on the relative susceptibility of shortleaf and loblolly pine root tips to *Phytophthora cinnamomi*. *Phytopathology* 79: 1114-1118.
- Gauthreaux, S.A., Jr. 1985. The temporal and spatial scales of migration in relation to environmental changes in time and space. In: Rankin, M.A. (ed.). *Migration: mechanisms and adaptive significance*. *Contrib. Marine Sci.* 27 (Suppl.), pp. 503-515.
- Goggans, R., Dixon, R.D. and Seminar, L.C.S. 1989. Habitat use by Three-toed and Black-backed Woodpeckers, Deschutes National Forest, Oregon. *Oreg. Dep. Fish and Wildl., Nongame Wildl. Program, USDA Deschutes Natl. For. Tech. Rep.* 87-3-02, 43 pp.
- Hakkarainen, H. and Korpimäki, E. 1994. Does feeding effort of Tengmalm's owls reflect offspring survival prospects in cyclic food conditions? *Oecologia* 97: 209-214.
- Hannon, S.J., Mumme, R.L., Koenig, W.D., Spon, S. and Pitelka, F.A. 1987. Poor acorn crop, dominance, and decline in numbers of acorn woodpeckers. *J. Anim. Ecol.* 56: 197-207.
- Haywood, S. and Perrins, C.M. 1993. Is clutch size in birds affected by environmental conditions during growth? *Proc. R. Soc. Lond. B.* 249: 195-197.
- Henderson, I.G. and Hart, P.J.B. 1995. Dominance, food acquisition and reproductive success in a monogamous passerine: the Jackdaw *Corvus monedula*. *Journal of Avian Biology* 26: 217-224.
- Hertert, H.D., Miller, D.L. and Partridge, A.D. 1975. Interaction of bark beetles (Coleoptera: Scolytidae) and root-rot pathogens in grand fir in northern Idaho. *Can. Ent.* 107: 899-904.
- Hildén, O. 1982. Winter ecology and partial migration of the Goldcrest *Regulus regulus* in Finland. *Ornis Fennica* 59: 99-122.
- Hogstad, O. 1970. On the ecology of the Three-toed Woodpecker *Picoides tridactylus* (L.) outside the breeding season. *Nytt Mag. Zool.* 18: 221-227.
- Hogstad, O. 1983. Wing length variation and movement pattern of the Three-toed Woodpecker *Picoides tridactylus* in Fennoscandia. *Fauna norv. Ser. C, Cinclus* 6: 81-86.
- Hogstad, O. 1990. Dispersal date and settlement of juvenile Willow Tits *Parus montanus* in winter flocks. *Fauna Norv. Ser. C, Cinclus* 13: 49-55.
- Hogstad, O. 1991. The effect of social dominance in foraging by the Three-toed Woodpecker *Picoides tridactylus*. *Ibis* 133: 271-276.
- Hogstad, O. and Stenberg, I. 1997. Breeding success, nestling diet and parental care in the White-backed Woodpecker *Dendrocopos leucotos*. *J. Orn.* 138: 25-38.

- Hunter, M.D. and Price, P.W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73: 724-732.
- Hutchison, F.T. 1951. The effects of woodpeckers on the Engelmann spruce beetle, *Dendroctonus engelmanni* Hopk. M.Sc. Thesis, Col. State Univ., Ft. Collins, CO. 78.
- Imbeau, L., Savard, J.-P.L. and Gagnon, R. 1999. Comparing bird communities of successional black spruce stands originating from fire and logging. *Can. J. Zool.* 77: 1850-1860.
- Imbeau, L. and Desrochers, A. 2002. Foraging ecology and use of drumming trees by Three-toed Woodpeckers. *J. Wild. Manage.* 66: 222-231.
- Koplin, J.R. 1972. Measuring predator impact of woodpeckers on spruce beetles. *J. Wild. Manage.* 36: 308-320.
- Koplin, J.R. and Baldwin, P.H. 1970. Woodpecker predation on an endemic population of Engelmann spruce beetles. *Am. Midl. Nat.* 83: 510-515.
- Korpimäki, E. 1988. Factors promoting polygyny in European birds of prey – a hypothesis. *Oecologia* 77: 278-285.
- Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica* 36: 97-125.
- Lekander, B., Bejer-Petersen, B., Kangas, E. and Bakke, A. 1977. The distribution of bark beetles in the Nordic countries. *Acta Ent. Fenn.* 32: 1-37.
- Lens, L. and Dhondt, A. A. 1994. Effects of habitat fragmentation on the timing of Crested Tit *Parus cristatus* natal dispersal. *Ibis* 136: 147-152.
- Lertzman, K. and Fall, J. 1998. From forest stands to landscapes: spatial scales and the roles of disturbances. In: Peterson, D.L. and Parker, V.T. (eds.). *Ecological scale: theory and applications*. Columbia University Press, pp. 339-367.
- Lundberg, P. 1985. Dominance behaviour, body weight and fat variations, and partial migration in European Blackbirds *Turdus merula*. *Behavioral Ecology and Sociology* 17: 185-189.
- Martikainen, P., Siitonen, J., Kaila, L. and Punttila, P. 1996. Intensity of forest management and bark beetles in non-epidemic conditions: a comparison between Finnish and Russian Karelia. *J. Appl. Ent.* 120: 257-264.
- Martikainen, P., Kaila, L. and Haila, Y. 1998. Threatened beetles in White-backed Woodpecker habitats. *Conserv. Biol.* 12: 293-301.
- Martikainen, P., Siitonen, J., Kaila, L., Punttila, P. and Rauh, J. 1999. Bark beetles (Coleoptera, Scolytidae) and associated beetle species in mature managed and old-growth boreal forests in southern Finland. *For. Ecol. Manage.* 116: 233-245.
- Martin, T.E. 1987. Food as a limit on breeding birds: a life-history perspective. *Ann. Rev. Ecol. Syst.* 18: 453-487.
- Martin, K. and Eadie, J.M. 1999. Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. *For. Ecol. Manage.* 115: 243-257.
- Marzluff, J.M., Raphael, M.G. and Sallabanks, R. 2000. Understanding the effects of forest management on avian species. *Wild. Soc. Bul.* 28: 1132-1143.
- Massey, C.L. and Wygant, N.D. 1973. Woodpeckers: most important predators of the spruce beetle. *Colo. Field. Ornithol.* 16:4-8.
- Mikusinski, G., Gromadzki, M. and Chylarecki, P. 2001. Woodpeckers as indicators of forest bird diversity. *Conserv. Biol.* 15: 208-217.
- Murphy, E.C. and Lehnhausen, W.A. 1998. Density and foraging ecology of woodpeckers following a stand-replacement fire. *J. Wild. Manage.* 62: 1359-1372.
- Newton, I. 1980. The role of food in limiting bird numbers. *Ardea* 68: 11-30.

- Newton, I. 1998. Population limitation in birds. Academic Press.
- Nilsson, J.-Å. and Smith, H. G. 1985. Early fledgling mortality and the timing of juvenile dispersal in the Marsh Tit *Parus palustris*. *Ornis Scandinavica* 16: 293-298.
- Nilsson, S.G. 1987. Limitation and regulation of population density in the Nuthatch *Sitta europaea* (Aves) breeding in natural cavities. *J. Anim. Ecol.* 56: 921-937.
- Nilsson, S. G., Hedin, J. and Niklasson, M. 2001. Biodiversity and its assessment in boreal and nemoral forests. *Scand. J. For. Res. Suppl.* 3: 10-26.
- Pakkala, T., Hanski, I. and Tomppo, E. 2002. Spatial ecology of the Three-toed Woodpecker in managed forest landscapes. *Silva Fennica* 36: 279-288.
- Pasinelli, G. 1999. Relations between habitat structure, space use and breeding success of the Middle spotted Woodpecker. PhD thesis, University of Zürich, Switzerland.
- Pechacek, P. 2004. Spacing behavior of Three-toed Woodpeckers (*Picoides tridactylus*) during breeding season in Germany. *Auk* (in press).
- Pechacek, P. and Krištín, A. 1993. Diet of woodpeckers, Piciformes in Berchtesgaden National Park. *Vogelwelt* 114: 165-177 (in German with English summary).
- Pechacek, P. and Krištín, A. 1996. Food and foraging ecology of the Three-toed Woodpecker *Picoides tridactylus* during the nestling period. *Orn. Beob.* 93: 259-266 (in German with English summary).
- Perrins, C.M. 1966. The effect of beech crops on Great Tit populations and movements. *Br. Birds* 59: 419-432.
- Pettersson, R.B., Ball, J.P., Renhorn, K.-E., Esseen, P.-A. and Sjöberg, K. 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. *Biol. Cons.* 74: 57-63.
- Pettersson, R.B. 1996. Effect of forestry on the abundance and diversity of arboreal spiders in the boreal spruce forest. *Ecography* 19: 221-228.
- Pinowski, J. 1965. Overcrowding as one of the causes of dispersal of young tree sparrows. *Bird Study* 12: 27-33.
- Post, K.E. 1984. Wood borer (Cerambycidae and Buprestidae) infestation, development and impact on wood quality in recently felled white spruce trees in the interior of Alaska. M.S. Thesis, University of Alaska, USA.
- Powell, H. 2000. The influence of prey density on post-fire habitat use of the Black-backed Woodpecker. M.S. Thesis, University of Montana, Missoula, USA.
- Rajasärkkä, A. 1997. Conservation of birds in Finnish old-growth forests. *Linnut* 2: 16-27 (in Finnish with English summary).
- Rassi, P. 2000. The new list of threatened bird species in Finland. *Linnut* 35: 6-13 (in Finnish with English summary).
- Rose, A.H. 1957. Some notes on the biology of *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae). *Can. Entomol.* 89: 547-553.
- Rykiel, E.J., Jr., Coulson, R.N., Sharpe, P.J.H., Allen, T.F.H. and Flamm, R.O. 1988. Disturbance propagation by bark beetles as an episodic landscape phenomenon. *Landsc. Ecol.* 1: 129-139.
- Salonen, K. 1973. On the life cycle, especially on the reproduction biology of *Blastophagus piniperda* L. (Col., Scolytidae). *Acta Forestalia Fennica* 127: 1-72.
- Sandberg, R. and Moore, F.R. 1996. Fat stores and arrival on the breeding grounds: reproductive consequences for passerine migrants. *Oikos* 77: 577-581.
- Schmiegelow, F.K.A. and Mönkkönen, M. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecol. Appl.* 12: 375-389.

- Sedinger, J.S., Flint, P.L. and Lindberg, M.S. 1995. Environmental influence on life-history traits: growth, survival, and fecundity in Black Brant (*Branta bernicla*). *Ecology* 76: 2404-2414.
- Siikamäki, P. 1995. Habitat quality and reproductive traits in the pied flycatcher: an experiment. *Ecology* 76: 308-312.
- Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecol. Bull.* 49: 11-41.
- Sipura, M. 1999. Tritrophic interactions: willows, herbivorous insects and insectivorous birds. *Oecologia* 121: 537-545.
- Smith, H.G. 1993. Seasonal decline in clutch size of the Marsh Tit (*Parus palustris*) in relation to date-specific survival of offspring. *Auk* 110: 889-899.
- Sorvari, V.-M. 1994. Kitsi forest fire area - a paradise for Three-toed Woodpeckers. *Linnut* 4: 28-32 (in Finnish with English summary).
- Stacey, P.B. and Bock, C.E. 1978. Social plasticity in the Acorn Woodpecker. *Science* 202: 1298-1300.
- Stacey, P.B. and Koenig, W.D. 1984. Cooperative breeding in the Acorn Woodpecker. *Sci. Amer.* 251: 114-121.
- Stark, R.W. 1982. Generalized Ecology and Life Cycle of Bark Beetles. In: Mitton, J.B. and Sturgeon, K.B. (eds.). *Bark Beetles in North American Conifers. A System for the Study of Evolutionary Biology.* Austin, USA, pp. 21-45.
- Stearns, S.C. 1989. The evolutionary significance of phenotypic plasticity. *Bioscience* 39: 436-445.
- Sutherland, W.J. 1996. *From individual behaviour to population ecology.* Oxford, England.
- Tikkanen, O.-P. 2000. Adaptation of a generalist moth, *Operophtera brumata*, to host plants. PhD thesis, University of Joensuu, Finland.
- Thomas, D.W., Blondel, J., Perret, P., Lambrechts, M.M. and Speakman, J.R. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* 291: 2598-2600.
- Tucker, G.M. and Heath, M.F. 1994. *Birds in Europe: their conservation status.* BirdLife International, Cambridge.
- Uimaniemi, L., Orell, M., Mönkkönen, M., Huhta, E., Jokimäki, J. and Lumme, J. 2000. Genetic diversity in the Siberian jay *Perisoreus infaustus* in fragmented old-growth forests of Fennoscandia. *Ecography* 23: 668-677.
- Väisänen, R. and Heliövaara, K. 1994. Hot-spots of insect diversity in northern Europe. *Ann. Zool. Fennici* 31: 71-81.
- van der Jeugd, H. P. and Larsson, K. 1998. Pre-breeding survival of barnacle geese *Branta leucopsis* in relation to fledgling characteristics. *J. Anim. Ecol.* 67: 953-966.
- Verboven, N. and Visser, M.E. 1998. Seasonal variation in local recruitment of great tits: the importance of being early. *Oikos* 81: 511-524.
- Virkkala, R., Heinonen, M. and Routasuo, P. 1991. The response of northern taiga birds to storm disturbance in the Koilliskaira National Park, Finnish Lapland. *Ornis Fennica* 68: 123-126.
- Visser, M.E. and Verboven, N. 1999. Long-term fitness effects of fledging date in great tits. *Oikos* 85: 445-450.
- Weibel, A.C. and Moore, W.S. 2002. Molecular phylogeny of a cosmopolitan group of woodpeckers (Genus *Picoides*) based on *COI* and *cyt b* mitochondrial gene sequences. *Mol. Phylogenet. Evol.* 22: 65-75.
- Wesolowski, T. and Tomialojc, L. 1986. The breeding ecology of woodpeckers in a temperate primaeval forest – preliminary data. *Acta Orn.* 22: 1-21.
- Wiehn, J. 1997. Food supply, parental abilities and parasitism in the reproduction of kestrels. PhD thesis, University of Turku, Finland.

- Wiktander, U. 1998. Reproduction and survival in the lesser spotted woodpecker. Effects of life history, mating system and age. PhD thesis, University of Lund, Sweden.
- Wiktander, U., Olsson, O. and Nilsson, S.G. 2000. Parental care and social mating system in the lesser spotted woodpecker *Dendrocopos minor*. J. Avian Biol. 31: 447-456.
- Willimont, L.A., Jackson, J.A. and Jackson, B.J.S. 1991. Classical polyandry in the West Indian woodpecker on Abaco, Bahamas. Wilson Bull. 103: 124-125.
- Winkler, H., Christie, D.A. and Nurney, D. 1995. Woodpeckers: a guide to the woodpeckers of the world. Pica Press, New York.
- Yeager, L.E. 1955. Two woodpecker populations in relation to environmental change. Condor 57: 148-153.
- Yunick, R.P. 1985. A review of recent irruptions of the black-backed woodpecker and three-toed woodpecker in eastern North America. J. Field. Ornith. 56: 138-152.
- Zink, R.M., Rohwer, S., Drovetski, S., Blackwell-Rago, R.C. and Farrell, S.L. 2002. Holarctic phylogeography and species limits of Three-toed Woodpeckers. Condor 104: 167-170.