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Top predator and interference competition modify the occurrence and breeding success of a specialist species in a structurally complex forest environment

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The three-toed woodpecker *Picoides tridactylus* favours structurally complex forest biotopes that are also preferred by its predators and competitors. Among them, the goshawk *Accipiter gentilis* is a top predator that may have a positive indirect effect on the woodpecker by its negative impact on other predators. We studied this predator–prey community in a forest-dominated area of 470 km^2 in southern Finland in 1987–2005 by controlling goshawk occupancy and habitat changes. Goshawk affected densities of bird predators and hole-nesting species and locations of the nest sites of woodpeckers. Goshawk (+) and great spotted woodpecker *Dendrocopos major* (–) were significantly associated with density changes and breeding success of three-toed woodpecker. Positive influence of goshawk was correlated with landscape fragmentation that indicates that goshawk could decrease mammalian nest predation on three-toed woodpecker. Territory quality of three-toed woodpecker may be substantially modified by species interactions and be mediated to its population development.

Introduction

Both the abundance and distribution of single species and coexistence of different species in space and time are simultaneously affected by several abiotic and biotic factors (*see* e.g. Andrewartha & Birch 1954, Krebs 1972). The role of species interactions, like competition, predation or mutualism may modify the structure of animal communities (cf. Connell 1975, Diamond & Case 1986, Ricklefs & Schluter 1993, Morin 1999). However, as different species interactions are connected with each other and also depend on the properties of the biotope studied, it is often difficult to separate effects of species interactions from those caused by spatial and temporal variation of habitat quality, especially in structurally complex environments. In addition, the interpretation of observed spatial patterns and densities of species are usually not straightforward because various processes may generate similar patterns and the results are dependent on

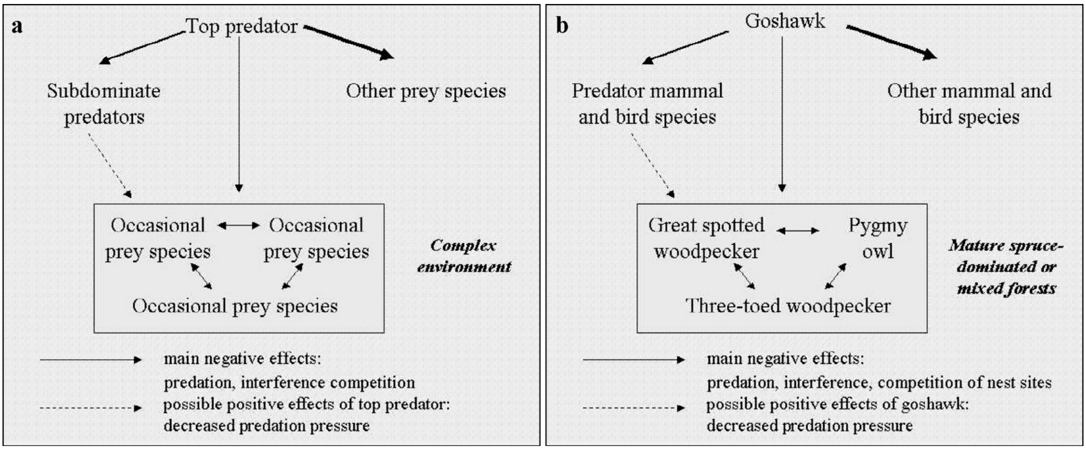

Fig. 1. — **a**: A schematic chart of the possible positive effects of top predator on occasional prey species that interfere with each other. Indirect effects of the presence of the top predator by decreasing numbers of other predator species may produce a net loss of predation pressure targeted at occasional prey species. The loss of total predation pressure caused by the top predator may, however, lead to increased competition between these prey species. The coexistence of prey species can then be promoted by the heterogeneity of the environment. — **b**: An application of the previous theme in a predator–prey assemblage of a forest ecosystem. Goshawk is a top predator that kills mammal predators (e.g. pine marten, stoat, least weasel and red squirrel), and preys upon and also interferes with bird predators (e.g. sparrowhawk, ural owl) of three-toed woodpecker, great spotted woodpecker and pygmy owl and may thus lower the overall predation pressure targeted at these three hole-nesting species. Although also itself a predator of three-toed woodpecker, great spotted woodpecker and pygmy owl, goshawk prefers other forest bird species (e.g. forest grouse, corvids, woodpigeon and thrushes) and mammals as prey and may thus offer a possibility of enemy-free space for these three species around its nest site. Goshawk nest sites are often in structurally diverse mature spruce-dominated or mixed forests that allow three-toed woodpecker, great spotted woodpecker and pygmy owl to coexist even though three-toed woodpeckers or their nests are interfered with or occasionally preyed upon by the two other species.

spatial and temporal scales used in analyses (cf. Wiens 1989).

In this study we focus on the predator–prey relation in a complex environment with a hierarchically structured predator assemblage and a guild of alternative prey species that interfere with each other and compete for suitable nest sites (Fig. 1a). We are especially interested in the possible positive effects of a top predator on the densities and breeding success of its prey species. Direct effects of predation by decreasing numbers of prey populations are often thought to modify competitive interactions simultaneously and thus may also facilitate coexistence of prey species by reducing competition (e.g. Paine 1966, Harper 1969, Connell 1971, Roughgarden & Feldman 1975, Grubb 1977, Huston 1979, Crowley 1981), although both in theoretical and empirical studies a variety of outcomes have been noticed for a long time (cf. Holt 1984, Sih *et al.* 1985). In a situation with shared predation, interactions of prey species resemble those of competition of species (Williamson 1957; "apparent competition": Holt 1977, 1984); we can think that prey species compete for enemy-free space (Jeffries & Lawton 1984, 1985). The respective competitive capabilities of different prey species depend thus also on their vulnerability to predators.

A top predator may have indirect effects by decreasing numbers of other predator species. The result can be a net loss of predation pressure targeted at prey species as compared with the situation when the respective top predator is absent, especially if a certain prey species or species group is already not preferred by the top predator (Fig. 1a). However, if there are several ecologically similar, above-mentioned non-favoured or occasional prey species, the loss of total predation pressure caused by the top predator may lead to increased competition between these prey species. The coexistence of prey species can then be promoted by the spatial, structural heterogeneity of the environment, and if prey species cannot coexist locally they still may coexist at larger, regional scales with species occupying different sites or same sites at different times (Danielsson 1991, McLaughlin & Roughgarden 1993, Holt 1997, Hanski 1999, Shurin *et al.* 2004).

If both the top predator and occasional prey species are mobile and territorial (as birds in this study) the prey species can be thought to optimise location of their territory or nest site in relation to the nest site of the top predator. Assuming that a territorial top predator usually kills and interferes with individuals of other predator species most efficiently in close surroundings of its nest site with a decreasing predation and interference rate as the distance from the nest increases, an occasional prey species would minimize the overall predation risk by selecting the nest site in close vicinity of the nest site of the top predator. In addition, the overall predation rates by the top predator can be low in nearest surroundings of the nest site and hence also lower the total predation risk (cf. Norrdahl *et al.* 1995).

In practice the nest site selection of prey species is influenced by several interconnected environmental factors that should be measured or kept constant before recognition of the effects of predation is possible. There are several studies of the effects of predation on prey populations in avian communities. These include various experiments with removal of predators, but with diverse results and alternative explanatory processes are often incomprehensively taken into account (*see* reviews in Wiens 1989, Newton 1993, 1998). Interspecific interactions including competition and predation have been observed among bird predators, i.e. raptors and owls (Uttendörfer 1952, Mikkola 1983, Kostrzewa 1991, Newton 1991, Solonen 1993, Hakkarainen & Korpimäki 1996, Serrano 2000, Hakkarainen *et al.* 2004a). These interactions can modify spatial patterning and occupancy of territories or nest sites of various species of owls and raptors in forest landscapes with largest species generally dominating smaller ones (e.g. Uttendörfer 1952, Lack 1971, Newton 1979, Janes 1985, Korpimäki 1987, Fiuczynski 1991, Solonen 1993, Hakkarainen & Korpimäki 1996, Fielding *et al.* 2003, Sergio *et al.* 2003, 2004, Hakkarainen *et al.* 2004a, Vrezec & Tome 2004). Bird predators may, in turn, directly or indirectly influence abundance and dispersion of their prey species. Density of potential prey species have been observed to decrease with closer distance from predators' nest sites (Eng & Gullion 1962, Meese & Fuller 1987, Sodhi *et al.* 1989, Suhonen *et al.* 1994, Norrdahl & Korpimäki 1998) but documented cases of lowered nesting success near predators' nest sites are rare (cf. Newton 1993, but *see* Eng & Guillon 1978, Geer 1978). Predation may also induce changes in spatial dispersion patterns of breeding prey species (Anderson & Wiklund 1978, Forsman *et al.* 1998, 2001, Forsman & Mönkkönen 2001). There are also some studies where bird species were positively associated with predators' nest sites and with increasing nest survival (e.g. Wiklund 1982, Paine *et al.* 1990, Ueta 1994, Norrdahl *et al.* 1995).

In this study, we investigate the effects of a top predator, the northern goshawk *Accipiter gentilis* (hereafter goshawk), on a coexisting predator–prey community and its possible positive effects on a hole-nesting bird species guild comprising occasional prey (the pygmy owl *Glaucidium passerinum*, the great spotted woodpecker *Dendrocopos major* and the three-toed woodpecker *Picoides tridactylus*) in mature boreal forest which is a structurally complex environment (Fig. 1b; for a closer introduction to the study species, *see* next chapter). Goshawk is known to influence predator numbers or their territory distribution by predation or competition (e.g. Widén 1987, Tornberg 1997, Krüger 2002a, 2002b, Petty *et al.* 2003a, 2003b, Hakkarainen *et al.* 2004a). Thus it may also lower predation pressure on potentially important bird and mammalian predators (e.g. the sparrowhawk *Accipiter nisus*, ural owl *Strix uralensis*, tawny owl *S. aluco*, pine marten *Martes martes*, stoat *Mustela erminea*, least weasel *M. nivalis*, red squirrel *Sciurus vulgaris*) of the above-mentioned hole-nesting species.

The three hole-nesting species interfere with each other and may compete for suitable nest holes and nest trees, but evidence of predation (by pygmy owl on the two woodpecker species during the breeding time and by great spotted woodpecker on three-toed woodpecker nests) is rare (Glutz & Bauer 1980, Cramp 1985, Winkler & Christie 2002; also T. Pakkala *et al*. unpubl. data, M. Lagerström and J. Miettinen pers. comm.). Special attention in this study is paid to three-toed woodpecker that is a specialist species which prefers mature forests with dead and dying trees and has been observed to be associated with goshawk nest sites (Linkola 1967). The possible positive effect of goshawk on territory quality of three-toed woodpecker could thus be especially important for this species, because occupied goshawk nest sites can then help it to maintain viable populations in fragmented, managed forest landscapes.

We test the following hypotheses:

1. The forest species (sparrowhawk, ural owl, pygmy owl, great spotted woodpecker and three-toed woodpecker) share similar overall habitat preferences and in particular favour the neighbourhood of goshawk nest sites.
2. Goshawk has a negative effect on subdominant predator species (sparrowhawk and ural owl) and a positive effect on occasional, hole-nesting prey species (pygmy owl, great spotted woodpecker and three-toed woodpecker) especially in close surroundings of its nest sites.
3. Interspecific interactions, especially interference competition among hole-nesting bird species influence their spatial dynamics.
4. Annual changes in density and territory quality of a forest bird species depend on interspecific interactions.

Material and methods

Study species

Goshawk is a holarctic, mostly resident hawk that occupies a variety of forest habitats (cf. Cramp 1985, Thiollay 1994), but it prefers to nest in old forests (e.g. Newton 1979, Hayward & Escano 1989, Selås 1997a, Penteriani & Faivre 2001, Penteriani 2002, Hakkarainen *et al*. 2004b), and open forest stands with large trees as feeding grounds (e.g. Widén 1989, 1997, Beier & Drennan 1997, Penteriani *et al*. 2001). Goshawk has been observed to be vulnerable to structural changes of mature forest stands caused by modern silvicultural practices. Forest management has an effect both on the availability of nest sites and suitable prey, especially in northern areas of its distribution (Crocker-Bedford 1990, Tornberg & Sulkava 1991, Widén 1997), but in some areas, especially in western and central Europe, it has become more adapted to human influence on the landscape (Bijlsma & Sulkava 1997). The diet of goshawk consists of various species of birds like forest grouse, corvids, ducks, woodpigeon *Columba palumbus*, and to a lesser extent of smaller birds, and of mammals like the red squirrel, mountain hare *Lepus timidus*, and voles (e.g. Höglund 1964, Sulkava 1964a, Opdam *et al*. 1977, Widén 1987). Forest grouse are the most important and preferred prey of goshawk. Prey selection depends on season and availability of prey species (Lindén & Wikman 1983, Tornberg & Sulkava 1990, 1991, Tornberg 1997).

Sparrowhawk is a Palearctic, widespread and abundant small hawk that inhabits various forest habitats of different ages from continuous forest landscapes to patchy cultured landscapes. Its northern populations are migratory, but in other areas in Europe it is mostly resident (Cramp 1985, Newton 1976, 1986, Selås 1997b, Selås & Rafoss 1999). Small- and medium-sized birds comprise usually more than 95% of its diet (e.g. Opdam 1978, Newton & Marquiss 1982, Selås 1993, Götmark & Post 1996, Solonen 1997, Rytkönen *et al*. 1998), but also small mammals may be caught, especially in peak years of voles in northern Europe (Sulkava 1964b, Selås 1993).

Ural owl is a medium-sized owl with a wide Palearctic distribution, preferring mixed coniferous dominated forests of the northern taiga zone. It nests in cavities of large trees or stumps, in nest-boxes and in old stick nests, especially those of raptors (*Accipiter*, *Buteo*, *Pernis*) (Mikkola 1983, Cramp 1985, Pietiäinen & Saurola 1997). Ural owl is a food generalist, and it preys upon a variety of vertebrate species when the abundance of preferred prey, *Microtus* voles, decreases (e.g. Lundberg 1981, Korpimäki & Sulkava 1987). Pairs of ural owls are resident and territorial year-round (e.g. Lundberg 1979, Saurola 1987). The proportion of breeding pairs varies in accordance to fluctuating vole numbers (Pietiäinen 1989, Saurola 1989).

Pygmy owl, the smallest of the Palearctic owls, inhabits boreal coniferous and mixed coniferous forests from Norway to the Sakhalin Peninsula with isolated, mostly mountain populations in central Europe (Dementev & Gladkov 1966, Glutz & Bauer 1980, Mikkola 1983, Cramp 1985). Pygmy owl lives in a variety of forest habitats, but favors mature forests (Mikkola 1983, Cramp 1985, Sonerud 1991, Lagerström & Syrjänen 1995, Svensson *et al.* 1995, Strøm & Sonerud 2001) that are structurally diverse and contain a mixture of different forest types (Scherzinger 1974, Gluzt & Bauer 1980, Solheim 1984a, Lagerström & Syrjänen 1995). It is a hole and cavity nester that mainly uses holes excavated by medium-sized woodpeckers, especially great spotted and three-toed woodpeckers (Mikkola 1983, Cramp 1985, Lagerström & Syrjänen 1995, Wiesner 2001). Cavities and holes are also used as roosting places or for catching surplus prey in autumn and winter (e.g. Mikkola 1983, Solheim 1984b, Cramp 1985, Lagerström & Syrjänen 1995). The diet of pygmy owl consists of a variety of birds, mostly small passerines and small mammals, especially voles and shrews (Kellomäki 1977, Mikkola 1983, Solheim 1984b, Cramp 1985) with a seasonal change with proportionally more mammals as prey in summer and autumn and more avian prey in winter (e.g. Mikkola 1970, Kellomäki 1977, Solheim 1984b, Ekman 1986, Suhonen 1993, Kullberg 1995, Lageström & Syrjänen 1995).

Great spotted woodpecker is distributed from the northern taiga through boreal and temperate to Mediterranean and alpine forest zones. It is in many parts of the range by far the commonest woodpecker (Dementev & Gladkov 1966, Winkler & Christie 2002, Michalek & Miettinen 2003). It inhabits all types of forest, also those in cultured landscapes (Pynnönen 1939, Durango 1945, Haapanen 1965, Glutz & Bauer 1980, Cramp 1985, Hansson 1992, Glue & Boswell 1994, Mikusiński & Angelstam 1997), but the densities are generally highest in mature unmanaged forests (e.g. Nilsson 1979, Scherzinger 1982, 1990, Wesołowski & Tomiałojć 1986, Angelstam 1990, Spitznagel 1990, Angelstam & Mikusiński 1994, Virkkala *et al.* 1994, Rolstad *et al.* 1995). The species is a hole-nester that uses alive or dead trees of different species and occasionally also nest-boxes (Pynnönen 1939, Dementev & Gladkov 1966, Blume 1977, Aulén 1988, Hågvar *et al.* 1990, Hansson 1992, Glue & Boswell 1994, Smith 1997, Mazgajski 1998, Kosiński & Winiecki 2004). It also has a diverse diet consisting mainly of various insects, in summer also of bird eggs and nestlings with a clear seasonal shift in more variable northern habitats where tree seeds, especially those of coniferous trees, pine (*Pinus* sp.) and spruce (*Picea* sp.), are important in winter (Pynnönen 1939, 1943, Glutz & Bauer 1980, Cramp 1985, Rolstad *et al.* 1995, Winkler & Christie 2002).

Three-toed woodpecker has a wide northern range of distribution that corresponds largely with that of spruce (*Picea* sp.) and larch (*Larix* sp.). It prefers mature boreal and mixed conifer forests (Dementev & Gladkov 1966, Winkler & Christie 2002), favouring especially forests with a good proportion of recently dead and dying trees, also with fallen logs (Hogstad 1970, Hess 1983, Pechacek 1995, 2004, Murphy & Lehnhausen 1998, Ruge *et al.* 1999, Imbeau & Desrochers 2002a, 2002b, Bütler *et al.* 2004). It also inhabits areas recently disturbed by fire, wind, snow, or other agents that increase the amount of suitable substrate for its insect prey (e.g. Blackford 1955, Yeager 1955, Knight 1958, Koplin 1969, Virkkala *et al.* 1991, Sorvari 1994). Its diet consists predominantly of insects, mainly conifer bark beetles (Coleoptera, Scolytidae) or longhorn beetle larvae (Coleoptera, Cerambycidae) (cf. Koplin 1972, Pechacek & Kristín 1993, 1996, Murphy & Lehnhausen 1998, Fayt 1999, 2003). Three-toed woodpecker is a hole-nester also preferring dead or dying trees for nesting (e.g. Linkola 1967, Ruge 1974, Hågvar *et al.* 1990, Stenberg 1996, Pechacek 2001, Pechacek & d'Oleire-Oltmanns 2004). Because of its close connection to forest habitats with natural dynamics and disturbances, three-toed woodpecker has suffered from intensive forest management practices (Goggans *et al.* 1989, Amcoff & Eriksson 1996, Dorka 1996, Mikusiński & Angelstam 1997; Bütler *et al.* 2004), and declines of breeding populations have been reported especially from northern Europe (Finland: Väisänen *et al.*

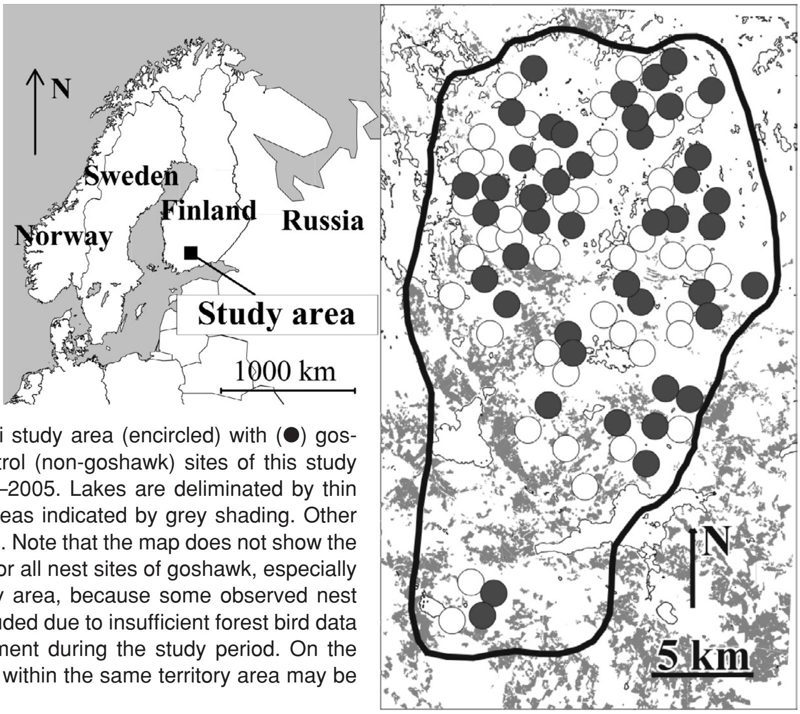

Fig. 2. Location of the Lammi study area (encircled) with (●) goshawk nest sites and (○) control (non-goshawk) sites of this study during the study period 1987–2005. Lakes are deliminated by thin black lines and agricultural areas indicated by grey shading. Other areas consist mostly of forests. Note that the map does not show the complete territory distribution or all nest sites of goshawk, especially in southern parts of the study area, because some observed nest sites and territories were excluded due to insufficient forest bird data or changes in forest environment during the study period. On the other hand, several nest sites within the same territory area may be presented.

1998; Sweden: Svensson *et al.* 1999) where long-term monitoring data are available.

Study area

The study area is located in the municipalities of Lammi, Padasjoki and Asikkala in southern Finland (61°15´N, 25°00´E; Fig. 2) with a total area of 470 km^2, of which 80% consists of forests. Spruce-dominated coniferous or mixed mature stands are the most common types of forest. The landscape is a mixture of forests of different ages, agricultural areas, lakes and scattered human settlements with a gradient from a southern agricultural-forest mosaic to northern forest-dominated areas.

Bird census methods

Territory mapping of all species

The study area was covered with breeding bird censuses in 1987–2005. Censuses were made using a modification of territory mapping method developed by the author (TP). This method is based on the method developed by Enemar (1959), on recommendations for an international standard for a mapping method (Anon. 1969), and on improvements of the method suggested by Tomiałojć (1980). Following extensive field tests of the efficiency and reliability of the territory mapping method in the Lammi study area in 1979–1986 (Tiainen *et al.* 1980, T. Pakkala & J. Tiainen unpubl. data), the method with 4–5 visits was applied by TP to census relatively large areas in forest environments. In this version of the territory mapping method, used also in this study, the key elements area: (1) proper timing of field visits during spring and summer in order to map efficiently territories of phenologically different groups of forest bird species; (2) optimising the field routes and speed of performing the census by e.g. the singing activity and landscape structure; (3) paying special attention to getting simultaneous records of several neighbouring territories of same species, i.e. "networks" of territories over large areas; (4) collecting extra field data of those species that are difficult to detect when needed; (5) standardizing the overall field effort and interpretation procedures of the results to ensure better comparability between different censuses (e.g. in the case of censuses in the Lammi study area all censuses and interpretations were made by the author TP). On average 30–35 field hours were used to map all the territories of breeding birds of an area of 1 km^2 in forest environment during the period between 15 April and 15 July.

Territory mapping excluding the most abundant species

Some of the censuses included in this study were made using the territory mapping method described above but with the exception that all the territories of 4–10 (depending on the forest type) most abundant forest bird species (e.g. chaffinch *Fringilla coelebs*, willow warbler *Phylloscopus trochilus*, robin *Erithacus rubecula*, siskin *Carduelis spinus*) were not mapped. Instead the presence/absence of these species was recorded usually in a 200 × 200 m grid. Typically in forest bird communities in southern Finland, chaffinch and willow warbler are 30% of the total number of pairs (cf. Solonen 1996), and in Lammi study area they are among the 4–10 most abundant species, usually 60%–75% (T. Pakkala & J. Tiainen unpubl. data; *see* also Pakkala & Väisänen 2000). The time saved by excluding these species from censuses can be used to increase the area of territory mapping, and on average only 20–25 hours/km^2 is needed to map breeding bird species of all territories with the similar effort as with the method described in the previous chapter. A modified version of the mapping method described above has been taken into use to census breeding birds in 1 × 1 km squares in Finland since 2000 (the summer bird atlas of Finland; Pakkala & Väisänen 2000, 2001, Pakkala *et al.* 2001).

Territory mapping of selected bird species and additional information

A relatively large amount of field effort was annually targeted at mapping territories of some selected bird species or groups of species, e.g. capercaillie *Tetrao urogallus* (Pakkala *et al.* 2003), woodpeckers (Pakkala *et al.* 2002), raptors and owls, and some passerine bird species, especially those associated with mature forests. These censuses were done using the territory mapping method that was described in the previous chapter, but with more rapid field visits; on average totally 5–7 hours were spent per 1 km^2 of forest area. In addition, large areas were annually visited before (in March and early April) and after (in July) the standard mapping period in order to check the presence of territories of the species and groups of species mentioned above, or to collect other information of, e.g., nest sites, nests, and breeding success.

Bird data

All data on breeding birds in this study were collected by the author TP and they include combined data from a field effort of about 16 000 hours in 1987–2005. These data can be classified into the following three categories representing data collected using census methods described above, respectively: (1) territory mapping of all bird species; total field effort: 4000 hours, total area covered: 130 km^2; (2) territory mapping excluding the most abundant bird species; total field effort: 7000 hours, total area covered: 300 km^2; (3) territory mapping of selected bird species and additional information; total field effort: 5000 hours, total cover of mapping 800 km^2 with overlapping areas in different years in these categories. All parts of the study area of 470 km^2 were covered with censuses, but as they were targeted to study forest birds and especially the species typically associated with mature forests, the northern parts of the study area were more thoroughly studied than the cultured landscapes of the southern parts.

Study design

Territories and nest sites of goshawk were searched and mapped with the methods described above. The total number of goshawk territories that were completely or partially within the study area was estimated to vary annually from 15 to 20 and the local population size seemed to be relatively stable during the study period. The census methods and effort were, however, insufficient to determine accurate numbers and borders of territories, especially in the southern parts of the study area. In all, 56 goshawk nest sites were detected in 1987–2005. Nest sites located > 1 km apart were classified as separate sites even if they were within the same goshawk territory. In many nest sites there were also groups of alternative nests built close to each other. Of all observed goshawk nest sites there were totally 44 nest sites with forest bird data covering at least a period of four years, and without any major changes in the forest environment (*see* Forest and landscape data) during the respective period, and with forest bird data either with goshawk and after goshawk occupancy (23 cases) or before and with goshawk occupancy (21 cases). These sites were taken into the analyses of this study. Because the nest site data cover relatively evenly the total study period and include comparisons in opposite time directions, possible errors caused by systematic trends in environment and forest bird densities are either smoothed out or can be estimated from different types of before–after comparisons.

From the forest bird data, the annual locations and numbers of nest sites and territories of three-toed woodpecker and four forest species — sparrowhawk, ural owl, pygmy owl, and great spotted woodpecker — considered important for the three-toed woodpecker were registered within 300, 500 and 1000 m radii from each goshawk nest site. Tawny owl was extremely rare around goshawk nest sites and it was thus excluded from the analyses of this study. All three-toed woodpecker territories in the surroundings of goshawk nests were in each census year classified as territories with nestlings detected or other territories. The distance of the nearest nest site of both woodpecker species from the goshawk nest site was also measured in each census year. If a nest was not found in the nearest woodpecker territory, the distance of the respective estimated territory centre from the goshawk nest site was used. If alternative goshawk nest sites, usually located < 500 m apart from each other, were used within the same goshawk territory, the numbers of forest bird territories were calculated by the location of the respective occupied nest site. The bird data were restricted to cover periods without any major changes in forest environment of the surroundings of each nest site, mostly caused by forestry practices that could affect numbers and territory locations of the studied bird species. A threshold value of 10% of the total land area of clear-cuts during the study period was used in each nest site and for each radius mentioned above (for forest environment data *see* the next chapter). Annual densities of forest bird species were calculated as the number of territories per area of forest land (including spruce swamps and pine bogs with trees) with the age of stand > 20 years for all species except for ural owl where the total area of forest land was used.

Goshawk nest sites were compared with control sites situated at the southwest corner of the nearest 1 × 1 km grid unit of the Finnish KKJ 3 Zone and located 2 km southwest of the above-mentioned nest site and at least 1 km from any other goshawk or control site, and the proportion of forest land on each study scale (300, 500 and 1000 m, respectively) had to be > 50%. If these conditions were not met, the location of a control site was moved the minimum distance either clockwise or counterclockwise along the 2 km distance radius in order to find the first suitable corresponding southwest corner to fulfill the conditions. The criteria for control sites were thus made rigorous enough to ensure comparability with goshawk and (non-goshawk) control sites. Pairwise patterning also guaranteed general similarity in cover of the study area (*see* Fig. 2). The forest bird data of the control sites were gathered using the same methods and criteria as used at the goshawk sites, except that each control site is represented by a 3-year dataset, and that territory mapping of great spotted woodpecker was done only on study scales of 300 and 500 m. In addition, potential spatial autocorrelations (e.g. Sokal *et al.* 1998) of the densities of study species were checked for both goshawk nest sites and control sites and these data sets were found separately and pooled to be free of spatially autocorrelated density patterns at the scales of this study.

Forest and landscape data

Based on land-use and forestry data and digital topographic maps made by the National Land Survey of Finland, aerial photographs of and extensive field information on the study area, habitat and landscape area values were calculated for the areas around goshawk nest and control sites. The following land classes and their areas were computed within radii of 300, 500 and 1000 m: water, agricultural land, open mires, young forests (< 20 years old, including clearcuts) and middle-aged and old forests (> 20 years old; including forests both on mineral and on peat soil). The amount of distinctive dry edges was also measured at each site by calculating the logarithmic ratio of the total areas of young and older forests. Changes in land use and forestry during the study period were also estimated by these data. The land-use and forestry data were selected to match the bird census years of the particular goshawk nest and control sites.

Territory quality of three-toed woodpecker

We used the proportion of years with nestlings detected to all census years in a territory as a measure of territory quality for three-toed woodpecker. This definition of quality is straightforward, and allows comparisons between different sites because of standard census efficiency. Moreover it summarises the overall breeding success of the territory.

Results

General habitat preferences of the studied forest bird species

Dependencies between abundances of five forest bird species were evaluated by calculating pairwise Spearman's rank correlation coefficients of mean densities from the pooled data of the periods at sites where goshawk was observed nesting during the study period but was not present ($N = 44$) and at control sites without nesting goshawk ($N = 44$) (Table 1).

Most of the pairwise correlations between densities of these five forest species were significantly ($p < 0.05$) positive showing the common habitat preferences of the species (Table 1). The exceptions were the correlations between ural owl and all other species at the smallest 300 m scale (sparrowhawk also at other scales; pygmy owl also at 500 m scale; great spotted woodpecker also at 1000 m scale) and the correlation between sparrowhawk and great spotted woodpecker at 300 m scale that were insignificant. Positive and mostly highly significant ($p < 0.001$) correlations were detected between the densities of the two woodpecker species and pygmy owl at all spatial scales. If the strength of the pairwise correlations are compared using the respective adjusted p with the Bonferroni

Table 1. Pairwise correlations of mean densities of study species at all sites (pooled data: $N = 88$, df = 86) where goshawk had been observed nesting but was not present ($N = 44$), and at control sites where goshawk was not observed nesting ($N = 44$). Data on the great spotted woodpecker are lacking at the control sites at 1000 m scale and the respective correlation coefficients were calculated from the observed goshawk sites only (df = 42). P of each pairwise test are shown. The adjusted p with the Bonferroni correction = 0.0017 ($\alpha = 0.05$; $n = 30$) and the significant pairwise correlations in this framework are set in boldface.

Species	Sparrowhawk	Ural owl	Pygmy owl	Great spotted woodpecker
Ural owl	$r_{300} = -0.093$; $p = 0.389$ $r_{500} = 0.108$; $p = 0.317$ $r_{1000} = 0.113$; $p = 0.295$			
Pygmy owl	$r_{300} = 0.221$; $p = 0.039$ $r_{500} = \mathbf{0.432}$; $p < \mathbf{0.001}$ $r_{1000} = \mathbf{0.359}$; $p < \mathbf{0.001}$	$r_{300} = 0.111$; $p = 0.305$ $r_{500} = 0.273$; $p = 0.01$ $r_{1000} = \mathbf{0.441}$; $p < \mathbf{0.001}$		
Great spotted woodpecker	$r_{300} = 0.257$; $p = 0.016$ $r_{500} = 0.297$; $p = 0.005$ $r_{1000} = 0.290$; $p = 0.056$	$r_{300} = 0.209$; $p = 0.051$ $r_{500} = 0.329$; $p = 0.002$ $r_{1000} = 0.133$; $p = 0.388$	$r_{300} = 0.293$; $p = 0.006$ $r_{500} = \mathbf{0.498}$; $p < \mathbf{0.001}$ $r_{1000} = 0.422$; $p = 0.004$	
Three-toed woodpecker	$r_{300} = 0.274$; $p = 0.01$ $r_{500} = \mathbf{0.372}$; $p < \mathbf{0.001}$ $r_{1000} = 0.263$; $p = 0.013$	$r_{300} = 0.154$; $p = 0.153$ $r_{500} = \mathbf{0.378}$; $p < \mathbf{0.001}$ $r_{1000} = \mathbf{0.496}$; $p < \mathbf{0.001}$	$r_{300} = \mathbf{0.588}$; $p < \mathbf{0.001}$ $r_{500} = \mathbf{0.668}$; $p < \mathbf{0.001}$ $r_{1000} = \mathbf{0.637}$; $p < \mathbf{0.001}$	$r_{300} = 0.306$; $p = 0.004$ $r_{500} = \mathbf{0.616}$; $p \mathbf{= 0.001}$ $r_{1000} = \mathbf{0.595}$; $p < \mathbf{0.001}$

correction (p = 0.0017, α = 0.05; the number of multiple comparisons = 30) there are still 12 significant, positive correlations out of 30 (Table 1). It is notable that most correlations between three-toed woodpecker and other species are significant, thus they indicate that areas with three-toed woodpecker territories are often favoured by the other four forest bird species.

We also compared the mean densities of the five forest bird species between the observed goshawk sites when goshawk was not nesting (N = 44) and control sites without nesting goshawk (N = 44) (Table 2). These density differences give a general view on the associations of the species in regard to habitats preferred by goshawk. Differences in densities of each species were estimated with Mann-Whitney U-test at the three spatial scales (300, 500 and 1000 m; except great spotted woodpecker only at 300 and 500 m). In all comparisons, except in the cases of sparrowhawk at all scales and of ural owl at 300 and 500 m scales, the densities were significantly higher in goshawk sites (adjusted p with the Bonferroni correction < 0.0036, α = 0.05, the number of multiple comparisons = 14). Also other densities were higher in goshawk sites, although the differences were not statistically significant. Thus, in general the studied five forest species share the same common habitat preferences with goshawk.

Effects of goshawk on the occurrence and densities of the study species

Possible effects of goshawk on the occurrence and densities of the five forest species were studied by comparing the density changes both at sites where goshawk was observed nesting in the first period but was not any more nesting in the second period (N = 23), and at sites with no goshawk in the first period but with it nesting in the second period (N = 21) (Table 3). Differences of these before and after densities of each species were evaluated with Wilcoxon signed rank tests at the three spatial scales of 300, 500 and 1000 m.

In both studied cases there were dramatic differences in occurrences and densities of the spe-

Table 2. Comparison of densities of study species between the observed goshawk nest sites when goshawk is not nesting (N = 44) and control sites with no observed goshawk nesting (N = 44). Data on the great spotted woodpecker are lacking at the control sites at 1000 m scale. The adjusted p with the Bonferroni correction = 0.0036 (α = 0.05; n = 14) and the significant differences in this framework are set in boldface.

Species	Density		U	P
	Goshawk areas with goshawk absent (N = 44)	Control (non-goshawk) areas (N = 44)		
Scale 300 m				
Sparrowhawk	0.64	0.52	880	0.47
Ural owl	0.60	0.08	787	0.13
Pygmy owl	**1.21**	**0.30**	**581**	**0.001**
Three-toed woodpecker	**1.61**	**0.12**	**362**	< **0.001**
Great spotted woodpecker	**5.67**	**3.60**	**493**	< **0.001**
Scale 500 m				
Sparrowhawk	0.77	0.49	662	0.01
Ural owl	0.41	0.13	692	0.02
Pygmy owl	**1.07**	**0.36**	**383**	< **0.001**
Three-toed woodpecker	**1.22**	**0.28**	**206**	< **0.001**
Great spotted woodpecker	**5.61**	**4.00**	**424**	< **0.001**
Scale 1000 m				
Sparrowhawk	0.38	0.32	815	0.20
Ural owl	**0.23**	**0.14**	**619**	**0.003**
Pygmy owl	0.54	0.38	644	0.007
Three-toed woodpecker	**0.62**	**0.26**	**315**	< **0.001**
Great spotted woodpecker	–	–	–	–

cies studied in relation to goshawk occupancy (Table 3). Only a few occasional territories of sparrowhawk and ural owl with goshawk present were detected at the 300 and 500 m scales, although both species were relatively common in goshawk sites before and after goshawk nesting. At 1000 m scale, sparrowhawk and ural owl coexisted with goshawk but their densities were then significantly ($p < 0.001$) lower as compared with their densities when goshawk was absent. The responses of these two predators were seen immediately in the next year after goshawk became absent when their densities increased significantly and continued to increase even during the second year after goshawk's absence (Fig. 3; paired t-test; sparrowhawk: AG1 *vs.* AF1; $t = 2.45$; df = 22; $p = 0.02$; AF1 *vs.* AF2; $t = 2.23$; df = 22; $p = 0.04$; ural owl: AG1 *vs.* AF1; $t = 2.78$; df = 22; $p = 0.01$; AF1 *vs.* AF2; $t = 2.97$; df = 22; $p = 0.007$). The reverse pattern was detected when goshawk occupied a place where it was previously absent: the densities of sparrowhawk and ural owl decreased rapidly and significantly (Fig. 3; paired t-test; sparrowhawk: BF1 *vs.* AG1; $t = -2.71$; df = 20; $p = 0.04$; AG1 *vs.* AG2; $t = -2.08$; df = 20; $p = 0.04$; ural owl: BF1 *vs.* AG1; $t = -5.15$; df = 20; $p < 0.001$). All other density differences between two successive years were insignificant ($p > 0.1$, adjusted p with the Bonferroni correction = 0.005; $\alpha = 0.05$; the number of multiple comparisons = 10 in both comparison sets above).

Pygmy owl and three-toed woodpecker had directly opposite responses to goshawk as com-

Table 3. The responses of study species to the disappearance (1 → 0) and appearance (0 → 1) of nesting goshawks. Comparison of differences in densities were made at sites where goshawk has been nesting in the first period but was not any more present in the second period ($N = 23$) and at sites with no goshawk in the first period but nesting in the second period ($N = 21$). The adjusted p with the Bonferroni correction = 0.0017 ($\alpha = 0.05$; $n = 30$) and the significant differences in this framework are set in boldface.

Species	Mean density when goshawk present	Mean change in density (and in %) goshawk 1 → 0 $N = 23$	Wlicoxon T	p	Mean density when goshawk absent	Mean change in density (and in %) goshawk 0 → 1 $N = 21$	Wlicoxon T	p
Scale 300 m								
Sparrowhawk	0.05	+0.63 (+1170%)	0	0.002	0.59	–**0.59** (–100%; no coexistence withgoshawk)	**0**	**0.001**
Ural owl	0.09	+0.83 (+870%)	0	0.008	0.25	–0.25 (–100%; no coexistence with goshawk)	0	0.25
Pygmy owl	1.90	–0.64 (–33.5%)	21	0.05	**1.15**	+**0.86** (+**75.1**%)	**2**	< **0.001**
Three-toed woodpecker	**2.69**	–**1.48** (–**55.1**%)	**0**	< **0.001**	**2.05**	+**1.05** (+**51.0**%)	**1**	< **0.001**
Great spotted woodpecker	6.23	–0.21 (–3.4%)	42	0.53	5.29	+0.08 (+1.5%)	76	0.70
Scale 500 m								
Sparrowhawk	**0.04**	+**0.76** (+**1930**%)	**0**	< **0.001**	**0.73**	–**0.68** (–**92.7**%)	**0**	< **0.001**
Ural owl	**0.03**	+**0.45** (+**1250**%)	**0**	**0.001**	0.32	–0.32 (–100%; no coexistence with goshawk)	0	0.004
Pygmy owl	1.16	–0.21 (–18.1%)	37	0.13	1.19	+0.11 (+9.2%)	8	0.19
Three-toed woodpecker	**1.55**	–**0.40** (–**25.8**%)	**0**	< **0.001**	1.30	+0.11 (+8.5%)	0	0.12
Great spotted woodpecker	5.73	–0.34 (–5.9%)	66	0.17	5.84	–0.23 (–4.1%)	69	0.49
Scale 1000 m								
Sparrowhawk	**0.24**	+**0.17** (+**71.0**%)	**1**	< **0.001**	**0.35**	–**0.13** (–**36.5**%)	**0**	< **0.001**
Ural owl	**0.09**	+**0.16** (+**186**%)	**0**	< **0.001**	**0.22**	–**0.19** (–**88.9**%)	**0**	< **0.001**
Pygmy owl	0.54	–0.06 (–11.1%)	12	0.03	0.47	+0.06 (+11.9%)	0	0.008
Three-toed woodpecker	0.71	–0.06 (–8.5%)	22	0.06	0.59	+0.02 (+2.8%)	17	0.33
Great spotted woodpecker	4.45	–0.08 (–1.8%)	90	0.59	4.17	+0.004 (+0.1%)	112	0.92

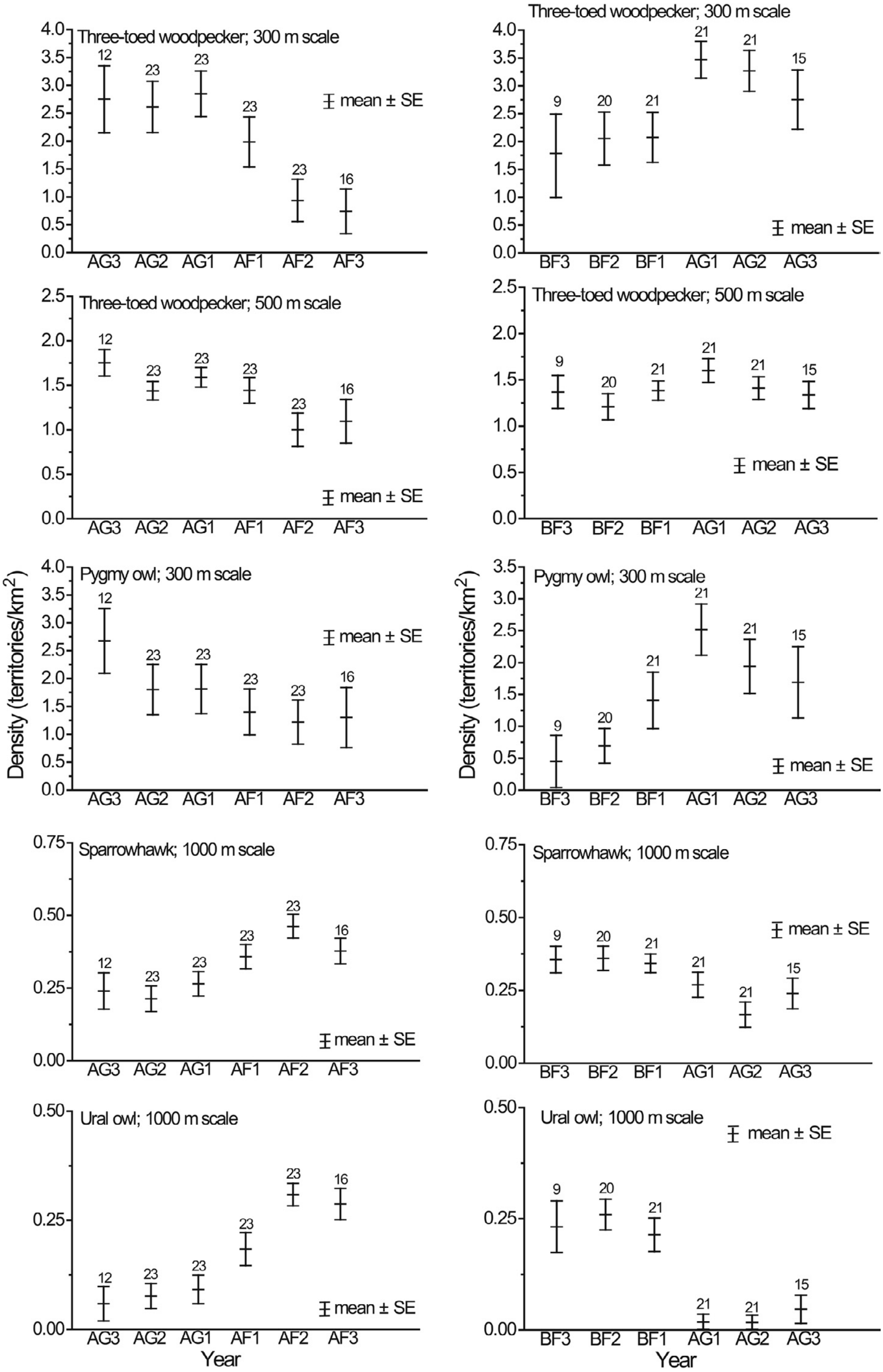

Fig. 3. Densities of three-toed woodpecker (300 and 500 m scales), pygmy owl (300 m), sparrowhawk (1000 m) and ural owl (1000 m) in surroundings of goshawk nest sites. Each panel shows a period of six years with either goshawk present in the first period (AG) and absent in the second (AF) (left-hand side panels); or goshawk absent in the first period (BF) and present in the second (AG) (right-hand side panels). Numbers above the standard error (SE) bars refer to the number of sites where data were available.

pared with those of ural owl and sparrowhawk: at 300 m scale the densities of both species were higher when goshawk was present, three of these density differences were significant ($p < 0.001$). At 500 m scale densities of these species were also higher when goshawk was present, but there were statistically significant ($p < 0.001$) density changes only in three-toed woodpecker with a decrease in density when goshawk disappeared. At 1000 m scale, the density change patterns of these two species were similar to the respective patterns in lower scales, but the density changes were relatively small. The responses of three-toed woodpecker were detected immediately in the next year after goshawk became absent when the densities decreased significantly and at the 300 m scale also one year after that (Fig. 3; paired t-test; 300 m: AG1 *vs*. AF1; $t = -2.45$; df = 22; $p = 0.02$; AF1 *vs*. AF2; $t = -1.94$; df = 22; $p = 0.07$). When goshawk occupied a previously unoccupied place a significant increase in densities of pygmy owl and three-toed woodpecker was observed directly in the first year of goshawk's occupancy (Fig. 3; paired t-test; pygmy owl; 300 m scale: BF1 *vs*. AG1; $t = 2.82$; df = 20; $p = 0.01$; three-toed woodpecker; 300 m scale: BF1 *vs*. AG1; $t = 3.14$; df = 20; $p = 0.005$; 500 m scale: BF1 *vs*. AG1; $t = -1.81$; df = 20; $p = 0.08$). All other density differences between two successive years were insignificant ($p > 0.1$, adjusted p with the Bonferroni correction = 0.0017; $\alpha = 0.05$; the number of multiple comparisons = 30 in the total data set above) except that of pygmy owl at 300 m scale where BF2 *vs*. BF1; $t = 2.04$; df = 19; $p = 0.06$.

Great spotted woodpecker was the only studied species with no significant or even nearly significant changes in the density in relation to goshawk occurrence.

Effects of goshawk on the location of nest sites of woodpeckers

The effects of occupied goshawk nest sites on the location of nest sites of the two studied woodpecker species were estimated by comparing the distances of the nearest nest site or territory centre of two woodpecker species from the goshawk nest site between two periods and at sites where goshawk had been nesting in the first period but was not any more present in the second period ($N = 23$), and at sites with no goshawk in the first period but with it nesting in the second period ($N = 21$). Differences between the before and after distances were evaluated with the paired t-test (df = 22 and 20, respectively) for the mean distances of the respective periods. In both cases, and for both species, their nest sites were situated significantly closer to the occupied goshawk nest sites than to unoccupied ones (Table 4).

We also studied the timing of the responses of the two woodpecker species to goshawk occupancy by comparing successive pairwise annual distances of nest sites to goshawk nest sites (Fig. 4). As in the case of annual density changes, periods of six years were used to guarantee adequate sample sizes. In total, 20 comparisons were made (2 species, 2 nest site types, 5 pairwise annual comparisons), the respective adjusted p with the Bonferroni correction equalled 0.001 ($\alpha = 0.05$). In cases where goshawk was present in the first period but the site was later unoccupied, the strongest response was seen immediately after the departure of goshawk; the mean distance of nest sites of three-toed woodpecker to the goshawk nest site increased by 111 m (the difference between years AG1 and AF1, *see* Fig. 4; paired t-test: $t = 4.71$; df = 22; $p < 0.001$) and that of

Table 4. The effect of goshawk on the location of woodpecker nest sites and territories. The adjusted p with the Bonferroni correction = 0.0125 ($\alpha = 0.05$; $N = 4$).

Woodpecker species	Mean distance (m) when goshawk present	Mean change in distance (m) goshawk 1 → 0 $N = 23$	t	p	Mean distance (m) when goshawk absent	Mean change in distance (m) goshawk 0 → 1 $N = 21$	t	p
Three-toed	216	+256	7.68	< 0.001	397	–108	–7.53	< 0.001
Great spotted	145	+50	7.99	< 0.001	211	–60	–8.75	< 0.001

great spotted woodpecker by 82 m ($t = 5.91$, df $= 22$, $p < 0.001$). The mean distance of three-toed woodpecker increased even after two years by 70 m (the difference between years AF1 and AF2; cf. Fig. 4; paired *t*-test: $t = 3.56$, df $= 22$, $p = 0.002$) but great spotted woodpecker did not show similar response, ($t = -0.36$, df $= 22$, $p = 0.73$). All other pairwise annual differences were insignificant.

In a situation where the site became occupied by goshawk the responses of both woodpecker species were seen immediately: the mean distance of nest sites of three-toed woodpecker to the goshawk nest site was 154 m shorter (the difference between years BF1 and AG1; *see* Fig. 4; paired *t*-test: $t = -4.97$, df $= 20$, $p < 0.001$) and that of great spotted woodpecker 70 m shorter ($t = -9.34$, df $= 20$, $p < 0.001$). All other pairwise annual distance differences were insignificant although a slight increasing trend of the nest site distances of three-toed woodpecker was seen during the goshawk occupancy.

Spatial dynamics and synchrony of the density changes of the hole-nesting bird species at goshawk nest sites

The association patterns of pygmy owl, three-toed woodpecker and great spotted woodpecker that form together a guild of hole-nesting forest bird species preferring similar types of mature forests were also generally similar in relation to goshawk presence although the responses of the great spotted woodpecker were weaker than those of the two other species. In spite of similar, clearly positive responses of both pygmy owl and three-toed woodpecker to goshawk, the responses to either disappearance or appearance of goshawk were not at all correlated in space. At 300 m scale, the correlation between density changes of pygmy owl and three-toed woodpecker after the disappearance of goshawk at 23 goshawk sites was $r_s = 0.03$ ($p = 0.88$, df $= 21$), and the respective correlation between the density changes of the same above species at 21 goshawk sites after appearance of goshawk was $r_s = -0.07$ ($p = 0.76$, df $= 19$). Also at 500 m and 1000 m scales, the correlations of density changes of the two species at various goshawk sites were small and insignificant ($0.01 < r_s < 0.23$; $p > 0.1$) in all cases.

In the previous analyses we used mean densities of the species during different study periods at different goshawk nest sites. To get a more accurate view of the patterns of synchrony between density changes we calculated pairwise correlations between all annual density changes of the three hole-nesting species studied. Pearson's correlation coefficient were calculated both at the 300 and 500 m scales and for both types of the goshawk nest sites (type 1: presence → absence; type 2: absence → presence of goshawk). In total, 12 comparisons were made, the respective adjusted p with the Bonferroni correction equalled 0.004 ($\alpha = 0.05$). At the 300 m scale, there was a negative and significant correlation between the annual density changes of the three-toed woodpecker and great spotted woodpecker at both types of goshawk nest sites (type 1: $r = -0.234$, $p = 0.012$, $n = 115$; type 2: $r = -0.383$, $p < 0.001$, $n = 105$). All other pairwise correlations between the annual density changes at 300 m and 500 m scale were small and insignificant (300 m: $-0.08 < r < 0.06$; 500 m: $0.04 < r < 0.16$; $p > 0.1$ in all cases) except that between pygmy owl and great spotted woodpecker at 300 m scale and at type 2 nest site with $r = -0.204$ and $p = 0.037$ indicating a negative association.

Interspecific relations and density changes of three-toed woodpecker

The goshawk seemed to influence the species composition and densities of the five forest bird species studied. Therefore, we also analysed changes in annual densities of three-toed woodpecker and the extent of their possible dependence on density changes of the other five studied species including goshawk. We used forward stepwise linear regression models with annual density changes ($Y - 1 \rightarrow Y$) of three-toed woodpecker as the dependent response-variable (Table 5). Models were constructed for all studied spatial scales (300, 500 and 1000 m) with the following independent variables:

- densities of sparrowhawk, ural owl, pygmy owl and great spotted woodpecker for the studied and larger scales in year Y,

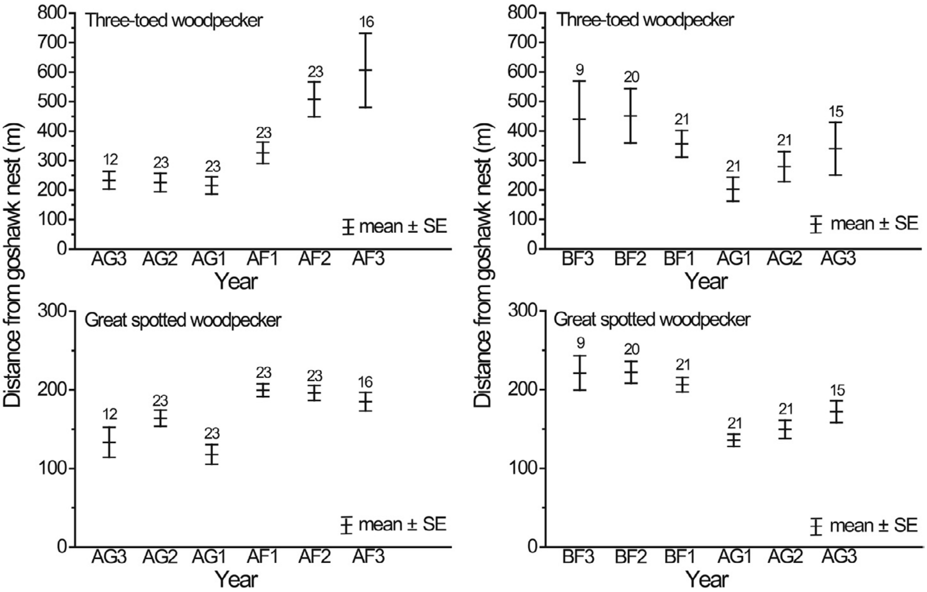

Fig. 4. Distances of the nearest nest sites of (**a**) three-toed woodpecker, and (**b**) great spotted woodpecker from the goshawk nest site. Each panel shows a period of six years with either goshawk present in the first period (AG) and absent in the second (AF) (left-hand side panels); or goshawk absent in the first period (BF) and present in the second (AG) (right-hand side panels). Numbers above the standard error (SE) bars refer to the number of sites where data was available.

- density changes of sparrowhawk, ural owl, pygmy owl and great spotted woodpecker for the studied and larger scales from year $Y - 1$ to Y,
- density of goshawk for 1000 m scale in year Y,
- density change of goshawk for 1000 m scale from year $Y - 1$ to Y,
- mean density of three-toed woodpecker of the study period for 500 m scale (for models of 300 m and 500 m scales), and
- mean density of three-toed woodpecker of the study period for 1000 m scale (for the model of 1000 m scale).

The mean density of three-toed woodpecker is expected to describe the general habitat suitability of the particular site for the species. Three data sets were used in the models: (1) pooled annual data from all goshawk sites; (2) annual data from goshawk sites where goshawk had been nesting in the first period but was not present in the second period and; (3) annual data from goshawk sites with no goshawk in the first period but with it nesting in the second period. At each scale two successive years with no three-toed woodpeckers present were excluded from the analyses. A criteria of $p < 0.05$ was used for the variables to enter the models.

At the 300 m scale with pooled data of all goshawk sites, the density change of great spotted woodpecker at the same scale was the strongest factor to influence annual density changes of three-toed woodpecker. The effect was negative and explained 11.4% of the total variation of annual change in three-toed woodpecker density. Another strong factor was the density change of goshawk (positive) with additional 6.1% of the total variation being explained by this factor. Thus, in all, 17.5% of total variation of annual change in three-toed woodpecker density was explained by these two above-mentioned factors that entered the stepwise regression model.

In cases where goshawk sites were divided into the two occupancy types described in previous chapters, the results were very similar with each other and also with the model with the pooled data: the most important factors were the density changes of great spotted woodpecker (negative), the density change of goshawk (positive), and the density change of sparrowhawk (at 300 m scale; negative). These two models explained 23.2% (with sites where goshawk disappeared) and 25.6% (with sites where goshawk appeared) of total variation of annual change in three-toed woodpecker density.

At 500 m and 1000 m scales it proved difficult to explain variation in three-toed woodpecker density with the selected factors. At 500 m scale with the pooled data the only significant factor that entered the model was the density of pygmy owl at the same scale with positive effect and explaining 2.2% of variation in annual change in three-toed woodpecker density. In models with different types of goshawk nest sites only the density of goshawk had a significant positive effect (with sites where goshawk disappeared; 3.7% of variation explained) and the density change of ural owl a significant positive effect (with sites where goshawk appeared; 10.3% of variation explained).

At 1000 m scale the only significant factor was the density change of goshawk with a positive effect (with sites where goshawk appeared; 4.7% of variation explained). Among other things, discussed more in the next section, one reason for low explanation power of the regression models at 500 m and 1000 m scales is probably the relative small amount of variation detected in three-toed woodpecker densities at

Table 5. Results of forward stepwise linear regression models with annual density changes ($Y - 1 \rightarrow Y$) of three-toed woodpecker as the dependent, response variable. At each scale two successive years with no three-toed woodpeckers present were excluded from the analyses. Only variables that entered the models (a criteria of $p < 0.05$ was used) are listed.

Scale and data set	Variables in the model	Coeff.	t	p	Cumulative % of variation explained
300 m: all goshawk sites ($N = 166$)					
	constant	–0.200	–1.07	0.29	
	density change of great spotted woodpecker at 300 m scale	–0.221	–3.19	0.002	11.4
	density change of goshawk at 1000 m scale	3.148	3.08	0.003	17.5
300 m: goshawk sites with goshawk presence→absence ($N = 80$)					
	constant	–1.001	–2.41	0.02	
	density change of great spotted woodpecker at 1000 m scale	–0.587	–2.74	0.008	11.2
	density change of goshawk at 1000 m scale	3.193	2.24	0.03	18.3
	density change of sparrowhawk at 300 m scale	–0.592	–2.19	0.03	23.2
300 m: goshawk sites with goshawk absence→presence ($N = 86$)					
	density change of great spotted woodpecker at 300 m scale	–0.31	–4.08	< 0.001	17.3
	density change of goshawk at 1000 m scale	4.41	3.04	0.003	25.6
500 m: all goshawk sites ($N = 204$)					
	constant	–0.257	–2.55	0.01	
	density of pygmy owl at 500 m scale	0.152	2.14	0.003	2.2
500 m: goshawk sites with goshawk presence→absence ($N = 108$)					
	constant	–0.30	–3.13	0.002	
	density of goshawk at 1000 m scale	0.850	2.31	0.02	3.7
	density of ural owl at 500 m scale	0.293	2.02	0.05	7.3
500 m: goshawk sites with goshawk absence→presence ($N = 96$)					
	constant	–0.015	–0.28	0.78	
	density change of ural owl at 500 m scale	–0.337	–3.29	0.001	10.3
1000 m: all goshawk sites ($N = 219$)					
	no significant variables				
1000 m: goshawk sites with goshawk presence→absence ($N = 115$)					
	no significant variables				
1000 m: goshawk sites with goshawk absence→presence ($N = 104$)					
	constant	–0.0036	–1.53	0.13	
	density change of goshawk at 1000 m scale	0.263	2.01	0.05	4.7

these scales. The relative variation of three-toed woodpecker annual density measured by variance-to-mean ratio was 13.2 at 300 m scale (N = 166), 6.9 at 500 m scale (N = 204), and only 1.9 at 1000 m scale (N = 219).

Species and landscape effects on territory quality of three-toed woodpecker

To study the effect of goshawk on the territory quality of three-toed woodpecker, we compared the dependence of proportion of observed territories of three-toed woodpecker with nestlings on the presence of goshawk. Territory quality was measured at three different distance classes: < 300 m, 300–500 m and 500–1000 m from centres of each goshawk nest site both at the presence and absence of nesting goshawks (Fig. 5). Differences of territory quality between the presence and absence of goshawk were evaluated using the Wilcoxon signed rank test within each distance class and those between distance classes at both the presence and absence of goshawk with the Kruskal-Wallis test. The proportion of three-toed woodpecker territories with nestlings was significantly higher in the nearest surroundings of the nest site when goshawk was present, still noticeably higher at the distance of 300–500 m, but no difference was detected at the distance of 500–1000 m (Wilcoxon signed rank test: < 300 m: $T_{40,30} = 25$, $p = 0.007$; 300–500 m: $T_{22,31} = 9$, $p = 0.06$; > 500 m: $T_{30,33} = 109$, $p = 0.83$) (Fig. 5). In the presence of goshawk, the proportion of three-toed woodpecker territories with nestlings differed significantly between distance classes (Kruskal-Wallis test: $H_2 = 15.64$, $p < 0.001$) and proportions between < 300 m and 300–500 m and < 300 m and 500–1000 m differed significantly from each other but the difference between 300–500 m and 500–1000 m was not significant (Dunn's non-parametric *a posteriori* test: $Q_{< 300\text{ m},\ 300\text{–}500\text{ m}} = 2.03$, $p < 0.05$; $Q_{< 300\text{ m},\ 500\text{–}1000\text{ m}} = 3.69$, $p < 0.001$; $Q_{300\text{–}500\text{ m},\ 500\text{–}1000\text{ m}} = 1.21$, $p > 0.10$). In the absence of goshawk no significant differences were detected between the distance classes (Kruskal-Wallis test: $H_2 = 1.37$, $p = 0.50$) although a slight decreasing pattern with distance was seen in the mean territory quality.

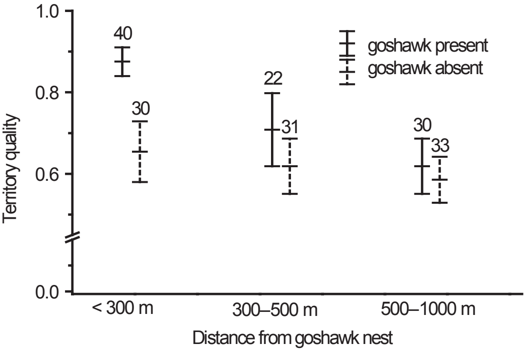

Fig. 5. Dependence of the territory quality of three-toed woodpecker on the presence of goshawk. Territory quality was measured as a proportion of territories with nestlings at three different distance classes: < 300 m, 300–500 m and 500–1000 m from centres of each goshawk nest site (n = 44; figure shows numbers of sites where three-toed woodpecker was present) both at the presence and absence of nesting goshawks.

We found previously that great spotted woodpecker had a negative effect on densities of three-toed woodpecker in surroundings of goshawk nest sites and that it may also affect the breeding success of three-toed woodpecker. In addition, the forest and landscape structures of the goshawk nest site, besides goshawk itself, may affect three-toed woodpecker, especially in relation to predation pressure linked to fragmentation. We, therefore, studied the relative importance of goshawk, great spotted woodpecker and landscape fragmentation in near surroundings (< 300 m) of goshawk nest sites using a complete logistic regression model with annual breeding success of three-toed woodpecker as the dependent variable (Table 6). As before, breeding success was measured as the proportion of observed territories of three-toed woodpecker with nestlings. To obtain standardised estimates, the presence of goshawk

Table 6. Effects of the presence of goshawk, great spotted woodpecker and landscape fragmentation on the breeding success of three-toed woodpecker in near surroundings (< 300 m) of the goshawk nest site.

Factor	Estimate	S.E.	*t* ratio	*p*
Constant	1.593	0.304	5.23	< 0.001
Goshawk	0.702	0.228	3.08	0.002
Great spotted woodpecker	–0.317	0.122	–2.60	0.009
Fragmentation	–2.570	2.563	–1.003	0.316

was handled as a categorical effect variable, and the effect of great spotted woodpecker was measured as the density difference between the density of the study year and the mean density at each nest site. The landscape fragmentation was calculated as the logarithmic ratio of the areas of young forests and older forests to estimate the total amount of distinctive dry forest edges. Presence of goshawk (positive) and relative density of great spotted woodpecker (negative) had significant effects on annual breeding success of three-toed woodpecker whereas the effect of landscape fragmentation was negative, but insignificant. The logistic model succeeded to classify correctly 73.3% of all cases ($n = 154$) (Table 6). However, we also found that although the mean breeding success of the three-toed woodpecker was only slightly and insignificantly associated with the landscape fragmentation ($r_s = –0.08$, $p > 0.10$, df = 38) in near surroundings (< 300 m) of goshawk nest sites; the amount of difference in mean breeding success of three-toed woodpecker between occupied and unoccupied goshawk nest sites, i.e. the effect of goshawk (cf. Fig. 5) was positively and significantly associated with the landscape fragmentation ($r_s = 0.395$, $p = 0.03$, df = 30). This indicates that the amount of distinctive edges contributes on breeding success of three-toed woodpecker, which may be connected to the general effect of mammalian predator pressure associated with forest fragmentation.

Discussion

Goshawk nest sites as potential “hot spots” of various forest bird species

We found that apart from sparrowhawk all other studied forest bird-species showed similar general habitat preferences that were especially clear among the three hole-nesting species. Densities of these species were also usually significantly higher at non-occupied goshawk nest sites as compared with that at other sites without observed goshawk nests. This indicates the structural diversity of goshawk nest sites and their surroundings that are important both for hole-nesting and predator birds. Results from several studies of goshawk’s nest site and territory selection point out both small-scale factors connected to both forest and habitat structures in near surroundings of goshawk’s nest site (e.g. Sulkava 1993, Penteriani & Faivré 2001, Penteriani *et al*. 2001, for a review *see* Penteriani 2002), and suitable forest and landscape structures for a successful goshawk territory (e.g. Kenward 1996, DeStefano & McCloskey 1997, Penteriani & Faivré 2001, Tornberg & Colpaert 2001, Hakkarainen *et al*. 2004b). To summarize, these results imply that goshawk nest sites and their surroundings — often mature forests with large trees surrounded by a structurally diverse forest-covered landscape — can be favourable sites for various different groups of forest birds and potentially even “hot-spots” of forest bird species associated with mature forests.

Top predator modifies predator community

We observed a clear negative association between the densities of goshawk and sparrowhawk, and goshawk and ural owl, respectively. These results are in concordance with the species interactions and spatial patterning of territories detected in hierarchical guilds of raptors and owls (*see* Introduction), and especially they were similar to negative associations found between goshawk and common buzzard *Buteo buteo* (Krüger 2002a, 2002b, Hakkarainen *et al*. 2004a), between goshawk and sparrowhawk (Newton 1986), and between goshawk and diurnal raptors and owls (kestrel *Falco tinnunculus* and short-eared owl *Asio flammeus*; Petty *et al*. 2003a). In our study, ural owl was found to use old stick nests of goshawk in five goshawk territories of the study area that emphasizes the possible competition of suitable nest sites and can be one reason for the significant negative association found between these two species. However, we do not have comprehensive data on the types of interactions between goshawk and sparrowhawk or goshawk and ural owl, but the results of long-term and large-scale territory mappings of forest birds within the study area indicate that goshawk rather has an effect on the locations of territories of sparrowhawk and ural owl than overall densities of these two species. The amount of preferred nesting habitats of many raptors and owls, namely mature forests (here: growing stock volume > 151 m^3 per ha) was relatively high (between 45%–65% of total land area) within our study area that promotes potential alternative nest sites for these species and thus may decrease possible population declines caused by interspecific competition.

Positive associations between top predator and occasional prey species

We found positive associations between goshawk occupancy and densities of pygmy owl and three-toed woodpecker. These associations were restricted to relatively close surroundings of goshawk nest sites and were not detected in the largest spatial scale (1 km radius from a goshawk nest site) where negative associations between both goshawk and sparrowhawk and goshawk and ural owl were still significant. As with sparrowhawk and ural owl, the density changes were mainly caused by changes in locations of nearest territories around goshawk nest sites, in this case towards goshawk's nest site. The shift in the location of territories was clear as the nearest nest sites of three-toed woodpecker and great spotted woodpecker were closer to the occupied goshawk nest site than to unoccupied ones. However, we did not detect any positive association between goshawk and the great spotted woodpecker densities. This result may be due to (1) generally high densities of this species as compared with that of pygmy owl and three-toed woodpecker (*see* Tables 2 and 3), i.e. in some years the forests are 'saturated' with great spotted woodpeckers and changes in territory locations are difficult; and (2) relatively large species density changes due to variation in seed crop of coniferous trees (*see* above in Study species) that are most likely independent of goshawk occupancy.

Linkola (1967) was the first one to present data indicating positive association between three-toed woodpecker nest sites and occupied goshawk nest sites, but neither he nor anyone after him was able to distinguish between habitat and interspecific effects. As we could control the habitat changes by considering only forest areas with small changes in the amount of suitable habitats during the study period, this is the first published study in which the positive role of goshawk itself is supported. Notably, the densities of pygmy owl and three-toed woodpecker were high around goshawk nest sites even when goshawk was absent, and thus we can interpret the positive density response of these two species to goshawk as a combined effect of suitable habitat and top predator.

Interspecific relations in the guild of hole-nesting birds

The previous conclusion is still not complete, because we have to take into account at least possible effects of interspecific relations within the guild of three-toed woodpecker, great spotted woodpecker and pygmy owl that have effects on densities of these species. Although the general density responses of pygmy owl and three-toed woodpecker to goshawk were similar, they were not correlated between different nest sites and annually within the same sites. The annual density changes of three-toed and great spotted woodpecker were significantly negatively correlated at the smallest scale, 300 m radius around goshawk nest sites. These results indicate negative associations between the three species, especially between the two woodpeckers. Observed negative associations are, however, not necessary linked to interspecific competition although it is also known that resource use of these species overlap, hence resource use by one species reduces its availability to another species (especially availability of suitable nest holes and nest trees) that make the strength of evidence for competition between species at least suggestive (e.g. Martin 1986, Wiens 1989).

A broadened view of territory quality: the three-toed woodpecker case

Three-toed woodpecker was the most thoroughly studied species of the three hole-nesting bird species within the study area, and our goal was to use this species as an example in estimating the relative role of interspecific relations in density and territory quality variations of forest bird species. Both the positive effect of goshawk and the negative effect of great spotted woodpecker were simultaneously significant factors in various models that tried to explain annual changes in density variation of three-toed woodpecker. Our results thus corroborate the importance of both the top predator and interference competition in territory occupancy of three-toed woodpecker, although the strongest effects were restricted to the closest vicinity of the goshawk nest sites. This result is, as discussed above, partly explained by the changes in location of territories whereas densities of three-toed woodpecker remained relatively stable within the larger areas around the goshawk nest sites.

Positive or negative associations between densities of different species do not, however, indicate that they are important for population development of the species in question. We therefore broadened our view to analyse the effects of interspecific relations on breeding success of three-toed woodpecker. Proportion of three-toed woodpecker territories with nestlings detected was used as a general measure of territory quality. A significant increase in territory quality was detected in close surroundings of the goshawk nest sites when we compared the situation between the occupied goshawk nest sites and the same nest sites unoccupied. If annual changes in territory quality were analyzed at the vicinity of goshawk nest sites, both the positive effect of goshawk and negative effect of great spotted woodpecker were significant.

If we consider the relation between goshawk and three-toed woodpecker only, our results resemble those of Wiklund (1982), Paine *et al.* (1990), Ueta (1994) and Norrdahl *et al.* (1995) where the occurrence and nest survival of bird species was positively associated with predators' nest sites. In these studies, the increased nest survival was linked to lowered predation rates by subdominant predators (especially corvids) preyed upon by the top predator. Mönkkönen *et al.* (2000) found that predation rates on artificial nests close (50–100 m) to goshawk nests tended to be lower than at medium (500–1000 m) or very long (2500 m) distances but distance to forest edges and forest type influenced how the distance from goshawk nests was related to predation rates.

It is obviously quite difficult for corvids to attack nests of hole-nesting woodpeckers although in central Europe crows *Corvus corone* and magpies *Pica pica* have been observed to try to catch great spotted woodpecker nestlings while those were waiting for food at nest entrances (cf. Michalek & Miettinen 2003). There are no observations in the Lammi study area of corvids even trying to rob nests of three-toed woodpecker (T. Pakkala *et al.* unpubl. data), thus the situation in our study was different from that in studies that deal with open-nesting species. On average, the nest losses of hole-nesting bird species are estimated to be substantially smaller than those of open-nesting ones (e.g. Nice 1957, Lack 1968, Nilsson 1984, Li & Martin 1990, Martin 1995, Wesołowski *et al.* 2002, but *see* Walankiewicz 2002), but published information about the causes of nest failures of woodpecker nests are few, and those of three-toed woodpecker are in practice missing (cf. Dementev & Gladkov 1966, Glutz & Bauer 1980, Cramp 1985, Winkler & Christie 2002). However, Pechacek (2006), considers nestling predation — probably by mammals — to have a significant effect on total nesting success of three-toed woodpecker. According to field observations from the Lammi study area (T. Pakkala *et al.* unpubl. data) and other studies in Finland (pygmy owl: Lagerström & Syrjänen 1995, M. Lagerström pers. comm.; great spotted woodpecker: J. Miettinen pers. comm.), mammalian predators — especially stoat and least weasel — seem be the most common nest predators of pygmy owl, three-toed woodpecker and great spotted woodpecker in boreal forests. In general small mustelids are considered the most important predators of hole-nesting species in temperate and boreal environments (cf. Sonerud 1985, Huhta *et al.* 2004). Other mammalian predators of three-toed woodpecker include pine marten which is too big to enter nesting cavities of three-toed woodpecker but can catch adult woodpeckers (Nyholm 1970, Pulliainen & Ollinmäki 1996), and red squirrel whose role in nest predation is poorly known (cf. Bayne & Hobson 1997). The above-mentioned mammalian predators belong to the diet of goshawk but with the exception of red squirrel they can be considered occasional prey (e.g. Lindén & Wikman 1987, Widén 1987, Tornberg 1997, Petty *et al.* 2003b).

We did not have data on abundances and density changes of mammalian predators around the goshawk nest sites, although several field observations of all of them were made at the sites. Thus, the true role of goshawk in decreasing predation of mammals remains speculative. On the other hand, the positive effect of goshawk as measured by the difference in territory quality of three-toed woodpecker was significantly increasing with increasing fragmentation of forest landscape in surroundings of the goshawk nest sites. As populations of various mammalian nest-predators are considered higher in fragmented forest landscapes (e.g. Storaas & Wegge 1987, Henttonen 1989, Andrén, 1994, 1995, Hansson 1994, Kurki *et al.* 1997, 1998, Chalfoun *et al.* 2002a, 2002b, Huhta *et al.* 2004), goshawk is at least a good candidate to decrease overall mammalian predation pressure on nests of woodpeckers and pygmy owl.

Of the birds of prey present around goshawk nest sites, adult woodpeckers are occasional prey of sparrowhawk (e.g. Opdam 1978, Selås 1993, Solonen 1997, Rytkönen *et al.* 1998), ural owl (e.g. Mysterud & Hagen 1969, Lundberg 1981, Mikkola 1983, Korpimäki & Sulkava 1987), and goshawk (e.g. Höglund 1964, Sulkava 1964a, Opdam *et al.* 1977, Widén 1987). Also pygmy owl may catch woodpeckers, but these events are rare and they practically occur outside the breeding season (Lagerström & Syrjänen 1995, M. Lagerström pers. comm., cf. Michalek & Miettinen 2003). We detected significantly smaller densities of sparrowhawk and ural owl around the occupied goshawk nests as compared with those around the unoccupied ones, but because of the rarity of woodpecker as prey items, it is difficult to exactly estimate if goshawk's presence actually decreases total predation pressure of avian predators (goshawk included) on adult three-toed woodpeckers and if it then influences the territory quality of the species.

Our definition of territory quality covers the breeding season of three-toed woodpecker from the settling of adults to breeding territories until the late nestling period. The survival of fledglings is thus not included in our calculations. The above-mentioned mammalian and bird predators are known to prey upon fledglings of woodpeckers (cf. Glutz & Bauer 1980, Cramp 1985, Winkler & Christie 2002, Michalek & Miettinen 2003). We assume that the role of goshawk in lowering overall predation pressure on three-toed woodpeckers continues also at least during the early fledgling period but as the woodpeckers move longer distances from their nest sites when fledglings get older (Cramp 1985, T. Pakkala *et al.* unpubl. data) the effect of goshawk also decreases.

Great spotted woodpecker had a significant, negative effect on territory quality of three-toed woodpecker in close surroundings of the goshawk nest sites. Within the Lammi study area, great spotted woodpecker is much more abundant than three-toed woodpecker, even in preferred habitats of the latter, with typically 2–5 territories of great spotted woodpecker overlapping with each territory of three-toed woodpecker (cf. Tables 2 and 3). Thus, three-toed woodpeckers are practically continuously in touch with great spotted woodpeckers. Published studies and observations about antagonistic behavior between these species report usually dominance of great spotted woodpecker (cf. Hurme & Sarkanen 1975, Glutz & Bauer 1980, Cramp 1985) that was corroborated by various field observations of this study (T. Pakkala unpubl. data). On the other hand, it has been pointed out that these two species in sympatry should occupy different strata of forest, especially for feeding, to reduce competitive pressure (Hogstad 1971, 1993, Ruge & Havelka 1993, Michalek & Miettinen 2003).

In most observed cases, great spotted woodpecker dominated three-toed woodpecker and rather strong interference was observed especially during great spotted woodpecker peak density years. In our study area, great spotted woodpecker had a frequent, disturbing effect on the onset of nesting of three-toed woodpecker by often starting nesting in close vicinity of the nest site three-toed woodpecker had selected or even in the same tree. Great spotted woodpeckers were also commonly observed to take over old nest holes of three-toed woodpecker to nest especially if there were longer cold periods during the onset of breeding in late April and early May (T. Pakkala *et al.* unpubl. data). We thus assume that the negative effect of great spotted woodpecker is both direct — the species decreases nesting efforts of three-toed woodpecker — and indirect

— the species forces three-toed woodpecker to suboptimal nesting habitats that, on average, are also situated at longer distances from goshawk nest sites.

Three-toed woodpecker in changing forest landscapes

Three-toed woodpecker is considered an important keystone species in coniferous-dominated natural forest and a potential umbrella species indicating general habitat quality of forest environment (e.g. Imbeau 2001, Mikusiński *et al.* 2001, Angelstam *et al.* 2003, Bütler *et al.* 2004, Pechacek & d'Oleire-Oltmanns 2004). The populations in Fennoscandia are in decline (Väisänen *et al.* 1998, Svensson *et al.* 1999) that is most probably mainly caused by modern forestry practices that decrease both the area of suitable habitat and quality of remaining habitat by removing old and dead trees (cf. Nilsson *et al.* 1992, Angelstam & Mikusiński 1994, Bütler *et al.* 2004).

In this study, we surveyed unchanged forest environments to be able to detect the role of possible interspecific relations, but it should be remembered that the change in forest habitats is the most important factor that affects population variation of three-toed woodpecker also within our study area: during the last two decades the breeding population of three-toed woodpecker has decreased by some 30% in Lammi study area and approximately 50% of this decrease can be directly linked to loss of suitable forest habitats caused most often by forest clear-cutting within central parts of territories (T. Pakkala unpubl. data).

We can, however, state that the effects of predation and competition are of importance if we estimate persistence of three-toed woodpecker in a forest environment at the level of single territories or local populations. As goshawk, great spotted woodpecker and three-toed woodpecker prefer similar forest habitats, species interactions concern a relatively large proportion of the three-toed woodpecker population. Great spotted woodpecker can be, of course, considered as a constant disturbance factor to three-toed woodpecker but our results indicate that the possibilities for three-toed woodpecker to coexist successfully with great spotted woodpecker are better in less fragmented forest landscapes with high structural diversity that offer more suitable alternative nest places within territory. Goshawk, on the other hand, may at first glance be classified as just an occasional neighbour of three-toed woodpecker in forest landscapes, but the proportion of three-toed woodpecker territories in close surroundings or near goshawk nest sites can be surprisingly high; e.g. in northern parts of our study area about 30% of breeding territories of three-toed woodpeckers were situated close to goshawk nest sites, and goshawk was a constant breeder in all four largest territory concentrations of three-toed woodpecker that comprised almost 50% of all permanent territories in that area. Thus the effects of competition and predation are here closely related to the structure of forest landscape matrix. Assuming that fragmentation in forest landscapes is likely to continue in the future with losses of suitable habitats for both predator species and the hole-nesting bird guild studied here, we predict that the relative role of species interactions are going to increase. Combined effects of habitat factors and interspecific relations may then substantially modify territory quality of three-toed woodpecker and probably also other ecologically similar forest bird species and their ability to maintain viable populations in dynamic forest landscapes.

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