

Density variation and breeding success of the Black Woodpecker *Dryocopus martius* in relation to forest fragmentation

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Density of the Black Woodpecker *Dryocopus martius* was examined and reproductive data collected, both in a forest landscape area (128 km²) and in a farmland area (123 km²) with highly fragmented forests (26% forest), in central Sweden during 1985–1990. The composition, age, and the management practices of the forests did not differ in the two areas. We found that the densities (about 0.15 territorial pairs/km² of forest land) were the same in the forest area and in the farmland area with highly fragmented forests. Furthermore, we found no differences in the reproductive rate, predation rate, body conditions of the young, or the breeding times between the two areas. The frequency distribution based on the duration in years of the territory occupation was also the same in both areas. We conclude that the Black Woodpecker is not excluded from highly fragmented forests and can successfully breed there, provided that tree composition and food supplies are suitable. However, we do not know what the lower limit of fragmentation is for the species. Further studies of the effects of habitat fragmentation on the Black Woodpecker are needed from northern Fennoscandia, where the density is lower than in southern Sweden.



1. Introduction

According to the theory of island biogeography by MacArthur & Wilson (1967), one could regard habitat fragments as islands. From this point of view, the number of species in small, fragmented habitat islands should be less than in large, uniform areas. However, where more than 30% of the original habitat remains, bird species impoverishment has not been found in fragmented coniferous taiga forests (Wegge & Rolstad 1986, Rolstad & Wegge 1987, Haila et al. 1987). One

explanation of this is that birds may include several separate patches of habitat in their territories (Nilsson 1977, Haila et al. 1987). However, some bird species, such as the Siberian Tit *Parus cinctus* in northern Finland (Virkkala & Liehu 1990), suffer from fragmentation of earlier uniform forests. Also, other sedentary species of old forests (Willow Tit *Parus montanus*, Crested Tit *P. cristatus*, Treecreeper *Certhia familiaris*, and Siberian Jay *Perisoreus infaustus*) have declined in northern Finland, this being explained mainly by fragmentation, but also by changes in the age

structure of the taiga forests (Helle & Järvinen 1986).

Angelstam (1990) found no effect on woodpecker species richness of habitat area in fragmented taiga forests. In contrast, he found that certain quality aspects (dead wood, tree species diversity, occurrence of stumps and logs, etc.) were much more important in explaining the number of woodpecker species present (see also Nilsson et al. 1992). However, Haila et al. (1987) found that scarce species such as woodpeckers tend to be more sparse in very small (< 6 ha) fragments of forests than might be expected on the basis of their occurrence in large fragments. Also, the occurrence of the Lesser Spotted Woodpecker *Dendrocopos minor* increased regularly with the amount of deciduous forest in 200 ha plots, and it was absent from most plots with less than 10% deciduous forest (Wiktander et al. 1992).

Of the seven woodpecker species in Sweden, the Black Woodpecker *Dryocopus martius* and the Great Spotted Woodpecker *Dendrocopos major* are more generalists than the other species in terms of habitat selection, and they can consequently subsist in managed forests (see Nilsson 1979a, 1979b, Angelstam 1990, Nilsson et al. 1992). These woodpeckers are keystone species for other hole-nesting birds, as nest hole producers. Since the Black Woodpecker breeds almost throughout Sweden, although more scarcely in northern Sweden (Ahlén & Tjernberg 1992), old nest-holes made by this species are often essential for several large-sized, hole-nesting bird and mammal species (Johnsson et al. 1990). The Black Woodpecker is a resident species, and has certain demands upon nesting trees (Ahlén & Tjernberg 1992, Nilsson et al. 1993, in press). Despite being a more generalist species than most other woodpeckers in Sweden, the Black Woodpecker certainly has special habitat requirements for survival (Angelstam 1990).

Information on Black Woodpecker densities in different types of forests exists from several places in Fennoscandia (Pynnönen 1939, Merikallio 1958, Haila & Järvinen 1977, Nilsson 1980, Wahlström 1982, Boström 1988, Johansen 1989, Wahlström & Joelsson 1992, Rolstad et al. 1992). However, these investigations have mainly been made in more or less homogeneous forests, and

only a few studies have dealt with typical agricultural areas, which contain a large number of fragmented woodlots.

In the present study, a Black Woodpecker population, in more or less homogeneous forests, was compared with a population living in highly fragmented woodlots in nearby agricultural areas. The purpose was to evaluate any possible differences in the population density per forest area, reproductive rate, body conditions of the young, and in the breeding season of woodpeckers inhabiting continuous or fragmented forest areas.

2. Study area

During 1985–1990, the territories of the Black Woodpecker were mapped in two different types of landscape; an extensive forest area and a pronounced agricultural area, both characterised by flat topography and situated in the county of Uppland, in central Sweden (approx. 59°45'N, 17°15'E; Fig. 1). The forests, lakes, and other geographical features were measured by digitising topographical maps (scale 1:25 000) with a digitising table (Table 1).

The study area of forest landscape (128 km² excluding lakes; directly connected to continuous forests further west, north and east) is covered by forests (80.1%), which are intersected by small farmland areas, such as infields, and some open mires and fens. The forest consists of one

Table 1. Area of different habitats in two areas in Uppland, central Sweden.

	Forest area	Farmland area
Total land area excl. lakes (km ²)	127.9	123.0
Area of lakes (km ²)	1.0	12.0
Area of forest (km ²) including clearcuts and wet forests and mires with trees	102.4	31.5
No. of separate woodlots	141	533
Area of wet forests and mires with trees (km ²)	8.7	0.02
No. of objects with wet forests and mires	288	6
Area of open mires and fens (km ²)	1.3	0.3
No. of open mires and fens	33	34

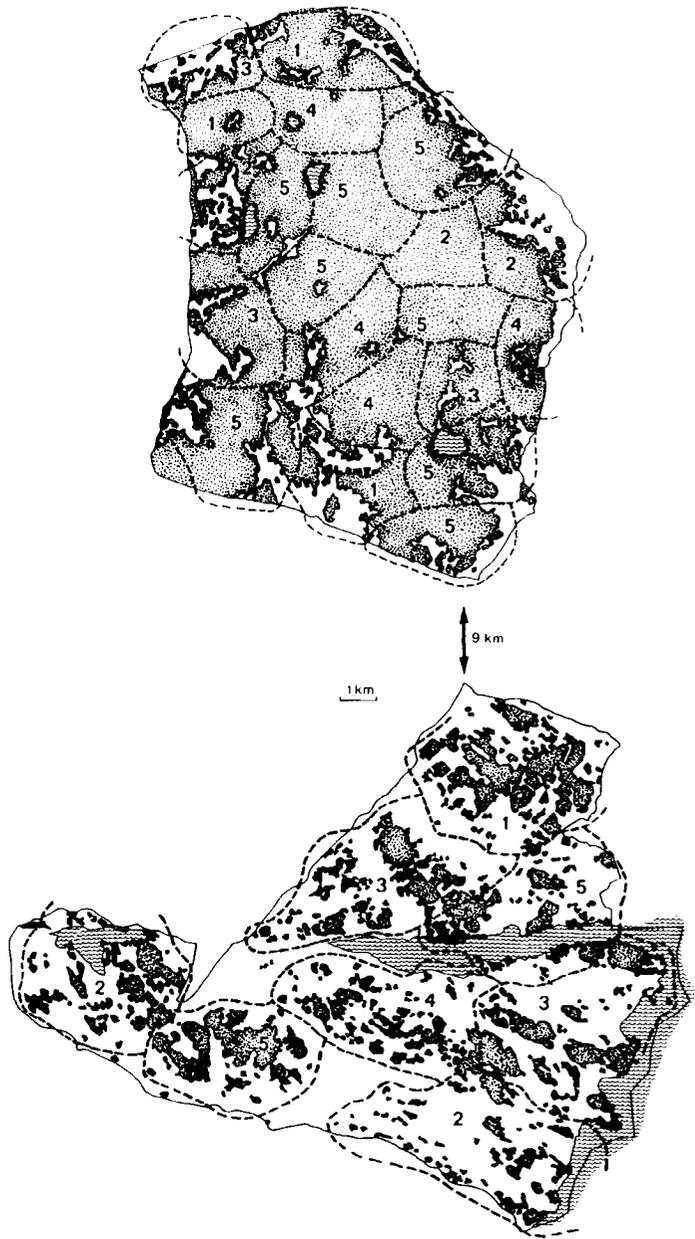


Fig. 1. Maps showing the investigated areas situated in Uppland, central Sweden; forest area in north and highly fragmented area in south. Shortest distance between the areas is 9 km. Open mires and fens are not shown on the maps. The theoretical maximum number of Black Woodpecker territories (21 in north and 8 in south) found during a five-year study are indicated on the maps with dotted lines. The dotted borderlines indicate theoretical areas for each territory, but the borderlines are also, to some degree, based on field observations. Figures (1–5) show the number of years the territories were occupied by a pair, or at least one resident Black Woodpecker, during the breeding season.

main continuous unit of 98.5 km² and 140 small forest patches. Only nine of these 140 forest patches exceed 0.1 km² (maximum 0.5 km²). Dominating tree-species are spruce *Picea abies* and pine *Pinus sylvestris* but also deciduous trees, mainly birch *Betula* spp., aspen *Populus tremula* and alder *Alnus glutinosa*, are common. About 8.5% of the forest area consists of wet forest

types, including mires with trees. The area is exposed to modern forestry management, with small- to medium-sized clearcuts, and one maximum clearcut area about 0.5 km². The average areas of clear-cuttings in the county of Uppland were 0.047 km² in 1987–1988 (Anon. 1990).

The study area situated in the farmland district (123.0 km² excl. lakes) and close to Lake

Mälaren, is characterised by large fields mainly used for crop production. This landscape is largely fragmented by a total number of 533 patches of forests, of which 53 are larger than 0.1 km² and 8 are greater than 1 km² (maximum 4.2 km²). The tree species composition and age are about the same as in the forest study area. However, in a few small places, mainly close to Lake Mälaren, the contribution of broad-leaved deciduous forests, with species such as oak *Quercus robur*, maple *Acer platanoides*, elm *Ulmus glabra* and ash *Fraxinus excelsior*, is striking. The proportion of wet forests, including mires with trees, is negligible in comparison with the extensive forest study area (see Table 1). The forests are exposed to modern forestry methods, but on a smaller scale than in the forest study area.

3. Methods

Territories of the Black Woodpecker were mapped during the breeding season, in March and April, 1985–1990. Each year four to six persons, mainly the same persons every year, intensively searched for the Black Woodpeckers in the two study areas. The forests were investigated by walking slowly through the forests during the morning. The investigations occurred several times each season. By using cars or bicycles on available roads, it was possible to cover large areas during the same morning. Taped calls and drums of the Black Woodpecker were regularly used to locate territorial individuals and to define territory boundaries. Great efforts were made to find nests. All identifications of the Black Woodpecker, such as observed birds, drumming or calling birds (can be heard at least 3 km away), were recorded on maps. Furthermore, all known, old Black Woodpecker holes were located and investigated in May, in order to find any pairs breeding in old holes. A territory was regarded as occupied when a nest was found, or when at least one Black Woodpecker was resident in a limited region during the breeding period. When no signs of territorial Black Woodpeckers were found after at least three visits, with each visit lasting several hours in the early morning and occurring in suitable weather, the territory was regarded as unoccupied. With the methods ex-

plained above, we are convinced that, in principle, every territorial Black Woodpecker was discovered, and those eventually missed would not have affected the results other than marginally. However, 1985 data from the forest study area were incomplete and reliable data are only available for the years 1986–1990. Territorial mapping was also incomplete in the farmland area in 1990, and data from this year were thus omitted. Located nests were regularly investigated until the juveniles were ringed and measured at 20 days old (end of May to early June).

The population density was calculated by dividing the total forest area by the number of territorial woodpeckers (pairs or single resident birds). Since birds' territories can be overlapping, and there might also be areas not utilised by the birds, this value of area of forest per territorial pair is not the same as territory size. However, a large fraction (25%) of the birds were individually colour-ringed and six individuals were followed using radio telemetry. Observations of these individuals indicate that the density value may be rather close to real territory size, as was also found in a study using telemetry in Norway (Rolstad et al. 1992). In our study, clearcuts were included in the forest area. The reason for this is that the small clearcuts occurring in the county of Uppland are important foraging habitats for the Black Woodpecker (our own observations and also observed in Norway by Rolstad et al. 1992). Furthermore, at many clearcuts there were stands of seed trees (pines), often used as breeding places for the species.

4. Results

During the five-year period 1986–1990, the number of Black Woodpecker territories varied between 10–17 (mean 14.8) in the forest study area. Corresponding figures for the farmland area, 1985–1989, were 3–7 territories (mean 5.0). Theoretically 6–7 km² of forests were available for each territory in both areas (Table 2). The mean nearest distances with standard deviation between occupied nestholes were 2.2±1.1 km (median 2.0 km, n = 60) in the forest area and 5.0±2.9 km (median 4.3 km, n = 14) in the farmland area (nearest distance 0.3 km in one occa-

sion in both areas, respectively). The median values were lower than the mean because some nests were not found, or because some territories were empty. Territories were regularly spaced in the study areas (Fig. 1, as also found in a Norwegian study; Rolstad et al. 1992).

During the study period the combined number of territories were 21 and 8 for the forest and farmland area, respectively (see Fig. 1). From large-scale observations in both study areas we conclude that Black Woodpeckers were faithful to breeding places from one year to another, that in single years some "territories" were unoccupied, and that "missing pairs", with certainty, had disappeared from the study areas. In order to find out if there were quality differences between territories in the farmland and forest area, we tested if there was any difference in the

number of years available territories were occupied during the five-year study-period. However, no such difference was found (Mann-Whitney U-test, $U = 70.5$, $P = 0.497$).

The number of eggs per clutch, mean date of hatching, number of fledged young per successful breeding, and the number of young per breeding (including failures), mean weight and mean wing length of juveniles (20 days old), did not differ between the two areas (Table 3). There was no significant difference in the exploitation of old nest holes as a breeding place between the two areas, 38% old nest holes in the farmland area, $n = 13$, and 27% old nest holes in the forest, $n = 49$ (Fisher's exact probability test (two-tailed), $P = 0.495$). Furthermore, no significant difference in predation rate was found between the farmland and the forest area, 15.4% ($n = 13$) and

Table 2. Observed number of territories of Black Woodpecker (pairs or single territorial birds) in the forest and farmland area, respectively, and density of Black Woodpecker territories (mostly pairs) per 100 km² forest during 1985-1990. The number of found nests with egg or young is given within brackets.

	1985	1986	1987	1988	1989	1990	Mean
No. of territories (nests)							
Forest area	–	10 (7)	16 (15)	17 (11)	16 (11)	15 (9)	15
Farmland area	7 (4)	5 (2)	5 (2)	3 (2)	5 (4)	–	5
Density of Black Woodpecker territories per 100 km ² forest							
Forest area	–	9.8	15.6	16.6	15.6	14.7	14.5
Farmland area	22.2	15.8	15.8	9.5	15.8	–	15.8

Table 3. Black Woodpecker reproduction data from the forest and farmland study areas, respectively. T-test, independent samples were used in all analysis.

	Forest	n	Farmland	n	P
No. of eggs per clutch (range)	4.56 (2–6)	41	4.71 (4–5)	7	0.491
Mean date of hatching (range)	May 5th (23.4–12.6)	31	May 5th (22.4–24.5)	10	
No. of young per successful breeding pair (range)	3.71 (1–5)	35	3.91 (3–5)	11	0.355
No. of young per breeding pair including failures	2.65	49	3.31	13	0.205
Mean weight (g) of 20-day-old young					
Males	268.5	60	270.7	16	0.685
Females	249.4	63	241.0	23	0.125
Mean wing length (mm) of 20-day-old young					
Males	137.8	60	137.8	16	0.992
Females	134.7	63	134.0	23	0.700

28.6% ($n = 49$), respectively (Fisher's exact probability test (two-tailed), $P = 0.484$).

5. Discussion

In northern Europe the Black Woodpecker is associated with more or less mature, continuous coniferous forests (Cramp et al. 1985). However, the present work shows that the species also occurs in farmland-dominated areas. The Black Woodpecker is not excluded from intensively farmed areas just because the patches of forests are fragmented and small. If the forest habitat is suitable (in this study forest composition and age are about the same in the forest landscape and in the agricultural landscape), the Black Woodpecker can be found with equal density per forest area in farmland districts, in spite of small and scattered forest patches, as in continuous forests at the same latitude. Also, the territories were occupied to the same extent in both continuous forest and in fragmented areas during the study period. These findings are in accordance with the statements in von Haartman et al. (1963–72) and Haila et al. (1987), that the Black Woodpecker often occurs in fragmented forests, using different areas widely dispersed from each other for foraging. Furthermore, we found similar reproductive parameters in the two study areas, indicating that the energy costs for flying between forest patches were not a limiting factor in the more fragmented landscape. Alternatively, the higher energy costs are compensated by more available food in the fragmented areas. In fragmented landscapes there has often been found an increased risk of nest-predation. This may be due to predators penetrating into the forests from the surrounding farmlands (for references see Angelstam 1992). However, in our study we found no difference in predation rates of the Black Woodpecker nests between fragmented and continuous forests. The main predator was the pine marten *Martes martes*, which inhabits both study areas.

The Black Woodpecker has certain minimum area requirements, probably determined by food resources. According to the present study, at least a total area of 4.5 km² of forests must be available for a territorial pair in an agricultural area in

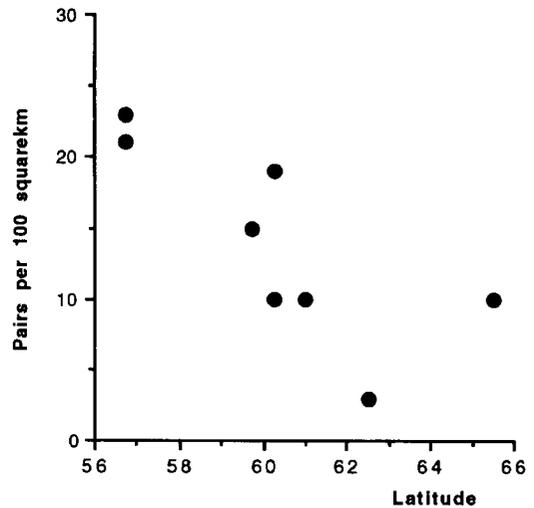


Fig. 2. Mean density (number of pairs per 100 km² of forest) at different latitudes in Fennoscandia (Spearman correlation, $r_s = -0.86$, $n = 8$, $P = 0.02$) [Lake Mökkelin, Sweden (56°45'N), 21 in mixed forest of conifer and deciduous (Nilsson 1980, 1981), Ljungby, Sweden (56°45'N) 23 in mixed coniferous forest (Wahlström 1982, Wahlström & Joelsson 1992), Varaldskogen, Norway (60°15'N) 19 in coniferous forest (Rolstad et al. 1992), Uppland, Sweden (59° 45'N) 15 in mixed coniferous forest (this study), Åland, Finland (60°15'N) 10 in coniferous forest (Haila & Järvinen 1977), southern Finland (about 61°N) 10 in coniferous forest (Merikallio 1958), central Finland (62°30'N) 3 in mixed forest (Pynnönen 1939), and northern Sweden (65°–66°N) 10 in virgin coniferous forest (Boström 1988)].

central Sweden. These patches (mean 76 woodlots per pair) were scattered over a land area of at least 17 km². However, there must be some limit of fragmentation where the Black Woodpecker cannot persist in the landscape. In our fragmented area, 26% of the area consisted of suitable habitat. We do not know the species' lower limit. In Sweden, the Middle Spotted Woodpecker *Dendrocopos medius* went extinct in an area when suitable habitat covered 6% of the area (Pettersson 1985). However, the ultimate cause for this extinction was probably due to environmental stochasticity and inbreeding.

In Fennoscandia the density of Black Woodpeckers decreases with latitude, the highest density being found in southern Sweden, the lowest in central Finland and northern Sweden (Fig. 2). In central Finland we calculated mean nest dis-

tance to be 6.4 km, from Pynnönen (1939). Likely explanations of this latitudinal decrease in density are: differences in food availability, and in northern Fennoscandia, food availability combined with a high degree of forest fragmentation. In general, the number of insect species, and perhaps also the density of insects, increases with a warmer climate and higher coil productivity (Palmgren 1930, Fisher 1960, Turner et al. 1987). This is probably the same for the main food of the Black Woodpecker, which is made up of ants (larvae, pupae and adults of Formicidae, above all *Campanotus*) and wood-boring beetles (Coleoptera; Cramp et al. 1985; see also Olesen & Olesen 1972 and Rolstad et al. 1992). In southern Sweden, the Black Woodpecker occurs in stable populations despite intensively managed forests. However, increasing wood biomass and forest area, in recent decades, probably compensates for decreasing forest quality in other respects (Nilsson et al. 1992), and fragmentation of forests due to clearcuts (mean 0.014–0.048 km² in different counties; Anon. 1990) does not affect the Black Woodpecker. However, in the taiga forests in northern Finland and northern Sweden the Black Woodpecker has shown a long-term decline during the last 40 years (Järvinen & Väisänen 1979, Väisänen et al. 1986, Ahlén & Tjernberg 1992). This decline has been explained as a result of modern forestry management, i. e., destruction of virgin forests, large clear-cuttings, draining of swamp forests and other forestry measures (Väisänen et al. 1986). Since very large clear cuttings are common in northern Sweden (average areas 0.25 km² in the 1980's; Anon. 1990), and natural forests have become rare, fragmentation may affect the Black Woodpecker in such a way that the birds must have larger territories, as we found in the county of Uppland (see also Pynnönen 1939). With larger territories in the north, and larger clear-cuts which are not used in winter (Rolstad et al. 1992), the effect of forestry may be more severe in northern, than in southern Fennoscandia. The food demands during winter are probably the limiting factor in this respect (see Nilsson et al. 1992), as described for the resident Nuthatch *Sitta europaea* (Nilsson 1987, Enoksson 1990) and Treecreeper (Kuitunen & Helle 1988). Furthermore, the Black Woodpecker depends on nesting trees of a certain

minimum stem thickness and size (S. G. Nilsson et al. 1993, in press), and in northern Sweden it could be a limiting factor.

Sammanfattning: Täthet och reproduktion hos spillkråka i relation till skogsfragmentering

Jämförande studier av täthet och reproduktionsframgång hos spillkråka utfördes mellan två områden i centrala Sverige 1985–1990. De två områdena utgjordes av ett stort sammanhängande skogsområde (128 km²) respektive ett jordbruksdistrikt (123 km²) med starkt fragmenterade skogar. Skogarnas utseende och ålder samt skogsbruksmetoder var ungefär desamma i bägge områdena.

Vi fann att tätheten av spillkråka (i medeltal cirka 0.15 par/km² skog) och utnyttjandet av reviren var densamma inom de två områdena under undersökningsperioden. Även reproduktionen, ungarnas kondition och tidpunkt för häckning var i stort sett identisk mellan det homogena och fragmenterade skogslandskapen. I det fragmenterade området var skogsdungarna (medeltal 76 per par) fördelade över en yta av minst 17 km², och 26% av ytan bestod av lämplig biotop.

Av resultaten kan slutsatsen dras att spillkråkan förekommer i starkt fragmenterade skogsområden om trädslagssammansättning är den rätta och nödvändig föda finns tillgänglig. Var den undre gränsen för fragmenteringsgraden går är dock fortfarande oklar. Fortsatta studier avseende fragmenteringens effekter på spillkråkan är därför angelägna, speciellt i norra Sverige och Finland där tätheten är lägre än i södra Fennoscandia.

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References

- Ahlén, I. & Tjernberg, M. (eds.) 1992: Artfakta. Sveriges hotade och sällsynta ryggradsdjur 1992. — Uppsala.
 Angelstam, P. 1990: Factors determining the composition and persistence of local woodpecker assemblages in taiga forest in Sweden – a case for landscape ecological studies. — In: Carlson, A. & Aulen, G. (eds.),

- Conservation and management of woodpecker populations: 147–164. Swedish University of Agricultural Sciences, Department of Wildlife Ecology. Report 17. Uppsala.
- 1992: Conservation of communities – the importance of edges, surroundings and landscape mosaic structure. — In: Hansson, L. (ed.), *Ecological principles of nature conservation*: 9–70. Elsevier Applied Science. London.
- Anon. 1990: *The natural environment in figures*. Official statistics of Sweden. — Third edition. Stockholm.
- Boström, U. 1988: Fågelfaunan i olika ålderstadier av naturskog och kulturskog i norra Sverige. — *Vår Fågelvärld* 47:68–76.
- Cramp, S. (ed.) 1985: *Handbook of the birds of Europe, the Middle East and North Africa*. — The Birds of Western Palearctic. Vol. 4. Oxford.
- Enoksson, B. 1990: Autumn territories and population regulation in the nuthatch, *Sitta europaea*: an experimental study. — *Journal of Animal Ecology* 59:1047–1062.
- Fisher, A. G. 1960: Latitudinal variations in organic diversity. — *Evolution* 14:64–81.
- Haila, Y. & Järvinen, O. 1977: Competition and habitat selection in two large woodpeckers. — *Ornis Fennica* 54 (2):73–78.
- Haila, Y., Hanski, I. K. & Raivio, S. 1987: Breeding bird distribution in fragmented coniferous taiga in southern Finland. — *Ornis Fennica* 64:90–106.
- v. Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–72: *Pohjolan linnut värikuvien*. — Otava, Helsinki.
- Helle, P. & Järvinen, O. 1986: Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. — *Oikos* 46:107–115.
- Johansen, B. T. 1989: Population, territory size and breeding success of Black Woodpeckers in Tilsvilde Hegn, northern Zealand, 1977–1986. (In Danish with English summary) — *Dansk Orn. Foren. Tidsskr.* 83:113–118.
- Johnsson, K., Nilsson, S. G. & Tjernberg, M. 1990: The Black Woodpecker; – a keystone species in European forests. — In: Carlsson, A. & Aulen, G. (eds.), *Conservation and management of woodpecker populations*: 99–102. Swedish University of Agricultural Sciences, Department of Wildlife Ecology, Report 17. Uppsala.
- Järvinen, O. & Väisänen, R. A. 1979: Changes in bird populations as criteria of environmental changes. — *Holarctic Ecology* 2:75–80.
- Kuitunen, M. & Helle, P. 1988: Relationship of the common Treecreeper *Certhia familiaris* to edge effect and forest fragmentation. — *Ornis Fennica* 65:150–155.
- MacArthur, R. H. & Wilson, E. O. 1967: *The theory of island biogeography*. — Princeton Univ. Press, Princeton.
- Merikallio, E. 1958: Finnish birds. Their distribution and numbers. — *Fauna Fennica* 5: 1–181.
- Nilsson, S. G. 1977: Density compensation and competition among birds breeding on small islands in a South Swedish lake. — *Oikos* 28:170–176.
- 1979a: Effect of forest management on the breeding bird community in southern Sweden. — *Biol. Conserv.* 16:135–143.
- 1979b: Density and species richness of some forest bird communities in south Sweden. — *Oikos* 33:392–401.
- 1980: Möckelnområdets fågelfauna. — Länsstyrelsen i Kronobergs län. Växjö.
- 1981: De svenska rovfågelbeståndens storlek. — *Vår Fågelvärld* 40:249–262
- 1987: Limitation and regulation of population density in the nuthatch *Sitta europaea* (Aves) breeding in natural cavities. — *Journal of Animal Ecology* 56:921–937.
- Nilsson, S. G., Olsson, O., Svensson, S. & Wiktander, U. 1992: Population trends and fluctuations in Swedish Woodpeckers. — *Ornis Svecica* 2:13–21.
- Nilsson, S. G., Johnsson, K. & Tjernberg, M. 1993: Age, dimensions and loss rates of Black Woodpeckers nesting trees. — In: Johnsson, K., *The Black Woodpecker as a key species in forests*. PhD-thesis. Report 24. The Swedish University of Agricultural Sciences, Dept of Wildlife Ecology, Uppsala, Sweden.
- Olesen, L. L. & Olesen, E. M. 1972: Sortspaettens fouragering. — *Flora och Fauna* 78:33–39.
- Palmgren, P. 1930: *Quantitative Untersuchungen über die Vogelfauna in den Wäldern Südfinnlands mit besonderer Berücksichtigung Ålands*. — *Acta Zool. Fennica* 7:1–218.
- Pettersson, B. 1985: Extinction of an isolated population of the Middle Spotted Woodpecker *Dendrocopos medius* (L.) in Sweden and its relation to general theories on extinction. — *Biol. Conserv.* 32:335–353.
- Pynnönen, A. 1939: *Beiträge zur Kenntnis der Biologie finnischer Spechte I*. — *Ann. Zool. Soc. Zool.-Bot. Fenn Vanamo* 7(2):1–171.
- Rolstad, J. & Wegge, P. 1987: Distribution and size of capercaillie leks in relation to old forest fragmentation. — *Oecologia (Berl.)* 72:389–394.
- Rolstad, J., Majewski, P., Rolstad, E., Gjerde, I., Wegge, P., Bakka, D. & Stokke, P. K. 1992: Økologiske konsekvenser av bestandsskogbruket for hakkespetter i sentrale barskogsområder. — *Rapport fra Skogforsk*, 13/92:45–59.
- Turner, J. R. G., Gatehouse, C. M. & Corey, C. A. 1987: Does solar energy control organic diversity? Butterflies, moths and the British climate. — *Oikos* 48:195–205.
- Virkkala, R. & Liehu, H. 1990: Habitat selection by the Siberian Tit *Parus cinctus* in virgin and managed forests in northern Finland. — *Ornis Fennica* 67:1–12.
- Väisänen, R. A., Järvinen, O. & Rauhala, P. 1986: How are extensive human-caused habitat alterations expressed on the scale of local bird populations in boreal forests? — *Ornis Scand.* 17:282–292.
- Wahlström, K. 1982: Spillkråkans populationstäthet och val av boträd i en sydsvensk skog. — *Milvus* 12:88–97.
- Wahlström, K. & Joelsson, H. 1992: Milrutan. — *Milvus* 22:23–27.
- Wegge, P. & Rolstad, J. 1986: The spacing of Capercaillie leks in relation to habitat and social organization. — *Behav. Ecol. Sociobiol.* 19:401–408.
- Wiktander, U., Nilsson, I. N., Nilsson, S. G., Olsson, O., Pettersson, B. & Stagen, A. 1992: Occurrence of the Lesser Spotted Woodpecker *Denrocopos minor* in relation to area of deciduous forest. — *Ornis Fennica* 69:113–118.