

Seasonal patterns in home range and habitat use of the Grey-headed Woodpecker *Picus canus* as influenced by the availability of food

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Seasonal patterns in diet, home range and habitat use of the Grey-headed Woodpecker *Picus canus* were recorded at the Varaldskogen study area, a managed boreal forest located on the Swedish–Norwegian border in southcentral Scandinavia. One successfully breeding pair was radio-monitored throughout a year. Additional telemetry data were collected in summer from a male in a pair that failed breeding. In summer the birds almost exclusively preyed upon ant colonies in soil and rotten stumps located in young conifer plantations. In winter, when snow or frost prohibited ground feeding, birds were feeding on bark-dwelling insects in old pine and dead trees. The winter shift in diet and feeding behavior was accompanied by an approximately 100 times enlargement in home range size, increasing from 50–100 ha ($n = 3$) in summer to 4 500–5 400 ha ($n = 2$) in winter. With reservations due to small sample size, our data suggests that availability of winter food is critical to the Grey-headed Woodpecker when snow or frozen ground prevents ground-feeding for soil-dwelling ants.



1. Introduction

The Grey-headed Woodpecker *Picus canus* is widely distributed throughout temperate deciduous and conifer forests of the Palearctic faunal region. Different subspecies also occur in the southeast Oriental region (Short 1982, Cramp 1985). Despite the wide distribution range, this medium-sized woodpecker consistently seems to occur at low densities (reviewed by Cramp 1985). Although modern forestry practices have been assumed to influence this species negatively (Ahlén & Andersson 1976), the ultimate

reasons for its rarity, by and large, remain unknown.

As most of the species in the *Picus* genus, the Grey-headed Woodpecker mainly relies on ants as staple food. However, it is considered less ant-specialized than its European congeneric, the Green Woodpecker *P. viridis* (Cramp 1985). Matsuoka and Kojima (1979) report seasonal diet in the Grey-headed Woodpecker in Japan, where the small black ant *Lasius niger* dominated the diet. Interestingly, when snow covered the ground, the proportion of *L. niger* in the diet decreased to almost zero. Because probing and

gleaning are the main feeding techniques, snow presumably prevented the Grey-headed Woodpecker from utilizing soil-dwelling ant colonies. Consequently, the diet shifted to other invertebrates, especially spiders, *Clubonia* spp., which were abundant under the bark of dead trees.

In Fennoscandia, the Grey-headed Woodpecker is perhaps the least known woodpecker. Except for some notes about diet and nest-sites (Ehrenroth 1973, Wabakken 1973), information about seasonal habitat selection and home range is non-existent. Here we present radio-telemetry data from one pair of Grey-headed Woodpeckers, monitored throughout a year. Although our sample size is small, the results demonstrate distinct seasonal shifts in diet, habitat use and home ranges, which indicates that the availability of winter food is a critical factor that may limit woodpecker numbers.

2. Study area

The Varaldskogen study area is a 15 000 ha large forest tract situated on both sides of the Norwegian–Swedish border in the middle boreal zone (60°10'N, 12°30'E; Ahti et al. 1968). The topography is characterized by gentle hills and valleys between 200 and 400 m above sea level. Climate is moderately continental with mean temperatures of 16.2°C and –7.3°C in the warmest (July) and coldest (January) months. Yearly precipitation averages 613 mm. Normally, snow covers the ground from mid-November to April–May.

The forest is dominated by two conifers, Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, with scattered deciduous trees of birch *Betula* spp., aspen *Populus tremula*, alder *Alnus incana* and rowan *Sorbus aucuparia*. Forested land covers 85% of the total area, with the rest comprised of lakes, wetlands and a few scattered holdings and pastures. A detailed description of vegetation types is given by Rolstad et al. (1988).

The forest has been intensively managed by means of stand replacement practices since the early 1950s. Clearcutting and replanting 5–50 ha units has created a landscape mosaic pattern of even-aged plantations less than 50 years old, covering 75% of the forested area in 1993. The remaining 25% comprises uneven-aged, multi-

layered stands up to 200 years old. The remnant patches of old forest have been subject to selective cutting for fuel and timber, which leaves a stand structure lacking big trees and snags. A more detailed description of the forest history and stand structure is reported by Rolstad & Wegge (1989a, 1989b).

3. Material and methods

The material consists of two males and one female, belonging to two pairs spaced 7 km from each other (Fig. 1). No other Grey-headed Woodpeckers were observed in the 15 000 ha study area in 1992. In spring 1993, two pairs were located 12 and 18 km, respectively, to the south of our 1992 southern nest. Their breeding performance was not monitored. Hence, the breeding density of Grey-headed Woodpeckers in this tract was about 1–2 pairs per 10 000 ha.

Birds were captured with a hoop net on a telescope pole at the roosting holes prior to incubation. They were fitted with a 7 gram (5–6% of body mass, inclusive harness) SS-2 type, backpack transmitter (Biotrack, UK), attached with a nylon harness enclosed in silicon rubber (Brander 1968). Transmitting distance varied between 300 m and 2 km depending on the local topography. Birds were reinstrumented at 3 month intervals according to the life length of the batteries. Daily monitoring was conducted with a portable receiver and a hand-held antenna. In winter, when birds moved extensively around, a dense network of forest roads and aircraft surveys helped localization.

At location A (Fig. 1) both sexes were captured in March and April 1992. The pair successfully bred in a retained aspen on a large clearcut. Eight eggs were laid and 7 young fledged, with 3 and 4 young following the male and female parent, respectively, for a 3 week period. One egg remained unhatched. This pair was monitored continuously until April 1993. At that time we failed to reinstrument the female so we lost radio-contact and did not observe her again within the study area. In early May 1993, the male was observed with an unmarked female at the 1992 nest site. However, shortly after he disappeared out of the study area and we

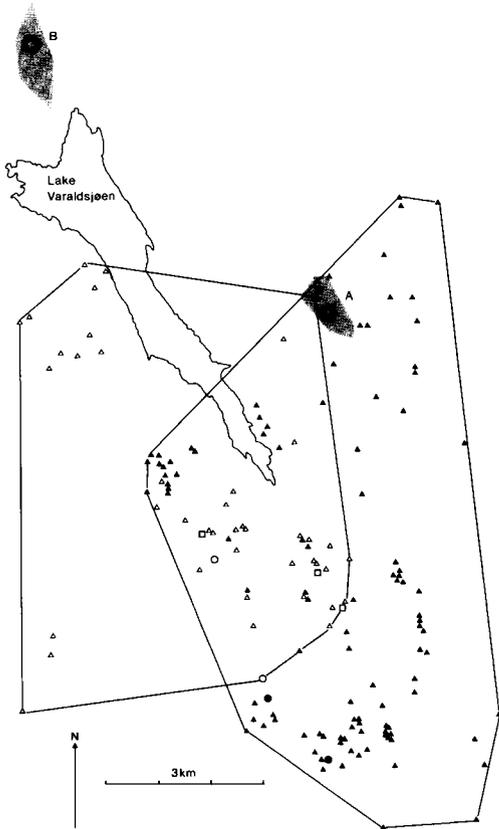


Fig. 1. Seasonal home ranges of a pair (location A) and a male (location B) Grey-headed Woodpecker at the Varaldskogen study area during 1992–93. Shaded areas indicate summer ranges and polygons indicate winter ranges of the male (filled symbols) and female (open symbols) at location A. Stars denote nest sites, triangles daytime locations, circles roosting sites and squares feeding tables.

lost radio-contact. The unmarked female remained displaying at the location, but also disappeared after a few days.

At location B (Fig. 1) only the male was radio-instrumented in early May 1992. This pair made two unsuccessful breeding attempts in an aspen on a new, large clearcut. The first attempt resulted in the male throwing out two freshly laid eggs. The second clutch contained 5 eggs from which 4 young hatched. All died during the third week, presumably because the female stopped feeding, and the male did not compensate for the lower feeding rate. However, both sexes stayed in the vicinity of the nest throughout June. We

failed to reinstrument the male, and although we intensively searched the location no birds were observed in the area in late summer, autumn and winter. In spring 1993 a single unmarked male displayed at the location, but no breeding attempt was recorded.

Home range size, based on direct observations, or cross-bearings and triangulations closer than 100 m, was estimated by drawing a polygon among the successive outermost plots (Mohr 1965). Habitat selection was assessed by comparing habitat use with availability. We assumed independency when successive daytime locations were temporally spaced at a minimum of 5 hours. However, less than 10% of the locations of a bird were recorded during the same day. Data on available habitats were extracted from detailed maps and computerized files from the forest owners. This information was carefully cross-checked in the field and from recent air photos to correct for recent forestry measures. We recorded forest stand age and dominating tree species in a 0.1 ha plot surrounding the direct observations and telemetry locations closer than 50 m. When data were pooled among birds, we weighed the available habitats with the number of locations obtained for each bird. Use of feeding substrate was noted from the direct observations, and prey items taken were checked from the feeding site after the birds had left.

The diet was quantified by collecting fresh faecal droppings ($n = 194$) at the feeding sites or roosting trees. Faecal droppings in roosting trees and nest remains were taken out with a portable vacuum cleaner. They were dried and food items were identified and counted using a binocular microscope. Most food items could be recognized from identifiable remains and they were categorized according to Appendix 1. One group of insects, *Diptera*, was impossible to count from the droppings. Hence, they were only quantified as a proportion of biomass. *Coleoptera* never constituted more than 5% of the biomass intake in any season and it comprised a variety of different species. Due to taxonomic difficulties we did not specify this group in detail. Numbers of prey items were transformed to biomass intake. This was done by collecting prey species, 100–1 000 individuals, at the feeding sites, killing by freezing to -18°C , drying at 105°C for 24 hours,

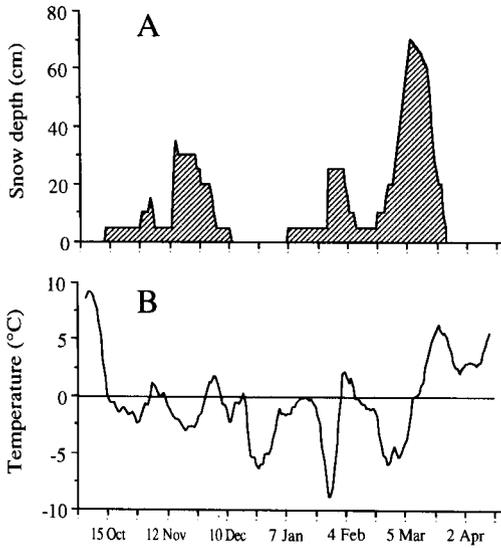


Fig. 2. Snow depth (A) and 7-days moving averages of daytime (12.00 A.M.) temperature (B) during 1 October 1992 to 20 April 1993 at the Varaldskogen study area.

and weighing on a scale with precision to 0.001 g (see Appendix 1). Availability of ant groups in summer was recorded at 24 plots in 10–20 year old conifer plantations within the home ranges of the birds. Within 10 × 10 m all ant colonies in soil and rotten wood were dug out and the number of ants was assessed visually.

To evaluate the impact of weather we recorded daily temperature about 12.00 A.M. from the first of October 1992 to the fifteenth of April 1993. Average snow depth was assessed at 3–5 sites within the birds home ranges (Fig. 2). Seasons were defined on the basis of marked shifts in the diet: spring (March–April), summer (May–October) and winter (November–February) (Fig. 3).

Throughout the paper we use the terms preference and avoidance for significantly greater or smaller use of resources than would be expected on the basis of statistical comparisons ($P < 0.05$) with availability, or what is obvious from graphical presentations.

4. Results and discussion

4.1. Seasonal diet and feeding substrate

Seasonal diet varied considerably (Fig. 3 and 4). (For a complete list of food items, see Appendix 1). During all snow-free seasons ants constituted the staple food, contributing more than 90% to the overall prey biomass (Fig. 4). Three groups of ants were dominant. The *Serviformica*-group prevailed as food throughout the year, except when snow covered the ground, contributing more than half to the prey biomass. Second was carpenter ants (*Camponotus* spp.), which constituted 2/3 of the biomass intake in winters with snow. Third was the mound-building red wood ants (*Formica rufa*-group), with a peak in April when low night temperatures prohibited their vigilance and ants could easily be licked directly from the mound. In midsummer a few faecal droppings contained the small black ant, *L. niger*. When not feeding on ants, different *Diptera* and *Coleoptera* species were preyed upon. During periods of snow-cover these prey groups constituted about 1/4 of the biomass intake (Fig. 3 and 4).

Snow and temperature influenced the availability of food in winter (Fig. 5). Except for two cases during snow melting in late March the birds were not recorded feeding on *Serviformica* when snow depth exceeded 5 cm. Neither were they seen feeding on *Serviformica* during snow-free periods when the ground was frozen. A few exceptions at 1–2 degrees minus could be explained by previous days of thaw. Since *Serviformica* ants colonized soil or well-rotten stumps and fallen logs (Fig. 6), frost presumably prohibited the birds utilizing this prey source.

When snow or frozen ground prevented *Serviformica*-feeding, carpenter ants were preyed upon in small galleries between the bark and sound wood at the basement of old pine trees (Fig. 6). These colonies were small, seldom exceeding a few dozen ants. Therefore, the birds were flying from tree to tree, picking a few ants at each site. This was in contrast to the *Serviformica*-feeding sites where the birds could dwell for hours at the same colony, which sometimes contained thousands of ants. Carpenter ants commonly colonize dead wood with a rather firm structure. Compared to the small galleries in the

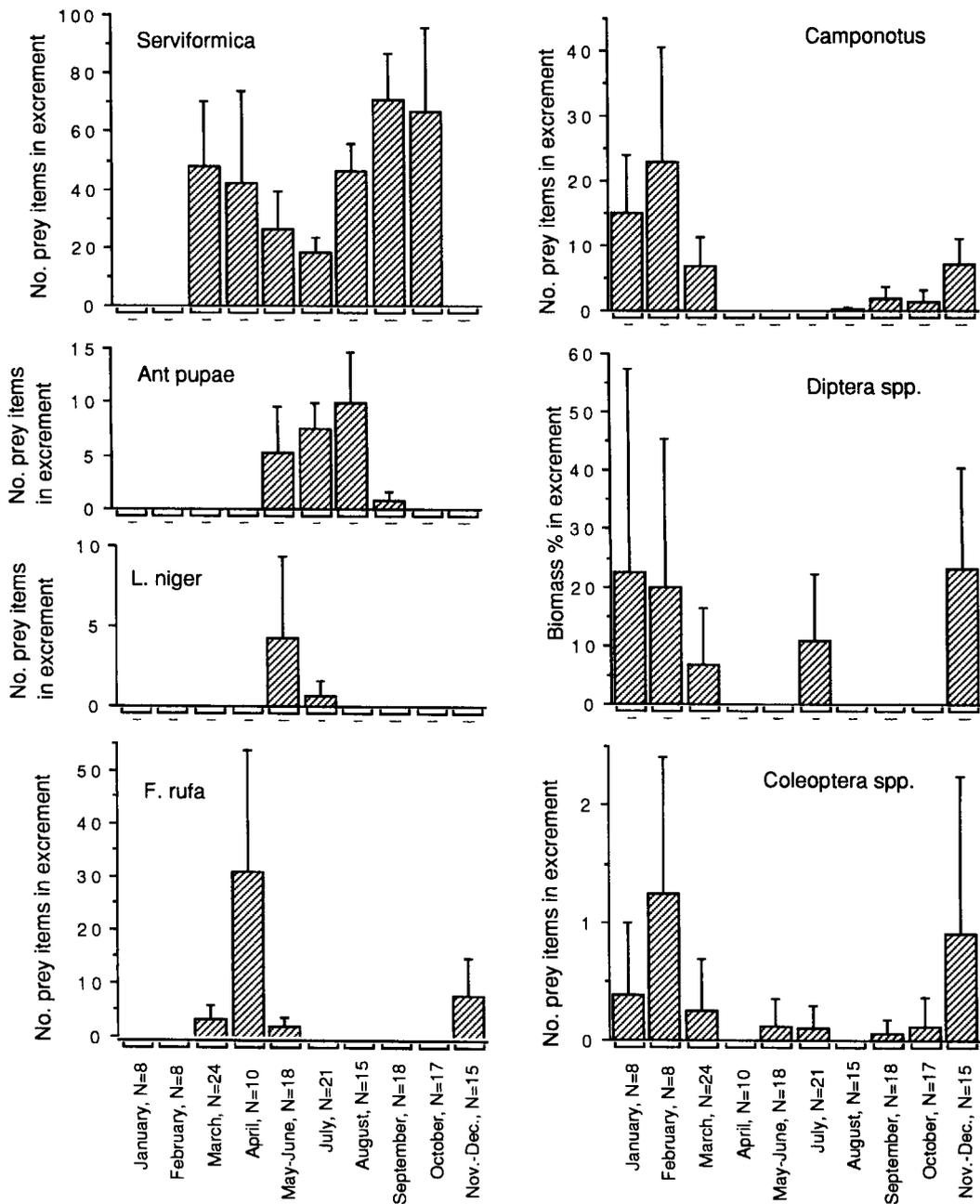


Fig. 3. Seasonal diet (excluding winter without snow) of the Grey-headed Woodpecker shown as monthly averages (+ 95% confidence interval) of the number of prey items in faecal droppings (N). Prey groups are specified in Appendix 1. (Note that *Diptera* spp. is shown as proportion of biomass).

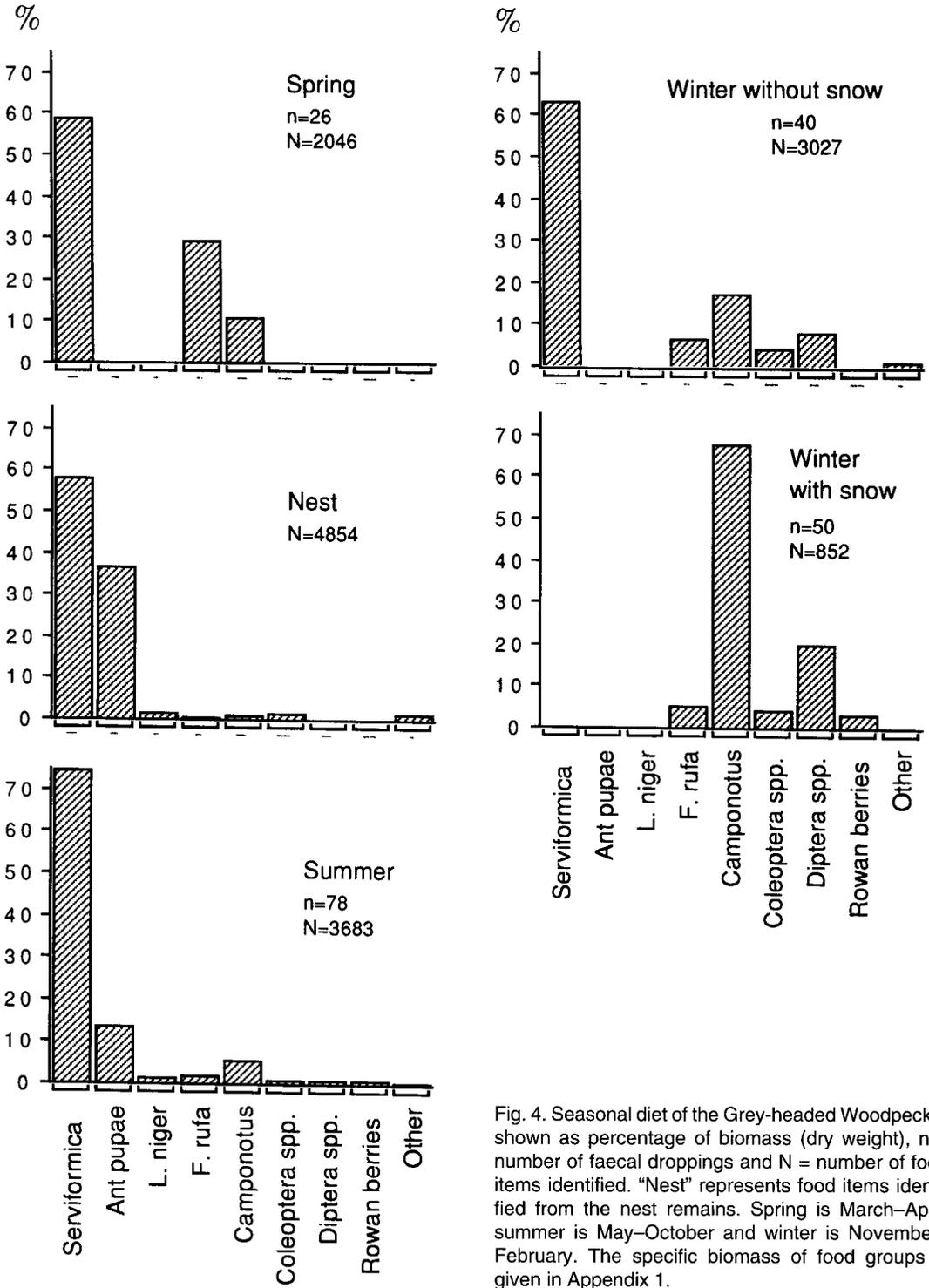


Fig. 4. Seasonal diet of the Grey-headed Woodpecker shown as percentage of biomass (dry weight), n = number of faecal droppings and N = number of food items identified. "Nest" represents food items identified from the nest remains. Spring is March–April, summer is May–October and winter is November–February. The specific biomass of food groups is given in Appendix 1.

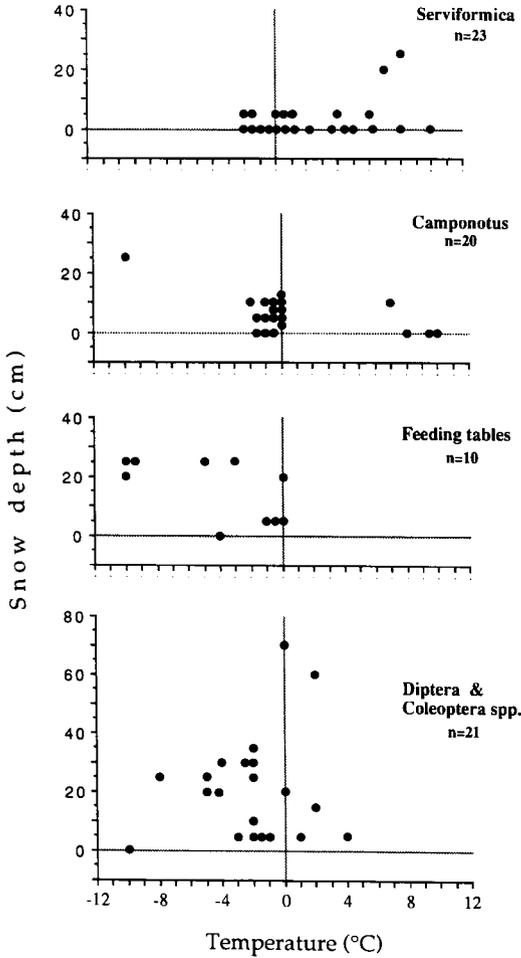


Fig. 5. Feeding observations of the Grey-headed Woodpecker categorized according to main food source, snow depth and ambient daily temperature. See Appendix 1 for specification of food items.

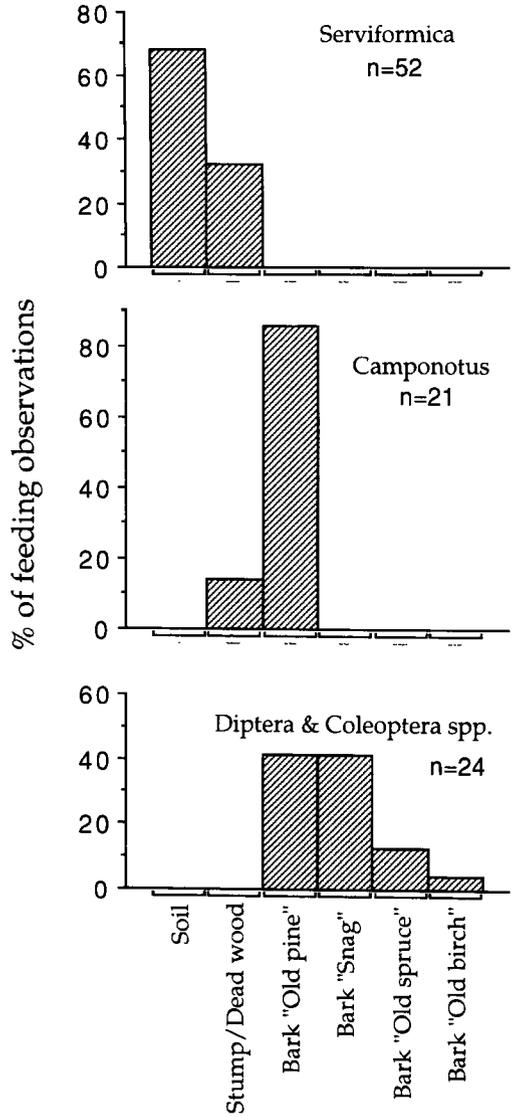


Fig. 6. Feeding substrate of Grey-headed Woodpecker in relation to main prey groups. Prey groups are specified in Appendix 1.

pine bark, carpenter colonies in stumps and dead wood are much larger, often counting ten thousand individuals (Saunders 1970, own observations). Probably due to the hard wood, this food source was inaccessible for the Grey-headed Woodpecker. A few times we observed the birds feeding on carpenter ants from this substrate, however, in these cases the wood had already been opened by the Black Woodpecker *Dryocopus martius* [a phenomenon termed autolyicism (see Matsuoka 1976)].

When snow depth exceeded 15 cm, or during longer periods of cold weather, the birds shifted their diet from carpenter ants to *Diptera* and

Coleoptera species, and tallow from feeding tables (Fig. 5). Whereas, the carpenter ants were taken close to the basement of pine trunks, *Diptera* and *Coleoptera* species were preyed upon both under the loose bark of dead trees and in the microstructure of the bark of old pine and spruce trees (Fig. 6). Hence, they were available at all heights of the stem. This presumably explains why *Diptera* and *Coleoptera* species were the only prey group during longer periods of snow (Fig. 5).

4.2. Prey selection

The *Serviformica*-group was the most important prey in summer, constituting 89% of the ant biomass (Fig. 4). However, because *Serviformica* also was the most abundant soil-dwelling ant, constituting 88% of available biomass, this prey group was not preferred. *L. niger* was rare and its distribution was very clumped within the birds' ranges. It constituted only 1% of available biomass, which also was the proportion of occurrence in the diet. Carpenter ants and the *F. rufa*-group constituted 8 and 2%, respectively, of summer biomass intake. This did not differ from available proportions, i.e., 5 and 6%, respectively.

One ant group was clearly avoided, *Myrmicinae*. This group was almost non-existent in the diet (Appendix 1), although it was common in soil and moss vegetation. Other prey groups, e.g., *Coptoformica* species, *F. sanguinea*, and *Diptera* and *Coleoptera* species, were negligible in the summer diet (< 5% of biomass intake), and we were not able to reliably quantify their availability.

The availability of prey groups was not assessed in winter. However, the consistent feeding on *Serviformica* during snow-free periods indicates that they were preferred compared with *Diptera* and *Coleoptera* (Fig. 4). When *Serviformica* became inaccessible due to snow

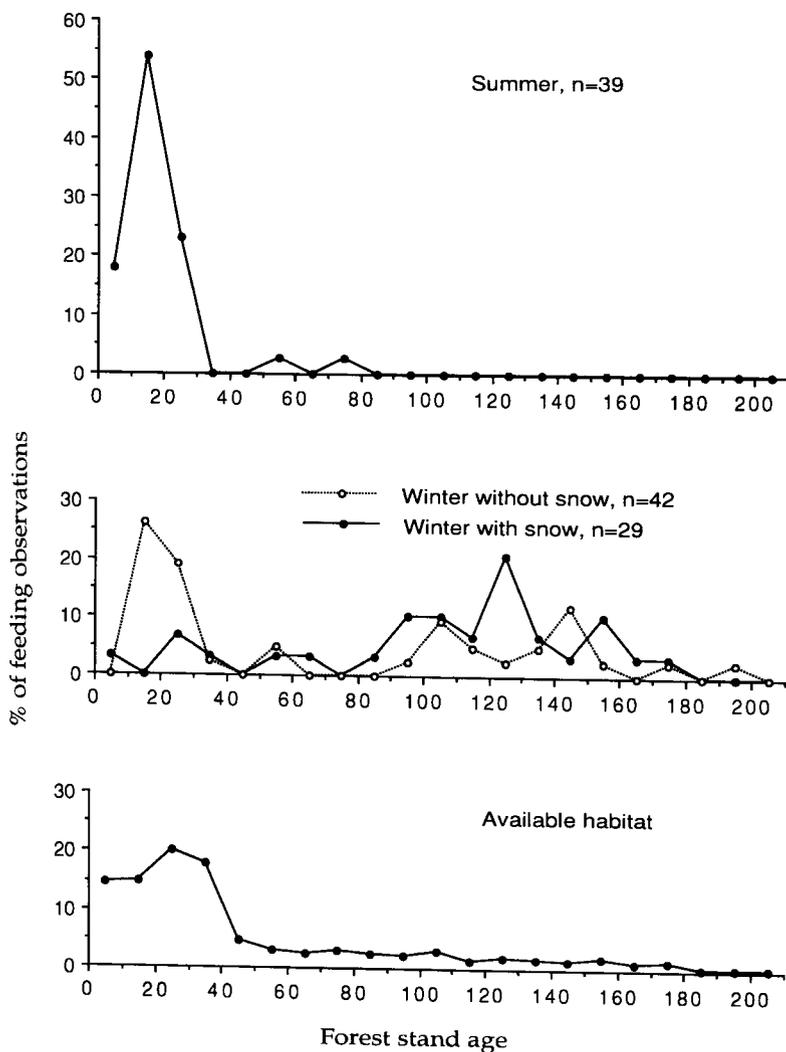


Fig. 7. Use and availability of forest stand age categories by feeding Grey-headed Woodpeckers.

and frost, birds first shifted to carpenter ants in pine bark. At snow depths exceeding 15 cm, the birds relied on *Diptera* and *Coleoptera* species (Fig. 5).

4.3. Habitat use

In summer, birds preferred young conifer plantations between 10 and 20 years old. Birds were feeding 4 times more often in this age class of the forest compared with availability (Goodness-of-fit: $G = 13.3$, $df = 1$, $P < 0.001$, $n = 39$) (Fig. 7). This habitat use coincided with the *Serviformica*-feeding (Fig. 8). In sharp contrast, birds preferred forest stands from 100 to 200 years old in winter (Fig. 7), both in periods with snow ($G = 21.4$, $df = 1$, $P < 0.001$, $n = 29$) and without ($G = 10.0$, $df = 1$, $P = 0.002$, $n = 42$). However, birds used old forests more often when snow covered the ground (test of homogeneity: $G = 5.8$, $df = 1$, $P = 0.02$, $n_1 = 29$, $n_2 = 42$), and in this period it was used 5 times more often than expected from availability. This coincided with the feeding on carpenter ants, and *Diptera* and *Coleoptera* species inhabiting old pines and dead trees (Fig. 8).

During snow-free winter periods birds utilized young plantations, and the age classes 0–30 years old were used 4 times more often than during periods with snow (test of homogeneity: $G = 10.8$, $df = 1$, $P = 0.001$, $n_1 = 29$, $n_2 = 42$) (Fig. 7). Compared with available habitat these age classes were used according to availability in snow-free periods (Goodness-of-fit: $G = 0.2$, $df = 1$, $P = 0.7$, $n = 42$), and avoided during periods with snow ($G = 10.7$, $df = 1$, $P = 0.001$, $n = 29$).

In summer a preponderance of the observations were in pine-dominated stands (Fig. 9), but it was not significantly different from availability (Goodness-of-fit: $G = 1.58$, $df = 2$, $P = 0.21$, $n = 33$). In winter we recorded a strong preference for pine-dominating stands ($G = 15.5$, $df = 1$, $P < 0.001$, $n = 70$) (Fig. 9), which corresponded to the feeding on carpenter ants in the bark of old pine trees.

Old pine and spruce forests (> 120 yr) covered 4 and 10% of the winter range (both sexes combined), respectively, and the stands were

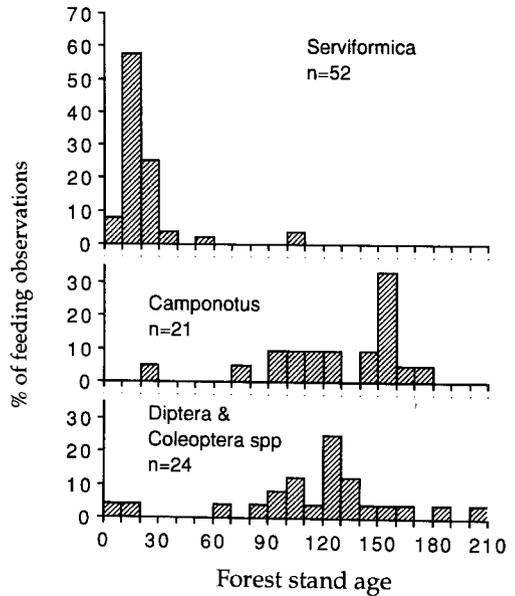


Fig. 8. Feeding sites of the Grey-headed Woodpecker in relation to main prey species and forest stand age.

highly fragmented (Fig. 10). When the birds were feeding on carpenter ants and insects in this habitat they moved restlessly from tree to tree, interrupted by longer flights between scattered old forest stands. When feeding on *Serviformica* in young forests, birds often stayed for hours and frequently revisited the same feeding site.

In summary, during summer the birds preferred young conifer plantations with easily accessible, large *Serviformica* colonies in soil and rotten wood. In winter they preferred 100–200 year old pine stands with scattered sources of carpenter ants, and old forest stands with dead trees hosting bark-dwelling *Diptera* and *Coleoptera* species.

4.4. Patterns of space use and movements

In summer the birds utilized fairly small ranges close to the nest (Fig. 1). Home ranges of the male and female at location A were 50 and 70 ha, respectively, whereas the male at location B used an area of 100 ha. During the period of nestling feeding the pair at location A collected food at a

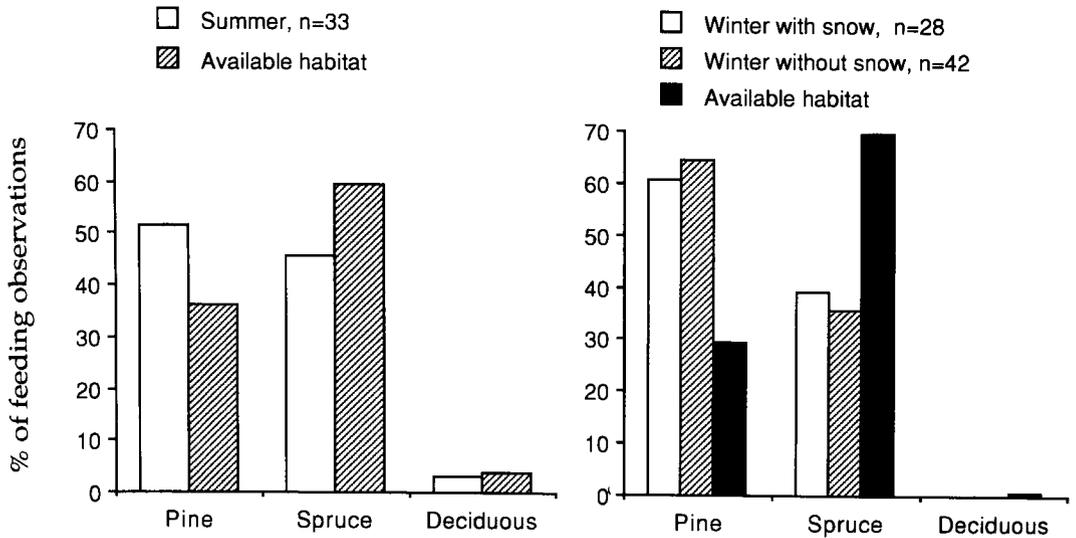


Fig. 9. Use and availability of forest stands, categorized by dominating tree species, by feeding Grey-headed Woodpeckers.

median distance of 365 m ($n = 60$ feeding bouts) from the nest. The shift to winter diet was accompanied by a marked enlargement of the home ranges, which increased about 100 times in size to 5 400 and 4 500 ha for the male and female, respectively, at location A (Fig. 1). Median distance between consecutive feeding observations was 2 515 m ($n = 38$) when the birds were feeding on carpenter ants and *Diptera* and *Coleoptera* species within old forest stands. During snow-free periods, when birds preyed upon *Serviformica*, the distance between consecutive feeding locations decreased significantly to a median 683 m ($n = 20$) compared to the old forest feeding activity (Mann-Whitney, $U = 534$, $P = 0.01$).

4.5. General discussion

Throughout snow-free seasons the Grey-headed Woodpecker relied on soil-dwelling ants as staple food. This is in agreement with the general notion that it is an ant-feeding, ground-dwelling woodpecker (Short 1982, Cramp 1985, Glutz von Blotzheim & Bauer 1980). Snow and frozen ground obviously prevented the birds from utilizing this abundant food source, and they shifted

to bark-dwelling carpenter ants and *Diptera* and *Coleoptera* species in winter. This agrees with the findings of Matsuoka and Kojima (1979), who reported that Japanese Grey-headed Woodpeckers shifted their diet from soil-dwelling ants to arboreal insects and spiders when snow covered the ground. Elsewhere, Grey-headed Woodpeckers also have been observed gleaning various insects from different substrates during the winter season (Collett 1921).

The shift in diet was accompanied by a corresponding shift in habitat use, which most probably reflected the availability of the different prey groups. Soil-dwelling ants are most abundant in younger successional stages (Punttila et al. 1991, own unpublished data), explaining the preference for 10–20 year old conifer plantations in summer and the use of this age class in winters without snow. At moderate snow depths carpenter ants dominated the diet. They were picked out from small galleries within the thick bark at the basement of old pine trees. Accordingly, birds preferred pine forests older than 100 years old. At larger snow depths and during longer periods with cold, birds were gleaning *Diptera* and *Coleoptera* species under the loose bark of dead trees. Such trees were most abundant in older stands, thus contributing to the old forest preference in winter.

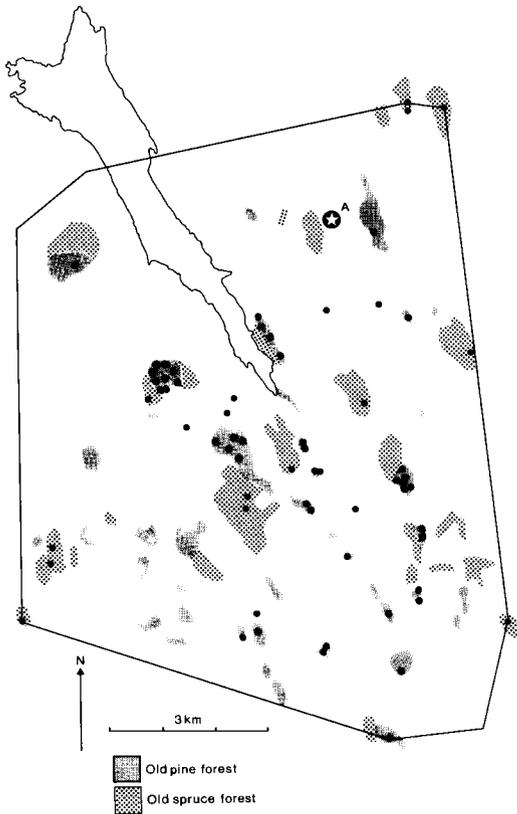


Fig. 10. Spatial pattern of the Grey-headed Woodpecker observations during winter while feeding on carpenter ants and *Diptera* and *Coleoptera* species. Observations of the male and female at location A are combined. The star denotes the nest location. Old pine and spruce forests are stands older than 120 years.

Along these lines, it is also tempting to explain the dramatic increase in home range size as a consequence of changed food availability. Snow-free winter periods also were accompanied by a marked decrease in daily movements. Winter prey groups may have been too sparse to support the birds within a restricted home range around the nest. Hence, they enlarged their range to encompass a fragmented habitat containing enough winter food for survival. However, it could also be that the birds in one way or another defended a kind of winter territory, to secure the availability of a variable winter food. Hogstad (1976, 1978) argues that this is the case for the Three-toed Woodpecker *Picoides tridactylus*,

although he did not report the size of the winter territories. Woodpeckers are relatively long-lived (7-10 yrs; Cramp 1985 and references therein), which may render “super-territories” (*sensu* Verner 1977) profitable. The 7 km distance between location A and B at Varaldskogen, and the consistent low density reported elsewhere within its range (see Cramp 1985), may indicate that the Grey-headed Woodpecker is winter territorial.

Why is the Grey-headed Woodpecker rare? Among boreal woodpeckers it has the highest production potential, with a clutch size of 7-9 eggs (Glutz & Bauer 1980). Ant-feeding behavior combined with the ability to regurgitate food to nestlings also imply that it has access to an abundant food source when breeding. This indicates that the Grey-headed Woodpecker rather should be a common species. Therefore, the reason for its rarity should be sought for in the winter situation. Two mechanisms may be at work, both of which are related to the winter food. Populations may suffer from high winter mortality, directly caused by food shortages. Accordingly, winter ranges should increase with decreasing availability of food. During mild winters, with access to soil-dwelling ants, survival should be higher and consecutive breeding densities should increase. Distance between nests should be highly variable with a minimum distance conforming to the breeding range (i.e., approximately 1 km according to our data). As a consequence, breeding numbers should be strongly correlated with previous years snow depth and temperature. Alternatively, the Grey-headed Woodpecker may claim large winter territories more or less independent of the actual food conditions. Adult survival should be fairly constant and breeding pairs should space out with a minimum distance set by the winter territories (i.e., 7 km according to our data). Surplus birds prevented from gaining territories should suffer high winter mortality. Accordingly, breeding densities should be weakly correlated to previous years weather conditions.

Anecdotal data from Finland lends support to the first hypothesis. At the southern (Helsinki) and western (Turku) coast of Finland, the density of Grey-headed Woodpeckers varies from 10-100 pairs per 10 000 ha (R. Virkkala and K. Ahola, pers. comm.). From the Upper Rhine

Valley in Germany, Spitznagel (1990) reports a breeding density of 35 pairs per 10 000 ha. These figures refer to temperate or coastal deciduous forest habitats with little or no snow during winter. In conifer forests in southcentral Finland, where snow regularly covers the ground, breeding density is roughly the same as in our study, i.e., 1 pair per 10 000 ha (R. Virkkala pers. comm.).

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Appendix

Appendix 1. Food items of the Grey-headed Woodpecker (N = 3 birds in spring and summer, N = 2 birds in winter) identified in faecal droppings (n = 194) and nest remains at location A at the Varaldskogen study area, southcentral Scandinavia, during April 1992-March 1993.

Prey group	Biomass (dry weight) g (100 ind.)	Spring n = 26	Nest	Summer n = 78	Winter		Total: Nest + n = 194
					without snow n = 40	with snow n = 50	
<i>Hymenoptera, Formicidae:</i>							
<i>Serviformica s.str.</i> ¹⁾	0.17	1567	3145	3082	2715	0	10509
<i>Lasius niger</i>	0.10	0	144	90	0	0	234
<i>Camponotus spp.</i> ²⁾	1.24	43	9	35	111	649	847
<i>Formica rufa</i> -group ³⁾	0.28	388	10	36	145	155	734
<i>F. sanguinea</i>	0.46	0	13	6	5	0	24
<i>Coptoformica s.str.</i> ⁴⁾	0.28	0	19	0	0	0	19
<i>Myrmicinae spp.</i> ⁵⁾	0.17	46	10	12	23	1	92
Ant pupae ⁶⁾	0.20	0	1494	414	0	0	1908
<i>Coleoptera</i> ⁷⁾	1.00	0	0	7	28	41	76
<i>Diptera</i> ⁸⁾	–	a)0% b)0%	c)– –	6% 46%	13% 44%	36% 56%	– –
Unidentified insects	–	0	0	0	0	0	10
<i>Sorbus aucuparia</i> (berries)	14.00	0	0	1	0	6	7
Total number of prey items		2044	4854	3683	3027	852	14460

¹⁾Mainly *Formica fusca* and *F. lemni*.

²⁾Including *Camponotus herculeanus* (dominant) and *C. ligniperda*.

³⁾Including *F. aquilonia* and *F. lugubris*.

⁴⁾Mostly *F. exsecta*.

⁵⁾Including *Myrmica* spp. and *Leptothorax* spp.

⁶⁾Ant group or species not specified.

⁷⁾Including *Myrrha octodecimguttata* (dominant) and *Thanasimus* spp.

⁸⁾Species in faecal droppings not identified. All checked feeding sites (n = 10) contained *Mycetophila caudata* (Staeger).

^{a)}Percent of faecal droppings containing *Diptera*.

^{b)}Percent *Diptera* (by biomass) in faecal droppings, excluding droppings without *Diptera*.

^{c)}The proportion of *Diptera* in the nest sample was not assessed.