Competition and habitat selection in two large woodpeckers

YRJÖ HAILA & OLLI JÄRVINEN

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Svärdson suggested in 1949 that *Dryocopus martius* and *Picus canus* compete. His hypothesis predicts that, when the density of one species changes, changes should be observed in the density and habitat selection of the other. During recent decades, the density of *canus* has increased on the island of Åland; simultaneously, the density of *martius* has considerably decreased and the range of its habitats has contracted. These conclusions follow from a comparison of census data from the 1920s with line transect data collected in 1975. Further censuses were made in 1976, on a small island group called Vargskär, 10—20 km east of Åland. The microdistribution pattern of the two species on Vargskär also suggests that competition exists between *canus* and *martius*. For example, the habitat range of *martius* is broader and its density higher on two islands where *canus* is absent than on one island where *canus* occurs. Causal relations are discussed, but no definite conclusions can be drawn.

Yrjö Haila, Fredrikinkatu 39 G 35, SF-00120 Helsinki 12, Finland
Olli Järvinen, Department of Genetics, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki 10, Finland

Introduction: Svärdson's hypothesis

In his monograph on the woodpeckers of the world, BLUME (1971:4) distinguishes between *Bodenspechte* and *Hackspechte*: for anatomical reasons, "je mehr z.B. eine Spechtart auf Hacken und damit auf festes Anklammern spezialisiert ist, desto schlechter klettert sie und umgekehrt." The two poles are naturally opposite ends of a continuum, and *Bodenspechte* and *Hackspechte* show us only the limits of woodpecker evolution. BLUME (p. 5) also refers to previous morphological studies, and gives evidence which suggests that the six Finnish woodpecker species should be ordered in the following series, from *Bodenspechte* to *Hackspechte: Picus canus, Dryocopus martius, Dendrocopos major, D. minor, D. leucotos, Picoides tridactylus.* During a survey of bird community structure in the Åland Islands, we studied the two first species, *canus* and *martius.* Both being classifiable as *Bodenspechte* and having similar ways of life, they promise to repay an investigation of their possible interaction.

In his classic review of habitat selection in birds SVÄRDSON (1949) noted that the Black Woodpecker *Dryocopus martius* seems to have filled the niches of the Green Woodpecker *Picus viridis* and the Grey-headed Woodpecker *P. canus* on the island of Gotland, where the two *Picus* species do not occur. On Gotland, *martius* is "more common than everywhere else in south Sweden and it also breeds in deciduous trees more often than on the Swedish mainland" (SVÄRDSON 1949:159). SVÄRDSON (p. 172) points out that Gotland could provide a good opportunity to elucidate the problems of competition in birds: if *canus* were introduced, it would be possible to study the effect on *martius* and to determine whether the absence of *viridis* makes any difference to *canus* or not. Although the southernmost parts of Finland are climatically and biogeographically similar to the areas inhabited by *viridis* in Sweden, *viridis* is absent and *canus* is present; thus *viridis* has evidently a strong adverse influence on *canus* (SVÄRDSON 1949:159).

SVÄRDSON's observation that *martius* has filled the niches of *viridis* and *canus* on Gotland implies that not only do the two *Picus* species compete, but that competitive interaction also occurs between these two species and *martius*.

To our knowledge, Gotland has not yet been used by ornithologists to make "a giant long-time field experiment" (SVÄRDSON 1949:172) — both *Picus* species are still absent. Instead, Nature has accomplished part of the experiment on the Åland Islands, about 300 km N of Gotland. Below, the largest island of this group is called the *mainland* of Åland (Sw. Fasta Åland) and the name *Vargskär* refers to the northern parts of the commune of Föglö, 10—20 km E of the mainland. Vargskär comprises exceptionally luxuriant islands with rich stands of southern deciduous trees (A. PALMGREN 1950).

The mainland of Åland

The mainland was studied ornithologically several decades ago. SNELLMAN (1929) reported that *canus* was very rare (p. 38: "En raritet härute.") and P. PALMGREN (1930) did not find the species at all in his extensive censuses. Thus, *canus* must have been very sparse on the Åland Islands in the 1920s (see also v. HAARTMAN et al. 1963—72:611), and possibly occurred only occasionally, not as a regular member of the avifauna (P. PALMGREN 1946 lists *canus* as absent from the Åland Islands).

In contrast, v. HAARTMAN et al. (1963—72:630) mention that *martius* has always been particularly typical of the Åland mainland. The censuses of P. PALMGREN (1930) support this claim, though it is difficult to estimate the densities exactly. They range from 0.5 pairs/km^2 to 3 pairs/km^2 in the main forest bird communities described by P. PALMGREN (1930:173—175), except in the relatively infrequent *Laubwiesen*, where *martius* was absent. As forests cover more than 50 % of the whole land area of the Åland Islands (e.g. P. PALMGREN 1935, KALLIOLA 1973), the average density on the Åland mainland may be estimated at about 1 pair/km^2. This is about 10 times the density typical of S Finland, 0.1 pairs/km^2 (MERIKALLIO 1958).

Thus *martius* appears to have been unusually abundant on the Åland mainland in the 1920s. Its previous habitats are known in some detail. P. PALMGREN (1930) reports 10 observations from his study area censuses: 3 from luxuriant deciduous forests, 5 from OMT forests (which are relatively productive, usually dominated by spruce) and 2 from pine forests growing on rocky hills.

The density of *canus* in 1975 may be estimated from the line transect censuses of HAILA (1976), which cover more than 170 km (9300 pairs of land birds observed). The linear model of JÄRVINEN & VÄISÄNEN (1975, JÄRVINEN 1976) gives the present average density of *canus* as 0.15 pairs/km^2. MERIKALLIO (1958) does not give any figures for the Finnish population of *canus*, but our estimate is certainly high compared with the density on the Finnish mainland (cf. the density of *martius* in southern Finland, above). According to SVÄRDSON's (1949) hypothesis, the density of *martius* should have decreased. (This does not imply that *canus* has driven out *martius;* it is equally possible that *martius* has decreased and *canus* has then increased.) In fact, the present average density of *martius* is 0.10 pairs/km². The dominance relationship of the two large woodpecker species has thus been reversed during the past half century. According to the results of winter bird counts, the increase of *canus* has been especially rapid in the 1970s (L. Laine, pers. comm.). Only two *martius* individuals were seen in the main belt of the line transect censuses of HAILA (1976): one of the observations came from OMT forest and the other from coniferous (mostly pine) forest on rocky hills. No observations were made in deciduous forest, even during the field excursions which took place after the censuses. The two *canus* seen in the main belt during the censuses occurred in luxuriant deciduous forest. The trends observed thus agree with SVÄRDSON's hypothesis.

Vargskär

In 1976 we both made censuses on 21 mostly small islands in Vargskär. Woodpeckers (Picinae) were found on three of the four largest islands. Table 1 gives the estimated densities of *canus* and *martius* (the linear model of JÄRVINEN & VÄISÄNEN 1975 used here too). The Great Spotted Woodpecker *Dendrocopos major* was observed only once (on Bänö), but its populations fluctuate strongly and no definite conclusions should be drawn from its scarcity on Vargskär. The data for the two large woodpeckers can be interpreted as follows.

TABLE 1. Densities (pairs/km²) of *Picus canus* and *Dryocopus martius* calculated from line transect censuses made on the four largest islands of Vargskär in June 1976. Seventeen smaller islands (up to 0.4 km²) without woodpecker records were interpreted as unsuitable for woodpeckers, and omitted in the calculations of average densities.

Island	Area (km²)	Censused (km)	Density	
			canus	*martius*
Ulversö-Överö	5.8	4.8	—	0.6
Nötö	3.6	4.2	—	—
Bänö	2.9	3.7	2.4	0.3
Mjölkö	1.1	1.5	—	0.6
Vargskär	13.4	14.2	0.17	0.10

First, it should be noted that the density estimate of *canus* is influenced by the large sampling variance, because the detectability coeffiecient *k* (see JÄRVINEN & VÄISÄNEN 1975, JÄRVINEN 1976) is very high. In consequence, each observation affects the estimates considerably, unlike the case with *martius,* whose *k* is quite low. We observed *canus* only once on Vargskär; one observation more would have yielded an estimate of 0.34 pairs/km² for the island group. Thus the high density of *canus* in Table 1 is not significant. As we did not find the species on any of our numerous excursions during one month (between 30 May and 7 July, 1976), *canus* is clearly rarer than *martius* on Vargskär.

Second, we may look at the densities found on single islands. On two islands where *canus* is absent the density of *martius* is high, as in P. PALMGREN's (1930) time on the mainland of Åland. As we were living on Ulversö-Överö, the absence of *canus* from that island is fairly certain. On Mjölkö also, the most likely habitats of *canus* were studied during a fairly long excursion after the census. The only *canus* island showed a lower density of *martius* than the two other *martius* islands. The census and the additional excursions failed to reveal any woodpeckers on Nötö, which is remarkable, because we believe that all the three species observed on the other islands could find suitable breeding habitats there.

We suggest the following interpretation of the density pattern: *canus* has been able to invade some islands in the area, and the densities of *martius* have decreased on these islands before or after the invasion of *canus;* further, *martius* (and other species) may be absent from some of the islands owing to chance extinction (e.g. MACARTHUR & WILSON 1967). This explanation is clearly derived from SVÄRDSON's (1949) hypothesis.

The above explanation is supported by data on the habitat range of *martius* on Vargskär. During numerous excursions on Ulversö-Överö, we often observed *martius* not only in pine-dominated forest, but also in luxuriant deciduous forest. The observations on the other islands came from pine(-dominated) forest. The wide habitat range of *martius* on Ulversö-Överö recalls the situation on Gotland or, in previous times, on the mainland of Åland.

Our data are admittedly scanty. Further studies should be made to elucidate the microdistribution pattern in other island groups.

Concluding remarks

The subject of competition between *martius* and *canus* has not been studied in detail since SVÄRDSON (1949), but ALATALO's (1975) calculations are of interest in this connection. He collected data on six Finnish woodpecker (Picinae) species, recording six environmental variables: date, commune, tree species, height of bird on tree, quality (alive/dead) and part of tree where bird was feeding (trunk/ branches and twigs). He then measured niche overlap by standard methods and found that the pair of species overlapping most was *martius* and *canus.* Wide niche overlap on a gradient is a necessary, even if not sufficient condition of strong competition. We may add that the two species are ant specialists (PYNNÖNEN 1943, BLUME 1966) and that they are certainly not geographical replacements. (The Three-toed Woodpecker *Picoides tridactylus* was also closely associated with *martius* and *canus* in ALATALO's niche matrices, but it is not an ant specialist; it differs morphologically, being a typical *Hackspecht* (see Introduction); it is relatively northern; and it is also quite small compared with *martius* or *canus,* needing smaller holes for roosting).

The scarcity of reports of behavioural interaction between *martius* and *canus* (e.g., see the recent review of HURME & SARKANEN 1975) suggests that "interference competition" is absent, i.e. fighting, etc. Sometimes *martius* responds to the calls of *canus* (v. HAARTMAN et al. 1963—72:612), but the ecological significance of this observation is obscure. HILDÉN (1955) observed that *canus* may also follow *martius,* perhaps because foraging is easier in a tree stump broken by *martius.* It is possible that *canus* reduces the food available for *martius* in deciduous forest, so that *martius* excludes *canus*-inhabited forest from its range of foraging habitats. This takes no account of the effect of *martius* on *canus.* If it is nil, the relationship between the two species should be designated as amensalism. On the other hand, it is possible that *martius* must first decrease if *canus* is to invade.

Modern forestry, one of the unknown variables in the problem, may lead to the decrease of *martius*.

The modern theory of competition (see May 1976; for a Finnish review of the subject, see Hanski & Järvinen 1977) does not identify competition with the occupation of identical niches, or suggest that competitive interaction prevents coexistence. It is necessary to ask whether the *degree* of niche overlap of two species is tolerable, and *how much* the overlap affects the populations of the competitors. The main argument used by Udvardy (1951:111, 115) against Svärdson's (1949) hypothesis is that *martius* and the two *Picus* species often coexist, but while true, this does not disprove the existence of competition. Ornithologists (e.g. v. Haartman et al. 1963—72:611) now seem to agree that the two *Picus* species compete, although this was also questioned by Udvardy (1951:111).

In summary, there is evidence (Svärdson 1949 and this paper) that the patterns of density and distribution in *martius* and *canus* are so often correlated that chance seems to be excluded. (Most observations are from islands, which suggests that the patterns are less clear on the mainland, owing to constant dispersal of the woodpeckers.) The mechanism of the suggested competition is still obscure. Do both species affect each other? Do they compete for food? Or suitable trees? Is competition important in all years? Or in all seasons? Does modern forestry play an important role? Do differences in the dispersal ability of the species affect the dynamics of woodpecker competition — could the poor dispersal ability of *canus* explain why its recent expansion on the mainland of Åland has not been followed by a similar expansion on Vargskär?

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Selostus: **Palokärjen ja harmaapäätikan kilpailu ja elinpaikan valinta Ahvenanmaalla**

Svärdson (1949) arveli Gotlannin havaintojen perusteella, että palokärki ja *Picus*-suvun tikat ovat jonkinlaisessa kilpailusuhteessa. Ahvenanmaan pääsaarella harmaapää on viime aikoihin asti ollut harvinaisuus, mutta vuoden 1975 laajojen linjalaskentojen perusteella sen tiheys näyttää ylittäneen Etelä-Suomessa tavallisen palokärjen tiheyden 0.1 paria/km^2. Samaan aikaan palokärjen tiheydet ovat laskeneet — 1920-luvulla pyöreästi 1 pari/km^2, nykyisin 0.1 paria/km^2 — suunnilleen eteläsuomalaiselle tasolle. Myös palokärjen elinpaikkojen valikoima näyttää kavenneen: 1920-luvun havainnoista huomattava osa on peräisin lehdoista, mutta kaikki vuoden 1975 havainnot tehtiin havumetsävaltaisilla biotoopeilla. Vuonna 1976 Föglön kunnan pohjoisosissa ("Vargskär") tehdyt laskennat täydentävät kuvaa. Taulukossa 1 on esitetty lajien tiheydet suurimmilla saarilla; 17 pienemmällä saarella ei havaittu ainoatakaan tikkaa. Koska laskentojen lisäksi eri saarilla — varsinkin Ulversö-Överöllä — on retkeilty runsaasti, näyttää jokseenkin varmalta, että harmaapään yleistiheys on selvä yliarvio. Tähän on syynä tekstissä lähemmin selvitetty tiheydenarviointimenetelmän tekninen ominaisuus. Kahdella suurehkolla saarella tilanne vastaa kaikin puolin Ahvenanmaan mannerta puoli vuosisataa sitten, kun taas kolmannella — ainoalla saarella, jolla harmaapää havaittiin — palokärjen tiheys on selvästi alhaisempi ja vastaa Ahvenanmaan nykytilannetta. Ilmeisestikään ns. häiriökilpailu (aggressiivisuus lajien välillä jne.) ei tule kysymykseen varteenotettavana selittäjänä. On mahdollista, että harmaapää pystyy käyttämään hyväkseen lehtomaisten metsien resursseja niin tehokkaasti, että palokärjen kannalta lehtomaiset metsät käyvät liian huonoiksi elinpaikoiksi, mutta esim. metsänhoidollisten toimenpiteiden vaikutus kumpaankin lajiin ja niiden väliseen suhteeseen on hämärä. Havaitun korrelaation syy- ja seuraussuhteet jäävät näin ollen avoimiksi.

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