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Methodology for studying the minimum habitat requirements of forest birds

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We discuss methodological problems in assessing the minimum requirements of breeding birds in a mosaic-like forest patchwork, created by modern forestry. In a small-scaled mosaic, the area of the habitat patches is not necessarily the most important characteristic to be measured — the birds may include several patches of different habitat types in their territories. We propose the following survey method, applicable within a region with characteristic habitat types: Locations of bird territories in different types of environments are mapped over several years and "frequency landscapes" constructed that show how frequently various habitat patches have been included within the territories of different species. Minimum combinations of habitats required by the species can then be identified, and detailed population studies directed at species that are threatened because of human-induced habitat changes.

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1. Introduction

In this paper we focus on using census data in assessing the effects of human-induced habitat changes on the bird fauna. Our study area is in the southern part of the Finnish coniferous forest, the taiga. As a consequence of human exploitation, southern Finnish forests are habitat mosaics that consist of mixtures of successional stands, and primeval forests have shrunk to small fragments isolated from each other by managed expanses. The aim of our field work is to evaluate the minimum requirements of forest birds as regards the structure and composition of habitat in their breeding environments in forest mosaics.

There are theoretical reasons for expecting that habitat fragmentation influences the composition of local bird faunas (MacArthur & Wilson 1967). A straightforward application of the theory of island biogeography to migratory birds such as those residing in the taiga is problematic, however (Haila et al. 1982, Haila 1983, 1986a). This is because immigration and extinction, key variables in the theory, lack meaning as population concepts when applied to a few pairs of migratory birds breeding in non-isolated habitat fragments.

Adherence to the MacArthur-Wilson equilibrium interpretation, even in situations where it is not applicable, results in conceptual problems (for examples, see Haila 1986b). An alternative theoretical framework is needed. We continue in the next section by elaborating upon the conceptual aspects in more detail, and present in subsequent sections methodological conclusions derived from our field experience.

2. Minimum habitat vs. minimum area requirements

"Minimum area requirements" is a familiar term in studies concerning habitat fragmentation. The idea is simple: as species number decreases with decreasing area of islands or habitat patches, one may think that each species is characterized by an inherent requirement of a minimum area, being excluded from habitat fragments smaller than this (see, e.g. Whitcomb et al. 1981).

The term "minimum area requirements" is fraught with theoretical problems, however. First, the level of ecological organization at which the term is applied is usually not made explicit. This is confusing because it has widely different meanings at the *population level* vs. the *individual level*. At the population level the term refers to a (relatively) closed local population that is entirely confined to a particular area. The survival of such a population depends on its size, as the probability of a chance extinction is higher the smaller the population (MacArthur & Wilson 1967); consequently, a viable population needs a certain minimum area (for a review of the problem, see Gilpin & Soulé 1986).

While this setting is realistic for birds in the tropics that often have a weak dispersal ability (Diamond 1975), it is not plausible for birds in the temperate or boreal zones. Most of the birds in the north are migratory and the majority of the others are efficient dispersers. At the population level northern birds are not confined to contiguous habitat "islands".

A positive correlation is, of course, commonly observed between the number of breeding bird species and the area of forest fragments in temperate and boreal zones (for recent reviews and references, see Wilcove et al. 1986, Askins et al. 1987). However, declining species numbers with fragment area do not demonstrate actual impoverishment of assemblages in small fragments because this trend is a "null" expectation even in random sampling (Connor & McCoy 1979; for data on northern birds, see Haila & Järvinen 1983, Järvinen & Haila 1984, Haila 1986a). The pattern of variation in species numbers in non-isolated habitat patches as a function of area is an epiphenomenon, resulting from the way populations and species assemblages vary in space (Williamson 1981, Haila 1983). Moreover, the characteristics of habitat fragments change regularly with area, which certainly influences bird assemblages as well ("area-mediated changes", as identified by Ambuel & Temple 1983).

At the individual level, in contrast, the term "minimum area" refers to the minimum area a pair needs for successful reproduction. In this sense minimum area requirements are real in all biogeographic zones alike. Territory size in birds, for instance, may be a factor precluding successful breeding in too small habitat fragments.

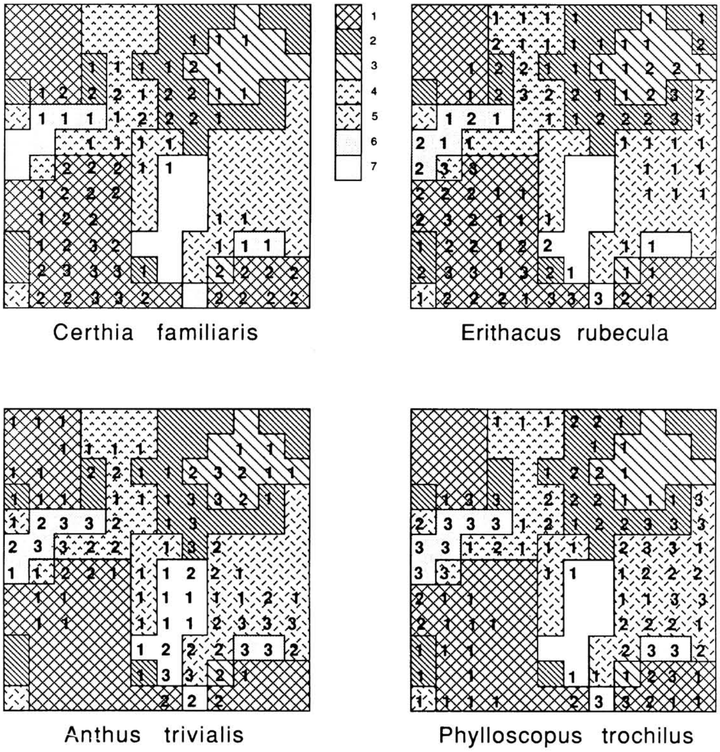
However, there is a conceptual problem of another kind involved in using the term minimum *area* requirements at the level of individual pairs. An emphasis on area implies that habitats are uniform, i.e., that area is the most important characteristic of breeding habitats. This is unrealistic. Habitats are mosaics of patches with variable characteristics, and birds breeding in habitat mosaics include patches of different types in their territories. This is evident in the case of species that nest in woods and forage on open ground, but may be true of forest residents as well (e.g. Haila & Hanski 1987).

Several combinations of different habitat patches may fulfil the requirements of individual bird species in a mosaic environment. A "null" expectation is that breeding sites vary from year to year, which results in "turnover" in species composition at any particular locality (Haila 1988). This effect is accentuated if the relative favourability of different microhabitats varies from year to year, e.g., in terms of food availability, or if bird populations fluctuate at the regional level due to factors other than the sum total of habitat available (i.e., suitable breeding habitats are not "saturated" by birds). Between-year variation in the way in which birds establish territories in habitat mosaics is one reason why habitat characteristics and the composition of breeding communities often disassociate (Verner et al. 1986).

The distinction between the population level and the individual level is not absolute, but they may grade into one another on the scale of a network of habitat patches which is inhabited by a (relatively) closed local population. The total amount of suitable habitat available for the whole population is important (Haila 1986a, Askins et al. 1987). The total range of the population may, moreover, be confined to a fairly small area although not to a single continuous habitat tract. Such a situation was demonstrated by Pettersson (1985) in his analysis of the recent extinction of the Swedish population of the middle spotted woodpecker (*Dendrocopos medius*).

When defining the minimum requirements of birds breeding in a mosaic-like patchwork of different habitats, "minimum area" is not an adequate unit to be interested in. We prefer the term *minimum habitat requirements*. The term refers to the needs of individual breeding pairs, and incorporates all the various aspects in the relationships between breeding birds and their habitat needs.

Evaluating the minimum habitat requirements of particular species must, naturally, be based on field data, but interpreting the data presents methodological challenges that result from the theoretical problems discussed above. First, an unknown amount of stochasticity is inherent in year-to-year site selection patterns. As a consequence, a "snapshot" picture of how breeding pairs are distributed in a single year over a habitat mosaic may be misleading. Secondly, the pairs observed are sustained only as a part of a



Certhia familiaris

Erithacus rubecula

Anthus trivialis

Phylloscopus trochilus

Fig. 1. A 36-ha study plot in the Seitseminen National Park; the picture is based on detailed habitat descriptions made in 10 m squares (see text). The blocks with different shading indicate the following, approximately uniform habitat types: 1 = tall (>25 m) spruce-dominated; 2 = high (about 20 m) mixed coniferous; 3 = high pine-dominated; 4 = medium high (about 15 m) mixed coniferous; 5 = pine sapling (<10 m); 6 = birch sapling; 7 = peat bog. Numbers on the maps show the number of years (out of three) different 1/4 ha squares of the plot were included in territories of the treecreeper, robin, tree pipit and willow warbler, respectively.

local population that can, however, be unambiguously defined only in exceptional situations. The difficult methodological problem follows that patterns observed in the data on the individual level may not reflect important population processes (e.g. Wiens & Rotenberry 1981, Van Horne 1983).

3. What kind of data are needed?

All habitats are mosaics of different patches at some level of resolution. Whether this matters or not in a particular situation depends on the size of habitat patches relative to the requirements and movements of the birds studied (Addicott et al. 1987).

We demonstrate our own research setting more concretely in Figs. 1 and 2. Fig. 1 shows habitat configurations in a study plot of 36 ha established within the Seitseminen National Park (61°55′N). About one third of the area is covered by primeval, spruce-dominated taiga (more than 120 years old), other parts comprising younger stands with recent traces of management, and small peatlands. We made detailed habitat descriptions of the plot in 10x10 m squares. Using 1/4 ha as a minimum unit and height and the species composition of tree stands as a criterion, the plot can be divided into 21 habitat blocks, indicated in Fig. 1. Thus, a typical patch of forests of different type in the plot is 1–5 ha. This scale of heterogeneity is representative of the whole national park, as shown by topographic maps and aerial photographs.

Fig. 2 shows similar habitat configurations in an area outside the national park, named by us "Forest island" (area S24 in Haila et al. 1987). The area is under intensive economic management. It comprises a forest fragment of 4.4 ha, surrounded by sapling stands that originated in clear-cuts in the late 1970s. Clear-cut areas are, naturally, originally homogeneous as regards tree stands, but become differentiated according to topographic details (which influence soil quality and moisture) and silvicultural measures. A moist depression on one side of Forest island is covered by a patchwork of young coniferous

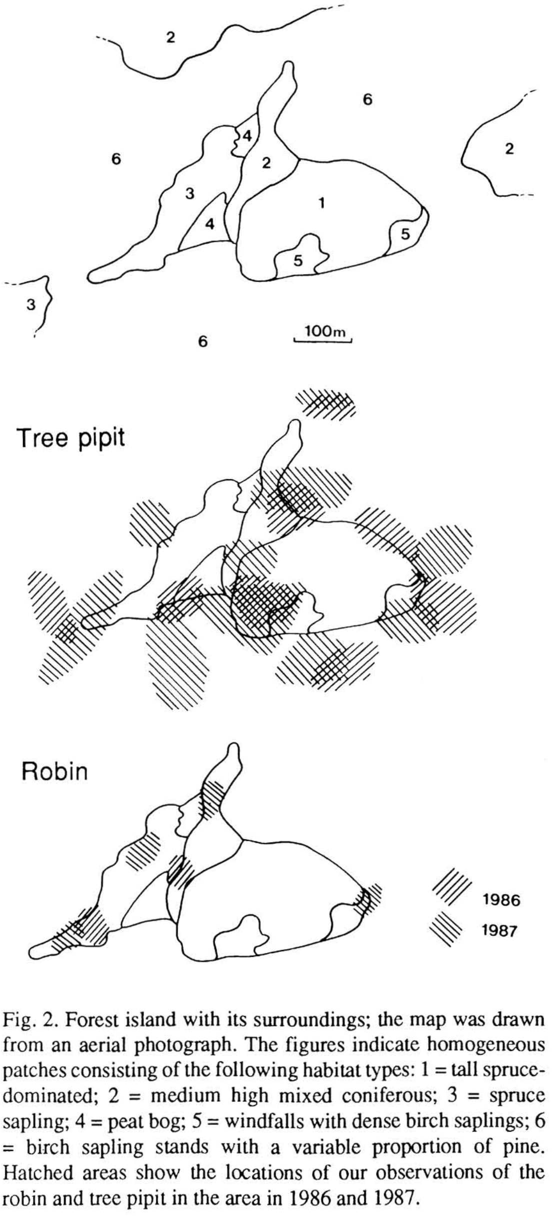


Fig. 2. Forest island with its surroundings; the map was drawn from an aerial photograph. The figures indicate homogeneous patches consisting of the following habitat types: 1 = tall spruce-dominated; 2 = medium high mixed coniferous; 3 = spruce sapling; 4 = peat bog; 5 = windfalls with dense birch saplings; 6 = birch sapling stands with a variable proportion of pine. Hatched areas show the locations of our observations of the robin and tree pipit in the area in 1986 and 1987.

stands. Homogeneous sapling stands often extend over tens of hectares in recent clear-cuts, but they are interrupted by networks of forests and scrub with a typical patch size of less than one hectare.

It is clear that data demonstrating merely the presence or absence of bird species in different patches — that is, data collected by one-visit censuses, even when observations are registered on a map — are completely inadequate for describing the minimum requirements of birds in environments such as those shown in Figs 1 and 2. Mere records of the "presence" of birds in particular habitat patches are of little use if we do not know what the breeding status of those birds is. This is also true of singing records: It is commonplace for birds to favour singing posts that may be far from their nests and separate from areas they use for foraging.

Reliable data on the actual location of bird territories in a habitat patchwork are clearly needed. Territory mapping ideally provides such data. However, there are potential pitfalls involved in interpreting mapping data. Density calculated per habitat patch is a misleading unit in cases where birds include several patches of different habitats in their territories. A single patch may include only a part of the territory, and the density estimate becomes inflated as a consequence of too small a denominator. Average densities per patch type are unrealistic and unreliable in mosaic-like habitats (Scherner 1981, Haila 1988).

Another problem with standard mapping is that it is, in practice, based on singing records but the birds may move around and forage in different areas when silent. This has become manifest in our radio-tracking of movements of individual chaffinch (*Fringilla coelebs*) males in the study plot shown in Fig. 1 (Hanski & Haila 1988, and unpubl.). Chaffinch males forage regularly throughout the breeding season in areas more than 1000 m off from their singing territories, and their "home ranges" include habitats (e.g., sapling stands, bogs) where one would hardly expect to find singing chaffinches.

These results on the use of space in the chaffinch are presumably applicable to several other forest species as well, as can be concluded from frequent observations of birds flying among habitat patches made during the censuses (see also Helle 1984). In other words, a forest stand where a particular bird male is observed singing does not equal its "minimum habitat requirements" because its home range may include surrounding habitats or be composed of a set of disjunct habitat patches.

An ultimate problem in drawing conclusions about habitat suitability from any kind of census data is that numbers of pairs do not necessarily reflect reproductive success, a basic measure of habitat suitability (Van Horne 1983). This is the case, for instance, in a "source-sink" situation in which a portion of a local population (in a "sink") is unable to reproduce successfully but is sustained by immigrants from a surrounding "source" (Wiens & Rotenberry 1981).

To conclude, for assessing reliably minimum habitat requirements we ought to have data on variation in reproductive success within local populations of birds as a function of habitat structure. For obvious reasons, this goal lies far ahead. A first substitute would be data on movements of individual birds in their home ranges in different types of environments throughout the breeding season. While radiotracking is technically feasible even for fairly small passerines, it is extremely time-consuming and can be applied only to one species at a time. A detailed territory-mapping with as good records on the location of territories as possible (not only estimates of numbers of pairs) seems the only available method for a survey covering the whole breeding fauna of an area. Data from several years are absolutely necessary in surveys, however, as discussed in the next section.

4. "Frequency landscapes" of territory selection

The amount of stochastic variation in the site selection of individual birds can be empirically estimated by comparing territory locations within a plot between years (Danilov 1980, Haila & Hanski 1987, Palmgren 1987), and by recording variations in territory size (Wiens et al. 1985). In Fig. 1 we demonstrate this effect within our study plot (see also Palmgren 1987). Using data from the years 1985–1987 we drew contour maps indicating how regularly different parts of our 36 ha study plot have been included within the singing territories of individual species, as revealed by territory mapping. Both forest-dwelling species, such as the treecreeper (*Certhia familiaris*) and robin (*Erithacus rubecula*), and residents of more open and bushy habitats such as the tree pipit (*Anthus trivialis*) and willow warbler (*Phylloscopus trochilus*), show similar patterns. Only a few parts of the plot have been inhabited in each of the three years.

Fig. 2 shows similar maps summarising territory locations of the robin and tree pipit in the surroundings of Forest island in 1986 and 1987. A similar variation to that in the study plot is apparent.

The frequency of a habitat patch being included in the territory of a particular species over a number of years is a natural measure of the relative preference the species shows for that patch. Contour maps such as those shown in Figs. 1 and 2 can be viewed as frequency lanscapes of habitat selection over a habitat mosaic. The prefered patches are presumably inhabited frequently, whereas variation in poorer habitats should be more pronounced, according to the classic buffer effect (Kluyver & Tinbergen 1953; see also Fretwell & Lucas 1970, O'Connor 1987).

Figs. 1 and 2 suggest that the method of constructing "frequency landscapes" is applicable within one plot, although data for many more years are needed to draw conclusions on the habitat correlates of sites favoured by different species. We believe that the approach can also be used for comparisons involving larger areas with varying habitat characteristics within the same region. For instance, we expect that numbers of pairs of forest birds vary less from year to year in our forested study plot (Fig. 1) than in the sapling mosaic surrounding Forest island (Fig. 2).

Birds may be able to track year-to-year variation in the relative quality of different habitats in their territory selection. This would be a deterministic factor causing changes in territory locations. The assumption is feasible. For instance, Haapanen (1965) observed that variation in the melting of snow in spring may influence the selection of nesting habitats by chaffinch males. Such a possibility only underlines the need for the censuses to extend over several years.

If the surveys representatively cover the variation available in habitat patchworks on a regional scale, the "frequency landscapes" obtained provide information on the minimum combinations of different habitat types acceptable to different bird species. This is what we mean by *minimum habitat requirements*. The measure is a relative one, because measures of habitat requirements must be related to what is actually available to the birds.

This qualification means, however, that the method of "frequency landscapes" is only applicable *within* local populations, where — ideally — individuals can mix within a few generations and freely choose from among all available environments each year. The method describes the actual habitat choice of the birds at the individual level and assumes that all individuals are identical. This assumption is not feasible for long-lived site-tenacious species (O'Connor 1987). The "source-sink" structure discussed above would also complicate the picture, and so would heritable differences in habitat preferences among individuals. These reservations again emphasize the need for long-term data in studying the dynamics of habitat use.

5. Birds in a mosaic of managed taiga

Our breeding bird censuses in the Seitseminen area since 1985 have thus far covered fairly extensively both mature forests of various ages and sapling mosaics. The time span covered by the censuses is too short for the drawing of reliable conclusions about minimum requirements. However, our data allow a preliminary classification of the bird species according to the role that extensive sapling mosaics play in their reproductive cycle. On the basis of our data we have defined four classes, and below we give examples of species belonging to each of them:

1) A few species breed in higher numbers in sapling mosaics than in mature forests. Representative species in this category are the tree pipit (*Anthus trivialis*) and willow warbler (*Phylloscopus trochilus*).
2) Several species usually regarded as forest birds breed regularly in sapling mosaics, but we lack detailed data on their territory size and reproductive success in mature vs. young forests that would permit an assessment of the relative suitability of the two environments. The species include, e.g. the dunnock (*Prunella modularis*), robin (*Erithacus rubecula*), song thrush (*Turdus philomelos*), redwing (*T. iliacus*), and brambling (*Fringilla montifringilla*).
3) Some forest species are commonly observed moving around in sapling mosaics throughout the breeding season but breed predominantly or exclusively in mature forests. This group includes, e.g., the great spotted woodpecker (*Dendrocopos major*), willow tit (*Parus montanus*), great tit (*P. major*), jay (*Garrulus glandarius*), chaffinch (*Fringilla coelebs*) and siskin (*Carduelis spinus*).
4) A few species are hardly ever observed in sapling mosaics during the breeding season. The list seems to be short, the wood warbler (*Phylloscopus sibilatrix*), chiffchaff (*Ph. collybita*), goldcrest (*Regulus regulus*) and treecreeper (*Certhia familiaris*) being the species included.

6. Concluding remarks: toward a research strategy

It seems that forest birds are a highly heterogeneous group concerning their minimum requirements in a habitat mosaic created by modern forestry. A few sensitive species have most probably already declined in our study area owing to changes in forest structure. Species such as the capercaillie (*Tetrao urogallus*), three-toed woodpecker (*Picoides tridactylus*), and crested tit (*Parus cristatus*) seem to favour primeval forest stands, and they are presumably affected by the decrease in the area of old forests. Winter may be critical for sedentary birds of the taiga.

A lingering threat toward a population should preferably be detected before any catastrophic changes take place. Defining the minimum habitat requirements of different species would be helpful for this purpose: If human-induced changes in the environment tend to impair the habitats available to a species, a population decline will certainly take place in the future. The capercaillie is an example of a species that has declined in northwestern Europe in recent decades because forests modified by intensive silviculture do not match its minimum requirements (Angelstam & Ringaby 1987, Lindén & Pasanen 1987, Rolstad & Wegge 1987). The capercaillie also demonstrates the need of detailed autecological data for reliable conclusions on minimum requirements: The whole life-cycle must be covered, crucial requirements of the capercaillie including lek sites, feeding areas for chicks, and high-quality forage in the winter.

Below we propose steps that would make up a research strategy toward assessing the minimum habitat requirements of birds. The first step is a survey of population distributions over different environmental types within the region studied. This indicates the regional abundances and gross habitat preferences of different species (see also Haila & Hanski 1984). The conclusions cannot be automatically extended to other regions because habitat requirements may vary according to the regional proportion of different environmental types (Collins 1983). The next phase is a mapping survey that extends over several years and covers study areas representing all relevant environmental types in the region. The aim of the survey is to construct "frequency landscapes" of habitat selection of the species. The frequency landscapes indicate which parts of the available habitat range are inhabited by various species. Species are thus pinpointed that are potentially endangered owing to a lack of suitable habitats. The final step comprises intensive population studies on these species.

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