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Methodology for studying the effect of habitat fragmentation on land birds

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Methodological problems of censusing land birds in archipelagoes of habitat fragments on the basis of practical experience from the Åland archipelago are discussed. Two main conclusions arise: (1) Quantitative data must be used; and (2) the scale of the census work must match the scale of the processes that are studied. Even when peculiar patterns are observed in the distribution of some species in habitat archipelagoes, the importance of habitat fragmentation *per se* as an ecological factor can be assessed only after competing explanations have been ruled out.

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1. Introduction

Fragmentation of formerly continuous habitats is a dominating theme in man-modified environments. The consequences of this process for nature conservation have been widely discussed in the ecological literature (see, e.g., Soulé & Wilcox 1980, Burgess & Sharpe 1981). The theory of island biogeography of MacArthur & Wilson (1967) has provided the conceptual framework for most of the conclusions. An established view seems to be that every species requires a certain minimum area in order to maintain a viable population; if the area of a habitat fragment decreases below this limit, the species is likely to go extinct from that particular plot. Support for this view has been sought from distributions of land birds in isolated woodlots (Galli et al. 1976, Forman et al. 1976, Terborgh & Winter 1980, Whitcomb et al. 1981).

There are two serious problems, however, that have not been solved satisfactorily in most of the ornithological studies on habitat fragmentation. First, a clear distinction should be made between habitat islands that are real isolates and those that are ecologically closely linked with surrounding areas (neighbouring habitat islands or the habitat "continent"). In the latter case the whole archipelago of habitat fragments, including the mainland, is the proper frame of research and it is doubtful what kind of ecological insight can be won by studying only small fragments in isolation (e.g. Williamson 1981). This situation is likely to be true for migratory birds at high latitudes (Haila 1983a).

Second, most of the studies are based on qualitative, presence/absence data instead of data on population numbers. The probability that a certain species is found in a habitat plot of a certain size is, however, greatly affected by its regional density (irrespective of whether the plot is part of a mainland or an island, Haila et al. 1983).

In this paper we discuss the methodological problems of censusing land birds in habitat fragments. We regard sampling design as a crucial part of methodology; indeed, when bird censuses are made in order to attack a specified ecological problem, an appropriate sampling design may be the most important precondition for the success of the study (see, e.g., James 1981, Rice 1981). Our conclusions are mainly based on census experiences on the Åland Islands, SW Finland; substantial results of the studies have been published elsewhere (Haila 1983a, Haila & Järvinen 1983, Haila et al. 1983) and are only briefly summarized below with respect to the habitat fragmentation issue (Sect. 4).

2. Sampling design

Research methods are tools that are used in order to achieve certain aims, i.e., to solve

problems that are deemed to be important and/or interesting. This is true also of the art of censusing birds (see Ralph & Scott 1981). In trying to develop adequate tools, the first step is a rigorous definition of the problem for which they are to be used.

The habitat fragmentation issue may be defined briefly as follows: What are the consequences of the increasing fragmentation of natural habitats for the community structure as well as population dynamics of birds residing in those fragments? The interesting point is the effect of the changing distribution of habitats ("insular" vs. continuous), not the effect of changes in their total area. However, a decrease in the total area of, say, natural forests would obviously affect forest birds and in practice it may be difficult to separate these two factors. Fragmentation is usually a consequence of habitat destruction.

2.1 Quantitative vs. qualitative data

In northern areas where most birds are migratory and isolation thus has a negligible role, island bird communities can be regarded as "samples" that are "drawn" by the islands from a surrounding avifaunal universe (Preston 1960, Haila 1983a). Because of chance effects inherent in sampling, the observed species number on a particular island in a particular breeding season is just a single observation from a probability distribution.

If the quantitative composition of the avifaunal universe is known, then an expected species number and its variance in a sample of a given size can be calculated by rarefaction (Simberloff 1978, 1979, James & Rathbun 1981). By using the data of Haila et al. (1980) on bird densities in the main habitats of the mainland of Åland we can estimate by rarefaction that a community of 50 pairs (expected in a plot of ca. 12 ha of luxuriant or 24 ha of barren coniferous forest) drawn randomly from communities of the main forest types is probably comprised of 17–19 species, with considerable sampling variance. Consequently, the communities of the main habitat types cannot be distinguished from each other solely on the basis of species number.

Furthermore, the species composition of small islands is subject to stochastic changes from year to year as well. In the avifaunal universe from which each island "draws" its sample of breeding pairs, the majority of species are relatively uncommon. The probability that they are included in the community of a particular island in a single year is less than one. Williamson (1981) called these species "casual breeders" (see also Haila 1983a). Due to the stochastic nature of actual colonization events they are expected to breed on a particular island every now and then but not every year.

This means, however, that qualitative data, i.e., mere species lists (or species numbers) are ecologically doubtful when characterizing bird communities of nonisolated islands (Haila 1983a). These problems can only be overcome by data on population numbers. Haila et al. (1983) proposed a method called "prevalence functions" for the quantitative analysis of colonization success (for an earlier version of the method, see Haila & Järvinen 1981). Prevalence functions are constructed by calculating expected population sizes of the species on the islands from mainland reference data and then comparing these expectations with observed numbers. If the efficiency of the census method is known, confidence limits can be calculated for both observed and expected popuation numbers. Prevalence functions give direct information that is relevant to the habitat fragmentation issue (Sect. 4).

2.2 The appropriate scale

All ecological processes have their characteristic space and time scales; relevant space scales range from local habitat plots to biogeographic regions, and time scales from a few hours in which ecophysiological responses of an individual take place to thousands of years needed for evolutionary adaptations to emerge. Wiens (1981) presented an overview of scale problems in ornithology. It is vital for any ecological study that the scale of the study and the scale in which the processes under investigation take place match each other. Thus, e.g., data on a single local community would be useless in making generalizations about faunal composition in the biogeographic region of which it is a part.

The ecological process that is important in the habitat fragmentation issue is local extinction (see, e.g., Terborgh & Winter 1980), but it is very difficult to determine rigorously what is an extinction for populations that are not isolated from each other (Simberloff 1976).

The crucial problem is, what role do small habitat plots have in the population dynamics of the species. Using Williamson's (1981) terminology, a "casual breeder" of a woodlot is certainly completely dependent on the dynamics of the regional population in the surrounding areas. However, "regular breeders" that breed in the woodlot each year in relatively high numbers, are probably also dynamically connected with the surrounding area; consequently, for instance, population changes in isolated plots may just reflect changes in the regional population.

There is no simple solution to this problem; the scale in which the dynamics of local populations residing in habitat patches becomes relatively independent from the dynamics of surrounding populations varies from species to species and from locality to locality. Therefore, it seems to us that bird ecological studies in fragmented habitats can be divided into two phases:

Phase 1 we call survey; the purpose of a survey is to find out whether the general distribution and abundance of different species in the study archipelago show any peculiarities that might be attributed to the fragmentation effect. The space scale should cover all island size classes, but also a control area on the mainland; a "pattern" observed in an archipelago may be completely explainable by the distribution of the species on the mainland as, e.g., mainland densities may correctly predict incidence functions or presence/absence of species in nonisolated archipelagoes (see Haila & Järvinen 1983, Haila et al. 1983, Järvinen & Haila 1984).

The time scale of a survey should cover more than one year. In the archipelago of Lake Inari, for instance, the population numbers of the Redpoll (*Carduelis flammea*) were considerably higher in 1979 than in 1977 (Haila 1983b). The observation is not unexpected because *C. flammea* is known to have wide population fluctuations in the north (von Haartman et al. 1963-72). The point is that combining longterm average densities from the mainland with island data for 1979 alone could mislead one into drawing wrong conclusions about the colonization pattern of *C. flammea*. Similarly, the colonization pattern of the Fieldfare (*Turdus pilaris*) in the Åland archipelago changed drastically between the years 1978 and 1979, presumably because of an exceptionally cold winter (Haila & Järvinen 1981, Haila et al. 1983). Consequently, very different pictures of the colonization success of *T. pilaris* would have been obtained from the breeding seasons immediately before and after the population change.

The second phase of the studies becomes necessary if peculiarities are found in the occurrence of some species; it comprises specific investigations of the mechanisms that have given rise to the observed peculiarities, i.e., the population dynamics of the species in the archipelago. Observed patterns alone cannot justify conclusions about processes that give rise to them. Usually several alternative mechanisms might have caused the patterns and competing explanations should be eliminated (for a review of the pattern/process problems in avian ecology, see Wiens 1983). The appropriate space and time scales are determined by the ecology of the species.

2.3 Comparability of the islands and the mainland

A common bias in many island/mainland comparisons has been the lack of concern for ecological differences between the study areas (Abbott 1980). Particularly important factors for breeding birds include differences in habitat microstructure (Haila et al. 1983, Haila 1983b) and the composition and abundance of food resources. Such differences may, of course, be caused by fragmentation itself (e.g. through increasing edge effects) but they also modify ecological processes in the habitat fragments. If one wants to show that increasing extinction probability in small habitat plots through decreasing area *per se* is an important factor, then obvious differences in the environmental conditions must be ruled out. This means that quantifiable measurements should be made of the environmental, especially habitat characteristics of islands and the mainland as an integral part of the research project (for methodology, see e.g. James & Shugart 1970, Anderson 1981, Wiens & Rotenberry 1981).

3. Census efficiency vs. economy

In the "survey" phase the whole breeding avifauna is the object of study and so it is reasonable to use some of the standardized general census methods (see, e.g., Berthold 1976, Shields 1979, Ralph & Scott 1981).

However, usually a relatively large number of islands needs to be censused in a short period of time, so a compromise may be necessary between census efficiency and coverage of different study areas (Haila & Järvinen 1981). It is often advisable to increase the number of sites sampled rather than to census a few sites intensively (Heck et al. 1975). Both theoretical arguments (Haila & Järvinen 1981) and results of a methodological test made on the Åland Islands (Haila & Kuusela 1982) support the view that one-visit censuses, with a census efficiency of around 70 %, give data that can be used in quantitative comparisons of general community characteristics as well as colonization patterns of single species. In the Åland conditions one-visit censuses are a good practical alternative. The validity of the conclusion should, however, be checked in other areas.

In the second, autecological phase of the study greater accuracy in the censuses is needed. But in studies on population dynamics of different species methodological issues diverge; no "standard" methods are available (see Ralph & Scott 1981).

4. The effect of habitat fragmentation on land birds in the Åland archipelago

Census data from 44 islands (with a size range of 0.5 to 582 ha) in the Åland archipelago were analyzed by prevalence functions that were constructed by using mainland habitat densities as reference data (Haila et al. 1983). In the majority of cases expectations and observations matched well. Several species were more abundant on the islands than expected but this is presumably a consequence of the patchy, mosaic-like structure of the island habitats; these species are mostly specialists of edges and bushy habitats.

The remarkable fact is that the list of opposite cases, species scarcer than expected on the islands, is short (Table 1). Table 1 includes all those species that might conceivably be impeded by the habitat fragmentation effect. As indicated in Table 1, however, for all but three species in the list an alternative explanation, and ecologically a more plausible one, can be given (see Haila et al. 1983 for details). The three exceptions are the Great Spotted Woodpecker (*Dendrocopos major*), the Crested Tit (*Parus cristatus*) (which is surprisingly scarce also in the archipelago of Lake Onega, Soviet Karelia (Hohlova 1977), and The Long-Tailed Tit (*Aegithalos caudatus*). The patchy habitat structure may impede the survival of the latter two species during the winter (Haila & Järvinen 1983, Haila et al. 1983), whereas reasons for the scarcity of *D. major* are obscure.

Table 1. Species that were scarcer than expected on small islands in the Åland archipelago; expectations were based on mainland habitat densities (scarce species excluded) (see Haila et al. 1983 for details).

Species	Status	Plausible reason(s)
Bonasa bonasia	Absent	Habitat lacking low dispersal
Numenius arquata	Absent	Habitat lacking
Dendrocopos major	Scarce	Obscure
Riparia riparia	Absent	Nest sites lacking
Anthus pratensis	Scarce	Nest predation by *Corvus corone*
Troglodytes troglodytes	Absent*	Habitat effects
Turdus pilaris	Scarce	Habitat effects
Saxicola rubetra	Scarce	Nest predation by *C. corone*
Acrocephalus schoenobaenus	Absent	Competition with *A. scirpaceus*
Sylvia atricapilla	Scarce	Tall trees lacking
Phylloscopus collybita	Scarce	Tall spruce lacking
Parus cristatus	Scarce	Wintering low dispersal(?)
Aegithalos caudatus	Absent	Wintering(?)
Nucifraga caryocatactes	Scarce	Habitat effects
Corvus monedula	Absent	Habitat effects

*An actively singing male observed in 1983

One may ask whether it is legitimate to regard real islands as habitat fragments. Small islands in the Åland archipelago certainly are ecologically different from mainland habitat patches as breeding environments of land birds (Haila 1983a). However, they differ from continuous forests even more than do mainland habitat fragments. The comparison is, consequently, conservative with respect to the habitat fragmentation issue.

To conclude, it seems on the basis of quantitative data that for the breeding land birds of the Åland Islands habitat fragmentation is a factor of minor importance. Occurrence of different species in the archipelago is mainly determined by their regional abundance and their habitat requirements. The few observed deviations from expectations should be studied more accurately at the autecological level.

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References

Abbott, I. 1980: Theories dealing with the ecology of landbirds on islands. — Adv. Ecol. Research 11:329-371.

Anderson, S. H. 1981: Correlating habitat variables and birds. — Stud. Avian Biology 6:538-542.

Berthold, P. 1976: Methoden der Bestandserfassung in der Ornithologie: Übersicht und kritische Betrachtung. — J. Ornithol. 117:1-69.

Burgess, R. L. & Sharpe, D. M. (eds.) 1981: Forest island dynamics in man-dominated landscapes: 125-205. — Springer-Verlag. N.Y., Heidelberg, Berlin.

Forman, R. T. T., Galli, A. E. & Leck, C. F. 1976: Forest size and avian diversity in New Jersey woodlots with some land-use implications. — Oecologia (Berl.): 26-8.

Galli, A. E., Leck, C. F. & Forman, R. T. T. 1976: Avian distribution patterns in forest islands of different sizes in central New Jersey. — Auk 93:356-364.

von Haartman, L., Hildén, O., Linkola P., Suomalainen, P. & Tenovuo, R. 1963-72: Pohjolan linnut värikuvin. — 1092 pp. Otava, Helsinki.

Haila, Y. 1983a: Land birds on northern islands: a sampling metaphor for insular colonization. — Oikos 41:334-351.

—"— 1983b: Colonization of islands in a north-boreal Finnish lake by land birds. — Ann. Zool. Fennici 20:179-197.

Haila, Y. & Järvinen, O. 1981: The underexploited potential of bird censuses in insular ecology. — Stud. Avian Biology 6:559-565.

—"— 1983: Land bird communities on a Finnish island: species impoverishment and abundance patterns. — Oikos 41:255-273.

Haila, Y. & Kuusela, S. 1982: Efficiency of one-visit censuses of bird communities breeding on small islands. — Ornis Scand. 13:17-24.

Haila, Y., Järvinen, O. & Väisänen, R. A. 1980: Habitat distribution and species associations of land bird populations on the Aland Islands, SW Finland. — Ann. Zool. Fennici 17:87-106.

Haila, Y., Järvinen, O. & Kuusela, S. 1983: Colonization of islands by land birds: prevalence functions in a Finnish archipelago. —J. Biogeogr. 10:499-531.

Heck, K. L., van Belle, G. & Simberloff, D. 1975: Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. — Ecology 56:1459-1461.

Hohlova, T. Yu. 1977: (Хохлова, Т.Ю.) 1977. Эколойофачнистическая Характеристка тнезфовой орнитофачнц Заонежья — Vestnik LGU, Seriya Biol. 15:22-30.

James, F. C. 1981: Summarizing remarks: sampling design. — Stud. Avian Biology 6:452-453.

James, F. C. & Rathbun, S. 1981: Rarefaction, relative abundance, and diversity of avian communities. — Auk 98:785-800.

James, F. C. & Shugart, H. H. 1970: A quantitative method of habitat description. — Aud. Field Notes 24:727-736.

Järvinen, O. & Haila, Y. 1984: Assembly of land bird communities on northern islands: a quantitative analysis of insular impoverishment. — In: Strong, D. R. Jr., Simberloff, D., Able, L. G. & Thistle, A. B. (eds.), Ecological communities: Conceptual issues and the evidence: 138-147. Princeton Univ. Press, Princeton, N.J.

MacArthur, R. H. & Wilson, E. O. 1967: The theory of island biogeography. — 203 pp. Princeton Univ. Press, Princeton, N.J.

Preston, F. W. 1960: Time and space and the variation of species. — Ecology 41:611-627.

Ralph, J. C. & Scott, J. M. (eds.) 1981: Estimating numbers of terrestial birds. — Stud. Avian Biology 6.

Rice, J. 1981: Summarizing remarks: sampling design. — Stud. Avian Biology 6:450-451.

Simberloff, D. S. 1976: The significance of species turnover and the status of equilibrium island biogeography. — Science 194:572-578.

—"— 1978: Use of rarefaction and related methods in ecology. — In: Dickson, K. L., Cairns, J. Jr. & Livingston, R. J. (eds.), Biological data in water pollution assessment: quantitative and statistical analyses. — Amer. Soc. Testing Materials STP 652:150-165.

—"— 1979: Rarefaction as a distribution-free method of expressing and estimating diversity. — In: Grassle, J. F., Patil, G. P., Smith, W. K. & Taillie, C. (eds.), Ecological diversity in theory and practice: 159-176. Int. Co-operative Publ. House, Fairland, MD.

Shields, W. M. 1979: Avian census techniques. — In: Dickson, J.G., Conner, R. N., Fleet, R. R., Kroll, J. C. & Jackson, J. A. (eds.), The role of insectivorous birds in forest ecosystems: 23-51. Academic Press, N.Y.

Soulé, M. E. & Wilcox, B. A. (eds.) 1980: Conservation biology. An evolutionary-ecological perspective. — 395 pp. Sinauer, Sunderland, M.A.

Terborgh, J. & Winter, B. 1980: Some causes of extinction. — In: Soulé, M. E. & Wilcox, B. A. (eds.), Conservation biology. An evolutionary-ecological perspective: 119-133. Sinauer, Sunderland, MA.

Whitcomb, R. F., Robbins, C. S., Lynch, J. F., Whitcomb, B. J., Klimkiewicz, M. K. & Bystrak, D. 1981: Effects of forest fragmentation on the avifauna of eastern deciduous forest. — In: Burgess, R. L. & Sharpe, D. M. (eds.), Forest island dynamics in man-dominated landscapes: 125-205. Springer-Verlag, N.Y., Heidelberg, Berlin.

Wiens, J. A. 1981: Scale problems in avian censusing. — Stud. Avian Biology 6:513-521.

—"— 1983: Avian community ecology: an iconoclastic view. — In: Clark, G. A. & Brush, A. H. (eds.), Pespectives in orhithology: 355-410. Cambridge Univ. Press, Cambridge.

Wiens, J. A. & Rotenberry, J. T. 1981: Censusing and the evaluation of avian habitat occupancy. — Stud. Avian Biology 6:522-532.

Williamson, M. 1981: Island populations. - 286 pp. Oxford Univ. Press, Oxford.

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