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On the relationship between distribution and abundance in birds breeding on Finnish mires: the effect of habitat specialization

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We tested Brown's (1984) explanation of the generally observed positive relationship between distribution and abundance of species. The hypothesis states that generalized species are widely distributed *and* locally common, and that specialized species are narrowly distributed *and* locally rare. The analysis is based on 327 censuses covering almost the whole north–south range of Finland, i.e., ca. 1100 km. The censused habitats cover 19 peatland habitat types, ranging from open flark fens to forested peatlands. The relationship between distribution and abundance was positive for the total avifauna, and also for wader and for passerine species. Since the number of observations may affect the number of peatland types where the species is observed, we used two indices to measure habitat amplitude (a rarefaction estimate and Hurlbert's (1978) B'). The species that were able to inhabit several mire types had large geographical ranges, but were not locally abundant. Thus, in general, the species with a wide habitat amplitude are regionally widespread, but not locally abundant. The results do not fully support Brown's explanation of the distribution–abundance relationship.

1. Introduction

In several taxa, species with a broad geographic range are usually locally abundant (Hanski 1982, Brown 1984, Gaston & Lawton 1988, Hanski et al. 1992). The causes of this relationship are, however, unclear. For example, Jackson (1974) found that the most widespread species of marine bivalves also have wide niches. To formulate a general hypothesis, Brown (1984) argued that generalized species are more widespread and locally abundant than specialized species. This implies that a specialized species is in fact unable to use resources efficiently and consequently occur locally in low densities, as stated by Brown (1984:273). This is contrary to the more traditional view, which states that specialists are efficient in using local resources and thus become locally abundant, but are not widespread (i.e., corollary of the statement "jack-of-all-trades-is-master-of none", Brown 1984).

It has recently been noted that the studies analysing the relationship between distribution and abundance may suffer from two methodological fallacies. First, the observed positive relationship may be a sampling artefact (Hanski et al. 1992, D.H. Wright, unpubl.). This is natural, since if a species is locally rare, the probability that it will be included in a sample is low. Thus the number of occurrences of a rare species should be low and consequently the distribution narrow. Second, the habitat where the local density of a species is obtained may largely determine whether the observed relationship is positive, non-significant or negative. A positive relationship can be expected only if the density is reported from a 'representative' habitat of a particular species (Gaston & Lawton 1990).

In this paper we address the following questions. (1) Is there any relationship between the distribution and abundance of Finnish peatland birds? (2) What kind of species are locally abundant? To answer the second question we more specifically ask whether locally common species are able to exploit a wide range of available peatland habitats, i.e., whether locally abundant and widespread species are habitat generalists — as argued by Brown (1984) — or habitat specialists. Proper analysis of the latter question poses several problems, because both distribution and abundance may affect almost any estimation of habitat amplitude. To overcome this problem we used two different measures of habitat range, which should reduce this bias.

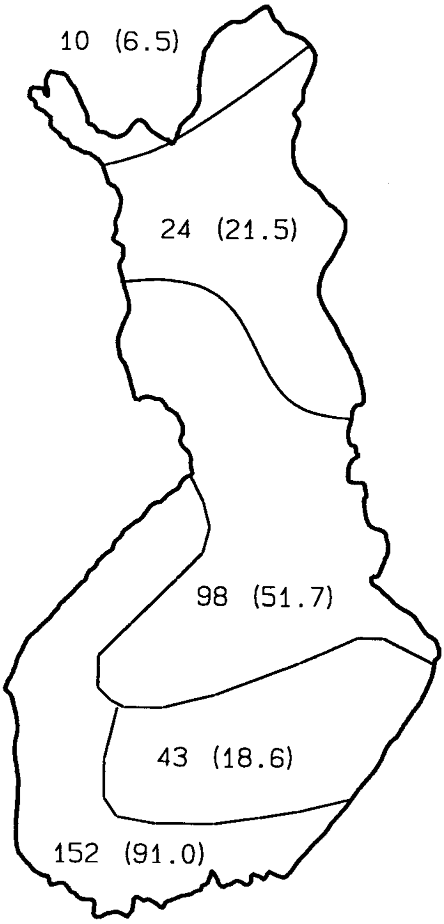

Fig. 1. Number and area (km^2, in parentheses) of census plots in different mire complex regions (Ruuhijärvi 1960, Eurola 1962) in Finland.

2. Material and methods

Since the terminology varies, we shall first define a few terms (see also Hanski et al. 1992). By *average density* we mean average local abundance of a species calculated over all those sites where the species is observed. Thus it could be more exactly termed average density-when-present. By *geographical range* (or distribution) we mean the distance between the northernmost and southernmost Finnish breeding record of a species in our data. We use the distance instead of the number of sampling points to avoid (or diminish) the sampling bias indicated above. This measure does not suffer from the low probability of observing rare species in single samples as much as does the number of points where the species is observed. Due to the longitudinal shape of Finland the estimate we use should also reliably measure the south-north geographical range of a species.

The density and range estimates of 28 species are based on single-visit sample plot censuses made during the breeding season over the whole Finland in 1963–1984 (Fig. 1). The range of the sample plots was about 1000 km. The total number of censuses was 327 (Fig. 1) and they covered an area of about 190 km^2. Censuses from early and late years were available from southern and northern Finland, so possible long-term trends in bird populations should not obscure the analyses. We restricted the analyses to the species that breed mainly on peatlands, since inclusion of forest species that are only occasionally observed in peatlands, such as *Fringilla coelebs* and *Turdus iliacus*, would clearly have confused the testing of the hypothesis (see also Gaston & Lawton 1990). The selection of species was based on the information in Hyytiä et al. (1983). A list of the species is shown in Appendix 1.

Single-visit censuses do not give correct estimates of 'true' densities, but reveal about 60% of the breeding population and 80% of the species (Kouki & Järvinen 1980). Thus the density values reported are underestimates. This should not have a marked effect on the analysis of the distribution-abundance relationship, because all the sites received single visits. Rare species are naturally more difficult to observe than abundant species. We tried to avoid the effect of this on the observed distribution by using range of observations to measure the distribution instead of the number of observations.

Each sample plot (mire) was allocated to a particular mire type or combination, according to peatland classification scheme used in Finland (e.g., Ruuhijärvi 1960, 1983, Eurola 1962, Pakarinen & Ruuhijärvi 1978, Eurola & Kaakinen 1979a, 1979b). The classification recognizes mainly the botanical characteristics of a mire, but is also associated with many factors that affect the general appearance of a mire, e.g., wetness and tree density. Thus the classification is probably also appropriate for bird-habitat relations (see also Kouki et al. 1992).

The analysis of habitat specialization was restricted to a) species that attain their highest densities in peatlands (as stated above), and b) species for which we had at least 20 observations. The first restriction is due to the fact that estimation of the habitat breadth of a species that typically breeds in other habitat types (e.g. forests) would have been irrelevant. The second restriction was due to the number of habitat classes we used, i.e., our estimates of habitat niche breadth would have suffered greatly in cases in which the number of records was lower than the number of habitat classes. After these restrictions, 19 species were left for the habitat analysis.

Habitat niche breadth was defined in two different ways. First, we used rarefaction (Simberloff 1978) to estimate the expected number of breeding habitats when the number of observed individuals is kept constant (20). Second, we used Hurlbert's (1978) habitat amplitude measure

$$B' = X^2 / [A\ \Sigma(x_i^2/a_i)],$$

where X is the total number of observations of a species, A is the total area of the census sites, x_i is the number of observations at habitat i and a_i is the total area of habitat i. Hurlbert's index measures whether the habitats are exploited in proportion to their availability. The value of 1.0 indicates that all habitats are used in proportion to their availability.

In analysing the data we used correlation analysis. We $\log_e$-transformed the density to linearize the observed relationship, but no other transformations were done.

3. Results

3.1. Distribution and abundance

In the whole of Finland and the whole species assemblage occurring on the peatlands, species that were widely distributed were also locally the most abundant (Fig. 2). The relationship accounted for about 26% of the original variation in average density. A similar pattern was observed separately in waders (R^2=47%), and passerines (R^2=59%), but not in the broad taxonomic group of other species observed in the censuses.

3.2. Habitat specialization

Among the 19 peatland species abundant ones did not occur in more habitat types than rare ones (Fig. 3). Thus it seems that habitat generalist are not locally more common than habitat specialists. However, both measures of habitat niche width were positively correlated with geographical distribution (Fig. 4). Thus habitat generalists are more widely distributed than habitat specialists.

4. Discussion

Järvinen & Sammalisto (1976) found that the constancies of Finnish peatland birds were posi-

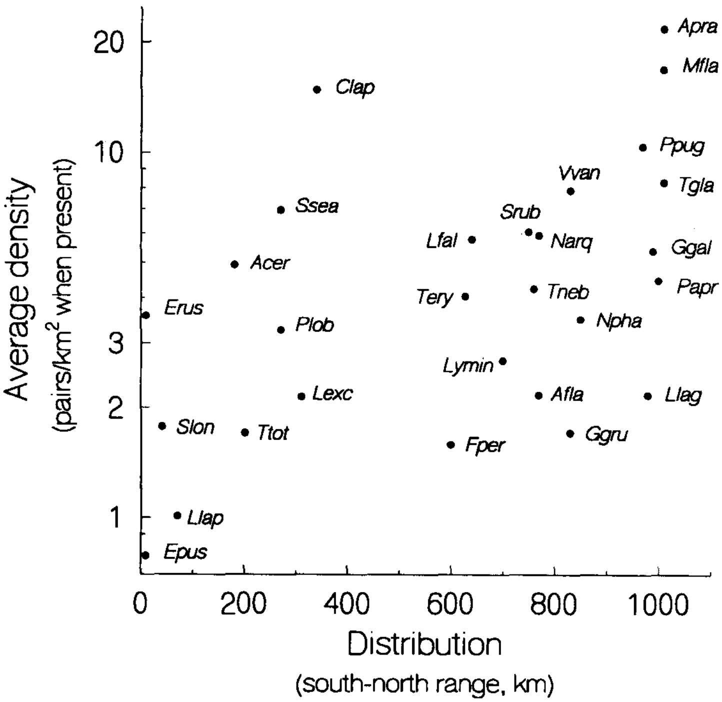

Fig. 2. The relationship between distribution and average density of the birds breeding in Finnish mires. The abbreviations beside the plotted points are explained in Appendix 1. The correlation for all species is r = 0.507 (P = 0.006, df = 26), for waders r = 0.686 (P = 0.007, df = 12), for passerines r = 0.765 (P = 0.027, df = 6), and for others r = -0.176 (P = 0.738, df = 4).

tively correlated with the frequencies within their almost arbitrarily defined regions; i.e., a positive relationship existed between distribution and abundance. Our results corroborate those of Järvinen & Sammalisto, but we have been able to extend the analysis further to cover a wider geographical range in Finland. We also demonstrated that wide geographical distribution in a species is closely linked with large-scale habitat niche breadth. Thus, species that exploit several peatland types tend to have wide geographical distribution.

Brown's (1984) explanation of the generally observed (see also Gaston & Lawton 1990) positive relationship between species distribution and local abundance was only partly consistent with our results. Namely, generalists were more widely distributed but not locally abundant. However, the result seems to invalidate Brown's explanation. As Brown's hypothesis implies that both abundance and distribution are related to ecological specialization, invalidation of either of these relationships also invalidates the hypothesis as a possible explanation of the positive distribution-abundance relationship.

Ford (1990) also found a positive correlation between abundance and distribution among Australian land birds, but the regression had a poorer fit than among the Finnish peatland birds. We suggest two reasons for the difference. Ford's material has a larger spatial scale (1° squares) and includes taxonomically more diverse group of species than our data. These factors probably disturb any relationship between distribution and abundance. Interestingly, Ford found that none of the measures of niche breadth he used was correlated with the geographical range of the species. Ford's measure of niche breadth, however, was on a different scale (e.g., foraging type) from our broad definition of habitat specialization. In testing Brown's (1984) hypothesis, the actual method used for classifying species as generalists and specialist is obviously extremely important.

We expected the lack of support for the second part of Brown's hypothesis, since we can think of no mechanistic reason why a species that is able to exploit several habitat types should become locally abundant. A wide foraging niche in a species would imply an ability to use several kinds of resources or microhabitats in each locality, thus conferring the potential for increasing local density, but the habitat width, which is

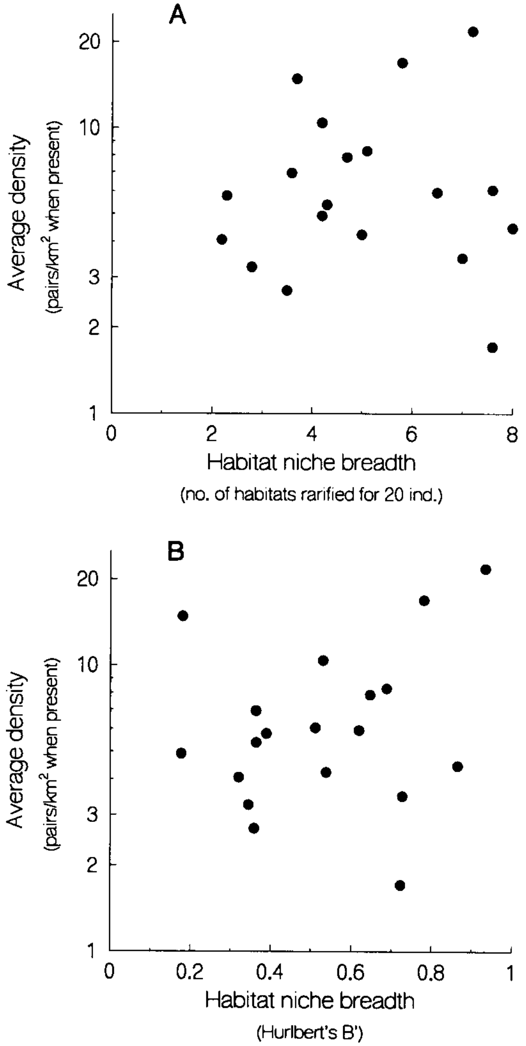

Fig. 3. The relationship between habitat niche breadth and average density in the birds breeding in Finnish mires. Habitat niche breadth is measured using (A) rarefaction and (B) Hurlbert's (1978) habitat amplitude index. The correlation for A is r = 0.026 (P = 0.917, df = 17) and for B r = 0.194 (P = 0.426, df =17).

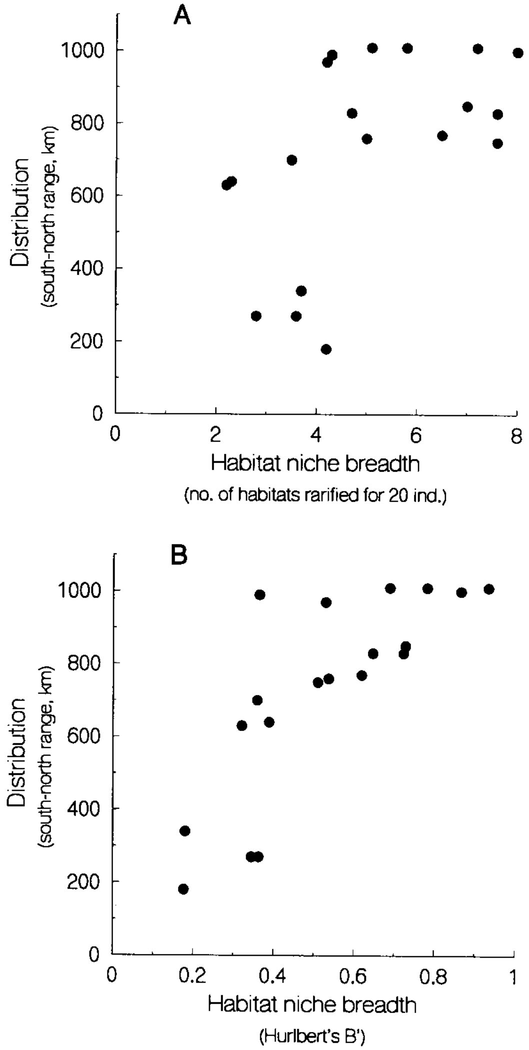

Fig. 4. The relationship between distribution and habitat niche breadth in the birds breeding in Finnish mires. Habitat niche breadth is measured using (A) rarefaction and (B) Hurlbert's (1978) habitat amplitude index. The correlation for A is r = 0.549 (P = 0.015, df = 17) and for B r = 0.783 (P = 0.000, df = 17).

more a property of the species, has not necessarily the same effect. However, the two niche dimensions may be correlated, but this is not a necessity.

Although we tried to remove the effect of number of observations on the habitat niche measure, our measure is evidently still insensitive to, e.g., the spatial variation in population processes (birth, death, immigration, emigration). These may largely affect the observed habitat use of a species. One possibility is that spatially different populations are related as source and sink populations (Pulliam 1988). Thus a species that finds one habitat very suitable may generate dispersers to less preferred habitats. The phenomenon of the use of less preferred habitats is also involved in the ideal free distribution (Fretwell and Lucas 1970), where all localities are used in proportion to their preference. Interestingly, neither of these alternatives predicts high local abundances *on average*, as does Brown's (1984) hypothesis.

We conclude that among the birds breeding in Finnish mires, wide-ranging species are able to use several habitat types, but are not locally more common than other species. The results thus partly support Brown's (1984) hypothesis, namely that generalists and specialists differ in their distribution, and these differences are probably inherent properties of the species. This is not the reason, however, for any relationship between distribution and abundance. To reach convincing explanations, there is an urgent need for further analysis, which would require a more detailed multi-dimensional niche analysis (see Kouki et al. 1992) and knowledge of spatial variation in the population processes.

Finally, our results have implications for the conservation of peatland birds. Clearly, populations with either narrow niches or low local densities are most prone to extinction (see also Bock & Ricklefs 1983, Gilpin & Soulé 1986). Our analysis showed that species restricted to a small geographical area are habitat specialists. Thus, for successful conservation, the particular habitat requirements of each species should be estimated, high priority being given to species with small rather than large geographical distribution. According to our results, however, local rarity does not necessarily mean that a species is dependent on only one or a few habitats. This implies that conserving a particular type of habitat for a locally rare peatland species is not necessarily a sufficient approach. To avoid extinction even rare species need a variety of habitats in a larger geographical area .

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Selostus: **Ovatko Suomen suolinnuston habitaattigeneralistit laajemmalle levinneitä ja paikallisesti runsaimpia kuin spesialistit?**

Testasimme Brownin (1984) hypoteesia, joka pyrkii selittämään, miksi lähes aina maantieteellisesti laajalle levinneet eliölajit ovat myös paikallisesti runsaita. Hypoteesin mukaan laajalle levinneet ja paikallisesti runsaat lajit ovat generalisteja. Harvinaiset ja harvalukuiset lajit puolestaan ovat spesialisteja.

Hypoteesia testattiin Suomen suolinnuston avulla. Aineistoomme kuului 327 koealalaskentaa eri puolelta Suomea. Koealojen yhteispinta-ala oli noin 190 km^2. Kukin koeala luokiteltiin yhteen 19 suotyypistä tai suotyyppien yhdistelmäksi. Lajin levinneisyys määriteltiin pohjoisimman ja eteläisimmän havainnon erotukseksi. Vain ne lajit, joiden tiedetään pesivän pääasiassa soilla otettiin huomioon analyysissä (lajit kuten peippo ja punakylkirastas jätettiin pois). Koska sekä runsaus että levinneisyys saattavat vaikuttaa havaittujen pesimähabitaattien määrään, käytimme kahta indeksiä habitaatin käytön mittaamisessa. Rarefaktion avulla laskettiin odotettujen esiintymishabitaattien määrä, jos havaituista yksilöistä poimitaan satunnaisesti 20. Lisäksi laskimme Hurlbertin (1978) esittämän habitaattiamplitudin mitan.

Lajien levinneisyyden ja paikallisen runsauden välillä oli odotettu positiivinen suhde sekä koko lintuyhteisössä että kahlaajilla ja varpuslinnuilla erikseen.

Esiintymishabitaattien määrä vaikutti positiivisesti lajin levinneisyyteen, mutta ei paikalliseen runsauteen. Generalistilajit olivat siis laajalle levinneitä, mutta eivät paikallisesti runsaita. Brownin hypoteesin toinen osa osoittautui siten oikeaksi, mutta tulos merkitsee kuitenkin sitä, että ekologinen erikoistuneisuus ei voi olla positiivisen levinneisyys-runsaus -suhteen syy.

Suolinnusto suojelun kannalta tulos tarkoittaa sitä, että suojeluponnistus tulisi kohdistaa suppealla alueella esiintyviin lajeihin, koska näiden habitaattivaatimukset ovat tiukimmat. Erityisen tärkeää olisi määrittää kvantitatiivisesti, mitkä ympäristön rakennepiirteet (suotyypin ohella) ovat ratkaisevia lajien esiintymisen kannalta. Tärkeää on myös, että menestyksellinen paikallisesti harvinaisten lajien suojelu edellyttää useiden suohabitaattien suojelua.

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Appendix 1. Species (and their abbreviations) that were classified as peatland species. The classification is based on the general description of the species in Hyytiä et al. (1983).

Species	Abbreviation	Species	Abbreviation
Group: other		*Numenius phaeopus*	NPHA
Falco peregrinus	FPER	*N. arquata*	NARQ
Lagopus lagopus	LLAG	*Tringa erythropus*	TERY
Grus grus	GGRU	*T. totanus*	TTOT
Stercorarius longicaudus	SLON	*T. nebularia*	TNEB
Sterna paradisea	SSEA	*T. glareola*	TGLA
Asio flammeus	AFLA	*Phalaropus lobatus*	PLOB
Group: Waders		Group: Passerines	
Pluvialis apricaria	PAPR	*Anthus pratensis*	APRA
Vanellus vanellus	VVAN	*A. cervinus*	ACER
Limicola falcinellus	LFAL	*Motacilla flava*	MFLA
Philomachus pugnax	PPUG	*Saxicola rubetra*	SRUB
Lymnocryptes minimus	LYMIN	*Lanius excubitor*	LEXC
Gallinago gallinago	GGAL	*Calcarius lapponicus*	CLAP
Limosa lapponica	LLAP	*Emberiza rustica*	ERUS
		E. pusilla	EPUS