Ornis Fennica 75:119–127. 1998

Guild indicator species on a landscape scale — an example with four avian habitat specialists.

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Received 30 January 1998, accepted 11 March 1998

The ability to predict the patch occurrence of a deciduous forest bird guild through an indicator species was tested using published data. Except for the indicator, the Long-tailed Tit (LT), the guild consisted of the Marsh Tit (MT), the Blue Tit (BT) and the Lesser Spotted Woodpecker (LW). All single species, as well as the entire guild, occurred more often like LT than expected by chance. Over all, 86% of the guild occurred in concurrence with LT. When LT was present the mean number of guild species was 3.52 and when absent 0.79. The occurrence pattern of the guild did not change when one multi-sampled region in Sweden was compared with patches scattered throughout four countries, whereas concurrence was more significant in studies from the boreal zone than from the nemoral zone. The guild showed a nested structure in patch occupancy, where the occurrence of LW strongly predicted that of the entire guild. However, because of the better overall statistical agreement in relation to the guild, the Long-tailed Tit, or rather, its known thresholds regarding habitat fragmentation, are suggested as suitable indicators for the occurrence of this guild.

1. Introduction

Indicators may be used in management for the evaluation of habitat quality, or for the surveillance of population developments (Morrison et al. 1992). The use of indicators, either species, structures or abstract indexes, in nature conservation is growing. For the selection of relevant indicators, traditional species studies are often replaced by systematic attempts to stratify the environment and to focus the proper spatial scale (Noss 1990, Angelstam 1997).

Plants are commonly used as indicators for habitat type or quality, whereas animal species are rare as indicators in landscape conservation (Furness and Greenwood 1993, Nilsson and Ericson 1997). However, animal species guilds have been proposed as units in which indication may work (Szaro and Balda 1982, Verner 1984), but few have been validated. So far, such systems have showed poor associations between the occurrence or behaviour of the indicator in relation the other species, often due to hazy and unstratified composition of the guild (Block et al. 1986, Szaro 1986). Guilds are often based on, for instance, body size, feeding behaviour and taxonomy (Patton 1987, Morrison et al. 1992). Such groupings, however, obviously do not imply that the species respond similarly to, for example, habitat changes. The difficulties in grouping species according to taxonomy can be seen with, for example, the Hazel grouse (*Bonasa bonasia*), whose movements in a landscape appear more similar to those of voles than other grouse (Åberg et al. 1995). Furthermore, another problem with animal indicator systems has been to select relevant measures of habitat

qualities, which apply to different species and seasons (Noss 1990, Wiens 1995).

Indicator systems usually deal with straight habitat-species relationships. Therefore, earlier tests of guild indicators have mainly been conducted on the scale of habitat stands or individual territories (DeGraaf and Chadwick 1984, Patton 1987). Along with small scaled habitat structures, the proportion and distribution of habitats are also often important, or even decisive, for sustainability of populations (Hanski and Gilpin 1991, Morris 1991). Determining possible threshold levels for such landscape relationships, would enhance conservation (Wiens 1995, With and Christ 1995). Furthermore, if such thresholds would also apply to whole sets of species, naturally, they would be more widely applicable.

I studied a guild of four insectivorous birds associated with mature deciduous or mixed forests (see Methods). The aim of this study was to investigate how well the presence of the Long-tailed Tit (*Aegithalos caudatus*), reflected the occurrence of the entire guild. That is, all species prefer the same habitat, but do they also show a close association in their occurrence measured on a large scale, i.e. in the choice among differently distributed habitat patches.

The Long-tailed Tit has a normal daily range within 1 km^2 (Nakamura 1969, Gaston 1973, Bleckert 1991), and is sensitive to habitat isolation, i.e. it occurs only in areas with a large number of patches of the preferred habitat (Enoksson et al. 1995, Hinsley et al. 1995, Jansson and Angelstam 1997). Long-tailed Tits in boreal landscapes use areas with more than 10% of the suitable habitat or less than 300 m between habitat patches (Jansson and Angelstam 1997). Such measurements are often easily obtained from appropriate maps and may be used in, for example, the planning of forest management. An obvious question, however, concerns the possible generality of such thresholds for the occurrence of other species and taxa.

2. Methods

The guild included the Long-tailed Tit (LT), the Marsh Tit (*Parus palustris*) (MT), the Blue Tit (*P. caeruleus*) (BT) and the Lesser Spotted Woodpecker (*Dendrocopos minor*) (LW). All of these species prefer mature deciduous mixed forests, often containing birches (*Betula* spp.) and alder (*Alnus* spp.) (Rosenberg 1988, Winkler et al. 1995, Harrap and Quinn 1996). The guild species were chosen because they are all resident species and none of them is a habitat generalist in boreal forests. Other possible resident species that could have been included, such as other Woodpeckers or the Nuthatch (*Sitta europaea*), were regarded as either too rare or did not usually occupy the studied habitat, at least not in Sweden. The four selected species are not threatened today on a national scale in western Europe, but they are not very abundant and show a fragmented distribution in many forested areas (Marchant et al. 1990, Harrap and Quinn 1996). These attributes are all suggested prerequisites for suitable indicator species (Landres et al. 1988, Noss 1990, Morrison et al. 1992, Angelstam et al. 1993, Furness and Greenwood 1993).

The size of patches usually occupied by Blue Tits may be quite small, even less than 2 ha, while the probability for the occurrence of the other three species is reported to be equal in patches measuring between 5–25 ha (van Dorp & Opdam 1987, Wiktander et al. 1992, Hinsley et al. 1996). However, even though the guild members differ somewhat regarding the size of their preferred patches, they may respond similarly to patch isolation.

To allow for more general results and to cover different landscape types, data were collected from a variety of regions in four European countries. Data from 39 bird inventories (28 in Sweden and 11 in continental Europe), published in scientific journals or in official reports from nature conservation agencies, were used (Table 1). The inventories included data on the occurrence of the four species (LT, MT, BT, LW) in 104 patches.

Bird studies were included in the analyses if the following criteria were fulfilled: 1) the inventoried patch(es) was situated within the distribution range of all four species. 2) The patch(es) contained suitable habitat for all guild species, i.e. forested areas with deciduous species well represented. 3) Study areas not exceeding 1 km^2 (100 ha), because occurrences of the guild species in areas larger than the normal daily range would be difficult to compare and may miss the aim of analysing occurrence similarities. The 1 km^2 limit was also used because habitat variability increases with

area; hence, the habitat description may be less accurate. 4) All patches were more than 1 km apart. That is, the distance should exceed the normal daily range of all four species to avoid replication of results. Inventoried patches which fulfilled all criteria, but where no guild species were observed, were also included in the study since absences, as well as presences, may reflect a similarity in the range of movements of the guild species.

For the analyses I–III, data were grouped according to the number of patches per study (I), the position of the study area (II) and the species

Table 1. Data on the 39 studies used in the analyses, showing the number of patches per study, patch habitat, vegetation zone and country of study. The two top studies make up the multi-sampled area Bergslagen (B). Under Habitat, the inventoried patches are described by the abbreviations: D = deciduous forest, DO = deciduous old-growth, Mix = deciduous and coniferous mixed, R = riparian and A = agricultural area.

Reference	No. of patches	Habitat	Vegetation zone	Country of study
Enoksson et al.1995(B)	30	Mix	Boreal	Sweden
Svensson 1973 (B)	20	Mix	"	"
Andersson 1990	1	Mix, R	"	"
Andersson, Malm. 1992	1	Mix	"	"
Anon. 1975a	1	Mix, R	"	"
Anon. 1975b	1	Mix, R	"	"
Anon. 1976	1	Mix	"	"
Anon. 1976	1	Mix	"	"
Anon. 1984	1	Mix, R	"	"
Anon. 1985	1	D, R	"	"
Anon. 1986	1	Mix, R	"	"
Fredriksson 1984	1	Mix	"	"
Führ 1973	1	Mix	"	"
Gustavsson, Nils. 1998	1	Mix	"	
Holmstedt 1986	1	Mix, R	"	"
Jansson 1996	1	Mix	"	"
Johannesson 1976	1	D	"	"
Jonasson 1995	1	Mix, R	"	"
Lundberg 1981	1	D	"	"
Lundberg, Molin 1982	1	D	"	"
Malmstigen 1976	1	Mix, R	"	"
Malmstigen 1976	1	Mix, R	"	"
Malmstigen 1990	1	Mix, R	"	"
Pettersson 1978	1	Mix	"	"
Pettersson 1981	1	D, R	"	"
Rosenberg 1972	1	D, R	"	"
Rosenberg 1979	1	D, R	"	"
Nilsson 1979	8	Mix	Nemoral	"
Hinsley et al. 1995	1	D, A	"	England
van Dorp, Opdam 1987	1	D, A	"	the Netherlands
Anon. 1983	5	D, R	"	Poland
Cieslak 1982	1	Mix	"	"
Cieslak 1991	2	Mix	"	"
Grabinski, Staw. 1986	1	Mix	"	"
Kujawa 1995	2	Mix	"	"
Nowicki 1983	1	D	"	"
Rzepala, Mitrus 1995	4	Mix	"	"
Tomialojc 1995	1	DO	"	"
Wolk 1982	2	DO	"	"
Σ 39 studies	104 patches		B = 27 N = 12	4 Countries

occurrences per patch (III), as follows:

I. Some of the studies included bird data from more than one patch, which all fulfilled the above criteria. To avoid the possibility that one multi-sampled region would bias the results, two subsets of data (Bergslagen and Mix) were put together and analysed separately. Data on the occurrence of the guild species were sorted as presence-absence per species and per patch. Bergslagen (n = 50), an area in south-central Sweden where coniferous forest dominates (Jansson and Angelstam 1997), consisted of data from two studies. These two studies contained 30 (Enoksson et al. 1995 plus unpublished data used with the permission of the authors) and 20 (Svensson 1973) patches, respectively. All other studies contained 1–8 patches, which were pooled and used as the subset Mix (n = 54). The percentage of patches with each of the guild species present were calculated when LT was present and absent, respectively. For the patches where LT was present, the proportion (%) of patches where the entire guild were present was also calculated. Furthermore, the mean number of guild species occurring in patches when LT was present and absent, respectively, was calculated. The similarity in the occurrence of the species was tested by contingency table analyses.
II. The data were also analysed as each study (regardless of patch numbers) representing one sample (n = 39), where all were categorised as being conducted in the boreal or the nemoral zone (Sjörs 1965). The proportion (%) of guild species that occurred like LT (no-no or yes-yes) was calculated for all studies, and the boreal and nemoral studies were compared (Mann-Whitney). The mean number of species present when LT was present and absent was also calculated for the boreal and nemoral studies, respectively.
III. The data on the occurrence of birds from all patches (regardless of area), with at least one of the guild species present (n = 87), was arranged in a species occurrence matrix (Patterson and Atmar 1986, Worthen 1996) according to the number of species present per patch (4–1). The occurrence pattern of the four guild species was tested for nestedness by comparing a simulated occurrence distribution (1 000 iterations) with the observed occurrence distribution using the simulation programme provided by Patterson and Atmar (1986, RANDOM 1). The analysis includes data on the number of patches (87), number of species per patch and the number of unexpected patch vacancies. The assumption is that if a species occurs in a patch with, for example, two species present it should also occur in all patches with three species present and so on.

3. Results

All four guild species were present in 40 of the 104 patches, 1–3 species occurred in 47 patches and in 17 patches none of them appeared. The entire guild occurred in full agreement (all species present or absent) in 55% of all studied patches. For all patches (n = 104), the mean number of guild species was 3.52 when LT was present and 0.79 when LT was absent.

Analysis I showed that in Bergslagen, the agreement in guild species occurrences was somewhat higher when LT was absent than when present. MT and LW were often absent when LT was present, whereas, when LT was absent, often only BT was present. Another pattern was observed in Mix. When LT was present, the other guild species were most often present as well, but both MT and BT also frequently occurred when LT was absent (Table 2). These relationships are shown both as the proportion (%) of patches with coinciding occurrences, and as the mean number of species present when LT was present and absent, respectively. The presence of an entire guild was significantly more likely in Mix than in Bergslagen ($\chi^2 = 49.02$, $p < 0.0001$), whereas other trends between the groups were unclear.

The degree of indicator-guild conformity in patch occurrence, i.e. whether the species are randomly distributed compared with LT, was tested for each species and region. All species occurred statistically more often with LT than would be expected by chance, in Bergslagen (MT: $\chi^2 = 15.28$, $p < 0.0001$, BT: $\chi^2 = 9.92$, $p = 0.0016$, LW: $\chi^2 = 9.17$, $p = 0.0025$), and in Mix (MT: $\chi^2 = 9.56$, $p = 0.002$, BT: $\chi^2 = 7.76$, $p = 0.0053$, LW: $\chi^2 = 17.48$, $p < 0.0001$) (Df = 1 in all cases).

Analysis II showed that the proportion of guild species that occurred concurrently with LT in the studies from the boreal zone (mean = 92%, n = 27) and from the nemoral zone (mean = 74%, n = 12) differed significantly, with a higher concurrence in the boreal zone ($p = 0.022$, $z = -2.3$, Mann-Whitney). The mean number of guild species present — except LT — when LT was present was 2.4 in the boreal zone studies and 2.7 for the nemoral studies. When LT was absent the corresponding numbers were 0.6 and 1.4, for the boreal and nemoral studies, respectively. The proportion of the guild that occurred like LT in all studies (n = 39), i.e. the boreal and nemoral zones combined, was 86%.

In analysis III, although the guild consisted of only four species, the occurrence distribution of the guild species among patches showed a significant nested structure ($z = -21.12$, $p < 0.0001$), i.e. there were much fewer patch vacancies than expected from a random distribution of the guild. Of the individual species, the occurrence of BT, LT and LW showed significant nested patterns ($p < 0.001$ in all cases), while MT did not ($z = -0.552$, $p = 0.29$). The insignificant nested pattern of MT was due to it being absent in several patches with two and three species, although it occurred alone in one patch (Fig. 1).

4. Discussion

The occurrence pattern of this guild showed that Blue Tits were the most common and widely spread, the Long-tailed Tit and the Marsh Tit had similar occurrence patterns, and the Lesser Spotted Woodpecker was the rarest of the guild members. The entire guild was present in full concurrence (all or none of the species) in 55% of all studied patches. Whether this implies conformity in the guild regarding the occurrence in differently distributed habitat patches, is an open question. However, the number of guild species present when LT was present (3.52) and absent (0.79) for the complete dataset, suggests that the ability to predict the presence of guild species based on the presence of LT was quite good. That is, all guild species may have similar preferrences regarding the distribution of habitat as do Long-tailed Tits.

This study showed a better concurrence of the presence of guild species than did other tests of guild indicator systems on smaller scales (e.g. Patton 1987) and on larger nationwide scales, when species richness of certain taxa should indicate local biodiversity (Kerr 1997, Prendergast 1997). Besides that the guild consisted of only four species, one possible reason for the close associations is that all species are connected to a well-defined habitat. That is, the important factor to be analysed is known, which may be necessary for the selection of proper guilds.

All species occurred significantly more like LT than expected from a random distribution, both in the Bergslagen region and in the more scattered studies (Mix). However, when LT was present it was a better predictor of an entire guild in Mix (81% and 3.8 species present, Table 2), while when LT was absent, the conformity was better

Table 2. The proportion (%) of patches with presence of the guild members when the Long-tailed Tit (LT) was present and absent, respectively, and of the full guild when LT was present in Bergslagen (n = 50) and Mix (n = 54), respectively. The mean number of guild species present per patch when LT was present and absent, respectively, is also shown.

	MT	BT	LW	Entire guild	Mean no. of spp. present
Bergslagen					
LT Yes (n = 18)	61	100	33	28	3.0
LT No (n = 32)	6	53	0	–	0.6
Mix					
LT Yes (n = 43)	95	100	81	81	3.8
LT No (n = 32)	55	73	9	–	1.4

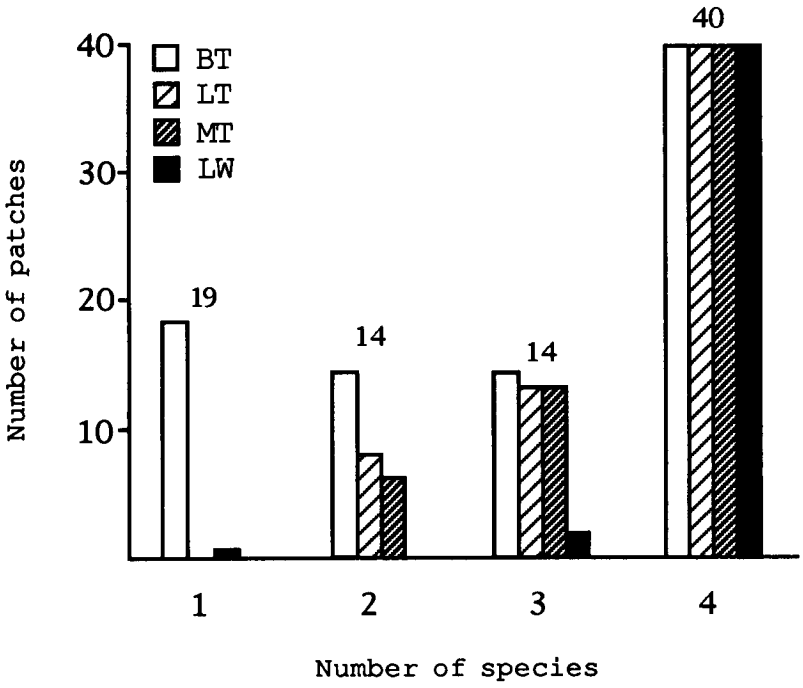

Figure 1. The number of patches with occurrences of Blue Tit (BT), Long-tailed Tit (LT), Marsh Tit (MT) and Lesser Spotted Woodpecker (LW), divided into classes of number of species present (1–4) in the patches. The number above bars shows the sample size per class, total 87 patches.

in Bergslagen (0.6 species). The latter relationship depended to a great extent on the fact that in Bergslagen all guild species were absent in several patches, which thereby lowered the mean number of species when LT was absent. Otherwise, possible reasons for the differences between Bergslagen and Mix are not readily apparent. They may, however, be related to the much lower abundance and greater fragmentation of suitable habitats in Bergslagen (Angelstam 1997).

However, when measured as a proportion of the guild species occurring like LT (II), concurrence was stronger in the boreal zone. Furthermore, in the nemoral zone more than twice as many species were present (1.4) when LT was absent, than in the boreal zone (0.6). That is, guild species occurred in higher conformity in patches in the boreal zone, where the habitat, in general, is more scattered. Such relationships, with higher correspondence in the distribution of ecologically similar species in patchy environments, was suggested by Brown (1984). Moreover, even without knowing the reasons why, it may not be surprising if the behaviour of species differs between regions with different habitat compositions.

When the Lesser Spotted Woodpecker was present, the other guild species were almost always present as well (Fig. 1). Hence, presence of LW was the best predictor of the presence of an entire guild. However, when LW was absent the other three species were often present, that is, the absence of LW could not be used to predict accurately the occurrence of the other guild species.

The Blue Tit was found in the majority of the studied patches (86 out of 104) and, unlike any of the other species, was also found in very small ones (< 1 ha). Hence, it was the most generalist of these four species, and, therefore, the least suitable species to predict the occurrence of this guild.

The Marsh Tit and the Long-tailed Tit were both semi-common and closely associated in their patch appearance, as was also found in other studies (Enoksson et al. 1995, Hinsley et al. 1995). However, MT showed a much higher variability in its nestedness and LT had the best mean values for the number of guild members in accordance, both when it was present and absent. Therefore, LT was the most suitable species to predict the occurrence of this guild. Furthermore, LT uses quite large areas compared with MT (Hinsley et al. 1996, Telleria and Santos 1997),therefore, its presence indicates the suitability of a larger area which is better than vice versa.

Altogether, the occurrence pattern of the guild

species suggests that, if anywhere, this indicator system could be regarded as reliable in the boreal zone. If so, the habitat distribution thresholds for the regular occurrence of the Long-tailed Tit (> 10% habitat coverage and < 300 m between patches) might be accepted as indicators for the presence of this bird guild in landscape planning in, for example, Scandinavian forest management.

Even though the conformity in the occurrences of the guild in patches was relatively high in this study, it may not be considered sufficient for the creation of a reliable indicator system. From a conservationist point of view, in addition to the classic question "how much (habitat) is enough?", one would also need to ask "how much probability is enough?". The often recognised discrepancy between biological relevance and statistical significance of a relationship is a frequent dilemma for ecologists.

However, to obtain reliable habitat or landscape assessments for different species and regions from indicator systems that include animal species, further investigations are needed (Nilsson and Ericson 1997). This study included only four species, but may serve as a useful example for planning possible indicator systems. Important matters for future studies are, for example, to cover the full range of variation of the tested variables among landscapes, the use of long-term data sets (Beshkarev et al. 1994, Jansson & Saari 1997), and perhaps to study sets of species rather than single species indicators (Angelstam 1997).

Acknowledgements. Henrik Andrén was most helpful with the nested statistics and with comments on the manuscript, as were also Per Angelstam, Åke Pehrsson, B. Hinsley and one anonymous referee. I also thank Grzegorz Mikusinski and Eva Ekholm-Pehrson for providing data. The study was supported by the private foundation Olle och Signhild Enqvists stiftelser.

Sammanfattning: **Indikatorsystem på landskapsnivå — ett exempel med fyra lövskogsberoende fågelarter**

Förmågan att förutsäga förekomsten av en grupp löv-blandskogsfåglar i lämpliga bestånd utifrån förekomsten av Stjärtmes testades med hjälp av publiserade inventeringsdata. Förutom den valda indikatorn Stjärtmes (LT), bestod artgruppen av Entita (MT), Blåmes (BT) och Mindre Hackspett (LW). Alla enstaka arter, liksom hela artgruppen, förekom oftare i likhet med Stjärtmesen jämfört med en slumpmässig fördelning. Överlag förekom 86% av artgruppen i enlighet med Stjärtmesen. Vid närvaro av Stjärtmes var i medeltal 3,52 av arterna närvarande och då Stjärtmesen saknades 0,79. Arternas förekomst i bestånd följde ett mönster ("nestedness"), visande tex. att då den Mindre Hackspetten var närvarande var så även hela artgruppen. Stjärtmesen visade dock överlag en bättre statistisk samstämmighet med hela artgruppen, den är även, till skillnad från Mindre Hackspetten, relativt vanlig samt inventeras med god säkerhet större delen av året och vore därför i fält lämpligast att spegla denna artgrupps förekomst. I tidigare studier har setts att Stjärtmesens förekomst i landskapet följer tydliga tröskelvärden angående biotopens fördelning. Arten förekommer regelbundet bara i områden med mer än 10% löv- eller blandskog och där sådana bestånd ej ligger mer än ca. 300 m isär. För praktisk planering vore troligen dessa tröskelvärden de indikatorer som enklast kunde användas i analyser av kart - och GIS - material för att gynna hela denna artgrupp.

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