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Marc-André Villard · Philip D. Taylor

Tolerance to habitat fragmentation influences the colonization of new habitat by forest birds

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Abstract We examined the relationship between the ability of bird species to persist in fragmented forests and their ability to colonize new forest habitat. Using a long-term data set on the colonization of a forest plantation, we tested the hypothesis that bird species tolerant to habitat fragmentation would detect and colonize the new habitat faster than intolerant species. The forest plantation under study is situated on an area of land reclaimed from the sea (a polder) in the central part of The Netherlands. We constructed an index of tolerance to habitat fragmentation and included it as a predictor variable in a set of three logistic regression models that compared the probability of colonization over four consecutive time periods. After controlling statistically for the effects of regional incidence, preferred habitat and life-history characteristics, there was a significant effect of tolerance to fragmentation on the ability of species to colonize the plantation, and a marginal effect on the timing of colonization. We then examined the effect of the same index of tolerance to fragmentation on colonization patterns over a larger spatial scale. Multivariate regression models showed that the proportion of three polders of different ages occupied by forest bird species was dependent upon the regional incidence of a species, its preferred habitat and its tolerance to fragmentation. The results support the hypothesis that species tolerant to habitat fragmentation detect and colonize new habitat faster than those intolerant to habitat fragmentation.

Key words Connectivity · Dispersal · Logistic regression
Landscape ecology · Netherlands Polders

Introduction

Understanding the effects of habitat fragmentation on plant and animal taxa is a major challenge for conservation biology because of the long time scales and large spatial scales generally associated with the phenomenon. Fragmentation effects have mainly been studied *a posteriori*, where it is assumed that past processes are reflected by present distributions of species in the remaining fragments of a formerly continuous habitat (e.g. Whitcomb et al. 1981; Gjerde and Wegge 1989; Lynch and Saunders 1991; van Apeldoorn et al. 1992).

Studies on the avifauna of fragmented forests have shown that some species are consistently absent or infrequent in the most isolated sites (Whitcomb et al. 1981; Lynch and Whigham 1984; van Dorp and Opdam 1987; Askins et al. 1990; Robbins et al. 1989). Various authors (Whitcomb et al. 1981; Lynch and Whigham 1984; van Dorp and Opdam 1987) have proposed that the selective extirpation of some species from the most isolated habitat fragments may result from their lower dispersal ability. By dispersal, we refer to both *natal* and *breeding* dispersal (sensu Greenwood and Harvey 1982). Since the species showing significant isolation effects include long-distance migrants, it was proposed that these species are not less vagile, but might be behaviourally reluctant to fly across open spaces (Whitcomb et al. 1981; Lynch and Whigham 1984; Opdam et al. 1984). The impact of this "barrier effect" on bird distributions might vary with the configuration of forest patches and with the nature of the matrix surrounding those patches (Whitcomb et al. 1981; van Dorp and Opdam 1987; Dunning et al. 1992; Taylor et al. 1993).

Most of the evidence for the reluctance of some forest bird species to cross gaps of open habitat is indirect, or remains unquantified (e.g. Willis 1974). To our knowledge, only Wegner and Merriam (1979) have directly quantified bird movements between forest fragments separated by open land. They found that these movements were uncommon relative to other types of movements (forest to field, forest to fencerow) and that they

M.-A. Villard (✉) · P.D. Taylor
Department of Biology, Carleton University,
Ottawa, Ontario, K1S 5B6, Canada

Present address:

¹Department of Zoology,
University of Alberta,
Edmonton, Alberta T6G 2E9, Canada

were largely restricted to only three species, suggesting that most other species using these fragments were reluctant to fly across open land. However, Wegner and Merriam (1979) could not distinguish "commuting trips" by these species [e.g. blue jay, *Cyanocitta cristata* (L.)] from dispersal movements.

Natal dispersal is always more extensive than breeding dispersal (Greenwood and Harvey 1982; Gauthreaux 1982). The post-fledging period, during which juveniles are believed to locate their future breeding region, is relatively brief, and characterized by high mobility and mortality (Baker 1993). For these reasons, direct measurement of the frequency of dispersal movements by birds among habitat patches is technically difficult. Another approach to this problem is to document the order of appearance of bird species in newly created habitat. Volcanic islands that emerge from the sea and are periodically destroyed by eruptions (e.g. Surtsey, Krakatau) provide such an opportunity. In this study, we analyse the colonization of forest plantations by birds. These plantations are situated on polders – areas of land that have been reclaimed from the sea.

The order of appearance, or colonization sequence, of bird species in polder plantations should reflect the pattern of forest succession. In European forests, vegetational succession is accompanied by a shift in the composition of the avifauna; trans-Saharan migrants are associated with early and mid-successional stages (Bilcke 1984; Helle and Fuller 1988) and year-round residents tend to occupy late successional stages (Bilcke 1984). However, variation in the density of the understorey of mature forests may complicate this relationship (e.g. Fuller and Crick 1992). The colonization sequence may also reflect the regional incidence of the different species. Chance dictates that more individuals of a widely distributed, abundant species will visit a given plantation and eventually breed there (Haila 1983, Haila and Järvinen 1983). Once the effects of the preferred habitat (vegetational composition, seral stage) and regional incidence of the bird species are controlled statistically, the colonization sequence of a given plantation or an entire polder should reflect the relative dispersal ability of the species. This approach provides a more direct assessment of the dispersal ability of different species than the analysis of avian extinctions on land-bridge islands (e.g. Willis 1974; Gotelli and Graves 1990) and other remnants of formerly more extensive tracts of habitat.

The objective of this paper is to test the following hypothesis: species tolerant to the fragmentation of their habitat will detect and colonize polder plantations more quickly than intolerant species. We test this hypothesis using data on the sequence of colonization of a single forest plantation by forest birds, and also, at a larger scale, using data on the pattern of occupancy of entire polders of different ages.

Methods

Study area

Our study is based on bird data from three polders of IJsselmeer, in the central part of The Netherlands (Fig. 1). These polders were reclaimed in three different decades: Noordoostpolder (NO) in 1942, Oostelijk Flevoland (OF) in 1957, and Zuid Flevoland (ZF) in 1968, and they all are about the same size: 480 km², 540 km², and 430 km² respectively. Noordoostpolder is adjacent to the mainland, while the Flevoland polders are adjacent to each other, but separated from the mainland by a lake (Fig. 1). Trees were planted at various times on each polder, creating an array of forest patches of various sizes and shapes. Tree planting in OF polder began in 1959, 2 years after the polder became dry (Mook 1971).

In OF polder, we focused particularly on Roggebotsbos (RB) (Fig. 1), a forest plantation of approximately 1700 ha where breeding birds have been censused intensively in most years since it was created. This plantation contains approximately equal areas of deciduous and coniferous stands, the dominant species being poplars (*Populus* spp.) and Norway spruce (*Picea abies*). Several other species were also planted, including English oak (*Quercus robur*), pines (*Pinus* spp.), and beech (*Fagus sylvatica*) (Bijlsma 1990).

The most probable source of immigrant forest birds to the polders is an extensively forested area called the Veluwe (Fig. 1). This sandy ridge of more than 1200 km² is adjacent to OF and ZF polders, and it is one of the few areas of The Netherlands that has remained forested throughout this century (Barends 1990). It is covered by deciduous and coniferous forest, interspersed with heathland. Coniferous stands cover 75% of the total area of woodland, the remaining 25% being dominated by deciduous tree species. Based on stand areas, the dominant tree species are Scotch pine (*Pinus sylvestris*), English oak, Douglas fir (*Pseudotsuga menziesii*), and beech. Norway spruce is only the third most com-

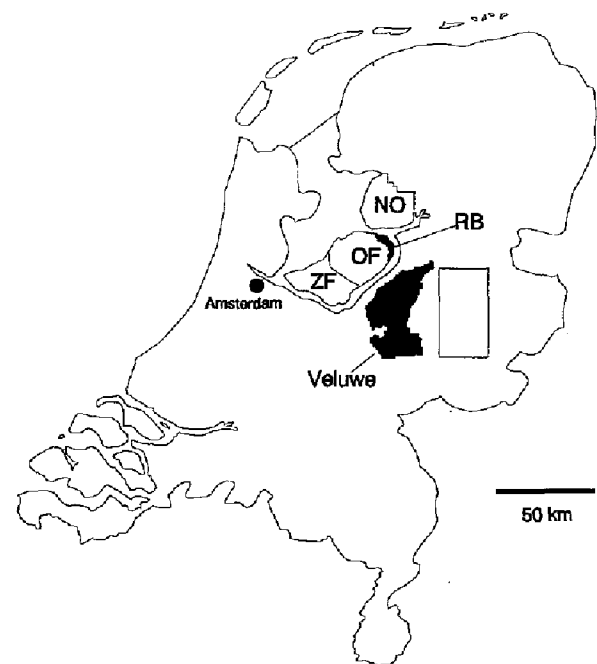


Fig. 1 Map of the study area, showing the location of the three polders (ZF Zuid Flevoland, OF Oostelijk Flevoland, NO Noordoostpolder) and the extensive forests of the Veluwe. The area enclosed by the open rectangle is characterized by fragmented forest

mon coniferous species in the Veluwe (Anonymous 1985). The main differences in tree species composition between the Veluwe and RB plantation are the higher proportion of coniferous stands and lower proportion of poplar stands in the Veluwe and the lower proportion of Douglas fir in RB plantation. These differences largely reflect evolution of forest management and silvicultural practices.

Data set

We compiled a list of forest-bird species of The Netherlands using information on habitat preference provided by SOVON (1987), and unpublished data from A. Schotman (IBN, Leersum, The Netherlands). The list includes 50 species that require at least a small patch of young or mature trees for nesting and that do not use human-built structures (see Appendix 1).

We selected seven independent variables for model building (Table 1). These included five life-history variables: foraging stratum (FORAGING), nest placement (NEST), migratory strategy (MIGRATION), preferred forest habitat (HABITAT) and preferred seral stage (SERAL). For FORAGING and NEST, we followed the classification of Ruitenbeek et al. (1990) and recognized four FORAGING strategies: ground, above-ground, aerial, no preference. We initially recognized several categories of nest type, but later collapsed the variable into a binary variable distinguishing HOLE NESTING species from non hole-nesters. For MIGRATION, we recognized three ordinal categories: migrants (mainly trans-Saharan), partial migrants (in which part of the population winters in The Netherlands), and residents following SOVON (1987). For HABITAT, we distinguished species most abundant in deciduous forest, coniferous forest, and species equally abundant in both. We recognized three ordinal categories of seral stage: early, middle and late. SERAL and HABITAT classifications followed densities reported in Grotenhuis et al. (1985) and Philippona et al. (1983).

One demographic variable was included: regional incidence – the proportion of all 5x5 km breeding bird atlas squares in the Veluwe for which breeding was probable or confirmed (Teixeira 1979). The Veluwe is the largest and, hence, most probable source of colonizing forest bird species to the plantation under study. The shortest distance between the extensive forests of the Veluwe and RB plantation is approximately 6 km (Fig. 1). The incidence measure will itself be a function, in part, of the independent variables HOLE NESTING, MIGRATION, SERAL and HABITAT. So as not to include their effects in further models, we first fitted a generalized linear model with these independent variables to the arcsine-square-root transformed incidence data, and used the deviance residuals (Chambers and Hastie 1992) from that model as a measure of the incidence of species in the Veluwe.

To assess the tolerance of each species to forest fragmentation (TOLERANCE), we compared the incidence (proportion of all bird atlas squares occupied) of each species in an extensively forested area (the Veluwe, described above) to that in a landscape of

the same area immediately adjacent to the Veluwe (Fig. 1). In this landscape (hereafter referred to as the “fragmented block”) woodland is present as a mosaic of small forest patches surrounded by agricultural fields. We reason that if a species has a greater incidence in the Veluwe than in the fragmented block, it is intolerant to the fragmentation of its habitat. If its incidence is equal or greater in the fragmented block, it is tolerant to habitat fragmentation.

The statistic derived using this approach will include two sources of unwanted variation. First, if there are differences in habitat between the two areas, a species that is found preferentially in one or the other may reflect these habitat differences rather than any effects of fragmentation. Second, the overall incidence of forest birds will naturally be lower in the fragmented block simply because there is less forest there. We eliminated the variation due to habitat differences in the following way. We first fit two separate generalized linear models. The dependent variable in each model was the arcsine-square-root of the incidence of forest bird species in each of the two areas – the Veluwe and the fragmented block. The independent variables were the same in each model: HOLE NESTING, MIGRATION, SERAL and HABITAT. These two models estimate the effects of habitat and life-history on the incidence of each species in each of the two areas. We then extracted the deviance residuals from each model, standardized them to mean zero and unit variance, which gives a measure of incidence of each species in each area, after taking habitat and life-history features into account. The procedure also accounts for differences in species' incidence that are due to differences in the extent of forest cover between the two areas.

To calculate the index of tolerance to habitat fragmentation we fitted a model II regression (a PCA on two variables) of the residual incidence of each species in the Veluwe versus the residual incidence of each species in the fragmented block. The residuals from the model II regression (the second principal component) measure the relative difference in the incidence of each species in the Veluwe and the fragmented block. Negative residual values indicate that a species tends to be intolerant to forest fragmentation; positive residuals indicate that a species tends to be tolerant to forest fragmentation.

A summary of variable names used frequently in the text is provided in Table 1. The complete data are presented in Appendix 1.

Plantation scale

We analysed the colonization of RB plantation using data collected by Jonkers (1986). Jonkers used the numerous paths dissecting the plantation as grid lines to map the territories of all species present in a 137-ha plot. He censused birds in 17 of the 22 years between 1964 and 1985. Details on the mapping method used are found in Hustings et al. (1985). In addition to the data of Jonkers (1986), the bird inventories of Cavé (1961) and van Elburg (1969) were used to establish a time series of bird species presence and absence (Table 2). These inventories cover the whole OF polder for the periods 1958-1960 and 1961-1966 respectively. Although the two polder-scale inventories did not pertain specifically to RB plantation, it was frequently visited since it is the largest forest plantation in OF polder and the first that was established. We assume that the first forest species that colonized OF polder were found in RB plantation, even though exact locations of the sightings were not always provided by Cavé (1961) or van Elburg (1969).

The time of colonization was defined as the year a species first appeared in the plantation, irrespective of its subsequent pattern of occupancy, since we wanted to emphasize the ability of a species to colonize, not its ability to maintain a breeding population over time. Using the colonization sequence, each forest species was classified into one of four periods of colonization: 1958-1966 (early), 1969-1976 (middle), 1978-1985 (late). A fourth class includes forest bird species which had not yet colonized RB plantation in 1985. These “non-colonizing” species were considered as potential colonizers since they breed in the Veluwe. Whether a species

Table 1 Names and explanations of independent variables used in the analyses

SERAL	seral stage of forest stands used for breeding – early, middle, late
HABITAT	woodland habitat preferred for breeding – deciduous, coniferous, indifferent
MIGRATION	migration distance – resident, short-distance, trans-Saharan
HOLE NESTING	type of nest built (used) by a species – tree cavity, other incidence in nearby continuous forest – continuous
INCIDENCE	incidence in nearby continuous forest – continuous
TOLERANCE	index of tolerance to woodland fragmentation – continuous

colonized the plantation in a given time period (or not) was the response variable at the plantation scale. To this response variable we fitted three logistic models (generalized linear models with binomial error terms and logit links; McCullagh and Nelder 1989) using the Splus statistical package (Chambers and Hastie 1992). The three models compared: (1) early colonizers with all other species; (2) early and middle colonizers with late and non colonizers; and (3) colonizers with non colonizers. The contribution of each term to reducing the deviance (a measure of the discrepancy between the fitted model and the data that is equivalent to the sums of squares in ANOVA; McCullagh and Nelder 1989) was tested for significance against a χ^2 distribution.

Polder scale

The predictions about colonization sequence derived from the plantation-scale models could not be formally tested because no complete data set exists at that scale. We considered however, that the proportion of squares occupied by a forest-bird species in any given polder during any time period represents an indirect measure of its ability to colonize polder plantations. To examine the patterns of colonization of polders by forest birds, the frequency of occurrence of forest birds on three polders was compared between the period of the breeding bird atlas of The Netherlands (1973–1977; Teixeira 1979) and the bird atlas of The Netherlands (October 1978 to September 1983; sovon 1987). For each of the three polders, we counted the number of 5×5 km atlas squares occupied by each forest bird species in the breeding bird atlas (Teixeira 1979), and on the maps corresponding to the two months best covering the breeding period of each species (as delimited by Hustings et al. 1985) in the sovon (1987) atlas. The number of atlas squares that a species occupies in the polder after a given amount of time is a measure of its ability to colonize that new habitat. A species still colonizing a polder should occupy a greater proportion of squares in the second period.

We then fitted a multivariate general linear model to these data to test the hypothesis that the extent of colonization of the six different polder-age combinations by forest birds was related to the life-history characteristics of the species, regional incidence, and tolerance to habitat fragmentation (the same set of independent variables as used in the plantation-scale analysis). The proportion of the total area of each polder occupied by each species was arcsine-square-root transformed to reduce non-normality. The model was fitted using the MGLH procedure in SYSTAT (Wilkinson 1990). The significance of each independent variable over all six models was measured using Wilk's λ . Comparing the signs and relative magnitude of the coefficients (from each of the six univariate models that made up the multivariate model) among each of the polder-age combinations and between the two scales of analysis, gives additional insight into the nature of the differences between colonization by forest birds at the scale of the plantation and the scale of the polder.

Results

Plantation scale

Substantial variability can be seen in the year of first appearance of the bird species that colonized RB plantation in the 28 years following the reclamation of polder (Table 2). The majority of species were present every year after they first appeared, but some species [e.g. *Anthus trivialis* (L.), *Phylloscopus sibilatrix* (Bechstein)] were recorded in RB plantation many years before their continuous occupancy was established. In the case of *P. sibilatrix*, it is uncertain whether or not a stable breeding

population was established at the end of the period examined (Table 2). It is noteworthy that the greatest year-to-year difference in the cumulative number of species occurred between years 6 and 7 after reclamation. This shows the difference in the intensity of the surveys at the polder scale (year 6) and the breeding bird censuses in RB plantation (year 7). This difference in censusing intensity should not affect the analysis since colonization data were pooled into multi-year classes, and each class contains at least one of the censuses of Jonkers (1986).

A summary of the three logistic models is presented in Table 3. The model coefficients show that seral stage and migration strategy each have consistent, significant effects on the probability of colonization for each of the contrasted groups. Early successional species were more likely to colonize in each time period, as were trans-Saharan migrants. The effects of habitat, hole nesting, and regional incidence had a significant effect only in the early stages of colonization (model 1). Early colonizing species included one hole nesting species (1/19) whereas hole nesters represented nearly one-half (3/7) of the species that colonized in the middle period, and two-thirds (6/9) of the late-colonizing species. No early colonizers were coniferous forest specialists (0/19), whereas 40% (6/15) of non colonizers were. These results suggest that once plantations have been established for about 10 years, there is an adequate mix of habitats and trees for hole nesting to satisfy most species. For example, *Parus palustris* L., one of the earliest hole-nesting species to colonize RB plantation, can extract nesting cavities in fast-growing, soft-wooded alders. Our results also indicate that species with a high regional incidence detected and colonized RB plantation relatively quickly, so that there was no detectable effect of this variable after the first 10 years.

The effects of tolerance to fragmentation increased in magnitude and significance from the first to third models. The effects were marginally significant in the model comparing early and middle colonizers to late and non-colonizers and highly significant in the model comparing colonizers to non-colonizers. Mean tolerance to fragmentation was positive for each group of colonizing species (early, middle, late), but negative for the non colonizers. In general, species that colonized early were those that were tolerant to habitat fragmentation and species that had not colonized the plantation after 30 years were those that were intolerant to habitat fragmentation.

The models can be summarized as follows: early seral-stage species that are trans-Saharan migrants, open nesters, prefer deciduous forests, and are regionally common, were more likely to colonize the plantation early than later seral-stage species that are resident, hole nesters, prefer coniferous stands, and are regionally uncommon. In addition, species intolerant to the fragmentation of their habitat, were less likely to colonize the plantation at all. FORAGING stratum did not contribute significantly to any of the models, possibly reflecting the lack of distinction between species mainly foraging in the sapling layer versus those foraging in the forest canopy.

Table 2 Colonization by forest birds of Roggebotsbos (RB) plantation, from the year following reclamation (1958, year 1) until 1985 (year 28). References: 1958–60: Cavé (1961); 1961–63, 1965–66: van Elburg (1969); 1964, 1969–76, 1978–85: Jonkers (1986). Data were collected in a 137-ha plot. [*P* species present in Oostelijk Flevoland (no evidence of breeding), + territorial male(s) recorded]

Species	Year after reclamation																											
	1	2	3	4	5	6	7	8	9	12	13	14	15	16	17	18	19	21	22	23	24	25	26	27	28			
<i>Sylvia communis</i>	P	P	P							+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Acrocephalus palustris</i>	P	P	P							+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Asio otus</i>		+		+		+	+	+	+																			
<i>Streptopelia turtur</i>				+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Sylvia borin</i>				+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Oriolus oriolus</i>				+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Cuculus canorus</i>				P	P	P		P	P	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Scolopax rusticola</i>					P					+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Phylloscopus collybita</i>						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Turdus philomelos</i>						+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Anthus trivialis</i>							+	+																+	+	+		
<i>Phylloscopus sibilatrix</i>							+	+																		+		
<i>Garrulus glandarius</i>							+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Turdus viscivorus</i>							+		+	+	+						+	+		+	+	+	+	+	+			
<i>Fringilla coelebs</i>							+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Phoenicurus phoenicurus</i>							+					+																
<i>Prunella modularis</i>								+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Sylvia curruca</i>							+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Sylvia atricapilla</i>							+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Erithacus rubecula</i>								+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Aegithalos caudatus</i>									+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Parus montanus</i>									+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Luscinia megarhynchos</i>										+	+																	
<i>Muscicapa striata</i>												+	+	+	+	+	+		+	+	+	+	+	+	+	+		
<i>Regulus ignicapillus</i>														+														
<i>Regulus regulus</i>															+	+	+	+	+	+	+	+	+	+	+	+		
<i>Dendrocopos major</i>																		+	+	+	+	+	+	+	+			
<i>Coccothraustes coccothraustes</i>																			+	+	+	+	+	+	+			
<i>Certhia brachydactyla</i>																										+		
<i>Ficedula hypoleuca</i>																										+		
<i>Turdus pilaris</i>																										+		
<i>Parus cristatus</i>																										+		
<i>Parus ater</i>																										+		
<i>Columba oenas</i>																										+		
<i>Accipiter gentilis</i>																										+		

Table 3 Logistic models showing the effects of independent variables on the probability of colonization of a forest plantation by birds. There are four time periods of colonization: (1) pre-1966; (2) 1969–1976; (3) 1978–1985; and (4) non-colonizers. There are three different models. In the first model, we contrast species that colonized in the first time period (i.e. pre-1966) with all others (post 1969 and absent). The model measures the impact of each independent variable on the probability of a species

colonizing up until 1966. In the second model, we contrast species from the first two time periods (i.e. pre-1976) with all others (post-1978 and absent). The final model contrasts the species that had colonized the plantation by 1985 with those that had not. For HABITAT, coniferous forest is the reference group. The first parameter compares deciduous forest with coniferous, the second parameter compares no preference with coniferous

Terms	df	Model 1			Model 2			Model 3		
		β	D	$P(\chi^2)$	β	D	$P(\chi^2)$	β	D	$P(\chi^2)$
Null model	49	-4.2	66.41		2.0	69.24		1.4	61.08	
SERIAL	1	-2.2	13.55	0.0002	-2.0	20.35	<0.0001	-1.3	5.48	0.02
HABITAT D	2	5.3	6.37	0.04	0.1	2.64	0.27	0.5	0.52	0.77
C+D		1.9			0.3			0.2		
MIGRATION	1	2.5	8.59	0.003	1.6	7.58	0.006	1.4	3.78	0.05
HOLE NESTING	1	-1.9	4.63	0.03	-0.8	1.07	0.30	-0.2	0.09	0.76
INCIDENCE	1	2.5	6.25	0.01	0.8	1.69	0.19	0.6	0.31	0.58
TOLERANCE	1	1.2	21.83	0.18	1.5	2.99	0.08	2.2	6.77	0.009
Residual	42		25.18			33.60			44.94	

Polder scale

The change in the frequency of occurrence of each species in each of the three polders (ZF, OF, NO) between the two periods of atlas recording is shown in Fig. 2. The number of species whose frequency of occurrence increased between the two periods gradually declined with time since polder reclamation (ZF to OF to NO). Many bird species colonized ZF polder within the first 15 years (Fig. 2A); 26 years after reclamation, some species were still colonizing OF polder (Fig. 2B), but by 41 years, colonization no longer was occurring in NO polder (Fig. 2C).

We included all independent variables used in the plantation-scale models in this polder-scale analysis in order to look at how parameter estimates changed through time, and across polders. Habitat, regional incidence and tolerance to fragmentation contributed significantly to the explanatory power of the polder models (Table 4). The signs of the parameter estimates for these variables are the same across the six univariate models, and also the same as in the plantation models, indicating that the direction of the effects of each variable on the timing of colonization of the plantation is identical to their effects on the extent of occupancy of the polders.

Discussion

Our results support the hypothesis that species able to quickly detect and colonize newly-available habitat are also more tolerant to the fragmentation of their habitat. This hypothesis is supported both at the scale of a single forest plantation and at that of entire polders. At the plantation scale, the effect of tolerance to fragmentation was most significant when comparing species that had colonized RB plantation by 1985 to potential colonizing species that were still absent. The fact that new species colonized RB plantation in 1985, and that several species were still expanding their distribution in OF polder in the 1979–1983 period (26 years after its reclamation) supports our contention that several forest bird species absent from RB plantation in 1985 can be considered as potential colonizers. A comparison of the variability in the proportion of atlas squares occupied by forest bird species among the three polders examined (Fig. 2) suggests that colonization and distributional expansion should continue to take place in OF polder for approximately another decade. Even though no substantial expansions occurred in NO polder (the oldest polder examined) between the two periods of atlas recording, four species [*Accipiter gentilis* (L.), *Regulus ignicapillus* (Temminck), *Carduelis spinus* (L.), and *Loxia curvirostra* (L.)] colonized this polder during this period.

Although a relationship between tolerance to habitat fragmentation and colonization ability points to dispersal as the key process involved, we cannot determine whether the patterns observed mainly reflect the physical (distance) or behavioural (response to contrasting habitat)

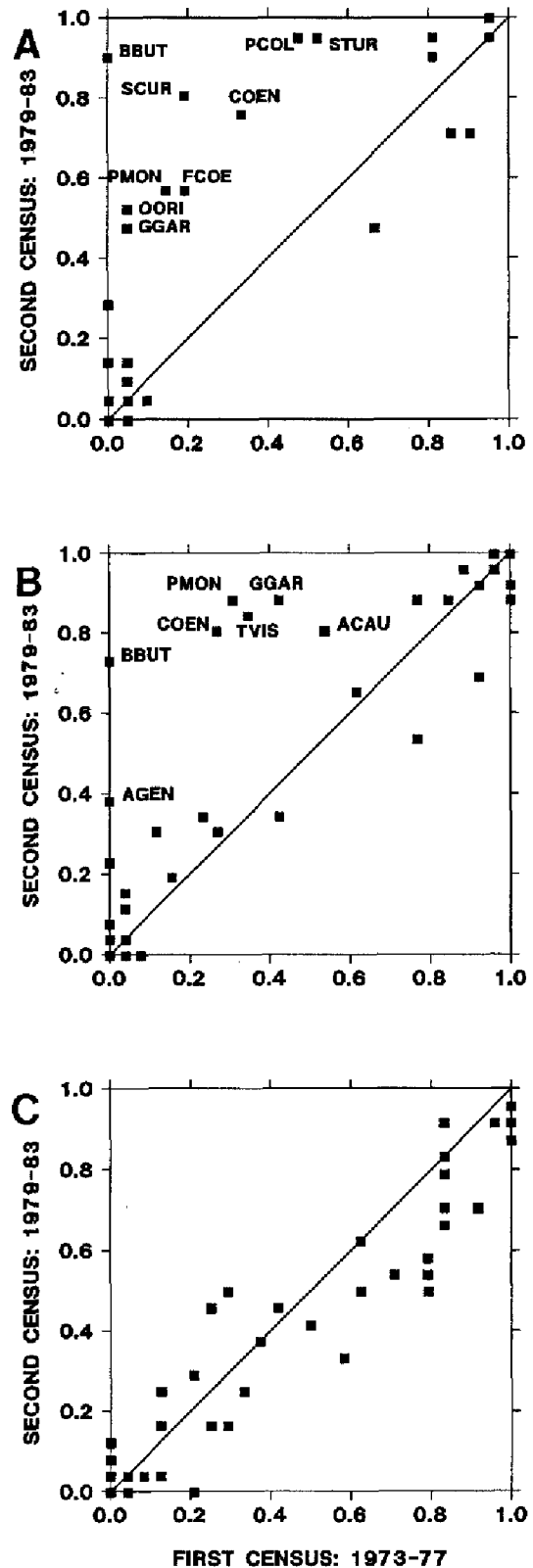


Fig. 2A–C Variation in the proportions of atlas squares occupied by woodland bird species in three polders of the Netherlands between 1973–1977 (Texeira 1979) and 1979–1983 (SOVON 1987). Points lying off the diagonal changed proportions between the two atlas periods. A ZF polder (reclaimed in 1968), B OF polder (reclaimed in 1957), C NO polder (reclaimed in 1942). Species codes are listed in Appendix 1

Table 4 Multivariate regression model showing the effects of independent variables on the proportion of each of the three polders occupied by forest birds in two time periods (1973–1977 and 1979–1983). The top table shows the mean-square variance and the probability of the type-I error for the multivariate effect of that term (measured using Wilk's λ); the bottom table shows the estimated effects of each independent variable for the six univariate models that make up the analysis. For HABITAT: D, coniferous forest is the reference group. The first parameter compares deciduous forest with coniferous, the second compares no preference with coniferous forest.

Terms	Polder						$P(W\lambda)$
	Zuid Flevoland		Oostelijk Flevoland		Nordoostpolder		
	1973–77	1979–83	1973–77	1979–83	1973–77	1979–83	
Constant	1.24	1.06	1.56	1.65	1.46	1.32	0.027
SERIAL	1.60	0.79	1.51	0.76	0.75	0.52	0.063
HABITAT	0.12	0.13	0.38	0.48	0.62	0.24	0.005
MIGRATION	0.36	0.61	0.57	0.27	0.42	0.21	0.338
HOLE NESTING	0.01	0.07	0.15	0.44	0.10	0.11	0.696
INCIDENCE	0.54	2.20	1.62	2.35	3.07	2.76	<0.001
TOLERANCE	1.31	1.90	1.63	1.76	1.86	1.06	0.005
Error	0.132	0.164	0.127	0.146	0.086	0.083	
Constant	0.80	0.74	0.90	0.93	0.87	0.83	
SERIAL	-0.30	-0.21	-0.30	-0.21	-0.21	-0.17	
HABITAT: D	0.11	0.11	0.14	0.04	0.07	-0.02	
C+D	-0.01	0.01	0.11	0.18	0.20	0.14	
MIGRATION	0.12	0.16	0.15	0.10	0.13	0.09	
HOLE NESTING	-0.03	-0.10	-0.15	-0.26	-0.13	0.13	
INCIDENCE	0.11	0.23	0.20	0.24	0.27	0.26	
TOLERANCE	0.33	0.40	0.37	0.39	0.40	0.30	

component of dispersal. Individuals from species scored as intolerant of forest fragmentation (e.g. *Scolopax rusticola* L., *Phylloscopus sibilatrix* – Appendix 1) were recorded in RB plantation many years before they established stable breeding populations. This suggests that some species have the physical ability to disperse to new sites, but for unknown reasons are less likely to do so.

To our knowledge, this is the first study reporting empirical evidence that species sensitive to habitat fragmentation are less efficient in detecting and colonizing new habitat, and hence may have a lower dispersal ability. The stochasticity inherent in dispersal movements of individual birds could have obscured the relationship between tolerance to fragmentation and timing of colonization. For example, assuming a negative exponential distribution of dispersal distances from the Veluwe forests (the presumed source of colonists), rare long-distance dispersal events could have led to the presence of individuals of a species in the polder plantations long before one would expect to detect that species based on its median dispersal distance. This phenomenon does not seem important here since most species occupied RB plantation more or less continuously from their year of first appearance.

Fine patterns in the colonization sequence of a forest plantation might reflect a gradual availability of new microhabitat features. We incorporated all predictors of colonization ability that we suspected to be important at a meso-scale in our analysis, but our classifications of these predictors were relatively coarse. Hence, the resolution of our models predicting the timing and extent of polder colonization was correspondingly coarse. The fact that these predictors were found to have significant effects on the response variables (at the plantation and polder scales) suggests that these finer, micro-scale habitat features are, on average, less important at larger scales.

The tolerance of a species to fragmentation has an important effect on colonization patterns at both medium and large scales even after considering habitat variables such as seral stage. The result has important implications for the conservation of forest birds and other mobile organisms. It suggests that the proper functioning of reserve networks for species intolerant to habitat fragmentation will depend on the ability of animals to move through the landscape – i.e. on landscape connectivity (Merriam 1984; Taylor et al. 1993). For most mobile organisms, the effects that changes in connectivity (such as those caused by habitat fragmentation) have on population dynamics at the landscape scale have not been investigated. Empirical studies comparing measures of movement abilities of the same species in fragmented and non-fragmented habitats are needed to both corroborate the general pattern we report, and to suggest means of altering landscape connectivity to ensure the persistence of target species.

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Appendix 1 Data included in the plantation scale and polder scale analyses. See Table 1 for the meaning of variable names.

Species	Code	Period of colonization ^a	MIGRATION ^b	HOLE NESTING ^c	TOLERANCE ^e	INCIDENCE ^d	HABITAT ^f	SERAL ^g
<i>Pernis apivorus</i>	PAPI	A	M	0	-0.998	82.2	C+D	L
<i>Accipiter gentilis</i>	AGFN	L	R	0	-0.257	86.7	C	L
<i>A. nisus</i>	ANIS	A	P	0	-0.473	100.0	C	M
<i>Buteo buteo</i>	BBUT	A	P	0	-0.050	100.0	C+D	L
<i>Scolopax rusticola</i>	SRUS	E	P	0	-1.584	100.0	D	E
<i>Columba oenas</i>	COEN	L	P	1	-0.368	100.0	D	L
<i>Streptopelia turtur</i>	STUR	E	M	0	0.219	100.0	C+D	M
<i>Cuculus canorus</i>	CCAN	E	M	0	0.106	100.0	D	E
<i>Strix aluco</i>	SALU	A	R	1	-0.519	100.0	D	L
<i>Asio otus</i>	AOTU	E	P	0	-0.437	100.0	C+D	M
<i>Jynx torquilla</i>	JTOR	A	M	1	-0.741	64.4	C+D	L
<i>Picus viridis</i>	PVIR	A	R	1	0.437	100.0	C+D	L
<i>Dryocopus martius</i>	DMAR	A	R	1	-0.457	100.0	D	L
<i>Dendrocopos major</i>	DMAJ	L	R	1	0.437	100.0	C+D	L
<i>D. minor</i>	DMIN	A	R	1	-0.064	77.8	D	L
<i>Anthus trivialis</i>	ATRI	E	M	0	-0.874	100.0	C+D	E
<i>Prunella modularis</i>	PMOD	E	P	0	0.196	100.0	C+D	M
<i>Erithacus rubecula</i>	ERUB	M	P	0	0.196	100.0	C+D	M
<i>Luscinia megarhynchos</i>	LMEG	M	M	0	1.089	46.7	D	M
<i>Phoenicurus phoenicurus</i>	PPHO	E	M	1	0.483	100.0	C+D	L
<i>Turdus pilaris</i>	TPIL	L	P	0	1.102	0	D	L
<i>T. philomelos</i>	TPHI	E	P	0	0.196	100.0	C+D	M
<i>T. viscivorus</i>	TVIS	E	P	0	0.263	100.0	C+D	L
<i>Acrocephalus palustris</i>	APAL	E	M	0	0.967	46.7	D	E
<i>Sylvia curruca</i>	SCUR	E	M	0	-0.373	100.0	D	M
<i>S. communis</i>	SCOM	E	M	0	0.106	100.0	D	E
<i>S. borin</i>	SBOR	E	M	0	0.106	100.0	D	E
<i>S. atricapilla</i>	SATR	E	M	0	0.219	100.0	C+D	M
<i>Phylloscopus sibilatrix</i>	PSIB	E	M	0	-0.527	88.9	C+D	L
<i>P. collybita</i>	PCOL	E	M	0	0.173	100.0	D	M
<i>Regulus regulus</i>	RREG	M	P	0	-0.115	100.0	C	M
<i>R. ignicapillus</i>	RIGN	M	P	0	-0.305	82.2	C	L
<i>Muscicapa striata</i>	MSTR	M	M	1	0.039	100.0	C+D	L
<i>Ficedula hypoleuca</i>	FHYP	L	M	1	0.039	100.0	C+D	L
<i>Aegithalos caudatus</i>	ACAU	M	R	0	0.107	100.0	C+D	E
<i>Parus palustris</i>	PPAL	A	R	1	-0.053	100.0	D	L
<i>P. montanus</i>	PMON	M	R	1	-0.073	100.0	C+D	M
<i>P. cristatus</i>	PCRI	L	R	1	0.241	100.0	C	L
<i>P. ater</i>	PATE	L	R	1	0.441	100.0	C	L
<i>Sitta europaea</i>	SEUR	A	R	1	-0.281	97.8	D	L
<i>Certhia brachydactyla</i>	CBRA	L	R	1	0.437	100.0	C+D	L
<i>Oriolus oriolus</i>	OORI	E	M	0	1.016	73.3	D	M
<i>Garrulus glandarius</i>	GGAR	E	R	0	0.173	100.0	C+D	M
<i>Corvus corax</i>	CCOR	A	R	0	0.590	11.1	C	L
<i>Fringilla coelebs</i>	FCOE	E	P	0	0.263	100.0	C+D	L
<i>Carduelis spinus</i>	CSPI	A	R	0	0.030	42.2	C	L
<i>Loxia curvirostra</i>	LCUR	A	P	0	-0.151	37.8	C	L
<i>Pyrrhula pyrrhula</i>	PPYR	A	R	0	-0.139	100.0	C+D	M
<i>Coccothraustes coccothraustes</i>	CCOC	L	P	0	-0.967	91.1	D	L
<i>Emberiza citrinella</i>	ECIT	A	P	0	0.130	100.0	C+D	E

^a (E early: 1958–1966, M middle: 1969–1976, L late: 1978–1985, A absent – species that had not yet colonized the plantation in 1985) (data in Table 1)

^b (M migrant, P partial migrant, R resident) (based on SOVON 1987)

^c (1 hole-nesting species, 0 species not nesting in tree holes or other cavities) (based on Ruitenbeek et al. 1990)

^d (Percentage of atlas squares occupied in the Veluwe ($n = 45$ squares), the largest area of woodland in the region (data from Texeira 1979))

^e see Methods (data from Texeira 1979). Tolerance to fragmentation increases with index value

^f (D deciduous, C coniferous, C+D no preference; species as abundant in C and D stands) (based on Grotenhuis et al. 1985; Philippona et al. 1983, and SOVON 1987)

^g (E early, M middle, L late)

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