

## **Migratory habits of birds breeding in different stages of forest succession: a comparison between the Palaearctic and the Nearctic**

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Mönkkönen, M. & Helle, P. 1989: Migratory habits of birds breeding in different stages of forest succession: a comparison between the Palaearctic and the Nearctic. — *Ann. Zool. Fennici* 26:323–330.

Forestry considerably alters the relative proportion of different forest succession stages nearly all over the world. Sedentary and migratory birds do not respond equally to habitat changes, as migrants may benefit or suffer from silviculture on both their breeding and wintering grounds. We examined the abundance of tropical migrants in temperate breeding passerine communities using 30 published (and one unpublished) studies of forest succession from North America, Europe and East Asia.

The proportion of tropical migrants is highest in intermediate stages of forest succession in Europe, whereas it increases with increasing stand age in eastern North America. In western North America the proportion is relatively even in intermediate and late phases of succession, after having increased from a low proportion in early successional habitats. In Japan, the proportion of tropical migrants in breeding assemblages is highest in the early stages, it then decreases, and increases again in late successional forests. Density trends of tropical migrants along the succession gradient follow the trends observed in relative proportion, except in Japan, where the density tends to increase.

We also studied the relationship between the migratory habit and breeding habitat structure of species using information provided in handbooks. There is a significant negative correlation between the length of migration and closeness of breeding habitat in passerine bird fauna in East Asia and Europe, whereas North America shows no significant relationship.

The results support the hypothesis of Bilcke that the habitat use of migrants in the breeding area is affected by the habitat availability in wintering areas. Of the wintering areas concerned, Africa includes the largest proportion of open habitats, whereas the Caribbean area and northern South America include mainly forests. We emphasize that it is impossible to give universally valid recommendations for the conservation of tropical migrant birds; instead we emphasize the greater importance of the specific requirements of each species.

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### **1. Introduction**

Forestry dramatically alters the distribution of habitats all over the world. Primeval forests in the areas of old civilization have been destroyed long ago; at present modern forestry is expanding into the most remote areas of the world, both in the tropics and the boreal forest zone. The impact of forestry on avian life on a local scale in particular has been studied

intensively since the pioneering study by Lack (1933) in Breckland, England. Thanks to this research we are able to ask more general questions on the effects of forestry on birds. One major phenomenon to be explained is: Why do tropical migrants prefer open or early successional habitats in their northern breeding grounds in Europe (e.g. Herrera 1978, Bilcke 1984, Helle & Fuller 1987), but mature forest in eastern North America (e.g. Whitcomb et al. 1981)? This is



Fig. 1. Passerine bird species breeding within the shaded areas were included in the breeding habitat vs. migratory habit comparison of this study (see text for details). The arrows indicate the main routes of holarctic passerines to their wintering grounds in the tropics (modified after McClure 1974).

an important question especially from the point of view of nature conservation. A related question is: Why are no 'area effects' due to forest fragmentation observable in Europe, whereas this seems to be the case in eastern North America (McLellan et al. 1986, Haila 1986, see also Helle 1985a).

Sedentary and migratory birds are not equally affected by forestry, as migrants may benefit or suffer from habitat changes that have taken place in both their breeding and wintering areas, and possibly along their migration route. The purpose of this study is to present both intra- and intercontinental comparisons of the habitat utilization patterns of tropical migrants in their temperate breeding grounds. This analysis is based on published results of quantitative breeding bird censuses conducted in different phases of forest succession. Secondly, we correlate the migratory habit and habitat requirements of passerine birds in North America, Europe and East Asia using information available in fieldguides and handbooks.

## 2. Material and methods

### 2.1. Forest succession analysis

Breeding-bird data for different stages of forest succession were culled from literature of three continents. The material represents the breeding areas of four major migration systems: Palearctic-African, East Asian and both western and eastern Nearctic-Neotropical system (see McClure 1974; Fig. 1). In the appendix we give the study areas and the data sources. The European and North American data contain information on both deciduous and coniferous successions, but for East Asia we were

obliged to restrict our analysis to deciduous forest succession in Japan.

The stages of forest succession were divided into four categories according to the height of vegetation (<1, 1–4, 4–10, >10 m). The Kruskal-Wallis test was used to test the differences between the successional categories within a study area. Absolute differences in successional categories between the continents are not important, as for example, 'tropical migrant' is a relative concept, but the main emphasis is on the comparison of the patterns obtained for each geographical area.

Migratory habit for each species was determined based on the following field guides:

North America	Scott et al. 1987
Europe	Bruun & Singer 1971
East Asia	Flint et al. 1984, King et al. 1986.

The density and relative proportion of tropical migrants were then calculated for each successional stage.

### 2.2. Migratory habit vs. habitat structure

We followed Bilcke's (1984) study in assessing the relationship between the migratory habit and breeding habitat structure of species. We grouped the breeding passerine species of the Soviet Far East, Finland (northern Europe) and eastern and western North America (see Fig. 1) into three categories according to their migratory habit:

- 1) sedentary species including partial migrants,
- 2) short-distance migrants and
- 3) tropical migrants.

The species were further divided into five categories according to the structure of their breeding habitat:

- 1) open habitat without trees or shrubs,
- 2) as category 1 but some trees or bushes present; reed-land,
- 3) shrubland, thickets,
- 4) open forest, parks and orchards,
- 5) forest.

These divisions are based on information provided by field-guides: Flint et al. (1984) for the Soviet Far East, Hildén (1974) for Finland, and Petterson (1962) and Scott et al. (1987) for North America. As to the general appearance of habitats this open ground – closed forest continuum is structurally analogous with the forest succession gradient of the succession analysis described above.

All the species of the Soviet Far East were included in the analysis, but for Finnish and American data we restricted the analysis to the most abundant species with the help of quantitative data (Merikallio 1958 and Robbins et al. 1986, respectively). The reasoning was based on

- 1) the more abundant the species the better its migratory habit and breeding habitat are known, and
- 2) this knowledge makes it possible to get equally large samples.

Bilcke's (1984) similarly collected material from Belgium was used as such in comparisons. Spearman's rank correlation technique was employed to test the relationship between migratory habit and habitat structure.

### 3. Results

#### 3.1. Forest successions

The breeding density of tropical migrants in bird communities increases in the course of forest succession in eastern North America (Fig. 2), and the variation among the vegetation height classes is significant (Kruskal-Wallis,  $H=14.8$ ,  $P<0.05$ ). Furthermore, the proportion of tropical migrants in breeding passerine communities increases during succession (Fig. 2,  $H=20.2$ ,  $P<0.001$ ). In western North America the density and proportion of tropical migrants is more or less constant in three later successional categories and there are no significant differences among categories (density:  $H=5.5$ , ns; relative proportion:  $H=4.3$ , ns).

In Europe, the density of tropical migrants is highest during intermediate phases of forest succession (Fig. 2). Density variation between vegetation height classes is significant ( $H=10.1$ ,  $P<0.05$ ). The proportion of tropical migrants in breeding bird assemblages in Europe peaks in the second vegetation height category (1–4 m), being at its lowest in forests more than 10 m in height (Fig. 2). These differences are also significant ( $H=15.4$ ,  $P<0.01$ ).

In Japan, the abundance of tropical migrants tends to increase in the course of succession. The proportion of tropical migrants in bird communities is highest in the pioneering stages of forest succession, low in the intermediate stages, and increases again in forests more than 10 m in height (Fig. 2). However,

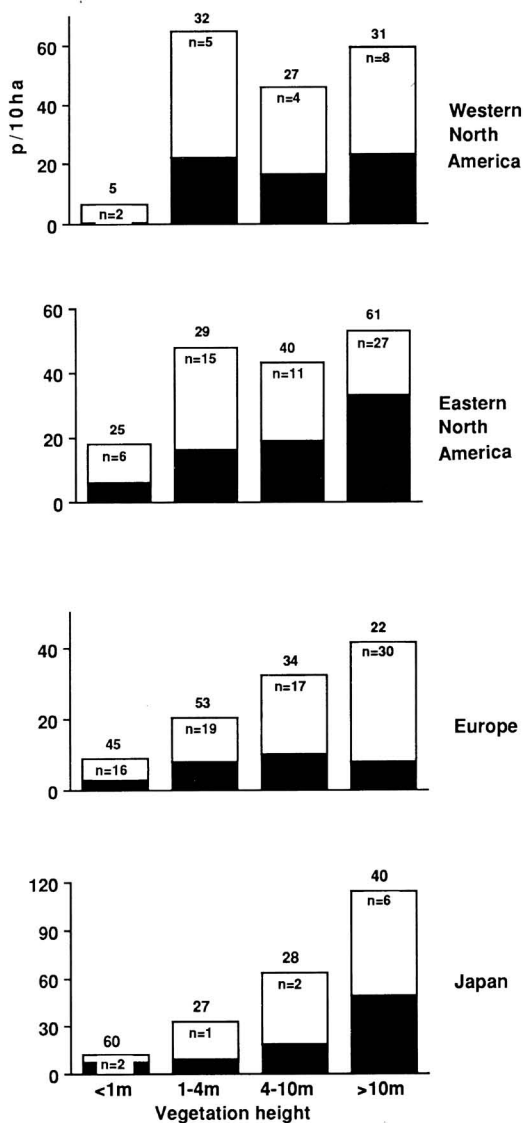


Fig. 2. Mean densities of breeding passerine birds (pairs/10 ha) in habitats of different heights of vegetation in the four geographical areas considered. The black area of bars indicate the density of tropical migrants. The figures above each bar denote mean relative proportion of tropical migrants in vegetation height categories. Number of communities studied is given inside each bar.

neither of these patterns is statistically significant ( $H=2.9$ , ns, and  $H=7.4$ , ns, respectively).

### 3.2. Migratory habit and habitat requirements

The following tabulation shows the rank correlation coefficients between the migratory habit (range 1–3) and breeding habitat structure (1–5) of passerines for each study area ( $n$  = number of species):

	$r_s$	$P$	$n$
Soviet Far East	-0.29	<0.01	105
Finland	-0.61	<0.001	70
Belgium (Bilcke 1984)	-0.26	<0.05	75
Eastern North America	+0.20	ns	73
Western North America	-0.10	ns	71

Significant negative correlations for the Soviet Far East and Europe indicate that relatively more resident species breed in forests than in open habitats and/or relatively more migrants in open habitats than in forests. Although neither of the two correlations for North America is significant, the coefficient for western North America is significantly smaller than the one for eastern North America ( $Z=1.78$ , 1-tailed  $P<0.05$ ).

Qualitative and quantitative analyses seem to provide quite similar results. Although the rank correlation coefficient for eastern North America is not significant, it is in the 'right' direction: relatively more migrants breed in forests than in open habitats.

Relative distribution of tropical migrant species into the five habitat categories in the qualitative analysis gives further support to the quantitative analysis. In Finland and Belgium, tropical migrants constitute a greater part of the bird fauna in intermediate categories than at the ends of the continuum (Table 1). The two European patterns and that for the Soviet Far East do not differ significantly from each other ( $P>0.05$  for all the comparisons,  $\chi^2$  test). In the Soviet Far East, tropical migrants' contribution is greatest in open habitats. The pattern for eastern North America deviates significantly from each of the Old World distributions ( $P<0.05$  in every case): tropical migrants form a much greater part of forest bird species than species of other habitats.

The proportion of tropical migrant species in the five habitat categories in western North America shows a clear peak in category 3 (shrubland, thickets), which deviates from the succession analysis. This pattern differs significantly from eastern North American and East Asian patterns, but not from European ones (Table 1).

The consideration of the proportions of tropical migrant species in different habitat categories (above) is not quite satisfactory, as the numbers of other

Table 1. The percentage of tropical migrant species in the breeding passerine fauna in five habitat categories distinguished in different geographical areas considered. 1 = open habitat without trees or shrubs, 2 = as category 1 but some trees or shrubs present, 3 = shrubland, thickets, 4 = open forest, parks and orchards, 5 = forest. The figures in parentheses indicate the number of tropical migrant species.

	1	2	3	4	5
Soviet					
Far East	63 (5)	67 (12)	54 (7)	33 (4)	33 (18)
Finland	25 (1)	72 (13)	67 (4)	25 (4)	12 (3)
Belgium	29 (2)	56 (9)	27 (4)	35 (6)	20 (4)
E North					
America	22 (2)	46 (6)	46 (6)	15 (2)	68 (17)
W North					
America	17 (1)	24 (4)	64 (7)	27 (4)	27 (6)

species may play a significant role. Table 1 shows the absolute numbers of tropical migrant species in the five habitat categories for the geographical areas considered. These figures are in agreement with the result of the succession analysis (Fig. 2) and percentages of species (Table 1). East Asia is somewhat exceptional, however. The two-peaked pattern clearly deviates from the percentage distribution, but resembles the pattern observed in the forest succession analysis (Fig. 2).

## 4. Discussion

### 4.1. Hypotheses of breeding habitat patterns of migrant birds

Our results, i.e. that the proportion of tropical migrants in their northern breeding grounds in Europe is greatest in early successional and in other open habitats, are well documented (Herrera 1978, Bilcke 1984, Potti 1985, Helle & Fuller 1987). It is equally well known that neotropical migrants in eastern North America mainly inhabit forest proper (Robbins 1979, Whitcomb et al. 1981). Comparative data from western North America and East Asia raise interesting questions. What factors are responsible for the differences observed? Three hypotheses have been proposed to account for the relative abundance of migrants in breeding communities, namely those of MacArthur (1959), Alerstam & Enckell (1979) and Bilcke (1984).

MacArthur (1959) hypothesized that the percentage of migrants is highest where the contrast in food

resources available for birds between summer and winter (seasonality) is largest. The hypothesis successfully accounts for the increase in the percentage of migrants, with increasing latitude in Europe (Herrera 1978, see also Helle & Fuller 1987) and between-habitat differences (e.g. coniferous vs. deciduous forest) in a given area (e.g. Willson 1976, Haila 1981). Since it is very improbable that forest successions (our succession analyses) or open habitat – forest continua (our qualitative analyses) differ between different continents in seasonality, MacArthur's hypothesis is not capable of explaining intercontinental or western vs. eastern North American differences. However, this hypothesis cannot be ruled out before it is properly tested.

Alerstam & Enckell (1979) proposed that migrants are better competitors in simple (open) habitats than in more complex ones (forests), because birds with simple niches can fit more easily into or find empty niche space in existing communities in their winter quarters, and they, therefore, have better chances to become migrants.

This hypothesis is in agreement with our European results and partly with East Asian results when considering percentages, but it fails to account for the North American patterns and density trends in all the study areas. Differences in niche space between birds with different migratory habits requires more consideration, (for example, are the niches of neotropical (or African) migrants simpler than those of sedentary species in Nearctic (or Palaearctic) forest), before the hypothesis can be satisfactorily tested. The problem is also conceptually difficult: although the structure of the preferred habitat of a species is simple, it does not inevitably mean that its niche is simple.

#### 4.2. Habitat preferences and vegetation in the tropics

Bilcke (1984) proposed that the habitat occupancy of migrant birds in their breeding grounds is determined by the proportions and geographical distribution of vegetation types in their winter quarters. The following tabulation shows rough estimates of the proportion of tropical forest to the total land area in the wintering areas of species breeding in areas of this study (based on vegetation maps):

Tropical	% forest
Africa	25
South America	70
Central America	50
East Asia	40

Bilcke's (1984) hypothesis is supported by the data of this study regarding percentage, but the density trends are not so clear. Several studies have shown that only a few Palaearctic migrants winter in deserts and evergreen forests in Africa, whereas they are abundant in savanna and other rather open habitats (e.g. Moreau 1961, Lack 1986).

In eastern North America, tropical migrants preferably inhabit forest proper, and their wintering grounds in South America contain mainly tropical forest. Neotropical migrants spend winter mainly in South and Central American forests and closed shrubs, and show an increasing proportion in local communities with increasing altitude, and they seem to avoid open habitats (Karr 1976). According to Hutto (1985), tropical migrants from western North America winter almost entirely within a narrow strip of the West Mexican mainland, from southern Sonora south to Guatemala. There is a great variety of habitats in that area, both open and forested, which fits well the pattern obtained from the breeding grounds of western North American tropical migrants. In tropical East Asia there are about as many open and forested habitats. This seems to fit well with our results which show that East Asian migrants have a two-peaked distribution along the open – forested habitat gradient.

Though Bilcke's (1984) idea is supported by the data of this study, a rigorous test is impossible to perform due to insufficient information on the wintering areas of many species. Bilcke's (1984) idea assumes that the breeding and wintering habitats of species are the same, which cannot be quite true (see Cody 1985; although the habitats are similar in their appearance, at least there are floristic differences).

#### 5. Concluding remarks

Interestingly, studies on the effects of forest fragmentation have also detected differences between Europe and eastern North America. There are more deep forest species (sensitive to fragmentation) in eastern North America than in Great Britain (McLellan et al. 1986, see also Haila 1986). McLellan et al. (1986) supposed that the difference might be due to histories of fragmentation in these areas: English woodland has been fragmented for at least 2000 years, whereas the woodland of North America was in its natural condition as late as in the 17th century. It is quite possible that the impact of human disturbance has had certain effects on the habitat selection of

tropical migrants also in the open habitat – forest gradient. It should be noted that the eastern North American pattern (many area-sensitive tropical migrants) is possibly valid only for deciduous forests. Several species which have been shown to be severely affected by forest fragmentation in deciduous forests of eastern North America seem not to be area-sensitive in boreal coniferous forest (Welsh 1987). Western North American tropical migrants breeding in coniferous forests are also not area-sensitive (Rosenberg & Raphael 1986). In addition, Robbins et al. (1987) have demonstrated that migrant species avoiding forest edges and small forest islands in the breeding season in eastern North America thrive quite well in isolated forest fragments and edge habitats in their wintering quarters in the neotropical region.

Regarding consequences of forest fragmentation for birds, the greatest concern in Europe is the sedentary species of old forests; most migrant species have in fact increased in numbers there during the past half century. In eastern North America, on the other hand, the tropical migrants have suffered most from forestry (however see Welsh 1987). This difference means that world-wide recommendations cannot be made, for example when planning conservation strategy for migratory birds.

*Acknowledgements.* Alice Exnerová kindly allowed us to use her unpublished data for which we are very grateful. Our thanks are also due to Yrjö Haila, Antero Järvinen, Raimo Virkkala and Daniel Welsh for their comments on this paper. Financial support from the Emil Aaltonen foundation (to MM) is gratefully acknowledged.

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## Appendix

Studies used in this paper. C and D refer to coniferous and deciduous successions, respectively.

Co-ordinates	Succession	Reference	Co-ordinates	Succession	Reference
Europe			E North America		
43°N, 7°E	D	Blondel 1981	33°N, 83°W	D	Johnston & Odum 1956
49°N, 8°E	C,D	Muller 1985	35°N, 83°W	C,D	Odum 1950
49°N, 14°E	C	Exnerová unpubl.	35°N, 94°W	D	Shugart & James 1973
50°N, 20°E	D	Glowacinski 1975	36°N, 83°W	C	Kendeigh & Fawver 1981
50°N, 20°E	C	Glowacinski 1979	40°N, 78°W	D	Yanner 1983
53°N, 4°W	D	Jones 1972	40°N, 91°W	D	Zimmermann & Tatschl 1975
53°N, 9°E	C	Dierschke 1971	45°N, 65°W	D	Morgan & Freedman 1986
55°N, 4°W	C	Moss et al. 1979	46°N, 78°W	C	Martin 1960
63°N, 28°E	C	Mönkkönen 1984	47°N, 73°W	C,D	DesGrandes 1980
66°N, 29°E	C	Helle 1985b	55°N, 93°W	C,D	McLaren & McLaren 1981
Japan			W North America		
43°N, 142°E	D	Hino 1985	37°N, 119°W	C	Kilgore 1971
43°N, 142°E	D	Fujimaki 1981	40°N, 123°W	C	Hagar 1960
43°N, 142°E	D	Fujimaki 1984	42°N, 112°W	C	Smith & MacMahon 1981
43°N, 143°E	C,D	Kobayashi & Fujimaki 1985	45°N, 123°W	C	Morrison & Meslow 1983
			48°N, 122°W	D	Stiles 1980
			60°N, 140°W	C	Theberge 1976

Received 15.XI.1987, revised 27.X.1989

Printed 22.XII.1989