

ON THE BREEDING DISTRIBUTION PATTERN OF EUROPEAN MIGRANT BIRDS: MACARTHUR'S THEME REEXAMINED

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ABSTRACT.—There is a conspicuous gradient in the proportion of passerine breeding communities contributed by tropical migrants (PPM) in Europe, with communities located in the northernmost areas showing the greatest percentages and those located to the south the smallest. I used multiple stepwise regression and regression on principal components to investigate the effects of a set of ecological, climatic, and geographical variables on migrant percentages in a sample of 55 European censuses distributed from northern Fennoscandia through southern Spain. When the main habitat types are considered individually, this geographic pattern is still significant. The best single predictor of PPM as revealed by multiple regression analyses is latitude, but when this variable is removed, the temperature of the coldest month provides almost equivalent predictions of PPM. Habitat type per se apparently does not influence substantially the percent of migrants in European breeding passerine communities.

These results contrast with those reported by MacArthur (1959) for North America, although they are consistent with some suggestions derived from the recent reanalysis of North American data carried out by Willson (1976). Intercontinental differences are perhaps due to sampling deficiencies in the North American areas studied, mainly derived from the restricted latitudinal range.

To explain the European pattern of PPM, I suggest that the percentage of migrants in a community during the breeding season depends on both the harshness of adverse winter conditions faced by the resident populations and on the total resource availability during the breeding period. Carrying capacity of the habitat during the severe season will to some extent regulate the size of resident populations in the following breeding period, which in turn must affect the abundance of migrants that may successfully colonize the habitat. Very harsh winters coupled to very productive breeding seasons favor the largest percentage of migrants. *Received 29 June 1977, accepted 31 August 1977.*

In analysing the contribution to North American breeding bird communities by neotropical, long distance migrants, R. H. MacArthur (1959) was able to show the existence of a pattern on a continental scale relating migrant percentages to habitat seasonality. No apparent geographical trend was found, however, and interhabitat differences alone appeared to account for the largest part of the variation in neotropical migrant proportions. Recently, MacArthur's analysis has been reinterpreted and some of his results questioned (Willson 1976). European breeding bird communities, as those in North America, are composed of a variable fraction of species (hereafter named "migrants") that migrate south in the autumn to spend the winter in the African tropics south of the Sahara Desert (Moreau 1952). They thus provide the opportunity for an analysis similar to that of MacArthur (1959); such intercontinental comparisons of geographical patterns may contribute substantially to our understanding of processes that configure breeding bird communities.

A preliminary investigation into this theme (Herrera 1977) revealed that, independently of structural quality of habitats, there is a strong geographical pattern in European percentages of migrant birds. The proportion of migrants increases northwards and reaches its highest values in Scandinavian communities, regardless of whether these are located in arctic tundra, boreal forests, or peatland bogs. Lowest values are displayed by southern European breeding communities. These latitudinal changes contrast with the results of MacArthur (1959) for North America. Are there

in fact different mechanisms underlying migrant percentages in Europe and North America or, alternatively, are the same causal factors operating differentially in both continents to give contrasting patterns? This paper aims to provide an answer to this question.

METHODS

The present study differs from MacArthur's analysis in two ways (which I believe to be unimportant). Owing to the relative scarcity of accurate census results for nonpasserine species, I have been concerned throughout only with passerine breeding communities. Normally, nonpasserines constitute only a small fraction of the total number of individuals, so I think any decrease in generality caused by ignoring them will be compensated largely by an increase in censuses available for analysis. This point will be further discussed in the final section of this paper. On the other hand, no special care has been taken in selecting censuses from undisturbed, natural habitats since, after some thousand years of heavy human landscape-use, pristine habitats are unfortunately very rare throughout Europe, especially in the southern half of the continent.

To eliminate possible irregularities derived from unusual spring conditions in single years, census data were preferentially chosen from studies over several consecutive breeding seasons. However, for the sake of geographical completeness, one-season censuses were used if neglecting them would have meant leaving a large area unrepresented. Hereafter, both one-season and several-seasons average censuses will be indiscriminately termed "censuses."

A total of 55 censuses was considered (Appendix 2) and three sets of data were recorded for each, related to the census itself (1-4 below), geographical features of the census locality (5-8), and climatic characteristics (9-16). Values for the last data set were obtained from the nearest station reported in Walter and Lieth (1960). Variables and symbols used are as follows.

1. Total passerine breeding density (TPD), in individuals/10 ha.
2. Migrant breeding density (birds/10 ha) (MD). Species considered as migrants were those which, according to Moreau (1952), do not winter to any extent in the Western Palearctic, their winter areas extending exclusively over the African and/or Asian continents, mainly south of 15°N (southern border of the Sahara Desert). This criterion eliminates some species that winter in Africa but also occupy large areas in the southern Palearctic (e.g. *Sylvia atricapilla*, *Phylloscopus collybita*, *Motacilla alba*). The migrant species are listed in Appendix 1.
3. Percentage of migrant individuals (PPM), equal to $(MD/TPD) \times 100$.
4. Structural quality of the habitat (SQH) scored from 1 to 5: herbaceous fields, tundra, etc. (1); shrubland (2); coniferous (3); deciduous (4); and mixed (5) forests.
5. Latitude (LATITU), expressed to the nearest half degree.
6. Altitude above sea level (AASL) in meters.
7. Shortest distance to the nearest coast (DISNEC) in km.
8. Shortest distance to the Atlantic coast, facing west (DISWFC) in km.
- 9,10. Monthly mean temperature of coldest (MTCM) and hottest (MTHM) month in °C.
11. Absolute yearly range of monthly mean temperatures (YRMT) in °C, obtained as the difference between MTHM and MTCM.
12. Relative range of temperatures (RRT) (YRMT divided by MTHM).
- 13,14. Monthly precipitation of driest (MPDM) and wettest (MPWM) month in mm.
15. Absolute yearly range of monthly precipitation (YRMP), obtained as the difference between MPWM and MPDM.
16. Relative range of precipitation (RRP) (YRMP divided by MPWM).

Climatic data were chosen to consider seasonal aspects of the annual cycle in an objective fashion. It is reasonable to assume that climatic indices of seasonality must be related in some way to ecological seasonality, the causal factor argued by MacArthur (1959) to explain the North American pattern of PPM. As the degree of seasonality is modified by altitude and continentality (Köppen 1923, Jansa 1969), several variables (6-8) were employed to measure such effects.

I used multivariate methods that have been shown useful in the analysis of geographical patterns (Vuilleumier 1970, Brown 1971, Ketterson and Nolan 1976). Multiple stepwise regression analyses were performed on census data using the BMD02R computer routine (Dixon 1968). In this program, one variable is added to the regression equation at each step. The variable added is the one that makes the greatest reduction in the error sum of squares; equivalently, the added variable has the highest partial correlation with the dependent variable partialled on the variables already included and is the variable

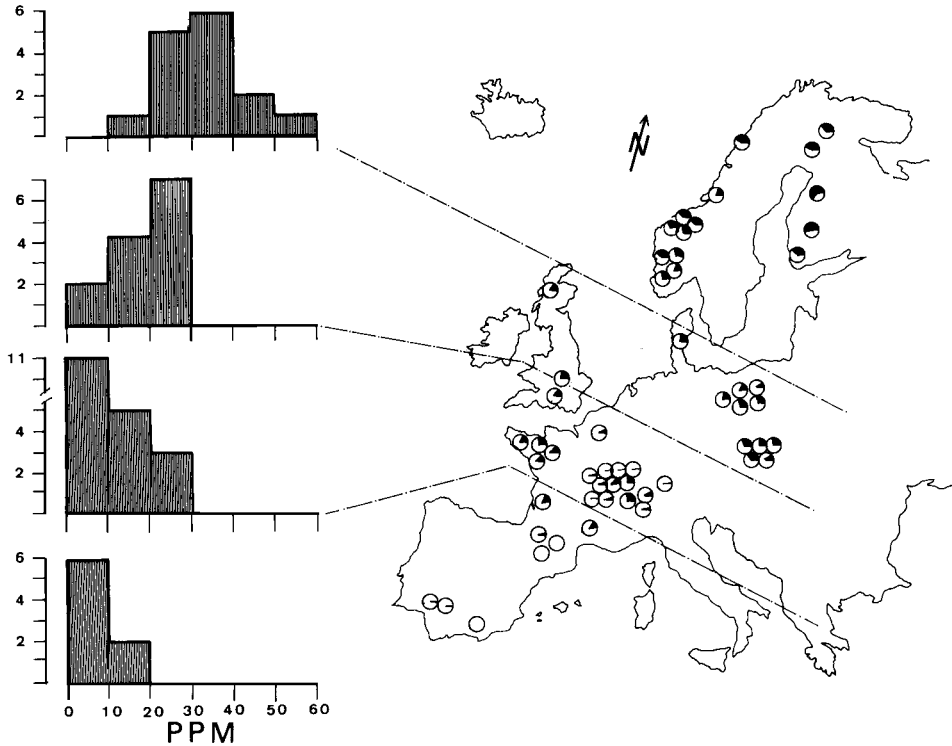


Fig. 1. Geographical pattern exhibited by the percentage of migrant individuals (PPM, black sectors of circles) in 55 European breeding passerine communities. Frequency distributions of PPM values within each latitudinal zone are shown to the left. Latitudinal areas were arbitrarily chosen.

that would have the highest F-value (Dixon 1968). Original data were used throughout with no transformation since there is no a priori reason to expect nonlinear dependences. Analyses were run taking as the dependent variable TPD, MD, and PPM, either deleting or not some of the independent ones.

In addition, a regression of PPM on the principal components resulting from the correlation matrix of the 13 environmental variables was carried out using the BMD02M computer program (Dixon 1968). This type of analysis provides a somewhat different view of the relationships between the dependent and independent variables. Whereas in stepwise regression variables are added one at each time and the relationships are assessed on the basis of individual variables, principal component analysis provides uncorrelated sets of related, linearly combined variables against which to regress the dependent ones. This procedure is particularly useful when dealing with independent variables among which there exist some highly correlated ones, such as the climatic variables under consideration.

To save space I omit the complete list of raw data, but it can be obtained from the author upon request. A list of localities, habitat types, and source references is given in Appendix 2.

RESULTS

A geographical pattern of PPM values is readily appreciated in Fig. 1. Passerine communities located to the northeast on the European continent contain a larger fraction of migrant individuals than those situated to the southwest. The frequency distributions of PPM values show a dependence upon latitude, although a rather slight longitudinal trend could perhaps be observed in Fig. 1 as well. Longitude was not considered among the geographical variables used in this study as, due to the peculiar distribution of land masses in western Europe, distance to the Atlantic coast

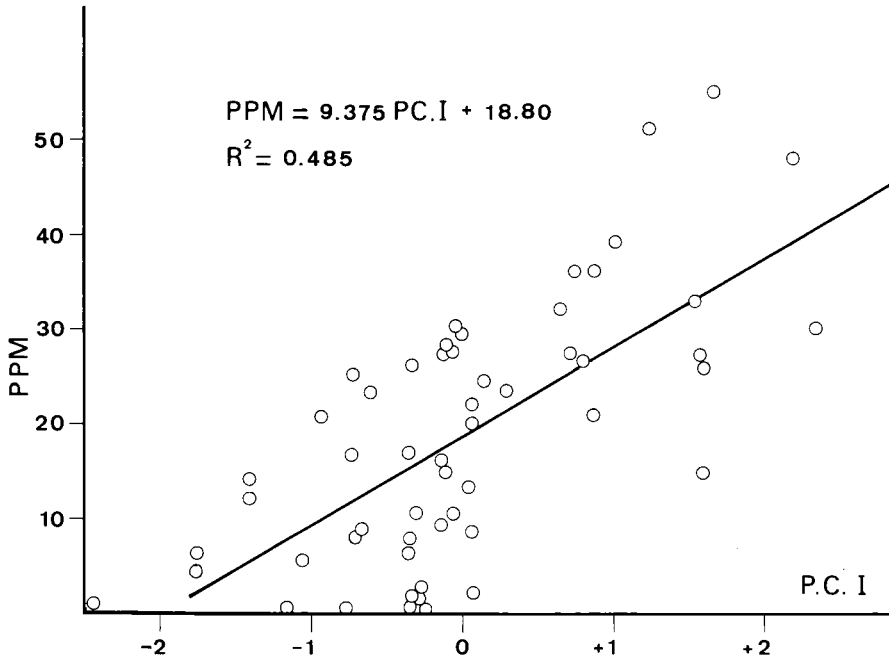


Fig. 2. Regression of PPM (percentage of migrant individuals) against P.C. I (first principal component). High values of P.C. I are associated with high latitude, low extreme temperatures (both coldest and hottest ones), and high seasonality in temperature, both in absolute and relative terms (Table 2). It can be seen that the proportion of migrants increases with the increasing values of P.C. I. Correlation is highly significant ($t = 7.07$, $n = 55$, $P \leq 0.001$).

appeared to be a better estimate of climatic continentality. Nevertheless, DISWFC does not appear to be significantly related to PPM (see below, Table 3).

Very distinct habitat types are pooled and intermixed in Fig. 1. However, no apparent relationship between habitat characteristics and geographical location of samples could be detected (correlation between LATITU and SQH, $r = -0.113$, $P > 0.4$). Furthermore, each habitat type taken separately exhibited a strong correlation between LATITU and PPM (Table 1). A test of homogeneity among the three correlation coefficients (Sokal and Rohlf 1969) revealed no significant differences ($\chi^2 = 1.81$, $df = 2$, $P > 0.3$), thus indicating that the relationship between migrant percentages and latitude is independent of the habitat type considered.

Is only latitude responsible for PPM variation or are there further associated environmental variables that contribute to the main sources of PPM changes? Principal component analysis reveals that, in addition to LATITU, there are four climatic variables that could potentially affect the percentage of migrant individuals in a significant way (Table 2, Fig. 2). They are MTCM, MTHM, YRMT, and

TABLE 1. Correlations^a between PPM and LATITU when the main habitat types are individually considered

	r	N	Significance
Coniferous forests	0.794	15	$P < 0.001$
Deciduous forests	0.626	21	$P < 0.01$
Grassland and shrubland	0.842	13	$P < 0.001$

^a Pearson product-moment correlation coefficient, r

TABLE 2. Principal component analysis of the correlation matrix of 13 environmental variables

	Principal component loadings ^a		
	P.C. I	P.C. II	P.C. III
LATITU	0.895	DISNEC 0.895	MPDM 0.914
MTCM	-0.958	DISWFC 0.905	
MTHM	-0.869		
YRMT	0.558		
RRT	0.930		
Eigenvalues	4.920	2.946	2.493
Proportion of environmental variance	0.378	0.227	0.192
Correlation coefficient with PPM ^b	0.697***	-0.097	-0.215

^a Only loadings greater than 0.4 are shown
^b *** = $P < 0.001$

RRT, which together with LATITU, gave the highest loadings on the first principal component (P.C.) (Table 2). Localities showing high scores on P.C. I are characterized by high latitude, low MTCM and MTHM values, and large values of YRMT and RRT. Percentage of migrants is highly and positively correlated with P.C. I scores (Fig. 2), and thus increases with increasing latitude, absolute and relative ranges of temperatures, and with decreasing values of extreme annual temperature, both coldest and hottest ones. It must be stressed that the relationship just described is between PPM and the combination of all the variables contributing to P.C. I in a significant way, but it tells us nothing on the possible relations between PPM and any of them considered individually.

No variable related to rainfall appears to account for any substantial amount of environmental variation in the set of localities studied. This was not unexpected, since except for four localities with a Mediterranean climate, rainfall is very evenly

TABLE 3. Results from multiple stepwise regression analyses

Independent variables	Dependent variable								
	PPM			MD			TPD		
	Order entered in equation	F-value ^a	Increase in R-square ^b	Order entered in equation	F-value	Increase in R-square	Order entered in equation	F-value	Increase in R-square
TPD	—	—	—	1	13.42***	0.202	—	—	—
MD	7	2.36	0.011	—	—	—	2	15.35***	0.164
PPM	—	—	—	6	2.19	0.026	—	—	—
SQH	6	13.96***	0.064	8	1.30	0.015	1	20.49***	0.279
LATITU	1	70.33***	0.570	—	—	—	6	1.28	0.013
AASL	3	2.32	0.016	5	1.87	0.023	4	1.26	0.013
DISNEC	10	0.60	0.003	10	0.38	0.004	10	0.29	0.003
DISWFC	9	0.56	0.003	4	2.57	0.032	7	2.93	0.030
MTCM	4	4.86*	0.030	—	—	—	8	0.89	0.009
MTHM	12	0.07	0.000	9	0.56	0.007	—	—	—
YRMT	—	—	—	12	0.77	0.009	—	—	—
RRT	5	4.32*	0.025	7	3.22	0.037	5	0.64	0.007
MPDM	2	10.89**	0.074	—	—	—	—	—	—
MPWM	—	—	—	11	0.78	0.009	9	0.47	0.005
YRMP	11	0.60	0.003	3	2.69	0.035	—	—	—
RRP	8	1.10	0.005	2	7.71**	0.103	3	1.96	0.021

^a Only F-values greater than 0.05 are shown. Significance levels: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$
^b Increases below 0.001 are not shown

TABLE 4. Results of stepwise regression of PPM when TPD, MD, and LATITU are removed

Variable ^a	Increase in R-square	F-value ^b	Coefficient in regression
MTCM	0.460	45.15***	-4.373
AASL	0.155	20.97***	-0.009
DISNEC	0.058	9.06***	-0.006
RRT	0.017	2.74*	-39.327
SQH	0.039	7.14***	-2.763
RRP	0.017	3.19**	14.146

^a Only significant variables are shown, listed in the order they enter the equation

^b Significance levels as in Table 3

distributed in time and space for the localities studied, all of which have a temperate climate (correlations between LATITU and either MPDM or MPWM are nonsignificant, $r = -0.020$ and $r = 0.069$, respectively, $P > 0.5$). A slight, negative correlation exists between PPM and P.C. III (Table 2), but statistical significance is not achieved ($0.1 < P < 0.2$).

Results of the stepwise regression analyses are shown in Table 3. Firstly, it must be noted that whereas PPM is very strongly influenced by geographical and climatic variables, this is not so for absolute measures of abundance (TPD and MD), whose variation is not substantially accounted for by any of the environmental variables I included in the analysis. If TPD were omitted from the list of independent variables, RRP would be the first variable entering equation with MD as dependent variable. This suggests some relationship between seasonality of precipitation (and thus seasonality of productivity), and abundance of migrant individuals. In any case, the relationships between either TPD or MD and environmental variables appear to be rather weak, since while 80.3% of PPM variation is related to these variables, they account for only about 35% of either TPD or MD variation. On the other hand, no close relationships exist between PPM and either TPD or MD. The percentage of migrant individuals (PPM) appears rather as a community-specific ratio which does not depend to any extent on absolute abundance of individuals. Migrant density (MD) and total passerine density (TPD) are, however, slightly interrelated, quite likely through a third, unknown variable, presumably of an environmental nature. It must be noted that TPD is significantly correlated with SQH, which is the first variable entering the equation (Table 3); this is not an unexpected result, as more complex habitats generally support denser passerine populations (e.g. Jones 1972, Blondel et al. 1973, Herrera 1977).

LATITU, MPDM, MTCM, RRT and SQH enter significantly into the regression equation of which PPM is the dependent variable (Table 3). Of these, LATITU is the best single predictor of migrant percentages and the first variable entering the equation, accounting for 57% of the total R^2 . The remaining four significant variables account altogether for an increase in R^2 of 0.193. The simultaneous effect of all five accounts for 76.4% of total PPM variation in the sample. The addition of the remaining 10 nonsignificant variables to the regression increases R^2 up to only 0.803, and unknown factors account for the rest of the variation (0.197).

The simplest predictive equation is

$$PPM = -47.795 + 1.285LATITU \quad (r = 0.755, df = 1,53, F = 70.33, P \ll 0.001)$$

Up to the sixth step, the regression receives the five significant variables plus the nonsignificant AASL (in brackets):

$$\begin{aligned} \text{PPM} = & 38.777 - 3.647\text{SQH} + 0.878\text{LATITU}(-0.005\text{AASL}) \\ & - 3.587\text{MTCM} - 43.946\text{RRT} - 0.152\text{MPDM} \\ & (r = 0.883, df = 6,48, F = 28.27, P \ll 0.001) \end{aligned}$$

According to this equation, the greater proportion of migrant individuals held by a community, the greater its latitude and the lower the monthly mean temperature of the coldest month (MTCM), rainfall of the driest month (MPDM), relative range of temperature (RRT), and structural quality of the habitat (SQH). As it is nonsignificant, AASL must be disregarded. Breeding communities located in northern localities with cold winters, relatively dry springs and/or summers, and inhabiting simple habitats are most likely to have a large proportion of migrant individuals.

At first glance, these results appear to differ slightly from those obtained with principal component analysis as, for instance, P.C. III (mainly influenced by MPDM) was there nonsignificantly correlated with PPM whereas MPDM emerges as a significant variable in stepwise regression. This discrepancy must be attributed to the fact that scores on any principal component result from the combination of several variables and when low-loading variables predominate on a given component (e.g. P.C. III), they may obscure correlations at certain times despite their small individual loadings.

As principal component analysis showed that several climatic parameters (MTCM, MTHM, YRMT and RRT) were associated with LATITU and strongly correlated with PPM, a stepwise regression was run taking PPM as the dependent variable and deleting LATITU from the set of independent ones. TPD and MD were removed as well. In this way, the influence of climatic variables alone could be assessed. Results are shown in Table 4.

Mean temperature of the coldest month (MTCM) alone explains 46% of PPM variation and it is the first variable entering the equation. It accounts for only a slightly smaller fraction of PPM variation than did LATITU alone when this latter variable was included in the analysis (Table 3), thus indicating that MTCM is almost as good a predictor of PPM as LATITU. After the first step, the resulting equation is

$$\text{PPM} = 17.335 - 1.711\text{MTCM} \quad (r = 0.678, df = 1,53, F = 45.15, P < 0.001)$$

thus revealing that communities facing the coldest winters hold the larger proportions of migrant individuals during next breeding season. This is an interesting result, since it suggests that PPM variation in Europe can be satisfactorily explained in climatic terms alone, disregarding the latitudinal location of communities. Although one must be well aware of the fact that correlation does not necessarily imply causation, it is tempting to assume that mean temperature of the coldest month is the critical parameter which largely regulates the proportion of migrant individuals in European breeding passerine communities.

DISCUSSION

Prior to comparing my results with MacArthur's (1959) and Willson's (1976) for North America, it is necessary to verify that my neglect of nonpasserines has not invalidated intercontinental comparisons. The absolute difference between the percentage of migrants computed according to MacArthur's criterion (PPM_1 , nonpasserines included) and mine (PPM_2 , only passerines), were obtained for individual censuses ($|\text{PPM}_1 - \text{PPM}_2|$). This was done for 18 North American censuses (Stewart

and Aldrich 1949, 1951; Odum 1950; Speirs 1972; Shugart and James 1973) and 17 European censuses chosen from those analysed in this paper—the only ones that provided adequate nonpasserine data. Mean absolute differences between figures yielded by the two methods were 1.86 ± 0.39 and $1.10 \pm 0.29\%$, for North America and Europe respectively (intercontinental comparison nonsignificant, $P > 0.05$). When the signs of differences are taken into consideration ($PPM_1 - PPM_2$), respective means for America and Europe are -1.79 ± 0.41 and $+0.59 \pm 0.37\%$, which in this case does differ significantly ($P < 0.001$). Although the latter result suggests some sort of intercontinental difference with regard to the degree of migratoriousness among nonpasserines, the small absolute differences found between figures arrived at by the two methods (ca. 1%) indicates that migrant percentages remain nearly unaltered by either deleting or including nonpasserines in the analysis.

The above results have revealed several important differences between Europe and North America in the geographical pattern of the percentage of tropical migrants (PPM). Whereas in Europe PPM values show a strong geographical component, this is lacking in North America, where migrant percentages vary according to habitat types (MacArthur 1959). Structural quality of the habitat (SQH) has a moderate negative influence on European PPM figures (Tables 3, 4), while according to MacArthur's results, wooded habitats of North America hold the highest percentages and simple habitats (prairie, desert) the lowest ones. A recent reanalysis of data covering part of the area dealt with by MacArthur suggests that his conclusions deserve some reassessment (Willson 1976). The clear-cut relations between habitat type and PPM that MacArthur found seem to be not too clear when examined using somewhat different criteria (e.g. differences between grasslands and northeastern deciduous forests appear nonexistent). When *all* migrants (not only tropical ones) are considered, average percent of migrant individuals is about the same in grassland (73%) and in deciduous forests (75%) and, as MacArthur found, is significantly greater in coniferous forests (94%) (Willson 1976). Although the criterion I have chosen to select migrant species is closer to MacArthur's, my European results are in fair agreement with Willson's suggestions for North America, as she pointed out (p. 585) that latitudinal differences in seasonality could be more a function of climate than of habitat type. My results demonstrate that in European breeding communities, geographical location with respect to latitude is the most important factor in determining the relative importance of tropical migrants and this relation continues to hold when the different habitat types are considered individually. However, latitude is not the only factor involved, as SQH, MPDM, RRT, and MTCM have significant effects on PPM as well (Table 3).

Neither MacArthur's nor Willson's contributions have revealed as strong an influence of latitude as my European results, but this fact must be related to the shape of the geographical area sampled by those authors. Of the 29 breeding communities analysed by MacArthur, only 2 came from Canada, and of 37 censuses handled by Willson only 9 were of Canadian origin. In both cases a relatively narrow range of latitude was sampled and under these circumstances it would be difficult to demonstrate a significant relationship to latitude. On the other hand, the range of habitats is much greater and more sharply defined in North America, and therefore American authors pay more attention to inter-habitat differences that can mask purely geographical patterns. Presumably, a restricted sampling design coupled to a well-defined habitat mosaic may have been responsible for the observed differences between North American and European results, although these are perhaps only

superficial. It is reasonable to expect that if more Canadian censuses were included in large enough numbers and latitude were equitably sampled, latitudinal trends would surely appear in North America.

In her discussion, Willson (1976) suggests the possibility of latitude affecting PPM values within a given habitat type, acting through variables such as length of summer growing season. Although this hypothesis remained untested in her paper, my results firmly support it. Despite the facts that many habitat types have been considered in the European analysis and that all of them are geographically intermixed, the effect of latitude on PPM is still clear whether habitats are combined or are considered separately, thus indicating that habitat type per se affects migrant percentages secondarily or not at all.

I have not considered length of summer growing season among the variables analysed. However, mean temperature of the coldest month emerges as a factor strongly affecting migrant percentages and this result has a fairly reasonable ecological meaning. Assuming that a breeding community is composed of two kinds of species only, namely migrants and strict residents, PPM values will be large when, given a total passerine density (supposedly regulated by the carrying capacity of the environment), migrants are relatively more abundant with respect to resident species. The latter are forced to live throughout the annual cycle in the same environment and successfully persist from one breeding season to the next. If breeding takes place only one time each year, population levels of resident species during a given breeding season depend not only on the success of reproduction during the previous summer, but also on the intervening successive carrying capacities of the habitat from summer to summer. Adverse seasons during this off-breeding period will impose a "bottleneck" to the "flow" of a resident population from summer to summer. If no substantial immigration from neighboring areas takes place, then lowered population levels will persist until the next breeding season, when migrant species will come in temporarily to colonize the habitat again. In this case, the latter will successfully appropriate a larger part of total available resources and reach higher densities. According to this reasoning, the narrower the bottleneck, the larger the fraction of migrants during the next breeding season. However, the percentage of migrant individuals should depend also on the total abundance of resources during the breeding season, which imposes a second constraint on PPM: the greater the total resource availability, the greater the total bird density exploiting it, and for a given narrowness of the bottleneck, the larger PPM as well. Seasonal "blooms" of insect prey are characteristic of environments with short summer growing seasons and these environments are usually found in high latitudes, just those having the greatest percentage of migrants in Europe.

It must be noted that it is not necessary to assume that populations of resident species are *exclusively* regulated during the non-breeding season, but only that this period plays at least part in regulation. Although this has been a traditionally controversial subject, recent studies suggest that this point may be essentially correct in some instances (e.g. Lack 1966, Fretwell 1972, Slagsvold 1975).

In Fig. 3 I propose that PPM values depend not only on total abundance of resources during the breeding season, but also on the severity of the winter season faced by resident birds. Relative magnitude of resource availability and/or accessibility during winter with respect to summer would be most closely related to PPM, as is suggested in Fig. 3. The absence of any significant correlation between PPM and either total passerine (TPD) or migrant (MD) density (demonstrated above) tends

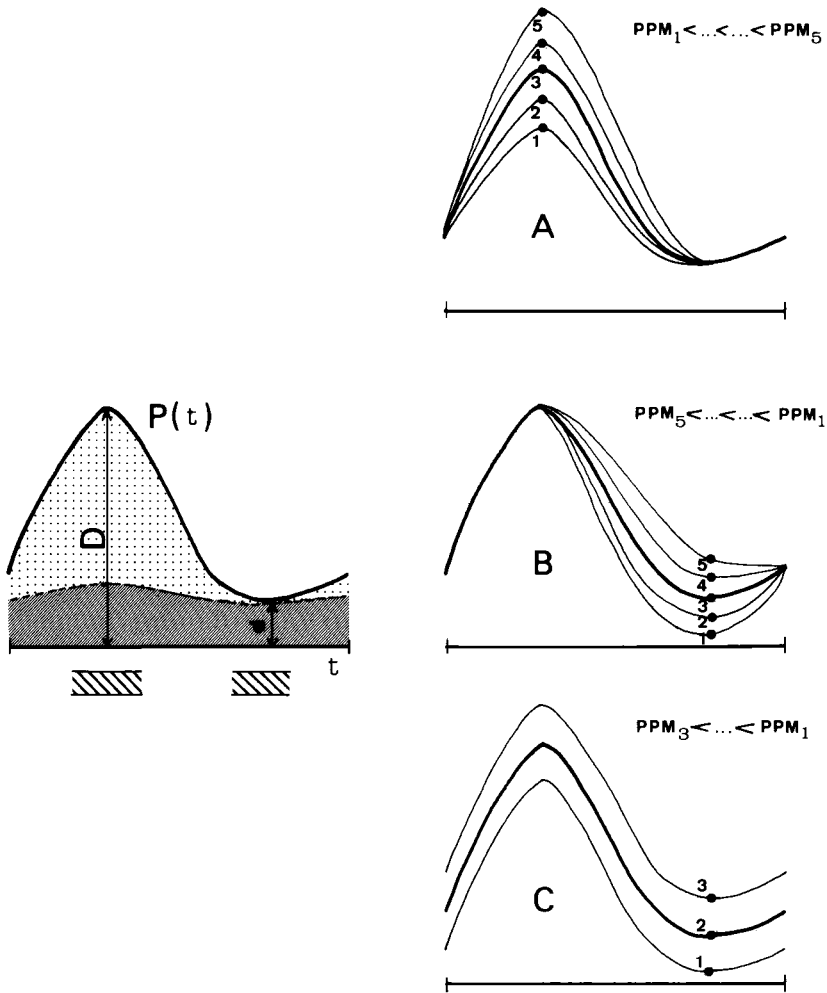


Fig. 3. A simple idealized graphical model to explain the observed differences in migrant percentages between communities under differing regimes of seasonality. It is assumed that communities are composed of year-round residents and summer migrants only. $P(t)$ describes the annual variations in carrying capacity of the environment to the birds, the peak (D) corresponding to the breeding season and the minimum (d) to the adverse season. The area under the curve is divided into two sections, corresponding to utilization by migrants (stippled area) and residents (shaded area), respectively. According to this model, PPM will depend simultaneously on D and d. **A:** For a given degree of severeness during the adverse season (d), PPM increases with increasing D; **B:** For a given resource abundance level during breeding season (D), PPM will decrease with increasing d; **C:** When D and d vary simultaneously, the final outcome will depend on the relative magnitude of D and d changes. In the case shown the curves are parallel to each other.

to support this hypothesis, as PPM appears rather as a community-specific ratio unrelated to the absolute magnitude of resource availability during the breeding season (which presumably affects TPD directly), but linked to the ratio between summer and winter conditions. Maximum figures of PPM are likely to be found in environments characterized by very harsh winters and summers with relatively high productivity. My results are concerned with the first aspect; assuming that ecological severeness of the adverse season must be related in some way to winter climatic

harshness, the correlation found between PPM and MTCM tends to support the former hypothesis. Mean temperature of the coldest month explains by itself 46% of PPM variation in the European sample when the effects of latitude are removed. On the other hand, evidence exists relating winter climatic features to community parameters such as bird species diversity (Tramer 1974, Kricher 1975), bird density (Shields and Grubb 1974), and foraging behaviour (Grubb 1975).

Length of the summer growing season was not considered in the above analysis and some of the unexplained variation of PPM may be attributable to this neglected variable. In any case, coldest climates in extreme latitudes are characterized by a short growing season and both variables should be correlated to some undetermined extent. Another source of unexplained variation may be the consideration of only tropical migrants instead of all migrant species, regardless of distance from breeding to wintering grounds. As Willson (1976) pointed out, there is no reason why seasonality should be reflected by tropical migrants only, and Fig. 3 is constructed taking account of this fact.

Obviously, I have made some simplifying assumptions that must be explicitly recognized. It is a common feature among temperate bird communities to contain in winter a variable fraction of non-resident birds that come in to overwinter there, and this fact was not considered at all when constructing Fig. 3. The effects of this neglected factor on model predictions must be especially noticeable in southern communities and less so in mid-latitude and northern areas. The study of geographical patterns of wintering passerines in temperate regions and their ecological correlates will undoubtedly modify our understanding of breeding bird community structure (Herrera 1977). Another critical aspect to be considered is why European tropical migrants exhibit a distributional pattern apparently similar to that shown in North America by *all* migrant species combined, as revealed by Willson (1976), whereas European-tropical (present study) versus North American-tropical (MacArthur 1959) comparisons show contrasting patterns. Keeping in mind these and perhaps other limitations, the above results must only serve to call attention to the significance that the non-breeding season can have in affecting the configuration of breeding communities. Further studies are needed before substantial conclusions can be drawn.

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Appendix 1

Breeding passerine species considered as migrants in this study. Only species occurring in any of the censuses are listed.

Alaudidae: *Calandrella brachydactyla*.

Hirundinidae: *Hirundo rustica*, *H. daurica*.

Motacillidae: *Anthus trivialis*, *A. cervinus*, *Motacilla flava*.

Laniidae: *Lanius senator*, *L. collurio*.

Muscicapidae: *Locustella naevia*, *Hippolais icterina*, *Sylvia hortensis*, *S. borin*, *S. communis*, *S. curruca*, *S. cantillans*, *Phylloscopus trochilus*, *P. bonelli*, *P. sibilatrix*, *Ficedula hypoleuca*, *F. albicollis*, *F. parva*, *Muscicapa striata*.

Turdidae: *Saxicola rubetra*, *Oenanthe oenanthe*, *Phoenicurus phoenicurus*, *Luscinia megarhynchos*, *Cyanosylvia svecica*.

Oriolidae: *Oriolus oriolus*.

Appendix 2

Summary of census material used in the present study.

Location	Habitat type	Number of censuses	Reference
NORWAY			
Nordmøre	Temperate and boreal deciduous	4	Røv 1975
Hardangervidda	Mountain tundra	4	Lien et al. 1974
Trondheim	Mixed forest	1	Hogstad 1967
Tranøy Island	Boreal deciduous	1	Myrberget et al. 1976

Appendix 2

Continued

Location	Habitat type	Number of censuses	Reference
FINLAND ^a			
SW Finland	Peatland bogs	1	Järvinen and Sammalisto 1976
Suomenselkä	Peatland bogs	1	Järvinen and Sammalisto 1976
Tornio-Kainuu	Peatland bogs	1	Järvinen and Sammalisto 1976
Forest Lapland	Peatland bogs	1	Järvinen and Sammalisto 1976
Fell Lapland	Peatland bogs	1	Järvinen and Sammalisto 1976
ENGLAND			
Chiltern Hills	Shrubland	1	Williamson 1975
Mid-Argyll	Temperate deciduous	1	Williamson 1974
Sussex	Yew woodland	1	Williamson and Williamson 1973
DENMARK			
Als	Temperate Deciduous	1	Joensen <i>in</i> Cody 1974
POLAND			
Niezgody	Floodplain deciduous	1	Mrugasiewicz 1974
Radziadza	Floodplain deciduous	1	Mrugasiewicz 1974
Niezgody	Mixed forest	1	Mrugasiewicz 1974
Borowiny	Temperate deciduous	1	Mrugasiewicz 1974
Rudy Milickiej	Coniferous forest	1	Mrugasiewicz 1974
CZECHOSLOVAKIA			
near Brno	Spruce forest	1	Pikula 1968
near Brno	Temperate deciduous	4	Pikula 1968
SWITZERLAND			
Cossonay	Mixed forest	1	Zollinger 1976
FRANCE			
Briançon	Mountain coniferous	3	Le Louarn 1968
Rambouillet	Temperate deciduous	1	Le Louarn 1971
Paimpont	Lowland coniferous	4	Constant et al. 1973
Vendée	Herbaceous field	1	Thiollay 1968
Camargue	Mediterranean shrubland	1	Blondel 1969
Jura	Coniferous forests	4	Frochot 1971
Dijon	Deciduous forests	5	Frochot 1971
SPAIN			
Pyrenees	Spruce dominated forests	1	Purroy 1972
Pyrenees	Pine forests	2	Purroy 1974
Almería	Coastal shrubland	1	García and Purroy 1973
Huelva	Evergreen-oak woodlands	2	Herrera 1977

^a Each of the five Finnish censuses is the average from a certain number of nearby localities