

# EXPERIENCE OF ANALYZING ANNUAL CHANGES IN BIRD POPULATION

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*Long-term data published on catches of birds on the Kursh spit were used for comparative analysis of annual changes in numbers of 41 species of birds. Original statistical processing (taking the logarithm, standardization, correlation and dispersion analyses) made it possible to investigate annual population fluctuations independently of other peculiarities of their dynamics. Associated fluctuations were noted for species with similar features of their winter ecology (wintering region, feeding place, and feeding objects), which supports the hypothesis according to which the size of populations is limited by the food reserve in the wintertime.*

Current views on the problem of the dependence of birds' populations on conditions in their nesting and wintering regions are based on D. Lack's idea that food resources are most limited during the nonnesting period; therefore, competition for food and death from starvation at that time should lead to limitation of the population's size. Developing N. P. Ashmole's hypothesis, R. E. Ricklefs (1980) came to the conclusion that, in conditions of seasonal climate change, in terrestrial communities two propositions are valid for most birds: 1) population density is determined primarily by winter mortality, and not by territorial behavior during the nesting season; and 2) population density influences the availability of resources for breeding individuals, which is reflected in the evolution of the optimum clutch size. Thus, the life cycle and demographic structure of a population should depend on the conditions determining winter mortality (Ricklefs, 1980, 1983). T. Alerstam and G. Högstedt came to similar conclusions (1982), basing them on the hypothesis that, although birds are freer to choose their habitats during the nonnesting period, due to high mobility, in the winter the area of suitable habitats for most European passerines is limited by a seasonal reduction in productivity or, for migratory species, an abundance of local competitors.

At the same time, many researchers note that, in spite of the logic of these statements, there is still no possibility of demonstrating them on sufficiently reliable facts (Alerstam and Högstedt, 1982; Ricklefs, 1983; Svensson, 1985; Greenberg, 1986; Holmes and Sherry, 1988).

In the present work, it is shown how published data on birds' population dynamics can be used to check theoretical predictions.\*

As initial material, we used annual data on numbers of birds caught during a season (from April through November) in the same three stationary traps on Kursh spit in the Baltic Sea. The dates of the traps' operation varied a little in different years, but they should change the total number of birds caught in a year only for certain early-arriving species and not by more than 8%. These data for 41 species over 22 observation seasons (from 1960 through 1981) were taken from the work of V. A. Paevskii (1985) without any changes and therefore are not given here.

The number of birds caught during a season varied in a wide range for each species. For 23 species, the differences between the maximum and minimum indices exceeded 10-fold, and for 5 species they differed by more than 100 times. In peak

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years, the numbers deviated from the average level more sharply than in the years of depressions. In this case, in place of the natural indices it is expedient to use logarithms of the numbers, since this method "reveals relative changes in numbers and makes the distribution of numbers symmetrical and almost normal" (Williamson, 1975, p. 36). Moreover, in analyzing population dynamics, "changes in the logarithm of the population's numbers are the most adequate characteristic of the process" according to the basic theory of population dynamics" (p. 15).

To evaluate annual changes in numbers, we employed a method based on use of the first difference between two adjacent terms of a series:

$$A(t) = \ln N(t) - \ln N(t-1) = \ln [N(t)/N(t-1)], \quad (1)$$

where  $N(t)$  is the evaluation of numbers in the  $t$ -th observation. From this quantity, it is easy to distinguish a linear trend (on a logarithmic scale), the average annual value of which is equal to

$$L = \frac{1}{T-1} \sum_{t=2}^T A(t) = \frac{1}{T-1} [\ln N(T) - \ln N(1)], \quad (2)$$

where  $t = 1, 2, \dots, T$ . Then, brief population changes in a pure form are characterized by the deviation of annual changes from the trend:

$$S(t) = A(t) - L. \quad (3)$$

As a result, annual changes in numbers are divided into long-term and brief ones. Long-term trends in the populations of birds migrating through the Kursh spit were considered previously (Dol'nik and Paevskii, 1979; Paevskii, 1985). Here, only brief changes are considered, as a phenomenon of independent interest.

Time series obtained in this way for each species were first tested for possible distortions introduced by the method of data collection. Changes in the numbers of seven species displayed significant positive correlation with the duration of the traps' operation. For them, the brief changes were decreased by the amount predicted by a regression equation according to the times of the corresponding traps' operation. Then, for each species we performed one more operation: standardization, which is necessary in order to analyze a dispersion complex with sharply differing variation indices. As a result, the time series acquired the following properties: zero mean, unit standard deviation, distribution of deviations close to normal, and the absence of a significant trend or correlation with the duration of trapping.

To seek the factors determining annual population fluctuations, we performed a preliminary analysis based on pair comparison of the series. As the measure for comparison, we used the coefficient of linear correlation. The matrix of coefficients of correlation enabled us to group the species that have significant correlations with each other. To obtain a graphic idea of the structure of interrelations between species, with the help of standard methods of multivariate nonmetric scaling (the CSS package of statistical programs), we carried out trivariate ordination of this structure, which significantly facilitated comprehension of it. Objective analysis showed that the species joined together are similar in certain peculiarities of their ecology that can significantly influence their survival rate at unfavorable times of the year and be the reason for synchronous fluctuations of their numbers. Information on the species' biology was clarified according to general and regional summaries ("Birds of the Soviet Union," 1954; Paevskii, 1971; Mal'chevskii and Pukinskii, 1983; Lack, 1971).

In conclusion, the species were once again grouped into classes, but this time not according to similarity of their dynamics, but according to ecological peculiarities that were put forth to explain the reason for changes in numbers. With the help of bivariate dispersion analysis, we evaluated to what degree such a classification of species explains the significant diversity of brief changes in numbers in the populations under consideration.

## RESULTS OF CORRELATION ANALYSIS

The matrix of coefficients of linear correlation, calculated for each pair of species with respect to brief changes in numbers during 21 annual intervals, is shown in Fig. 1. These coefficients of correlation determine the species' relative location on an ordination diagram (Fig. 2): the more similar the species' population fluctuations are, the closer they are to each

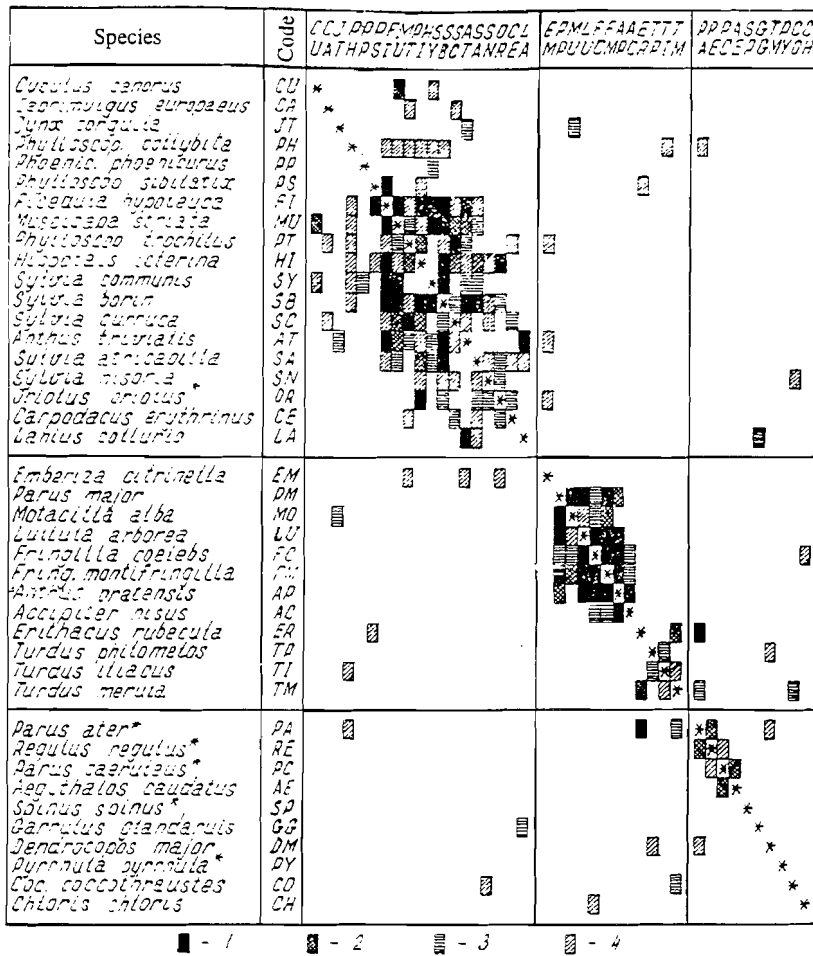


Fig. 1. Matrix of interspecific coefficients of correlation (explanations in the text). Positive coefficients of correlation: 1)  $r > 0.588$  ( $P < 0.005$ ); 2)  $r > 0.536$  ( $P < 0.01$ ); 3)  $r > 0.457$  ( $P < 0.025$ ); 4)  $r > 0.387$  ( $P < 0.05$ ). The dividing lines group species according to their wintering places (from the top down): distant migrants, near migrants, settled, and nomadic. For the species marked with an asterisk, the dependence on duration of the traps' operation was preliminarily eliminated.

other. Unavoidable distortions arising as a consequence of the structure's multivariate nature are reduced to a minimum thanks to the use of formal methods. The structure's basic peculiarities are thus preserved and reflect objective interrelations.

The largest and tightest grouping (in the left part of the ordination diagram) is represented by species that winter south of the Sahara. The few tropical migrants, the correlation of which with members of the group is not depicted, are located in direct proximity, since they have weaker, but reliable correlations with members of the group (see Fig. 1). Another compact grouping, in the right part of the diagram, is formed by migratory species that winter in Europe. Four more species (Turdidae wintering in the same region) are also located together in the lower part of the diagram, but not so compactly. The division of near migrants into two groups differing in the species' taxonomy suggests the thought of ecological peculiarities connected with this that determine the best winter survival rate in the same region in different conditions specific to each group. Settled and nomadic species are scattered over the diagram. Of them, common features of dynamics were reliably manifested only for species entering into winter tit flocks. The rest of the species wintering near their nesting regions have an insignificant correlation with each other and with other species, which agrees with the high specialization of their winter feeding on seeds of a certain type, and with the dependence of changes in numbers on the dynamics of the corresponding food plants' fruiting.

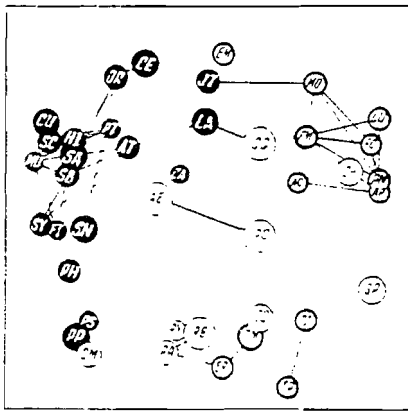


Fig. 2. Trivariate ordination of species on the basis of similarity of the dynamics of brief changes in their numbers. The third measurement ("depth") is depicted by the size of the circles: dark circles - distant migrants, circles with dark border - near migrants, light circles - settled and nomadic species; see Fig. 1 for the species' codes; species with a coefficient of correlation  $r > 0.50$  are connected by lines.

Thus, preliminary analysis makes the connection of birds' population dynamics with their wintering places and peculiarities of their winter ecology fairly obvious. We will consider in greater detail the trends that were noted.

The internal structure of the grouping of distant migrants apparently reflects the distribution of species by regions of wintering in the tropics. Separate positions in different parts of the block are occupied by *P. collybita*, part of which does not cross the Sahara and stays in Mediterranean countries, and by *L. collurio*, which winters primarily in the southern tropical belt of Africa (Lack, 1971). *F. hypoleuca* and *P. sibilatrix*, which winter primarily in West Africa, and *P. phoenicurus*, the European populations of which probably winter nearby, occupied the lower part of the block of tropical migrants on the diagram. The correlation is particularly high between the first two species ( $r = 0.70$ ,  $P < 0.01$ ), since among the usual migrants from the Palearctic they are the only ones that settle in wet equatorial forests (Svensson, 1985). *O. oriolus* and *C. erythrurus*, the wintering regions of which apparently include Indostan, were found in the upper part of the block. Closely connected with them are *S. atricapilla* and *S. nisoria*, which migrate from the Kursh spit through the Eastern Mediterranean and settle in East Africa with the greatest density. The wintering regions of species located in the center of the block encompass Central Africa and adjacent parts of the continent. We can also note differentiation among them: for example, the more southerly *A. trivialis* and *P. trochilus* are close to *L. collurio*, while *S. communis*, which winters west of Tanzania, gravitates toward *F. hypoleuca*.

It is hard to judge how much the Baltic populations of three species of nonpasserines, *C. canorus*, *C. europaeus*, and *J. torquilla*, the places of African wintering of which have not been precisely established, follow the general rule. We can only say for sure that their dynamics had little in common with the dynamics of birds wintering in Europe (the average coefficient of correlation  $r = 0.01$ ,  $n = 66$ ). But even with tropical migrants of the Passeriformes order their correlation is much weaker ( $r = 0.14$ ,  $n = 48$ ) than that of the latter with each other ( $r = 0.35$ ,  $n = 120$ ). It may be that weakening of the correlation is connected with a reduction in mortality of nonpasserines.

Our attention is drawn to the high integrity and unity of groupings of distant migrants, especially passerines, while species wintering in Europe are represented by a looser structure, through it would seem that the wintering places in Africa are more disconnected than in Europe. This must point to common causes of death for tropical migrants on their flyways, primarily in flying across the Sahara. The correlation of the birds' annual survival rate with the abundance of precipitation in the southern Sahara has been established for individual species by direct comparison (Hjort and Lindholm, 1978; Marchant, 1982; Svensson, 1985; Mead, 1987). The distinctiveness of the indicated nonpasserines' dynamics indicates that the flight across the Sahara may not be so critical for them.

Near migrants include species the northern European populations of which make regular flights to Southern and Central Europe. The center of their tight grouping in the upper part of the diagram is formed by *F. montifringilla* and *F. coelebs*, which base their winter feeding on fallen beechnuts and other seeds collected on open ground surface in forests, parks, and agricultural lands (Lyuleeva, 1982; Lack, 1971; Asensio, 1986). *L. arborea* and *A. pratensis* feed on herbaceous seeds on

forest edges, fields, and wastelands, which makes them close to the two preceding species. In these biotopes, and also near water and in populated points, *M. alba* (Davis, 1982) and *E. citrinella* eat foods found openly on the ground. At the same time, part of the population of *M. alba* probably winters in Africa, in the dry belt south of the Sahara (Lack, 1971), while *E. citrinella*, on the other hand, is partially settled or wanders short distances. This may explain their separation from the enumerated species and from each other.

Populations of *P. major* from Scandinavia and Eastern Europe are migratory to a significant extent (Paevskii, 1971). In the winter, in contrast to other tits, they half change to ground feeding on seeds, among which beechnuts occupy a special place (Perrins, 1966; Lack, 1971), making them close to representatives of Fringillinae. Habitation in populated points may make them close to *M. alba*. It is important that all of the indicated species are united by feeding on objects found openly on the ground surface, the accessibility of which drops sharply when snow falls. This factor apparently determines the population dynamics of many species wintering near the "snow boundary." For *F. montifringilla*, this dependence has been confirmed by direct observations (Jenni, 1982; Jenni and Neuschulz, 1985). Investigation of North American terrestrial granivores wintering in Arizona showed that their numbers also depend on the seed reserve and change similarly for different species, especially for those that feed in flocks in open habitats (Dunning and Brown, 1982).

*A. nisus* demonstrated a high correlation with birds that gather food from the ground, since its main victims in its wintering places are mass species included in this group (Dol'nik and Paevskii, 1984).

Near migrants of the Turdidae family formed a separate grouping in the lower part of the diagram. Feeding on the ground, in contrast to representatives of the preceding group, they extract food from under fallen leaves, from forest litter, and from diverse coverings, or find it under a canopy of dense underbrush and young growth (for example, Debussche and Isemann, 1985), and they should endure snowfall more easily. Besides invertebrates, tree and shrub berries eaten from the ground, as well as from branches, serve as an additional food for them, and their main one during the most severe periods. Therefore, on the whole, Turdidae probably winter further north than terrestrial granivorous birds, but they respond acutely to prolonged cold spells and poor berry crops (Langslow, 1983; Hilden and Saurola, 1985; Pettersson, 1986).

In Figs. 1 and 2, species the greater part of the population of which stays for the winter in relatively high latitudes, in regions with persistent snow cover, are called "settled and nomadic." There is no clear boundary between true migratory and "nomadic" species, and some of them, such as *E. citrinella*, *P. major*, *C. chloris*, and possibly even *C. coccothraustes* and *R. regulus*, occupy an intermediate position. In spite of this, the trait of migratoriness is convenient for diagnosis, since it is at least correlatively connected with population dynamics. Another trait is more closely and, apparently, causally connected with the dynamics of winter mortality: these species' aboveground feeding (in crowns of trees and shrubs) in the wintertime on plant fruits and dormant invertebrates, which makes them less vulnerable to cold spells and snowfall in comparison with species that feed on the ground.

Of the the species considered, four, *P. ater*, *P. caeruleus*, *R. regulus*, and *A. caudatus* more or less regularly enter into the composition of mixed "tit" flocks. They are united by a comparatively broad food ration and specialization not so much for feeding objects as for places for seeking and ways of obtaining food. We can suppose that their survival rate is determined by the availability of food during the most severe period. In fact, in Finland, for species entering into the composition of tit flocks similar population fluctuations have been noted, which are connected with the severity of the winter in regions close to their nesting places (Vaisanen, 1984). In this case, the most lethal for them were not snowfalls or cold spells by themselves, but sharp temperature changes, icing of branches, and other unpredictable anomalies (Hilden and Saurola, 1986).

The rest of the species of this group are specialized for consumption of seed foods of a specific type: *D. major*, pine and spruce; *G. glandarius* oak; *C. coccothraustes*, white birch, bird cherry, blackthorn; *P. pyrrhula*, ash and mountain ash; *S. spinus*, alder; *C. chloris*, herbaceous plants. Representatives of Carduelinae are considered the most specialized granivores among palearctic passerines (Nekrasov, 1978), with their specialization being based precisely on winter foods (Lack, 1971). The dependence of each species on the harvest of specific food objects leads to a situation in which they do not correlate in population dynamics either with the rest of the species or with each other. This corresponds to their scattered position on the diagram (Fig. 2; it should be noted that a large or small representation corresponds to a position in the foreground or background, respectively). Analysis of these species' maximum correlations with others, including unreliable ones, still deserves attention (see Fig. 1). Considering that, in studying a large number of pair coefficients of correlation for a limited number of years, some of them may reflect random coincidences, we will throw out the pairs *G. glandarius*-*L. collurio*, *C. coccothraustes*-*S. nisoria*, and *D. major*-*T. philmelos*, the commonality of which has no explanation. Other correlations of these species may indicate additional factors limiting the population of each of them. Thus, *P. pyrrhula* and *C. coccothraustes*

TABLE 1. Classification of Bird Species according to Winter Ecological Peculiarities and Some Characteristics of Group Variation of Brief Changes in Their Numbers

Type of seasonal migrations	Winter places for seeking food	Main objects of winter feeding	Species*	Indices**		
				Da/De	F	P
Distant migrants	Various	Primarily various invertebrates	CU, CA, JT, PH, PP, PS, FI, MU, PT, HI, SY, SB, SC, AT, SA, SN, OR, CE, LA	30,4	8,27	<0,001
Near migrants	Open ground surface	Various seeds***	EM, PM, MO, LU, FC, FM, AP, AC	50,6	7,53	<0,001
	Ground coverings, crowns	Berries, invertebrates	ER, TP, TI, TM	55,6	3,94	<0,001
Settled and nomadic species	Crowns of trees and shrubs, upper parts of herbaceous plants	Invertebrates, various seeds	PA, RE, PC, AE	42,8	2,36	<0,01
		Alder seeds	SP	100,0	—	—
		Oak acorns	GG	100,0	—	—
		Conifer seeds	DM	100,0	—	—
		Ash and mountain-ash seeds	PY	100,0	—	—
		Bird-cherry, hornbeam, and black-thorn seeds	CO	100,0	—	—
		Herbaceous seeds	CH	100,0	—	—

\*See Fig. 1 for full names of species.

\*\*Da/De) Portion of intragroup variation connected with synchronous changes in numbers (%); F - Fisher's ratio test; P - level of significance.

\*\*\*For MO) Primarily invertebrates; for AS - birds entering into the given group.

have their maximum similarity with *T. philomelos* and *T. merula*, which may be based on their dependence on berry harvests. Facultative feeding on seeds scattered on the ground probably links *C. chloris* and *F. coelebs*. Finally, *D. major* and *P. ater* should experience the effect of fluctuations in fruiting of spruce.

## RESULTS OF DISPERSION ANALYSIS

Dispersion analysis enables us to quantitatively evaluate what part of the overall variation (sum of the squares of deviations) of a dependent variable is due to the effect of a particular factor (trait) represented in the form of gradations. In this case, as the dependent variable in dispersion analysis we took standardized values of brief changes in the species' numbers over 21 annual intervals. As factors we took: A - difference in time (gradations - years of observations), B - difference in the species' ecological peculiarities (gradations - groups of species distinguished in the preceding section), and AB - the combination of these factors (gradations - groups of species in individual years of observations). It is not hard to notice that brief changes in numbers, computed according to formulas (1)-(3), are equal to zero on the average for each species.

TABLE 2. Results of Bivariate Dispersion Analysis of Brief Changes in Numbers of 41 Species of Birds over 21 Annual Intervals

Source of variation	df	D/Dt	F	P
Factor A . . .	20	6,5	4,07	<0,001
Factor B . . .	9	0,0	—	—
Combination AB	180	41,7	2,91	<0,001
Residual . . .	651	51,8	—	—
Total . . .	860	100,0	—	—

**Remark.** Gradations of factor A) years of observations; gradations of factor B) groups of species from Table 1; df) degrees of freedom; D/Dt) portion of variation connected with the factor's action in relation to total variation (%); F) Fisher's ratio test; P) level of significance.

Therefore, the factor B is fictive and by itself cannot be used to explain the variation. But its action is manifested in the combination AB, since, in each specific period, brief changes in the species' numbers are not equal to zero, but are similar for species belonging to one group and differ between groups.

Results of the classification of species described above according to peculiarities of their winter ecology, and characteristics of each group are given in Table 1; and general results of dispersion analysis corresponding to this classification, in Table 2. From them, it follows that a small, but reliably significant part of the variation of annual changes in numbers (6.7%) is common to all of the populations under consideration. It may be due to climatic changes in the nesting region or in the place where they were caught, or to changes in vegetation in the vicinity of the traps (Paevskii, 1985), etc. The greater part of the explained variation (41.7%) is connected with peculiarities of the species' winter ecology, reflected in their subdivision into 10 groups. Within the groups, species display similar population changes from year to year, while the dynamics of different groups differ significantly. This provides a basis for suggesting that annual variations in numbers of the populations under consideration are determined mainly by the winter conditions of their existence.

## DISCUSSION

One of the method's assumptions is that, if any group includes just one species, then 100% of the variation from year to year in the increment of this species' population is connected with traits characteristic of the given group (see Table 1). In particular, all changes in numbers of *D. major* are supposed to be due to the dynamics of fruiting of pine and spruce. In reality, this is obviously not so, and at least part of the variation must reflect random deviations from the dependence, however strict it may be. But, in the sample there is no second species dependent to a similar degree on the harvest of conifer seeds (for example, *Loxia curvirostra* could be one). Consequently, the derived evaluation of the role of winter factors is overstated for those species that are the sole representatives of their groups, and also for the entire set. At the same time, there is no doubt about the clearly expressed specificity of limiting factors for each of the species specialized for objects of winter feeding: combination of them into one group showed the insignificance of the overall component in annual variations in their numbers ( $P > 0.05$ ).

On the other hand, in groups including a large number of species, the explained variation is understated, due to incomplete consideration of the groups' internal structure, which may be connected with the same general patterns. Thus, distant migrants not only have common differences from birds that spend the winter in Europe, but they also possess peculiarities of dynamics characteristic of more specific regions of wintering and migrations. This is easily seen in more

TABLE 3. Variation of Brief Changes in Numbers of Passerines Wintering in Different Regions of the Tropics

Primary wintering regions	Species	$Da/Dt$	$F$	$P$	
Variant 1					
North Africa	PH	100,0	—	—	
South Africa	LA	100,0	—	—	
West Africa	FI, PP, PS	53,1	2,37	<0,01	
East Africa and South Asia	SA, SN, OR, CE	58,8	4,49	<0,001	
Central Africa	MU, PT, HI, SY, SB, SC, AT	59,9	9,41	<0,001	
Bivariate dispersion complex:		$Da/Dt = 34,9$ $Dab/Dt = 25,7$	36,2 27,2	11,41 2,14	<0,001 <0,001
Variant 2					
North and Central Africa	PH	100,0	—	—	
South and Central Africa	LA, PT, HI, AT	56,9	4,15	<0,001	
West and Central Africa	FI, PP, PS, MU, SY, SB	52,1	5,71	<0,001	
East and Central Africa, South Asia	SA, SN, OR, CE, CA	54,5	5,03	<0,001	
Bivariate dispersion complex:		$Da/Dt = 34,9$ $Dab/Dt = 21,0$	36,2 20,8	10,61 2,04	<0,001 <0,001

**Note.** Data on the wintering regions are taken from the following works: "Birds of the Soviet Union," 1954; Paevskii, 1971; Lack, 1971. See Fig. 2 for conventional notations of species; notations of variation indices as in Tables 1 and 2.

detailed analysis of the dynamics of passerines wintering in different regions of the tropics. To avoid subjective interpretation of information about the primary regions of wintering, we give two variants of the grouping of species (Table 3). The same could be said of near migrants, but in relation to biotopic confinement.

Thus, for bird populations migrating through Kursh spit in the Baltic Sea, knowledge of peculiarities of their winter ecology and wintering places can explain a significant part of the variation in brief population fluctuations. This supports the hypothesis of decisive influence of mortality factors outside the nesting season on birds' population dynamics.

If there is another system of factors that more fully explains the differences between species in annual population fluctuations, then such a system must, first of all, more fully explain the same grouping of species according to coefficients of correlation, which was discussed above (see Fig. 2). Secondly, such a system must give a different causal interpretation of the connection of population dynamics with the noted peculiarities of winter ecology, since they have already explained about half of the variation in dynamics, and new factors, at least the most significant ones, will unavoidably correlate with factors of winter ecology.

In seeking a different interpretation of the correlations that have been revealed, we used available information on nesting ecology (Mal'chevskii and Pukinskii, 1983; Lack, 1971) to classify the species according to their preferred habitats and nest locations. These traits were taken as factor B. Dispersion analysis showed that the difference in nesting habitats (4 gradations) and the places where nests are built (4 gradations) can explain 9.8% ( $P > 0.05$ ) and 8.0% ( $P > 0.05$ ) of the total variation, respectively, which is considerably less than the informativeness of peculiarities of winter ecology. Each grouping of species linked by close mutual correlation with respect to dynamics (see Fig. 2) includes nearly the whole spectrum of representatives with different specialization during the nesting period. On the other hand, it turned out that species with similar specialization, as, for example, nesting on the ground, which, it would seem, should experience similar changes in predation pressure or the weather and phenological conditions of nesting, did not have a reliable joint variation in annual increment. In those groups where such variation was found, for example, for species nesting in open biotopes (16.3%,  $P < 0.01$ ), it is more fully explained from the standpoint of winter ecology, which is not only connected with the similarity of these species' dynamics with each other, but also with their difference from other species.

Undoubtedly, there must also be more informative species differences reflecting summer specifics. One of them is apparently the difference in foraging tactics, since winter and summer peculiarities of foraging are similar for many species. However, if we suppose that provision with food in the summer has a decisive effect on numbers, then there is no clear explanation for the high correlation of the dynamics of such species as *M. striata*, *S. borin*, and *A. trivialis*, the feeding niches



of which in the summertime have no point of contact, or such as *F. montifringilla* and *F. coelebs*, the nesting ranges of which overlap slightly.

One more factor capable of acting on evaluation of population changes and determining the correlation between them for individual species is the procedure for collecting data. In S. E. Svensson's opinion (1978), the number of birds caught during migrations may reflect not so much the level of abundance of the nesting population as the random nature of the flow of migrants' passage through the trapping site, due to meteorological conditions on days of the migration's peak. In this case, annual changes in evaluation of the numbers of species migrating at close times, with the same variations of weather conditions, may be more similar.

In the present work, data are given which differ from those used by S. E. Svensson. They combine birds caught during the spring migration, nesting, and fall wanderings and migration. The average annual volume of the sample and the duration of observations are very impressive, thanks to which population changes in a year, for regular migrants, usually did not go beyond two-fold variations. For invasion species, they were much stronger, but since most authors consider the rate of invasions as a response to an increase in population (Dol'nik, 1975; Formozov, 1976; Paevskii, 1985), I believe that it is valid to use data on capture of migrating birds to calculate the correlation of various species with respect to changes in numbers, in spite of the fact that in absolute value such an evaluation probably far exceeds the actual one. Then, judging from the data given by V. A. Paevskii (1985), evaluations of changes in numbers of the same species at different trapping sites in the Baltic region are fairly similar. Finally, the comparatively high similarity of the dynamics of all distant migrants and lack of similarity of the rest of the species seems, in the first approximation, not to correspond to the degree of similarity of the times of these groups of species' mass migrations. On the contrary, a number of near and distant migrants caught at similar times differ sharply in the dynamics of their numbers. Nonetheless, the effect of migration times on the number of birds caught, as well as on the size of nesting populations deserves more detailed study.

Thus, disruptions of the level of abundance during the summer half of the year can sometimes be significant, but do not have a decisive effect on the dynamics of annual fluctuations. In the analysis that was conducted, they must account for part of the unexplained variation. Some part of the explained variation may correlate with both winter and summer factors simultaneously. However, the structure of the correlations, which has to reflect the action of summer disruptions at least no worse than winter ones, it seems, cannot be explained by anything other than the species' differences with respect to wintering places and winter peculiarities of foraging. In fact, in the data that were used the majority of individuals are yearlings caught during postnesting wanderings and fall migrations. Consequently, if the conclusions discussed here are true, then the action of factors determining winter mortality shows up at the level of abundance all the way until the end of the fall migration at the observation point.

The reality of the conclusions that we drew agrees with the results of investigations of individual populations. On the basis of the same data on numbers of birds caught during a season on the Kursh spit, V. A. Paevskii (1985) evaluated the correlation of numbers of *F. coelebs* and *P. trochilus* with the successfulness of breeding as +0.62 and +0.52, which corresponds to 38 and 27% of the dispersion. In the northern population of *F. hypoleuca*, the annual variations in nesting density were 1/3 due to differences in losses during breeding and 2/3 due to mortality in the remaining seasons; in central parts of the range, the effect of external conditions during the breeding period is supposed to be less significant (Virolainen, 1984).

The analysis that was conducted of the dynamics of populations migrating through the Kursh spit also enabled us to note certain trends that can be suggested as working hypotheses for additional investigations:

- 1) The amplitude of annual variations in numbers of birds decreases with an increase in the distance of seasonal migrations.
- 2) The predominant means of winter ecological isolation of species in northern latitudes by division of feeding objects is progressively replaced further south by division of places for seeking food, habitats, and geographic wintering regions.
- 3) The nature of changes in numbers agrees with the hypothesis that winter limitation by physical environmental factors and yield of food plants acting in moderate latitudes is replaced in the tropics by the action of diffuse competition, including on the part of aboriginal fauna.
- 4) In the same direction, the means of maintaining population homeostasis on account of movements within a significant part of the range is replaced by regulation at the level of local nesting populations through the successfulness of breeding, depending on density.

Deeper analysis of the factors responsible for annual changes in numbers would be possible with separate recording of the results of spring and fall catches. It would also be desirable to employ more detailed ecological knowledge reflecting the species' adaptation, data on the dynamics of corresponding environmental factors, and causal analysis of their effect.

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