

Mieczysław JÓZEFIK

**Studies on the Squacco Heron, *Ardeola ralloides* (SCOP.). Part V. Intraspecific isolation and the ecological zones of the range**

**Studia nad czapłą modronosą, *Ardeola ralloides* (SCOP.). Część V. Izolacja wewnątrzgatunkowa a strefy ekologiczne zasięgu**

**Исследования по желтой цапле, *Ardeola ralloides* (SCOP.). Часть V. Внутривидовая изоляция и экологические зоны ареала**

[with 1 map, 4 tables and 16 graphs in the text]

Introduction

Index of existence prosperity

Interdependence of the basic parameters of the spatial distribution

Biological mechanisms of isolation effect

Exponential increase of the isolation effect

Existence prosperity — survival — environment resistance

Ecological gradation of levels of index  $Z_{pe}$

$Pr_{ex}$  — index of the biological situation of the species

Ecological zones of the range

Conclusions

References

#### INTRODUCTION

Together with a deeper approach to problems of intraspecific changes, together with the development of populational genetics, and particularly with the study of the mechanisms conditioning the flow of genes, together with more attention being devoted to conditions under which speciation processes take place and to the working out of such concepts as the evolutionary destiny of the species, studies on the spatial structure of the species have acquired considerable importance. The key problem is here the question of intraspecific isolation. The descriptions of the phenomenon and effects of isolation in its various aspects which have been put forward so far (e. g. HUXLEY's dependent and independent species (1942), zones of primary and secondary intergradation, geographical isolation of MAYR (1965), etc.), have not given due consi-

deration to such important moments as a) tendency of the species to integrate spatially and overcome the limiting effect of isolation, b) peculiarities of the flock structure affected by the pressure of intraspecific competition and external reducing factors, c) variations of isolation forms in the annual cycle.

In the present work the author treats isolation in its effects as a) a real ecological limiting factor, b) an evolutionary factor playing a significant role in divergent processes. When referring to isolation in this first aspect I have in mind the effect being the result of the spatial distribution of the species in conditions of an insufficiently high level of group formation, that is in conditions of a weak gregarious effect when at the same time distances between separate groups (flocks, micropopulations) are considerable. At a high pressure of reducing factors (predators) its limiting effect is evidently magnified. Certain aspects of these problems have already been discussed in other parts of the cycle (cf. JÓZEFIK, 1969 a, b, 1970). I explained and proved then that the size of breeding sites is negatively correlated with the degree of spatial isolation, and that this correlation is curvilinear in its character — the limiting effect of isolation is intensified exponentially as it is arithmetically increased. I also analysed there the mechanisms of oscillations in the degree of isolation in respect of the numerical fluctuations of the species. I recorded that irrespective of numerical changes the species maintains a defined level of density not exceeding the critical degree of intraspecific isolations. It is only the synanthropization of the species which enables the birds to exist in the conditions of larger dispersion. The limiting effect of isolation is more prominent in the meridian cross-section than in the parallel one (JÓZEFIK, 1969b, 1970). As a limiting factor it affects, similarly as the biogeophysical conditions of the environment, the formation of the ecological zones of the range. This problem will be given the pride of place in the present, fifth, part of the cycle devoted to studies on the Squacco Heron.

#### INDEX OF EXISTENCE PROSPERITY

##### General assumptions

I have already devoted much attention to connections between the degree of isolation and the biological situation of the micropopulation in another part of the cycle (JÓZEFIK, 1970) when discussing interdependences between the size of breeding sites ( $y$ ) and distances ( $x$ ) to other sites neighbouring upon them. And as  $y$  and  $x$  were highly negatively correlated with each other, their ratio  $y/x$  (below referred to as index  $Z$ , when necessary corrections are taken into account as index  $Z_{pe}$ , and when it is given a logarithmic form it is termed as an index of existence success expressed in "prexes") will determine in a sufficient degree the biological situation of the given micropopulation. And thus:

$$Z = \frac{y}{x}. \quad (1)$$

The concept "biological situation" of the given micropopulation is for our purpose much too wide. As we are interested in a specific complex of environmental factors which determine the existence success (or ecological prosperity) of the micropopulation inhabiting the given site, a good pointer to such a prosperity would be, for instance, the size of sites in relation to the unit of area of the breeding habitat. As I have pointed out (JÓZEFIK, 1970) the correlation between these two parameters is very low as the size of sites is very much affected by the degree of isolation. And thus if the degree of existence prosperity is considered only for the breeding period, i. e. in a narrow ecological aspect, different variants of the "spatial" index will undoubtedly turn out to be a useful comparative instrument. On the other hand, in a cycle of many years, or even in the annual cycle, when the size of sites is determined by the survival rate of the micropopulation in the period of migrations, during wintering, etc., their survival depends on the size of the flock, the period of its absolute isolation in relation to other micropopulations (distances covered during migrations and the degree of danger threatening the birds while migrating), the existence prosperity is determined *sensu lato* by the cumulative effect of isolation. This does not however mean that in the concept of the mathematical expression of index  $Z$  the effect of local environment conditions (habitat capacity, biocenotic relations, etc.) are pushed into the background. They are expressed in formula (1) by  $y$ , assuming that  $y$  is not a rectilinear function  $x$  for different levels of  $Z$  (there only occurs a high correlation between them). Hence in zoogeographic investigations the above suggested index  $Z$  seems to be the most convenient way of estimating the degree of existence success when it is treated dynamically, or, as in our case, taken as an average value. The reason for the introduction of index  $Z$  into the studies on the spatial structure of the species lies mainly in considering in its "construction" the element of intraspecific relations being the result of isolation. Only after analysing separate characteristics of index  $Z$  in connection with the history of the species, with data bearing on the rate and character of its changeability, and after comparing it with the rate of habitat transformation can an attempt be made to discuss the state of the biological situation of the species under consideration.

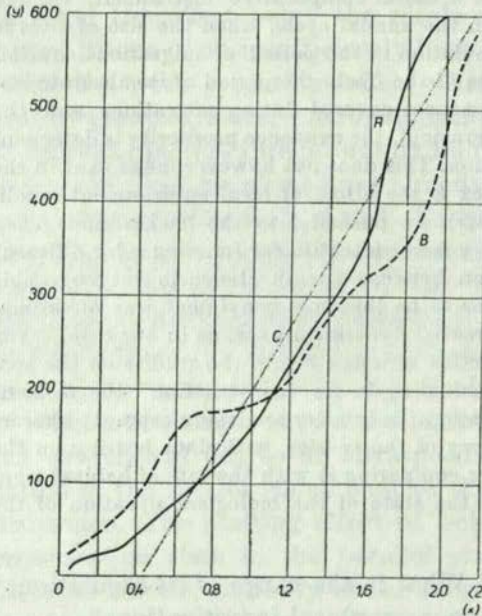
What is then the essence of index  $Z$ ? What is the range of its oscillations? What is the usefulness of this index in zoogeographical investigations?

As far as the first question is concerned the answer can be presented thus:  $Z$  is a general, relative (as its value is comparable only within one single species) and indirectly determining index of the degree of stabilization and of a final balance indicating the course of life occurrences of a given micropopulation inhabiting this particular breeding site in the complex of conditions provided by this habitat, that is to put it more tersely, it is an index of existence covering a longer period of time. The second problem will be discussed in the ensuing chapters of this part, while the answer to the last question is left to be dealt with by the reader. Let us pass now to certain characteristics of index  $Z$ .

#### Certain characteristics of index $Z$

Graph 1 presents, on the basis of data calculated for the two last centuries jointly, the curves of regression: a) average value of  $Z$  in relation to separate classes of site size (curve  $A$ ), and b) average size of sites in respect of separate limits of the value of  $Z$  (curve  $B$ ). Practically, the course of curve  $A$  from the lowest values of the co-ordinates until the level of 500 pairs, can be assumed as approximating a rectilinear one (cf. deviations from curve  $C$ ). The correlation

occurring between the size of sites ( $y$ ) and index  $Z$  is evidently a very high one ( $r_{yz} = +0.942$ ). Above this level of 500 pairs the increase in the value of  $Z$  gets more rapid — curve  $A$  forms here an arc (in Graph 1 it is shown only fragmentarily in view of the confinement of scale  $y$  to 600 pairs). As there is only a small number of sites inhabited by more than 500 pairs (4.2 %), we can assume for the moment that, on average, the value of  $Z$  characteristic for each of the breeding sites determines, more or less proportionally within the limits



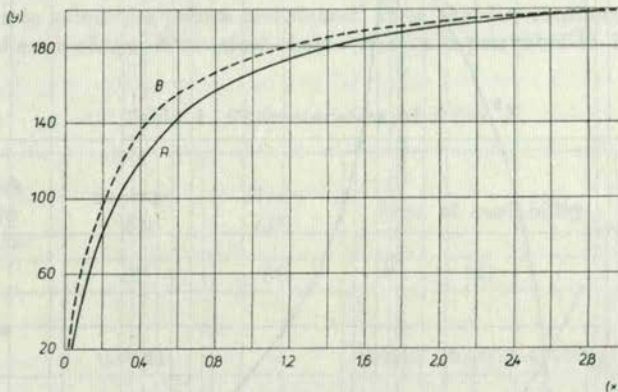
Graph 1. Correlation between the size of sites and index  $Z$ .  $y$  — size of sites expressed in breeding pairs,  $x$  — scale of the values of index  $Z$ ; curves of regression:  $A$  — average value of index  $Z$  in respect of breeding sites differing in size,  $B$  — average size of sites in respect of the scale of index  $Z$ ;  $C$  — deviation from curve  $A$  when we assume a rectilinear dependence of index  $Z$  in the size of sites.

of the deviation of  $x$  and  $y$  known to us (cf. Graph 5), the degree of existence prosperity of the micropopulation inhabiting the given breeding site (corrections which have been taken into consideration are presented on page 18). This is also indicated by the regression of the average site size in respect of the scale composition of index  $Z$  (curve  $B$  — Graph 1). And thus the higher is the value of  $Z$ , the higher and the more stabilized is the degree of „biological flourishing” displayed by the given micropopulation. The gradient connected with the attachment of the proper ecological significance to separate ranges of index  $Z$  and the introduction of necessary corrections into its calculation will be discussed when analysing Graph 5.

Parameter  $y$  in expression (1) can theoretically oscillate from the critical minimum size of sites up to the moment when the carrying capacity of the environment occupied is reached. Assuming that  $y$  of the given site is not limited in the breeding period by environment extremes and by the environment resistance in general, then its value depends, to a certain degree, inversely proportionately on the value of  $x$  (and more precisely on  $xa$  — cf. page 18). On the other hand  $x$  can oscillate from 10 to 15 km., i. e. from the moment when the site barely retains its autonomy to the critical degree of isolation tolerated by the species. Thus, although the correlation between  $x$  and  $y$  is quite high (JÓZEFIK, 1970), as well as the correlation

between  $y$  and  $Z$ , the oscillations of  $x$  and  $y$  for the respective values of  $Z$  are wide and gradually decreasing when the values of  $Z$  are lowest and highest (cf. Graph 5). Can we assume the degree of existence prosperity to be equal in the case of such wide oscillations of  $x$  and  $y$  for sites characterized by the same value of  $Z$ ? The answer will be attempted when analysing Graph 5.

Let us consider now a theoretical case of the variability of  $Z$  for a single site, assuming first its increase and then its decrease connected with, for instance, a general numerical increase of the population in a certain part of the range, that is with the setting up of new sites in the vicinity of the theoretical one, and later on with their disappearance. Let us use for this purpose data obtained with the help of the already mentioned equations of regression:  $x = 560 - 2.95y$ ;  $y = 165 - 0.24x$  (cf. JÓZEFIK, 1970). The variability of  $Z$  is presented in the form of curves in Graph 2.

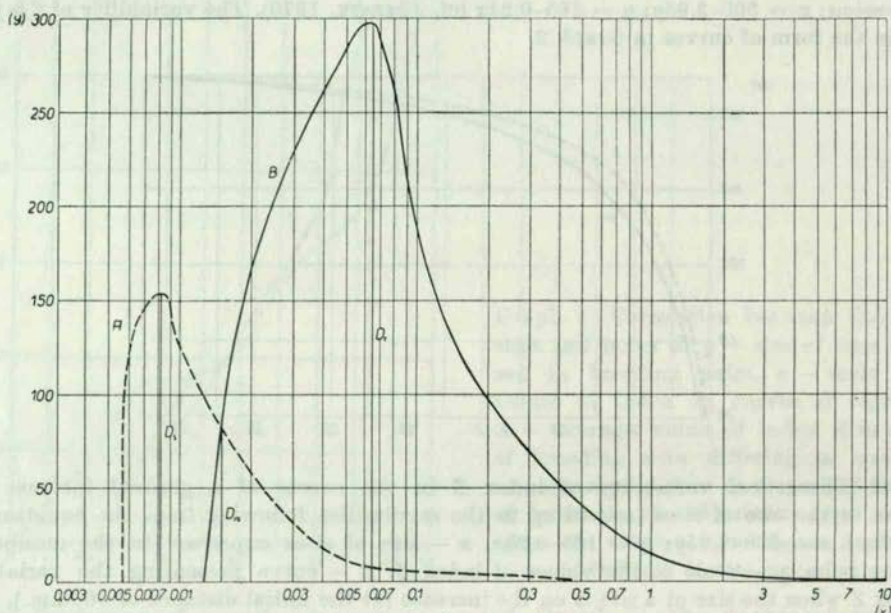


Graph 2. Theoretical variability of index  $Z$  in the course of a gradual increase and decrease in the size of sites (according to the regularities following from the equations of regression:  $x = 560 - 2.95y$ ;  $y = 165 - 0.24x$ .  $x$  — size of sites expressed in the number of breeding pairs,  $y$  — scale of the values of index  $Z$ ,  $A$  — curve presenting the variability of index  $Z$  when the size of a site is on the increase (at the initial distance of 600 km.),  $B$  — curve presenting the variability of index  $Z$  when a site declines numerically (at the initial distance of 70 km.).

The divergence of curves  $A$  (increase) and  $B$  (decrease) follows from the specific character of the mechanisms described (cf. JÓZEFIK, 1970), and their course assumes the form of a hyperbola. When comparing Graphs 1 and 2 we can record certain common features in the course of the curves, i. e. above certain values of  $y$  these curves form an arc. In the theoretical curve the progressive increase in the value of  $Z$  is a result of neglecting two important points when carrying out the calculations: a) progressive overcrowding of the sites whose size is constantly on the increase, and the fact that their carrying capacity has been reached, are here left out of reckoning, b) the fact that the shortening of distances is negatively correlated with the increase in  $y$  only to a certain specified limit, and when this is exceeded the correlation between  $x$  and  $y$  becomes positive (cf. JÓZEFIK, 1970) (equations of regression can be used here in the case of situations when there is no overcrowding and when the birds are considerably dispersed). And as for the theoretically assumed infinitely increasing overcrowding this was reflected in the progressive increase of  $Z$ , we seem to be entitled to put forward the following conclusion: in the case of sites whose value of index  $Z$  differs considerably from the level of the curve presenting the dependence of this co-efficient on the size of sites (e. g. breeding sites situated above the levels of curves  $A$  and  $B$  in Graph 5) we can reasonably expect, beside a perfect ecological prosperity, definite signs of overcrow-

ding. The tendency of curve *A* to deviate to the right in Graph 1 when representing large sites (more than 500 pairs) inclines us to suppose that we have detected signs of overcrowding in them. As sites with high values of index *Z* are rare in the range, it seems worthwhile to devote more attention to their certain particular features.

And thus of the total number of 211 breeding sites recorded for the last two centuries only 34 (16.1 %) were characterized by the value of *Z* higher than 1.0. In the XIXth century there were 31 (91.2 %) such sites, while in the XXth century this figure was cut down to 18 (52.9 %). Thus 16 (47.1 %) sites having in the XIXth century  $Z > 1.0$  disappeared in the present century, while 3 (8.8 %) new sites were set up. Of these 34 sites 7 (20.1 %) were



Graph 3. Distribution of index *Z* in relation to the average number of breeding sites. *x* — logarithmic scale of the values index *Z*, *y* — number of sites expressed in ‰, *A* — sporadic sites, *B* — regular sites, *D<sub>s</sub>* — mode of the distribution of sporadic sites, *D<sub>r</sub>* — mode of the general distribution of the breeding sites (curve of this distribution has not been presented in the graph), *D<sub>r</sub>* — mode of the distribution of regular sites.

situated in the western regions of the Caspian Sea drainage area (sites 22, 26–29, 31, 32 — JÓZEFIK, 1969 b) and only 4 of them still existed in the XXth century. The remaining sites, outside the Dniester Delta, are located in the drainage area of the Danube. In the middle reaches of the Danube and its drainage area (higher from the Iron Gate) 19 sites were recorded (sites 77, 81, 82, 84–88, 90, 97, 103, 109–112, 124–126, 130 — JÓZEFIK, 1969). Out of this number 4 remained until the present century and 2 new sites were set up. In the lower course of the Danube (mainly in the delta) the situation is at present most favourable for the species: 7 sites recorded there (sites Nos. 142, 144–149 — JÓZEFIK, 1969) are characterized by indices which are highest in the entire range (exceeding even the level recorded for them in the XIXth century). Clear signs of overcrowding have been recorded there in recent years.

The range of the variability of  $Z$  within the area inhabited by *A. ralloides* is very wide as it is between 0.0057 and 25.4721. Quite naturally this concerns only average values of  $Z$  for separate breeding sites (e. g. in certain periods of the species prosperity some of the sites reached even higher values of index  $Z$ , cf. Graph 5, in which the circles indicate the turning points in the variability of  $Z$  recorded for separate sites (hence the number of circles exceeds the number of sites). In view of this diversity the percentage distribution of the values of  $Z$  presented in Graph 3 in the form of curve  $A$  for sporadic sites and in the form of curve  $B$  for regular ones had to be plotted on the horizontal axis in the logarithmic scale. In connection with this, in order to read correctly the course of curve  $A$ , calculated for each 0.001, and when the curve exceeds 0.01 its value should be multiplied by 10, while after 0.1 it should be multiplied by 100. Curve  $B$  is calculated for each 0.01 (distances are ten times larger), and analogously when the curve exceeds 0.1 its value should be multiplied by 10, and when it exceeds 1.0 by 100. The axis has a scale expressed in ‰. Analysing the graph we ought to bear in mind the points mentioned. Thus the distributions are clearly asymmetrical and similar in shape. Numerical characteristics is presented in Table 1.

Table 1. Characteristics of index  $Z$ .

Characteristics of index $Z$ in respect of sites:	average ( $\bar{x}$ )	Mode ( $D$ )	Area of variability	Comments
(1)	(2)	(3)	(4)	(5)
In the extreme zone (6)	0.0561	—	0.0593 (0.0057–0.0650)	
In the optimum zone (7)	1.8599	—	25.4071 (0.0651–25.4720)	
Regular (8)	1.4658	0.0650*)	25.4571 (0.0150–25.4720)	*) with the class intervals = 0.01 (11)
Sporadic (9)	0.0610	0.0081**)	0.4668 (0.0057–0.4725)	** ) with the class intervals = 0.001 (12)
Taken together (10)	1.0691	0.0150***)	25.4664 (0.0057–25.4720)	*** ) with the class intervals = 0.01 (13)

### Critical value of $Z$

$D_{rs}$ , i. e. the mode of the general distribution of sites from both these categories (sporadic and regular), and at the same time the point of intersection of curves  $A$  and  $B$ , (Graph 3), similarly as it was already discussed in the case of the distribution of site sizes (JÓZEFIK, 1970), which occurs at the value of  $Z = 0.015$ , it marks the critical (minimum) level of  $Z$  below which only sporadic sites can exist. This value does not differ much from the critical

(minimum) value of  $Z$  (0.0081) for sporadic sites determined by the mode ( $D_s$ ) of their distribution. In the two distributions the initial steep sections of the curves, so characteristic for social species occurring in an island-like pattern, mark the highest possible, in the direction of the lowest (critical) values, deviation of  $Z$  from modes  $D_s$ ,  $D_r$ , and  $D_{rs}$ . It ought to be pointed out here that the general distribution of sites (not included in Graph 3), which includes mode  $D_{rs}$ , was drawn by plotting values of  $Z$  at 0.01 intervals.

The most valuable index for us is mode  $D_{rs}$  of the general distribution, i. e. the critical (minimum) value of  $Z$ , below which regular sites lose their character and either become sporadic or disappear completely.

### Critical value of spacing

When we know the critical value of the size of regular sites (which amounts to 17.5 pairs, JÓZEFIK, 1970, we can substitute it to formula (1), and then we shall have a simple equation  $0.015 = 17.5/x$ , the solution of which will give us the highest critical value of the isolation degree tolerated by the species. It amounts to 1,160 km.

With the exception of only one case (site No. 3 reached in the XXth century the average distance of 1.270 km when the numbers were between 20 and 50 pairs; cf. JÓZEFIK, 1969 a) none of either regular or sporadic sites exceeded the highest degree of isolation tolerated by the species, although admittedly some of them reached average distances approximating this critical value. And thus, for instance, sites nos. 167 and 168 exceeded in the XIXth century the distance of 850 km, sites nos. 166 and 173 exceeded in the present century distances of 870 and 830 km. An ecological analysis of the critical indices for the species will be undertaken in the ensuing parts of the cycle (i. e. parts dealing with the flock structure, migrations, as well as breeding and mortality dynamics).

### Introductory assumptions for singling out ecological zones of the range

The differentiation of the degree of existence prosperity for separate micropopulations, the exponent of which is  $Z$ , is connected with the previously singled out ecological zones (cf. JÓZEFIK, 1970) (extreme and optimum) of the palearctic part of the range. Then the numerical level of breeding pairs at separate sites was taken to be the criterium of the estimate. Hence all small dependent sites (up to 20 breeding pairs), although they could be characterized by a relatively high index of  $Z$ , were placed in the extreme zone. Other, somewhat larger sites, which for significant reasons should be covered by the extreme zone, turned out to be either in the optimum or in the suboptimum zone. As it follows from the data presented in Table 2, the error (i. e. deviation from the average of the data calculated with two other methods) is insignificant and amounts to 3 %. Applying the characteristics of the distribution of index  $Z$  as a criterium of the estimate, we have obtained lower results though they do not differ sufficiently from the correct one to warrant their rejection. Pro-



Table 2. Presentation of certain, calculated with different methods, characteristics of the extreme and optimum zones in the palearctic part of the range of *A. ralloides*.

Zones (2) Method of calculating	Extreme (3)			Optimum (4)		
	index <i>Z</i>	number of sites (%)	numbers of the species (%)	index <i>Z</i>	number of sites (%)	numbers of the species (%)
(1)	(5)	(6)	(7)	(8)	(9)	(10)
On the basis of the ecological analysis of separate sites (11)	0.0809	52.19	8.28	2.0969	47.81	91.72
On the basis of the data from the curve of concentration (JÓZEFIK, 1970) (12)	—	49.50	6.06	—	50.50	93.94
On the basis of the distribution of index <i>Z</i> (13)	0.0312	37.56	5.83	1.6229	62.44	94.17
Average (14)	0.0561	46.42	6.72	1.8599	53.58	93.28

bably the best method was a laborious analysis of the data concerned with ecological factors, the degree of isolation, and the history of the growth of all sites providing grounds for apportioning them to their respective zones. The results of such an analysis are presented in Table 2 and they do not differ too much from the average value (difference amounts to 5.7 %). Thus similar results were obtained by using three different methods, and they enable to determine, in per cent, not only the number of breeding sites dispersed in separate zones, but also to calculate precisely, also in per cent, the numerical state of *A. ralloides* inhabiting these zones. Quite naturally the data mentioned above should be treated as average for the last two centuries, and thus, to a certain extent, as static; however, they can be considered as being one of the more important characteristic features of the species.

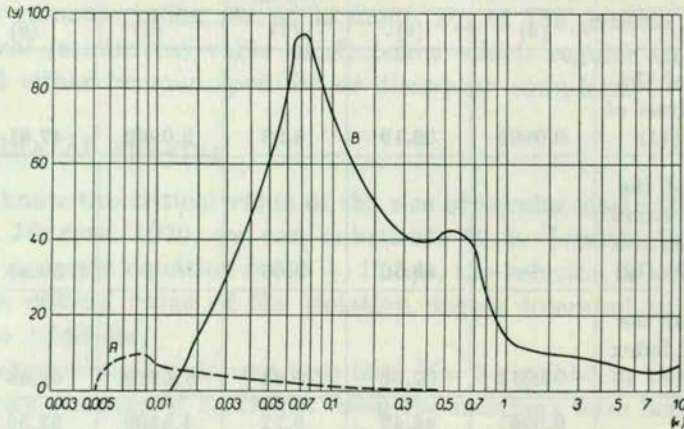
As each of the discussed methods for calculating revealed a tendency to yield either lower or higher results, I have come to the conclusion that it would be most reasonable to use average values obtained from data being the result of calculating them with three different methods when taking them into account in the ensuing parts of the cycle, particularly in those which deal with the ecological aspect.

The assumptions for breaking the range down into zones, put forward previously (JÓZEFIK, 1970), were not explained fully enough to render any further elaboration superfluous and I would like to add a few more comments now.

The extreme zone is characterized by a relatively frequent occurrence of lethal amplitudes of environmental factors preventing the population inhabiting the zone to maintain a positive balance between mortality and reproduction over a longer period of time. This zone comprises breeding sites whose values of index *Z* are lower than mode  $D_{rs}$ , i. e.  $Z \leq 0.065$  (Table 1). 46.42 % of all the breeding sites are situated in the conditions of this zone (cf. Table 2). When we deduce from this figure sporadic sites (41.55 %), then we realize that there are there also about 5 % of regular sites. A high degree of isolation can be quoted as one of the basic limiting factors.

The numerical distribution of the species in the extreme zone is not less characteristic — only 6.72 % of the total *A. ralloides* population are relegated to the environment extremes. They determine the specific character of the species concentration (cf. JÓZEFIK, 1970). This leads to a different shape of the curves presenting the distribution of index *Z*, not in relation to the number of sites, as in graph 3, but in respect of the number of breeding pairs inhabiting these sites (Graph 4).

Indices characteristic for the optimum zone are presented in Tables 1 and 2. This zone is the proper area of the species existence.



Graph 4. Distribution of index *Z* in relation to the average numerical level of the species. *x* — logarithmic scale of the values of index *Z*, *y* — numbers of the species expressed in the number of breeding pairs and presented in ‰. *A* — numbers of the species inhabiting sporadic sites, *B* — numbers of the species inhabiting regular sites.

#### INTERDEPENDENCE OF THE BASIC PARAMETERS OF THE SPATIAL DISTRIBUTION

Practical uses of index *Z* can only be appreciated when considering the interdependence of the more important structural parameters of the distribution presented in graph 5. This graph presents synthetically the dependence of the site size on the degree of isolation, it gives a good idea of the maximum degree of the species overcrowding and spacing, it reveals connections occurring between regular and sporadic sites, and besides enables us to consider more comprehensively the biological situation of the species. This graph can also be treated as a basis for further studies on spatial isolation and the index of existence prosperity.

The construction of the graph is based on four scales. The size of breeding sites expressed in the number of pairs is given on logarithmic scale *y*. Curves *A*, *B*, *C*, *D*, and *E* should be read against this scale. Irrespective of that, class limits of the site size are marked with continuous horizontal lines on scale *y*, which is closely connected with the distribution of the turning points of *Z* variation for separate sites (such points are marked with small circles) and with the construction of curve *F* based on average values for separate class intervals.

Logarithmic scale *x* reflects the degree of isolation which is expressed in average distances between separate breeding sites (in km.).

Scale  $z$  marked by broken horizontal lines can be applied only to curves  $J$  and  $K$ , and it determines the percentage relation between the number of breeding sites and the numbers of the species in separate class intervals of average distances.

The fourth successive scale is formed by slanting lines representing the respective levels of the value of index  $Z$ . The remaining elements of the graph, with the exception of  $F$ ,  $J$ , and  $K$ , should be read against these lines.

As I have mentioned before (cf. page 7), the turning points of  $Z$  variation for separate breeding sites are marked with small circles, and hence the number of circles exceeds considerably the number of sites. However, inasmuch as  $Z$  variation for separate breeding sites fluctuated within a small range, then their value is plotted in the graph in only two variants: a) characteristic for the XIXth century, b) characteristic for the XXth century. The operation mentioned was carried out in order to mark out the area of  $Z$  variation, and hence separate curves representing average values of this index, characteristic for separate categories of sites or zones, can not be the resultant values plotted on the diagram of points. These curves (movable means) were calculated from the working correlation tables.

The boundaries of the area of  $Z$  variation (curves  $a_1$ ,  $b_1$ ,  $c_1$ , and  $c_2$ ) were drawn graphically, and thus their values are not the result of extrapolation calculations. In spite of this simplification they will still be useful in our considerations.

Curves  $A$  and  $B$  represent the distributions of average values of index  $Z$  in the optimum zone ( $A$ ) and of regular sites ( $B$ ), and at the same time they are regression lines of the average site size in relation to the scale of distances ( $x$ ). Curve  $C$  has a similar double significance as it shows the distribution of index  $Z$  and the regression of all the breeding sites treated jointly.

The distributions of index  $Z$  and the regression of breeding sites within the extreme zone are illustrated by curve  $D$ , while curve  $E$  represents sporadic sites.

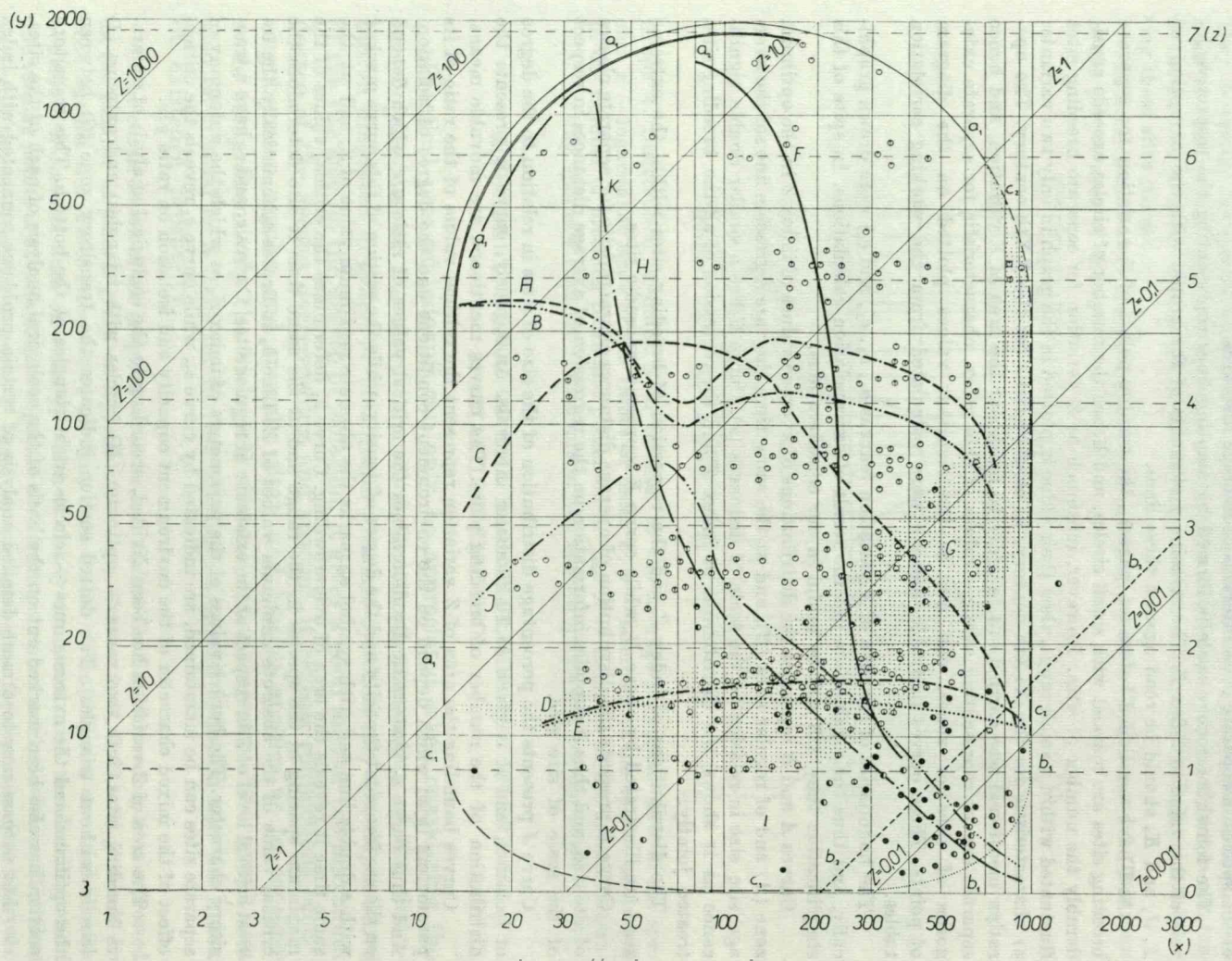
Curve  $F$  presents the distribution of average distances characteristic for separate classes of site size, and thus it supplies information on the regression of average distances in respect of the scale of site size.

Curve  $J$  presents the percentage distribution of the size of sites in relation to the degree of isolation, and it is given at 10-kilometer intervals. Analogously, curve  $K$  presents the distribution of the number of breeding pairs. The curves mentioned are movable means.

Curves bounding the area of  $Z$  variation represent the critical values of the ratio of its parameters ( $y/x$ ) which depend on the environment conditions and the degree of isolation. And thus curve  $a_1$  systematically determines the critical values of ratio  $y/x$  which depend on the environment capacity and the degree of density, while the section of this curve marked with a double line and with symbol  $a_2$  marks the absolute maximum value of  $Z$ , and at the same time it reveals the area of overcrowding. Curve  $b_1$  determines the critical values of the maximum spacing of the species in the range and at the same time it also determines the critical value of the absolute minimum values of  $Z$ . Line  $b_2$  indicates schematically the lowest critical level of  $Z$  in respect of the existence of regular sites. Curves  $c_1$  and  $c_2$  have a transitory character. The border values of the parameters of index  $Z$ , at which the autonomy of separate sites can be maintained, are indicated by curve  $c_1$ , while curve  $c_2$  reveals the critical effect of the mixed character of the environment capacity and isolation on ratio  $y/x$ .

The area of  $Z$  variation has been divided, according to the ecological analysis of separate breeding sites, into two zones — optimum ( $H$ ) (circles with triangles) and extreme ( $I$ ) (circles without triangles). The dotted section indicates the transitory zone ( $G$ ) between the optimum and the extreme ones — circles with triangles at the bottom. This transitory section has also been marked out on the basis of the ecological analysis of each of the sites.

Let us pass now to a more detailed analysis of certain problems connected with index  $Z$ . Problems dealing with other aspects of the species distribution within the breeding area, although they are to a large extent illustrated by graph 5, will be discussed later.



Graph 5. Outline of the area within which the variability of index  $Z$  is calculated and interdependences of more important parameters concerning the structure of the palearctic part of *A. ralloides* breeding range.  $y$  — size of sites (number of pairs),  $x$  — average distances degree of isolation (in kilometers),  $z$  — percentage relation between the number of breeding sites and the species numbers within separate class intervals of average distances; curves presenting the average values of index  $Z$ :  $A$  — sites in the optimum zone,  $B$  — regular sites,  $C$  — sporadic and regular sites together,  $D$  — sites of the extreme zone,  $E$  — sporadic sites; theoretical curves presenting the critical values of ratio  $y : x$  — curves enclosing the area of the variability of index  $Z$ :  $a_1$  — critical values of index  $Z$  in relation to the environment capacity and the degree of species density,  $a_2$  — section of maximum values of index  $Z$  indicating the area where the species density is highest,  $b_1$  — section of minimum values of index  $Z$  and critical values of the maximum dispersion of the species,  $b_2$  — the lowest critical level of index  $Z$  for the existence of regular sites,  $c_1$  — critical values of the parameters of index  $Z$  with a mixed impact of the environment capacity and isolation; the remaining symbols:  $F$  — curve presenting the average degree of site isolation according to separate class intervals,  $G$  — area of the variability of index  $Z$  in the transitional zone between the optimum and extreme zones,  $H$  — area of the variability of index  $Z$  in the optimum zone,  $I$  — area of the variability of index  $Z$  in the extreme zone,  $J$  — curve presenting the percentage distribution of the number of sites in relation to the degree of isolation (size of the class interval = 10 km.),  $K$  — curve presenting the distribution of the species numbers in relation to the degree of isolation (size of the class interval = 10 km.); skew lines indicate the respective levels of the value of index  $Z$ , circles mark the turning points in the variability of index  $Z$  for separate sites, here are their symbols:  $\bigcirc$  — regular sites in the XIXth century,  $\textcircled{\circ}$  — regular sites in the XXth century,  $\bullet$  — sporadic sites in the XIXth century,  $\textcircled{\bullet}$  — sporadic sites in the XXth century, circle with triangle at the top indicates the position of the site in the optimum zone, with triangle at the bottom — in the transitional zone, with no triangle — in the extreme zone.

## BIOLOGICAL MECHANISMS OF THE ISOLATION EFFECT

As it can be seen from graph 5 discussed above, sites having the same values of index  $Z$  are not in the identical situation as far as the degree of existence prosperity is concerned, as it was initially assumed in the second chapter. This is indicated by the composition of transitory zone  $G$ , the configuration of the critical values of index  $Z$ , and it also follows from the specific regression of the parameters of index  $Z$  in respect of each other. Let us consider now the composition of the transitory zone ( $G$ ), or rather the boundaries between this zone and the optimum ( $H$ ) and extreme ( $I$ ) ones, assuming that the degree of existence prosperity of breeding sites situated along each of these boundaries is very similar or even identical. This assumption is based on the following premises:

1) The degree of the micropopulation stabilization over a longer period of time can be considered to be a comparative scale of the degree of existence prosperity for the given micropopulation. This stability, in turn, depends on the size of the micropopulation, or strictly speaking on the range of its numerical oscillations. On the basis of the working material I can conclude that the most intensive numerical oscillations can be recorded in the case of small sites, and that the frequency and range of amplitudes are negatively correlated with the size of sites (this vast problem has not been yet comprehensively discussed in this cycle devoted to *A. ralloides*). This dependence has considerable causal connections (that is why I have accepted the size of sites as one of the parameters of index  $Z$ ).

2) The site is, to a certain extent, affected by the environment capacity, or more precisely, its volume and the final balance of reproduction and mortality rate of the micropopulation inhabiting it. Reproduction rate, or rather its effect, i. e. population increase, depends on the biocenotic composition of the environment, its capacity, and abiotic factors. The factors mentioned affect also mortality rate in the breeding period. However, the species remains in the breeding range for only one third of the annual cycle, hence the value of mortality rate during the remaining eight months affect decisively the size of sites. Here is the crux of the causal connection between the degree of isolation and the size of sites.

3) It has been proved experimentally that within specified limits there is a correlation between individual survival and the flock size, while separate individuals within the flock lose much less life energy than those outside it, the so-called flock effect (PONUGAYEVA, 1950). In the post-breeding period young individuals form, as a rule, separate flocks, while the survival rate of *A. ralloides* in the first year of life, calculated from ringing recoveries, amounts to 54.7 %, and in the first two years even exceeds 80 %. Thus the biological sense displayed by small flocks joining in larger ones is quite evident. Let us also assume, without risking much and in a simplified form, that the period

of absolute isolation of the flock after leaving the breeding site is proportional to the average distance between the sites. Naturally we are concerned here with the moment when two or more flocks join together in the period of post-breeding nomadic movements or migrations, coming from two or more sites neighbouring upon each other but situated at a long distance from each other (cf. JÓZEFIK, 1970). The probability of flocks encountering each other and joining together decreases as distances between sites get longer, and probably there is no rectilinear function here (an attempt to solve mathematically this problem will be undertaken in the ensuing parts of the cycle). I have touched here only upon the problem of autumn migrations. Mortality rate in the course of spring migrations, after disintegration, also remains, to a considerable extent, dependent on the route covered by the flock in order to reach their breeding site. Hence the following conclusion can be drawn: the survival rate of the flock (micropopulation) during its absolute isolation in the post-breeding period determines the maximum spacing of the species in the breeding range (cf. curve  $b_1$  — graph 5). It should be explained here that the survival rate of adult individuals increases considerably in the breeding period. Two distinct points are here decisive: a) *A. ralloides* is perfectly adapted to the breeding environment, b) it assumes the role of a commensal (or even more frequently of a mutualist) in respect of other species habitating together in the breeding colonies. And thus, inasmuch as the degree of isolation in the breeding period does not affect negatively, in any direct way, on the effectiveness of the breeding cycle, then this isolation assumes considerable importance in the post-breeding period as a limiting factor. This explains the high correlation between the size of sites and average distances on the one side and the lack of overcrowding at more distant breeding sites on the other, which leads in effect to increasing oscillations of the size of sites towards the edges of the range, the extreme case of which are sporadic sites, and this moment conveniently reveals the reasons for pulsations in the area boundaries.

4) An increased degree of isolation is connected, as a rule, with the necessity, for separate flocks (micropopulations), to overcome in the course of migrations habitats biologically alien to the species. This prolongs the period when they are exposed to conditions not infrequently disastrous in their effects particularly in the case of alien habitats. Most probably it is here we can find one of the basic reasons contributing to intensive reductions, which lead in consequence to considerable oscillations in the size of sites. And thus an increasing degree of spatial isolation affects destructively, through temporal isolation, the stability of sites and the maintenance of the homeostatic state within the given part of the range. Hence the ecologically equally valuable degree of stabilization, the measure of which we have accepted index  $Z$ , will cover gradually larger sites, as the degree of isolation is increased, and it will ultimately reach the critical value determined by the limiting effect of the environment capacity (rarer cases), or by the combination of two factors, isolation and the environ-

ment capacity (cf. curve  $c_2$ , graph 5). This combination consists in the limiting effect of the environment capacity only when the micropopulation reaches its highest numerical level, and besides in the effect of isolation on the amplitudes of oscillations.

When carrying out the ecological analysis of each of the sites and apportioning them to one of the zones, we have taken into account, first of all, the degree of stabilization displayed by each of the sites. Thus regular sites displaying intensive numerical fluctuations were accredited to the transitory zone, as well as sites whose period of existence was not very long (up to 20–30 years), and moreover sporadic sites at which the Squacco Heron nested altogether longer than the period when there were no Squacco Herons there. After deciphering the basic mechanisms of isolation, I have high hopes that the ecological assumption put forward on page 3 and concerned with the sameness of index  $Z$  (i.e. the same degree of existence prosperity along the boundaries of the transitory zone) will be accepted by the reader as reasonable and well grounded. The same can be applied to the value of index  $Z$  along curve  $b_1$ , i. e. the boundary of the maximum spacing of the species in the range.

When discussing the mechanisms of isolation, I would also like to stress quite an important moment: index  $Z$  indicates the existence prosperity of the given micropopulation not only in the breeding period but also in the entire annual cycle and treating it differently would be unjustified. If we are to single out an index covering only the breeding period and reflecting the environment conditions of the site, then the most obvious and reasonable one seems to be the average number of fledglings leaving one nest.

#### EXPONENTIAL INCREASE OF THE ISOLATION EFFECT

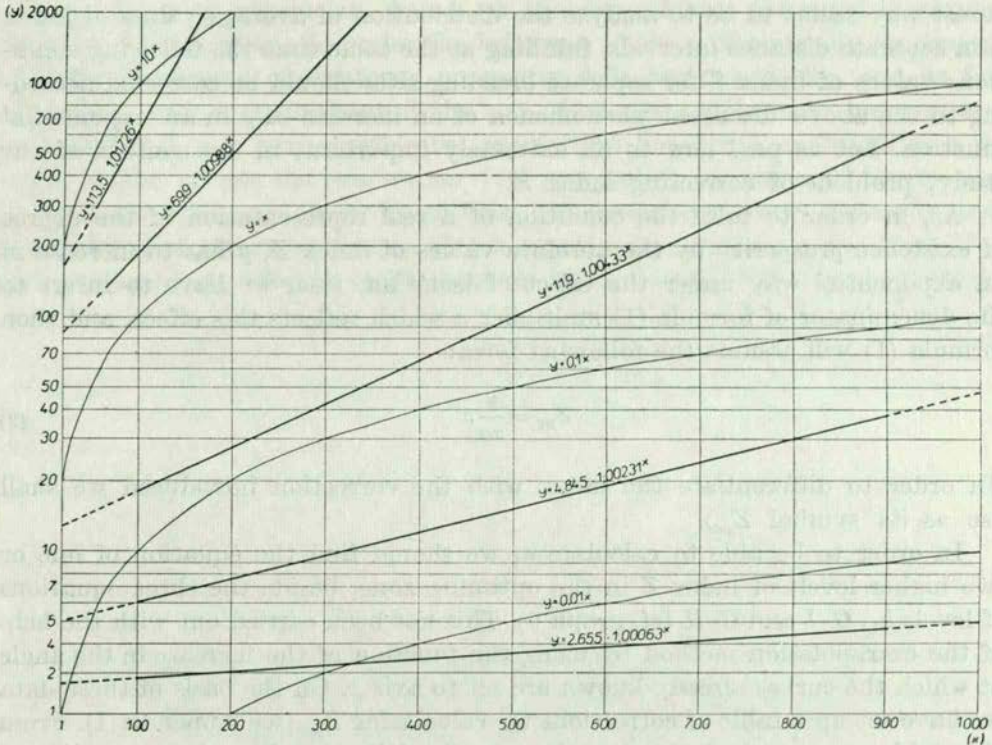
A completely different problem is the character of the functional interdependence between ecologically identical levels of index  $Z$ , the degree of isolation, and the size of sites. The rectilinear character of formula  $Z = f(y/x)$  assumed at the beginning of this chapter, had working purposes in mind, while the data from graph 5 (i. e. the above discussed boundaries of the transitory zone and curve  $b_1$ ) testify that this function is much more complicated when we apply successively different formulas for different levels of index  $Z$ . Let us now analyse the character of this function transforming the values of  $Z$  parameters from the boundaries of the transitional zone and from curve  $b_1$  on the logarithmic scale of graph 5 to the semilogarithmic scale (Graph 6, curves  $b_1$ ,  $G-I$ ,  $H-G$ ). We make sure straightaway that we are dealing here with exponential curves whose equations are of the following type:

$$y = kt^x.$$

And thus the exponential equation of curve  $b_1$  can be expressed as follows:

$$y = 2.655 \cdot 1.00231^x,$$





Graph 6. Interdependence between the size of sites and average distances when the impact of isolation has an exponential character.  $x$  — average distances,  $y$  — size of sites; thin lines — rectilinear interdependence for the initial (working) concept of index  $Z$  (equations of the type:  $y = ax$ ); thick lines — real curvilinear interdependence revealed (which can be expressed by exponential equations of the type:  $y = kl^x$ ) (in the graph the equations of separate curves are presented).

while for curve  $G-I$  it will assume the following form:

$$y = 4.845 \cdot 1.00231^x,$$

and another one for curve  $G-H$ :

$$y = 11.9 \cdot 1.00433^x.$$

I have proved that as distances between breeding sites get longer, the same level of existence prosperity (or speaking more graphically — the standard of the ecological situation) attained by the micropopulation inhabiting these sites can be maintained only in the conditions of the growth of sites in size according to an exponential function. Naturally the expression of this function varies for different levels of index  $Z$ . And thus when we want to express it in a more general way, i. e. to present it in a mean form and by that characterize generally the effect of isolation on the degree of existence prosperity, the simplest and

surest way seems to be to analyse the distribution of average values of index  $Z$  in separate distance intervals, fulfilling at the same time the following condition: values of index  $Z$  for separate breeding sites should be corrected according to the above discussed phenomenon of an increase in  $y$  in an exponential function. Let us pass now to an extremely important, in the context of our study, problem of correcting index  $Z$ .

As, in order to fulfil the condition of a real representation of the degree of existence prosperity by the absolute values of index  $Z$ ,  $y$  has to increase in an exponential way under the effect of isolation, then we have to insert to the denominator of formula (1) multiplier  $a$  which reflects this effect, and then formula (1) will assume the following form:

$$Z_{pe} = \frac{y}{xa}. \quad (2)$$

(In order to differentiate the index with the correction introduced we shall use as its symbol  $Z_{pe}$ ).

In order to be able to calculate  $a$ , we should find the equation of one or two higher levels of index  $Z$  in the optimum zone, beside the three equations of levels  $b_1$ ,  $G-I$  and  $G-H$  (cf. graph 6). This has been carried out with the help of the extrapolation method by using the function of the increase in the angle at which the curves already known are set to axis  $x$ . On the basis of these data we have set up a table of corrections for calculating  $Z_{pe}$  (see Appendix I). From this table  $a$  was calculated according to the following formula:

$$a = b \pm Zc \quad (3)$$

where,  $a$  = coefficient of the curvilinear effect of isolation on the degree of existence prosperity,  $b$  = coefficient of the curvilinear effect of isolation at the given level of index  $Z$ ,  $c$  = interpolational correction for calculating  $b$ ,  $Z$  = previous uncorrected index of existence prosperity calculated according to formula (1).

Substituting formula (3) to equation (2) we shall have the corrected formula for calculating  $Z_{pe}$ :

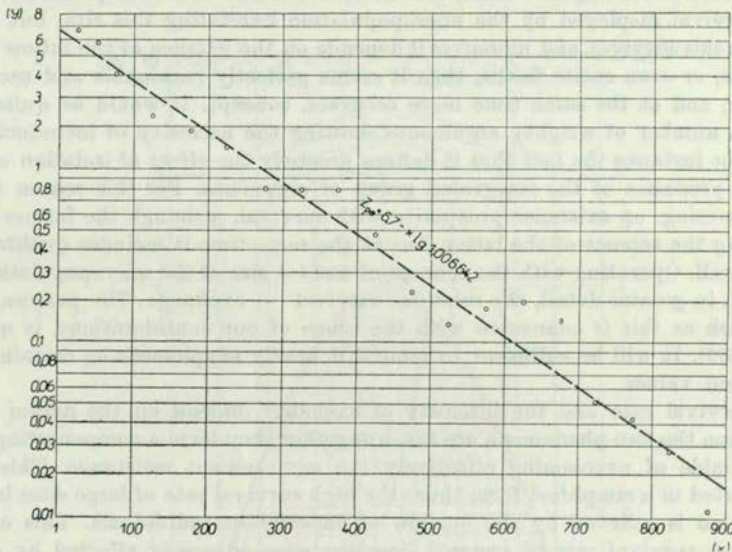
$$Z_{pe} = \frac{y}{x(b \pm Zc)}. \quad (4)$$

The use of formula (4) and of the table of corrections facilitates our task as it helps to do away with complicated calculations connected with correcting  $Z$ .

According to the assumption put forward on page 3, the general distribution of index  $Z_{pe}$  has been constructed in relation to the scale of distances. This distribution is presented in graph 7 — the curve falls logarithmically and its equation assumes the following form:

$$Z_{pe} = 6.7 - x \lg 1.006642.$$

The following conclusion, based on the dependences presented in graphs 6 and 7, can be drawn: as under the influence of the arithmetically increasing isolation the degree of existence prosperity falls logarithmically, and as for this degree to remain unchanged the size of sites would have to increase exponentially, then it is reasonable to assume that the spatial isolation, as a limiting factor, affects the relative survival rate and the numbers of the species in an exponential way. In order to define this conclusion more generally and to expand it at the same time so that it would cover species having their biology similar to *A. ralloides* (and there are quite a number of them), we have



Graph 7. General distribution of index  $Z_{pe}$  in relation to the degree of isolation.  $x$  — average distances (km.) — degree of isolation,  $y$  — logarithmic scale of index  $Z_{pe}$  (the graph includes the equation of the distribution curve).

to present it in a slightly modified way: any social species habitating the breeding range in an island-like pattern is decisively affected by spatial isolation, which is then one of the more important limiting factors. The mechanism of its effect realized in the post-breeding period assumes the form of temporal isolation. The increase of the spatial isolation in an arithmetical progress coincides with the growth of its effect in an exponential function.

This is one of the most important conclusions of the present paper which enables, among others, to provide reasons for the previously explained (cf. JÓZEFIK, 1970) integrating tendency of the species. The equation presented above ( $Z_{pe} = 6.7 - x \lg 1.006642$ ) is a general mathematical support of ALLEE'S rule when applied to *A. ralloides*. It also belongs to one of the most significant characteristic features of the species.

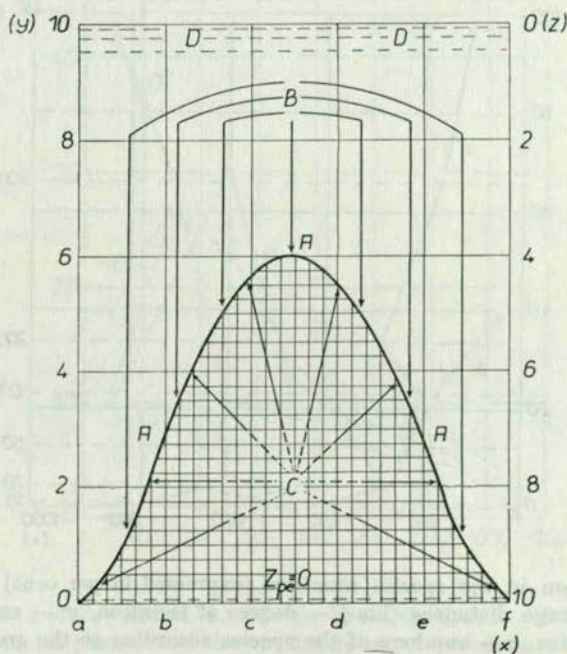
## EXISTENCE PROSPERITY — SURVIVAL — ENVIRONMENT RESISTANCE

The problem of confronting the newly introduced concept of „existence prosperity” with the more widely used ecological terms seems important enough to warrant a brief explanation. The term „existence prosperity” can be applied exclusively to micropopulations inhabiting the given breeding site, or alternatively to a group of sites in any part of the range but then in its mean form. As soon as we assume that there is no individual exchange between separate sites, i. e. the sort of rotation described previously (cf. JÓZEFIK, 1969a), and accordingly the survival of separate individuals determined by the environment conditions contributes to the general effect of the micropopulation survival rate, then there is no need to introduce any new term. However, as the size of sites depends not only on the degree of survival displayed by the micropopulation inhabiting this site, but it also decisively affects this survival, and moreover it depends on the balance of the inflow and outflow of individuals, or even entire flocks, then it seems perfectly reasonable and useful to introduce a wider, and at the same time more accurate, concept. It would be quite possible to quote here a number of weighty arguments showing the necessity of introducing this new concept, as for instance the fact that it defines precisely the effect of isolation on the course of biological processes of the integrated group of organisms. For this reason there are no grounds for mixing up existence prosperity with survival, although the former term covers in its meaning the essence of the latter, but at the same time it includes qualitatively other elements as well. Operating with the concept of size (= size of the micropopulation) we have not analysed, in greater detail, the relation: survival — exchange. The pattern of this relation, inasmuch as this is connected with the scope of our considerations, is quite evident (JÓZEFIK, 1969). It will be sufficient to remind it briefly supplementing certain points with newly-acquired values.

Both survival rate and the intensity of exchange depend on the action of isolation. However, when the two phenomena are taken together they form a compensating mechanism which is capable of overcoming effectively the environment resistance. This mechanism can be presented in a simplified form thus: the high survival rate of large sites leads to overcrowding which is relieved by the outflow of superfluous individuals. This excess makes up for the low survival rate of exposed breeding sites adversely affected by environment extremes, as a rule small ones. The index of existence prosperity presents the effects of this co-operation as a measurable relative gradient. As we can see, one term can not be substituted for the other, particularly in the case of the qualitatively different stress of the phenomenon. On the other hand, as we use the expression “existence prosperity” when referring to the species as an integrated biological unit, then it loses its meaning because, leaving aside the known sporadic, and rather pathological, cases, we know of no facts which would indicate the interspecific (genetic) exchange. A better expression seems to be here “survival rate of the species”, but even here it is differently coloured. Probably the best expression here would be the “biological situation of the species”.

It might be useful to compare here the expression proposed by the author with the one widely used and easily applied which has been introduced by CHAPMAN (1928), namely „environment resistance”. Broadly speaking, these two notions originate from two contrasting assumptions. The measure of environment resistance is the difference between the highest possible potential ability of the species to increase numerically and the real increase recorded. This concept assumes an increase in the infinite environment, and that one of the parameters can be determined only theoretically, and even then only after overcoming serious difficulties. The concept “existence prosperity” takes as its starting point an empirical (and so far only indirect) determination of the level of the complex of environmental factors (critical values of the parameters of index  $Z_{pe}$ ) at which the possibility of the micropopulation's existence approaches zero. Index  $Z_{pe}$  presents on a relative scale at which level,

above these critical values, the given micropopulation can exist. In both cases we are concerned with the determination of the „balance” being the result of the following relation: micropopulation, population — environment. In the former case (existence prosperity) the result of the integrated group's co-operation in the fight for survival is quite clearly stressed, while in the latter case (environment resistance) no clear-cut picture is obtained. We could cite here also some other parallels but this might exceed the scope of the present part of the cycle. Leaving aside a number of subtleties, it is possible to assume that both these concepts supplement each other which is well illustrated by the small scheme enclosed (graph 8). I have naturally assumed here the possibility of reducing the indices of environment resistance and existence prosperity to a common comparable scale, which seems to be possible only in an empirical way. However we shall return to this problem at the right moment.

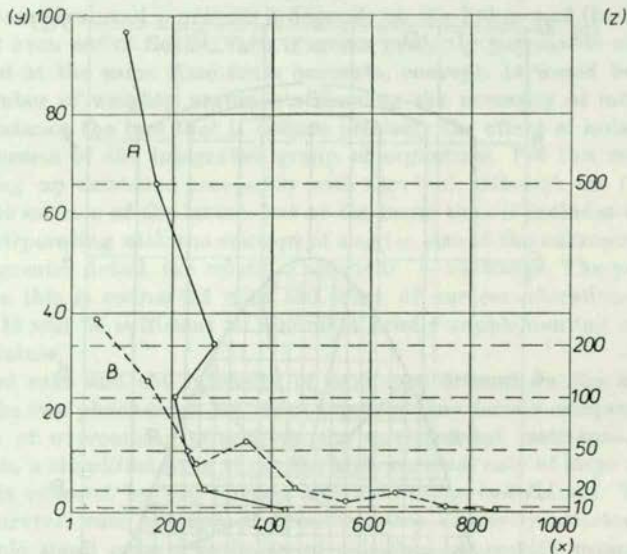


Graph 8. A simplified scheme of interdependences between existence prosperity and the environment resistance.  $x$  — (temporal)-spatial scale of the micropopulation existence (of the population or of the species),  $y$  — scale of the relative dependence between  $Z_{pe}$  and the potential realized,  $z$  — relative fiducial scale of the environment resistance,  $A$  — (temporal)-spatial variability of the relative values of index  $Z_{pe}$  and the difference: biotic potential-potential realized and (temporal)-spatial variability of the environment resistance,  $B$  — total impact of all the factors limiting of environment,  $C$  — effectiveness of the fight for survival,  $D$  — level of biotic potential.

#### ECOLOGICAL GRADATION OF LEVELS OF INDEX $Z_{pe}$

It is very important from the point of view of the ecological classification of the range zones to analyse the problems connected with attaching a specified ecological significance to respective levels of index  $Z_{pe}$  which would reflect

the gradation of their absolute values. As it has been shown in the previous chapter, the correlation ratio between the size of sites and average distances, presented as  $\eta_{xy}$  and  $\eta_{yx}$  is bilaterally connected causally, or to put it differently, the degree of isolation affects not only the size of sites, but also the size of a site, in its turn, as overcrowding is intensified there, leads to the setting up of new sites in the nearest vicinity, as much as the topographical conditions render it possible, which invariably brings about some shortening of distances between separate breeding sites (JÓZEFIK, 1970). As I do not want to make the course of the argument too cumbersome by illustrating it mathematically, I shall confine myself to assuming only as the starting point the



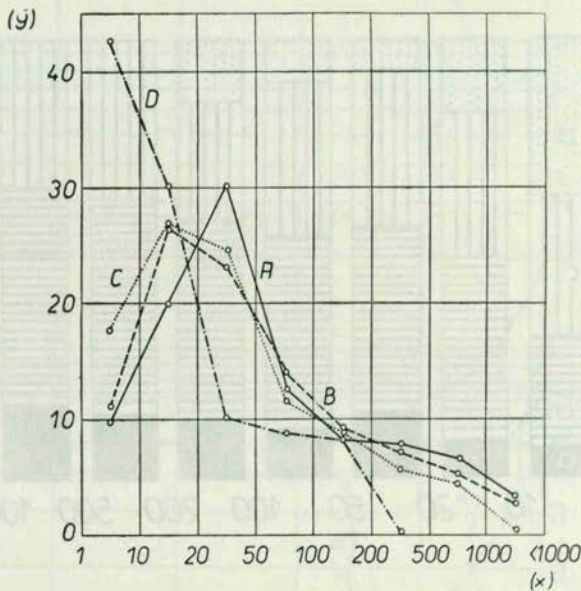
Graph 9. Regression in the species numbers (expressed in per cent) and of the degree of isolation.  $x$  — average distances (km.) — degree of isolation,  $y$  — numbers of the species in percentage relation,  $z$  — numbers of the species according to the groups of concentration (size of sites),  $A$  — regression of the degree of isolation according to the groups of numerical concentration,  $B$  — numerical regression in relation to the degree of isolation.

discovered regularity in the logarithmic decrease of the degree of existence prosperity under the effect of the arithmetically increasing isolation, and then it will not be difficult to reconstruct (naturally with certain approximation) the mechanism determining the way in which  $y$  affects  $x$ , and in which  $x$  affects  $y$ , in respect of their interdependence expressed by the value of index  $Z$ .

Let us consider now correlation ratio  $\eta_{xy}$  which reflects the effect of isolation on the size of sites. This effect can also assume an exponential character, i. e. at high and highest values of index  $Z$  this effect is reduced almost to zero, while at the lowest parameters of  $Z$  this effect is intensified up to the point of becoming the biological barrier (critical values of index  $Z$ ).

The effect of the size of sites on the increase in the degree of isolation (i. e.  $\eta_{yx}$ ) is lessened logarithmically as distances are lengthened arithmetically, and vice versa, that is this effect is intensified exponentially as the degree of isolation declines arithmetically.

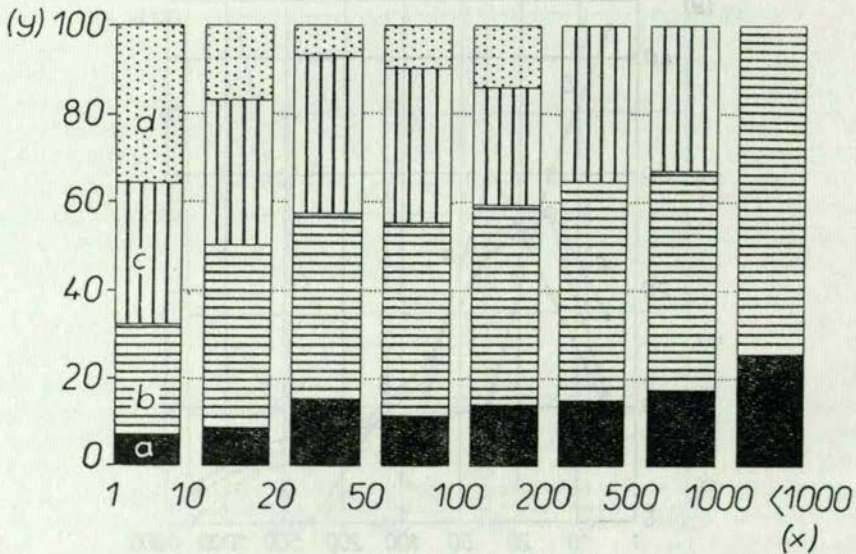
A significant moment of our further research would be to find out such a value of index  $Z_{pe}$  (naturally an average one) at which the effect of  $y$  on  $x$  would be reduced to zero. Having that object in mind, let us analyse the numerical regression of the species and the degree of isolation presented in graph 9. For the largest groups of birds down to those comprising 500 pairs the decrease in the degree of isolation is slow. Below the level of 500 pairs (down to 200



Graph 10. Distribution of the size of *A. ralloides* breeding sites in relation to average distances between them (in per cent of the total number of breeding sites within the given range of distances).  $x$  — class intervals of the size of sites,  $y$  — number of breeding sites within the given range of distances in per cent, curves of distribution within the range: *A* — up to 50 km., *B* — between 50 and 200 km., *C* — between 200 and 500 km., *D* — over 500 km.

pairs) the isolation is gradually intensified. Most probably groups of breeding sites bracketed between 500 and 200 pairs are the last ones for which the effect of  $y$  on  $x$  can be recorded, as the rapidly increasing degree of isolation clearly indicates that no more dependent sites are set up in their vicinity. The fall of curve *A* along the section presenting the groups smaller than 200 pairs is very characteristic and it indicates that we come up here against quite a large group of “dependent” sites dispersed around large breeding sites. Let us assume that average distances between large sites and their “satellites” do not display

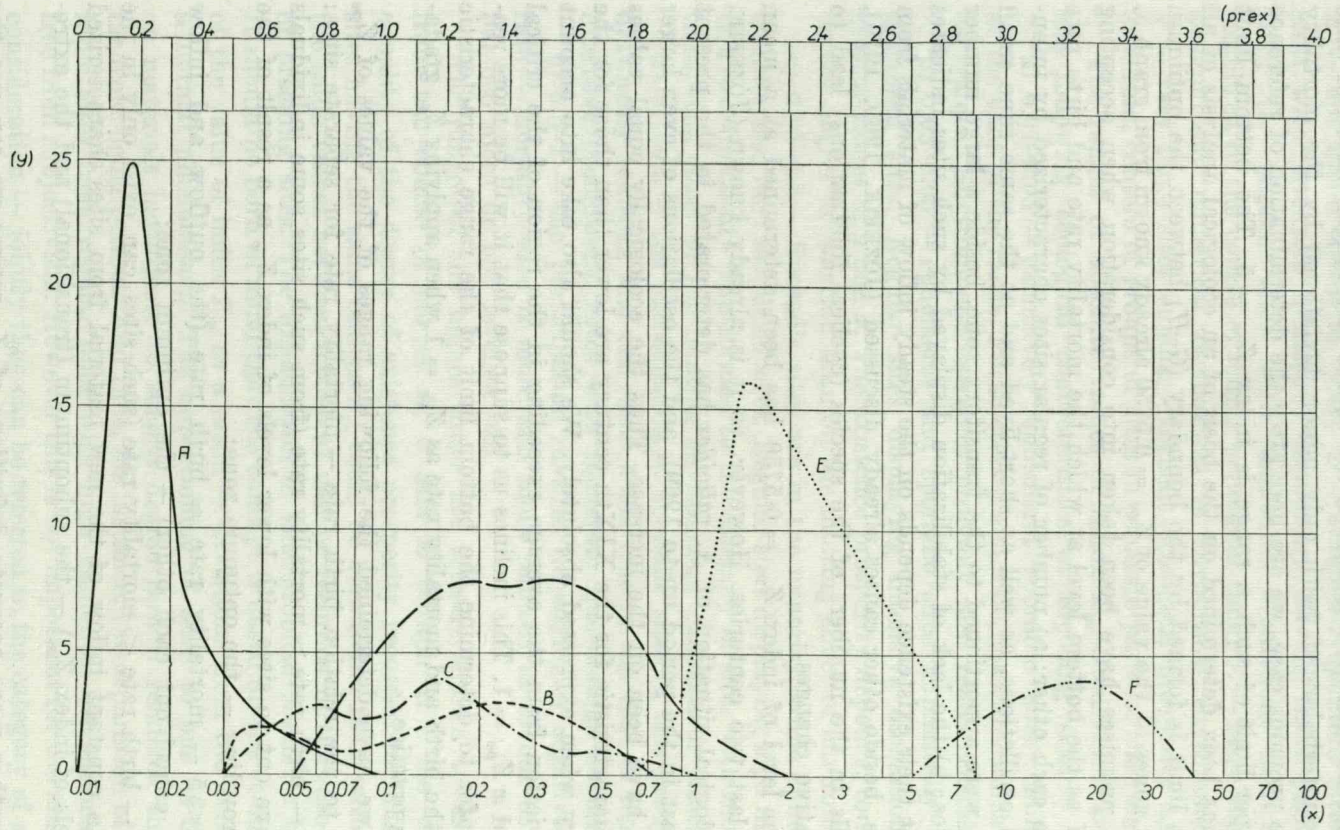
any significant differences (cf. graphs 10 and 11). And as the average distances of small breeding sites were reduced down to almost 200 km (the bend in curve A, graph 9), the effect of large sites on the setting up of "satellites" can be recorded, on average, within the limit of 200 km. Let us now closely scrutinize curve A (graph 9) — it shows that such distances represent groups of up to 400 pairs which comprise more than 42 % of all the Squacco Herons in the area. This indicates in turn that 42 % of the total numbers are concentrated in groups with the populations where the birth rate exceeds permanently the mortality rate. Obviously this conclusion has to be treated with a large degree of scepticism. Most probably this per cent is even higher, especially when we



Graph 11. Diagram presenting the percentage relation of average distances within separate class intervals of the size of breeding sites.  $x$  — size of sites,  $y$  — number of sites within separate ranges of distances expressed in per cent, ranges of distances:  $a$  — up to 50 km.,  $b$  — between 50 and 200 km.,  $c$  — between 200 and 500 km.,  $d$  — over 500 km.

consider that the surplus of individuals leads not only to the formation of new „dependent” sites but it also moves to many parts of the range characterized by a considerable dispersion of breeding sites. This level ( $y = 400$ ,  $x = 200$ ) corresponds to index  $Z_{pe} = 6.3700$ , but when we take into account the reservation mentioned above, the index ought to be lowered. And thus we shall assume, with only a small risk involved, (cf. graph 12), that in all sites with index  $Z_{pe} > 5$  the birth rate (population increase) exceeds the mortality rate, and this leads to the outflow of the surplus of individuals from such sites to those with lower  $Z_{pe}$ . Below the level of  $Z_{pe} = 5$  we can record the effect of the size of sites on the degree of isolation.





Graph 12. Distributions of index  $Z_{pe}$  for sites in different categories.  $x$  — logarithmic scale of the values of index  $Z_{pe}$ ,  $y$  — number of sites,  $A$  — ephemeral sporadic sites,  $B$  — stabilized sporadic sites,  $C$  — regular sites with considerable numerical oscillations,  $D$  — regular sites with a moderate degree of oscillations,  $E$  — regular sites with a positive balance birth rate — mortality rate, and with a good ecological prosperity,  $F$  — regular sites with a positive balance birth rate — mortality rate, and with an excellent ecological prosperity, overcrowded. In the upper part of the graph there is a nomogram of the transformation of absolute values of index  $Z_{pe}$  into the scale of  $prexes$ .

We still have to determine the range of  $Z_{pe}$  values at which the population increase of separate micropopulations in the course of a longer period of time is generally counterbalanced (with only minor deviations) by the mortality rate. As in the previous case, we are here after the determination of reference levels. The upper limit of such a range is index  $Z_{pe} = 5$ . The bottom limit of the range has been determined on the basis of an ecological analysis of all the sites. This limit is formed by the boundary ( $G-H$ ) between the optimum and transitory zones at the value of  $Z_{pe} = 0.5750$  already known from graph 5. The following premises have been taken into consideration when accepting boundary  $G-H$  as the bottom level at which the mortality rate and birth rate counterbalance each other: a) number of regular sites characterized by intensive numerical oscillations, as well as short-lived and at the same time small breeding sites, were apportioned to the transitory zone, beside a large number of sporadic sites; b) the lack of stabilization displayed by such sites indicates invariably that their existence depends on the steady inflow of materials from outside. Hence, beside other causes already discussed (JÓZEFIK, 1969, 1970), even small falls in the numbers of the species (cyclical fluctuations) lead to drastic qualitative changes.

The bottom level of index  $Z_{pe} = 0.5750$  has been determined as a mean value for the last two centuries. However, as it is already known (JÓZEFIK, 1969), the biological situation of *A. ralloides* has deteriorated in the present century (at least in the period up to 1960), and the oscillations of even larger breeding sites have been on the increase. Thus the ecologically equal values of index  $Z_{pe}$  characteristic for the XIXth century are lower than those for the present century when expressed absolutely. We should also take into account the upper deviation from the average exceeding in the region of the critical values of  $y$  and  $x$   $Z_{pe} = 1$ . This inclines us to suppose that it will be more reasonable and safer to determine the bottom limit of the range characteristic for sites with the birth and mortality rate as  $Z_{pe} = 1$  when applying  $Z_{pe}$  gradation later on in practice.

And thus we have determined the following ranges of the values of  $Z_{pe}$  corresponding to the relation birth rate — mortality rate for separate sites:

a)  $Z_{pe} > 5$  — birth rate  $>$  mortality rate (from such sites some individuals constantly move out to sites with lower levels of index  $Z_{pe}$  as a result of the state of overcrowding — the optimum zone;

b)  $1 \leq Z_{pe} \leq 5$  — mortality rate  $\approx$  birth rate (the outflow and inflow of individuals cancel out each other) — the optimum zone;

c)  $Z_{pe} < 1$  — birth rate  $<$  mortality rate (such sites can exist only in the conditions of a constant inflow of the new material from sites characterized by higher levels of index  $Z_{pe}$ ) — the suboptimum (transitional) and the extreme zones.

For any further more accurate definitions of  $Z_{pe}$  ranges we can use the characteristics of  $Z_{pe}$  distribution of breeding sites broken down, according to

the ecological analysis (cf. graph 12, table 3), into the following groups: A — ephemeral sporadic sites; B — stabilized sporadic sites; C — regular sites with intensive numerical oscillations having short periods of prosperity; D — regular sites with moderate oscillations and relatively well stabilized in the course of longer periods of time; E — large regular sites with insignificant numerical oscillations in favourable environment conditions; F — very large sites enjoying excellent ecological prosperity and making up, as a rule, centers of groups of sites in separate parts of the range.

The ranges of absolute values of index  $Z_{pe}$  cited below correspond with the following ecological characteristics of breeding sites:

a) 0.01–0.03 — exclusively ephemeral sporadic sites mainly distributed at the ends of the range. Parameters  $y$  and  $x$  do not differ much from the critical values. Environment extremes probably also reach critical values.

b) 0.03–0.05 — ephemeral and sporadic sites numerically counterbalance stabilized sites. Regular sites displaying intensive oscillations realize here critical values of  $y$  and  $x$ . The existence prosperity depends, to a larger extent, on the degree of isolation than on the limiting effect of environment extremes.

c) 0.05–0.1 — Sporadic sites are in the minority, while ephemeral ones are transformed into stabilized sites. Regular sites displaying high indices of oscillation are drastically transformed to the category of sites with moderate fluctuations. The effect of the limiting environment extremes is clearly visible here.

d) 0.1–0.5 — the participation of sporadic sites in this group is even more drastically reduced, and the same holds true in the case of regular sites with intensive oscillations. Sites with moderate fluctuations dominate here.

e) 0.5–1 — the participation of sites displaying a negative balance birth rate — mortality rate is more and more reduced in favour of sites with the balance more or less levelled off.

The ranges of the higher order are already known to us. As it follows from the course of curves *B*, *C* and *D* (Graph 12), the concept of the equality of the degree of existence prosperity recorded for different breeding sites having the same indices  $Z_{pe}$  could be here found fault with. For instance, the same values between 0.05–0.07 can be recorded in the case of four groups of breeding sites. The explanation of this problem seems to be worth-while. It should be born in mind that the concept is based on the ecological gradation of the value of index  $Z_{pe}$  as a mean — deviations from the average values are a normal phenomenon. The apportioning of sites to one of the groups was on materials incomplete to such a degree that it rendered the classification far from being perfect. And thus, for instance, the separation of stabilized sporadic sites from regular ones with high numerical oscillations has not been free from subjectivism. However this is not important for the main point of our consideration — jointly they can be referred to the category of sites with a low degree of stabilization.

However it has been man who has played the most important part in enhan-

cing the heterogenous character of sites with values of index  $Z_{pe}$  within the range of 0.03–1. The data presented in graph 12 comprise the last two centuries — i. e. the period of a very intensive expansion of man in respect of nature. A large per cent of small and medium-size breeding sites standing a fair and natural chance of a stabilized prosperity in the course of tens of years have been, and still are, destroyed in certain regions of the range (it is not so easy to destroy larger sites — cf. the situation of *Ardeidae* in the Danube Delta in the fifties of the present century — JÓZEFIK, 1969b). But for this circumstance, sporadic sites would most probably comprise (judging by the course of curve *D*) the range of index  $Z_{pe}$  between 0.01 and 0.1, and not, as it is illustrated by curve *B*, the range up to 0.7. Although the destructive effect of man in many fields of ecology ought to be treated as a natural action of the limiting factor (or a complex of factors), in our particular case, in view of its rapid rate (cf. JÓZEFIK, 1969b, 1970), there are good reasons for treating this action as a pathological phenomenon.

Table 3. Statistical characteristics of the distribution of index  $Z_{pe}$  according to the ecological gradient.

Intervals of $Z_{pe}$ (2)	Percentage distributions in relation to separate class intervals (3)					$Z_{pe}$		
	0.01	0.1	1	5	10	50	$\bar{x}$	$\sigma_{\bar{x}}$
Category of sites (1)								
ephemeral sporadic ( <i>A</i> )	50.7	1.5	—	—	—	—	0.0236	0.0168
stabilized sporadic ( <i>B</i> )	14.5	15.9	1.9	—	—	—	0.2093	0.1866
regular with considerable numerical oscillations ( <i>C</i> )	20.3	14.7	—	—	—	—	0.1803	0.1976
regular with moderate oscillations ( <i>D</i> )	14.5	62.3	13.2	—	—	—	0.5010	0.4244
regular ecologically prosperous ( <i>E</i> )	—	4.4	84.9	70.0	—	—	3.2011	1.7492
regular with excellent ecological prosperity, overcrowded ( <i>F</i> )	—	—	—	30.0	100.0	—	17.8754	9.3436
sites in the extreme zone (4)	85.5	32.4	1.9	—	—	—	0.0983	0.3898
sites in the transitory zone (5)	39.1	73.6	5.7	—	—	—	0.3013	0.3091
sites in the optimum zone (6)	14.5	67.7	98.1	100.0	100.0	—	3.5728	6.3660

We have obtained the gradation of  $Z_{pe}$  in an indirect way, and it characterizes generally the state of environment conditions under which each of the micropopulations can exist in the annual cycle. The gradient of the factors

of the breeding habitat will be discussed at large in the parts dealing with the autecology of the species. The situation seems to be less favourable as far as the data referring to environment conditions under which the species has to live in the post-breeding period are concerned. However, also in this case it will be necessary to undertake attempts to systematize the material.

PREX — INDEX OF THE BIOLOGICAL SITUATION OF THE SPECIES

The application of absolute values of index  $Z_{pe}$ , particularly in the case of a comparative estimate of  $Z_{pe}$  for separate breeding sites, is quite difficult as the size of class intervals of  $Z_{pe}$  increases logarithmically (cf. graph 12). Hence it would be more rational to use the logarithm of index  $Z_{pe}$ . The upper part of graph 12 presents a nomogram transforming the absolute values of index  $Z_{pe}$  into their logarithms, and in order to avoid logarithms with negative mantissa the transformations were carried out by multiplying  $Z_{pe}$  by 100, and that is why the final form of the transformation was as follows:

$$\lg Z_{pe} + 2.$$

The new scale obtained in this way has a number of useful applications and positive qualities: the initial part of the scale corresponding to the critical values of index  $Z_{pe}$  has the value of zero; the lowest values of stabilized sporadic sites and regular ones characterized by intensive oscillations start from 0.5; from the value of 1 an intensive increase of sites with moderate oscillations is initiated; value 2 forms a boundary between the sites with a negative balance birth rate — mortality rate and those sites with a levelled off or even positive balance; the highest values of  $\lg Z_{pe} + 2$  reach up to 3.6; neither in the past nor in the future (even more so) did the species or will it, exceed value 4 — this figure can be thus accepted as the final one in the scale. However the greatest asset of the new scale is an uncomparably greater adequacy of its absolute values in respect of the gradient of factors determining the degree of existence prosperity displayed by the given micropopulation. This enables to use the values of  $\lg Z_{pe} + 2$  in specified circumstances (e. g. for comparisons) as a sort of absolute units measuring existence prosperity. Bearing in mind the practical aspect I suggest accepting 1 *prex* (from Latin *pr*(osperitas) *ex* (istentiae)) as a unit for measuring the degree of existence prosperity in the case of separate micropopulations. And thus 1 *prex* =  $\lg Z_{pe} 0.1 + 2$ , and the general formula of the transformation can be presented in the following way:

$$n_{prex} = \lg m Z_{pe} + 2, \tag{5}$$

where  $n$  is the number of *prexes*, while  $m$  is the value of index  $Z_{pe}$ .

Realizing that theoretically in ecological sciences the transformation from the level of indices to the level of units of measurements is enormously complicated and often completely impossible, particularly when we have to deal with the possibility to measure a phenomenon which is the result of a mutual effect of the practically immeasurable number of factors, I am not going to attempt to give a definition of one *prex* (it is undoubtedly a unit of relative reference). And that is why I have left the theoretical expounding of the basis of this problem as an open and debatable point.

#### ECOLOGICAL ZONES OF THE RANGE

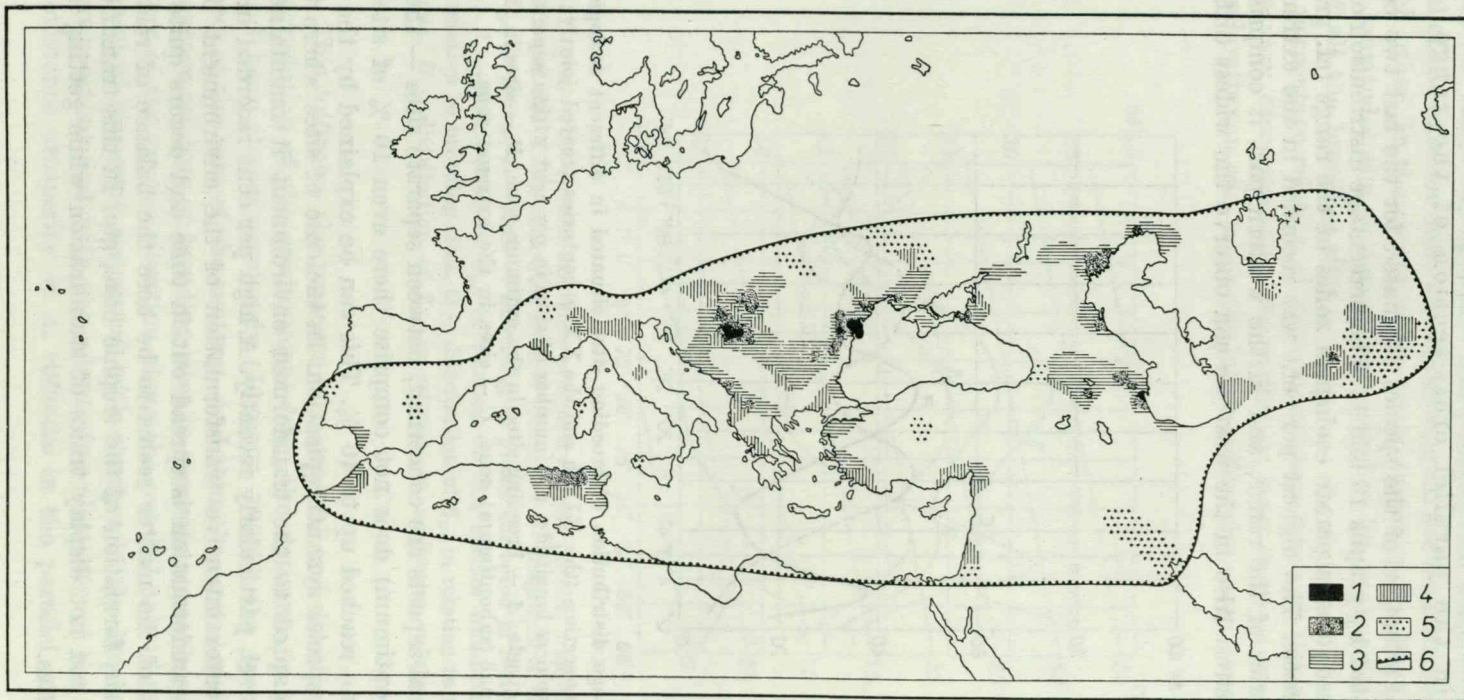
##### Izoprexes

I have determined previously (cf. page 9), with the help of three different methods, the proportion between the number of sites and the numerical state of the species in separate ecological zones, as well as giving characteristics of these zones according to the levels of index  $Z_{pe}$  (Table 3). Taking into account the reduction of the values of index  $Z_{pe}$  to *prexes*, the characteristic features of the extreme and optimum zones together with the transitional area (suboptimum zone) can be presented in the following way:

Table 4. Characteristic features of the ecological zones of *A. ralloides* range according to the gradation of the index of existence prosperity ( $Z_{pe}$ ) expressed in *prexes* (in brackets ranges of index  $Z_{pe}$  in their non-transformed form).

Zones	Ranges of $Z_{pe}$ in <i>prexes</i>	Index $Z_{pe}$ non-transformed	$\bar{x}_{Z_{pe}}$ ( <i>prex</i> )
(1)	(2)	(3)	(4)
extreme (5)	0-1.7	(0.01-0.5)	0.993
transitional (suboptimum) (6)	1.7-2.0	(0.5 -1.0)	1.479
optimum (7)	2.0-4.0	(1.0 -100.0)	2.804

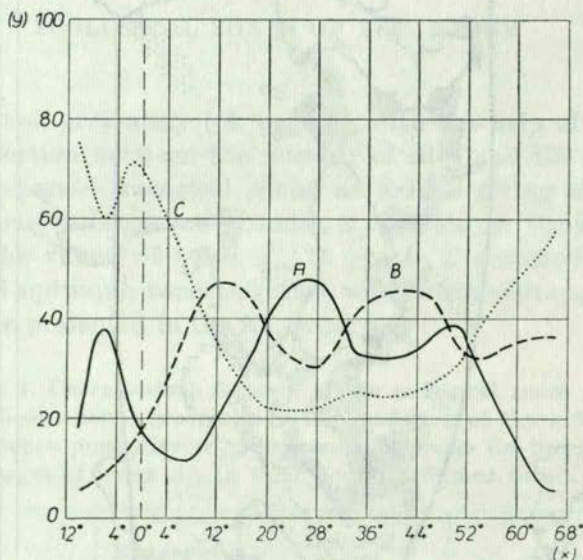
Using the scale of *prexes* I have marked in map 1 the so-called izoprex-areas, i. e. those indicating the composition of the optimum (symbols 1-2), suboptimum (symbol 3), and extreme (symbols 4-5) zones. Obviously, as the map is based on materials covering the last two centuries, it can not represent the actual composition of the ecological zones. As it is quite clear from the map, the optimum zone covers only a relatively small area although it is inhabited by over 90 % of all *A. ralloides* individuals in the range. The extreme zone comprises, on the other hand, more than 45 % of breeding sites (I have not included in these calculations the suboptimum zone).



Map 1. Ecological zones in the palearctic part of *A. ralloides* range — areas of izoprexes. 1 — optimum zone, izoprexes within the range 3.0–4.0; 2 — optimum zone, range 1.7–3.0 prexes; 3 — transitional zone (suboptimum), range 1.0–1.7 prexes; 4 — extreme zone, range 0.5–1.0 prex; 5 — extreme zone, range 0.0–0.5 prex; 6 — boundaries of the range.

### Zones in the parallel cross-section of the range

The biological situation of the species estimated for the last two centuries jointly is illustrated by graphs 13 and 14. The percentage distribution of breeding sites dispersed over separate ecological zones of the range (cf. graph 13) is very characteristic. The highest per cent was recorded in the extreme zone near the boundaries of the range, and in the western part it comprises over 60 % of all the sites. Also in the west we can observe the widest differences,



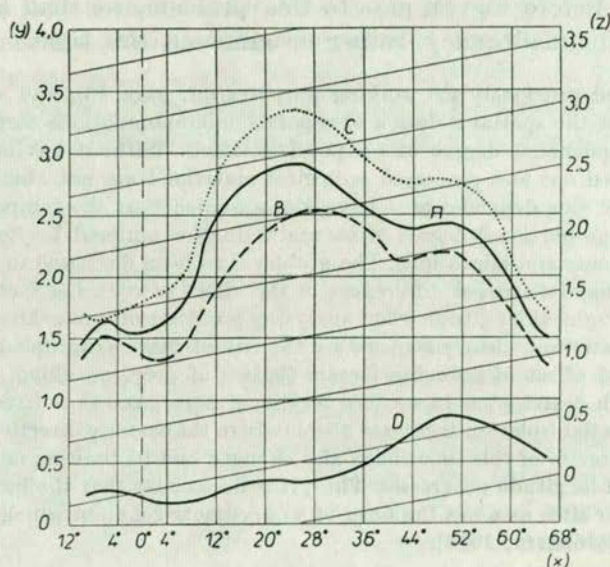
Graph 13. Percentage distribution of breeding sites situated in different ecological zones — the parallel cross-section (the XIXth and the XXth centuries treated jointly; movable means).  $x$  — geographical longitude,  $y$  — number of sites in per cent within separate classes of geographical longitude,  $A$  — breeding sites in the optimum zone,  $B$  — sites in the transitional (suboptimum) zone,  $C$  — sites in the extreme zone.

as far as ecological aspects are concerned, between separate sites — the transitional zone (suboptimum) does not comprise there even 10 % of sites, while the optimum zone reached up to 40 %. This can be explained by the specific character of the species synanthropization. In the case of sites where the species was well adapted to the transformed environment it maintained itself on a stabilized level, particularly recently. A high per cent recorded in the extreme zone indicates intensive transformation of the environment by man. The process of transformation is spread out in time and occurs quite specifically — the crux of the matter seems to be here the balance of relations in the new biocenosis, formation of the trophic base, etc. In this transitional period the species can not display traits of stabilization while getting adapted to new possibilities.



Inside the range the optimum and suboptimum zones exceed considerably the level of the extreme zone and depending on the local situation they compensate each other. In the center of the range (between the lines of 24° and 32° of eastern longitude) the optimum zone reaches its peak and comprises nearly 50 % of all the breeding sites.

The percentage relation of sites in separate zones at the eastern end of the range is very characteristic. The optimum zone there is gradually overtaken by the suboptimum one, while the latter suffers the encroachments of the extre-



Graph 14. Degree of the species existence prosperity in the parallel cross-section of the range (the XIXth and the XXth centuries treated jointly).  $x$  — geographical longitude,  $y$  — scale of index  $Z_{pe}$  in prexes,  $z$  — scale of index  $Z_{pe}$  in prexes corrected in relation to geographical longitude,  $A$  — distribution of  $Z_{pe}$  in relation to the species numbers,  $B$  — distribution of  $Z_{pe}$  in relation to breeding sites,  $C$  — distribution of  $Z_{pe}$  in relation to their maximum deviations,  $D$  — distribution of  $Z_{pe}$  in relation to minimum values of this index.

me zone. This indicates the presence of a gradual and directionally fixed ecological degradation of the environment from the optimum to pessimum conditions. As I have shown previously (JÓZEFIK, 1969b) the species regressed in this respect at the turn of the century. And thus the course of curves presenting the percentage relation of breeding sites in separate zones, beside giving a statical picture of the species situation along the parallel axis of the range, reveals also dynamical processes connected with changes in the biocentric composition of the environment and with the adaptative plasticity of the Squacco Heron.

The existence prosperity of *A. ralloides* in the parallel cross-section is il-

illustrated by graph 14. The movable mean of the minimum values of index  $Z_{pe}$  expressed in *prexes* (curve D) rises gradually from west to east. This is connected with an increase in the critical values of not only regular sites (cf. JÓZEFIK, 1970), but also of sporadic ones. I have determined previously (cf. page 29) the level of *O prex* as the critical value of index  $Z_{pe}$ . As curve D (graph 14) is a movable mean, its value must reach above the level of *O prex*. A general increase in its value towards the east forces us again (cf. page 33) to reassess the adequacy of the absolute value of the *prex* scale in respect of the real ecological situation of micropopulations habitating at different geographical longitudes. Before we can pass to this problem, we shall have to analyse the reasons of this inadequacy, rather insignificant this time.

I have assumed previously for working purposes (cf. page 15), and without an analytical approach, that the spatial isolation of separate micropopulations corresponds approximately to the proportional degree of temporal isolation. Without having at my disposal any properly worked out and processed ecological material I am not able to determine the functional aspect of this dependence. I have also assumed that the temporal isolation corresponds with the proportional degree of natural reduction suffered by flocks in the course of nomadic movements and migrations. The problem has been discussed in a general way for the entire area. I have discussed differences in the effect of reducing factors in relation to the degree of geographical longitude when analysing problems of synanthropization (JÓZEFIK, 1970). This differentiation, clearly stressed by the rise of curve D (graph 14) consists in the increasing eastward effect of reducing factors (beasts of prey, poaching — we are mainly concerned here with desert areas in western regions of Asia). And thus, irrespective of whether the degree of spatial isolation increases absolutely in the easterly direction (JÓZEFIK 1970), the qualitative character of this isolation is also changed and its limiting action is augmented as the geographical longitude progresses. Thus, it is no wonder that the increase in the critical values of regular sites assumes the form of a curvilinear function which has already been discussed at large (JÓZEFIK, 1970).

A number of important conclusions can now be drawn: a) the limiting action of the environment capacity and of the degree of isolation are clearly differentiated in the parallel cross-section. The environment capacity acquires dominating importance in its limiting action in western regions of the range, while the impact of the degree of isolation is more marked as a limiting force in eastern regions. b) The levelling off of the limiting impact of isolation is a result of the positive action of the anthropogenic factor (specific protection over the entire annual cycle). In recent decades all over western Europe, and particularly in the valley of the Rhône in the region of Swiss lakes, the observers recorded in late spring separate *A. ralloides* flocks most probably in the process of searching for new breeding sites (GÉROUDET, 1958, 1960, 1961). This phenomenon would confirm all along the conclusions put forward above. A more remote and indirect proof of this regularity is the existence of isolated sites of *Platalea leucorodia* L. and *Nycticorax nycticorax* (L.) in Holland (VOOUS, 1960). c) The levelling off of the limiting impact of isolation is one of the indis-

pensable conditions for the occurrence of synanthropization. In future, in the conditions of a complete elimination of the limiting action of isolation by man, it will be possible to maintain even small isolated populations of migratory species. What the consequences are bound to be, we can foresee, to a certain extent, even now (e. g. sharp intensification of divergency processes).

Correction  $Z_{pe}$  in the parallel cross-section should thus include a qualitative differentiation of the limiting impact of spatial isolation. The difference between the critical value of index  $Z_{pe}$  at the western end and at the eastern one amounts to 0.7 *prex* (in the west to 0.1 *prex*, while in the east to 0.8 *prex*). Thus the correction has not only theoretical but also practical significance. It would assume more importance if we analysed the degree of existence prosperity in the actual situation of the species, i. e. with the impact of isolation in the western regions neutralized by protective undertakings in the last decade. A nomogram of this correction has been taken into account in graph 14 — scale  $z$  and skew lines connected with this scale.

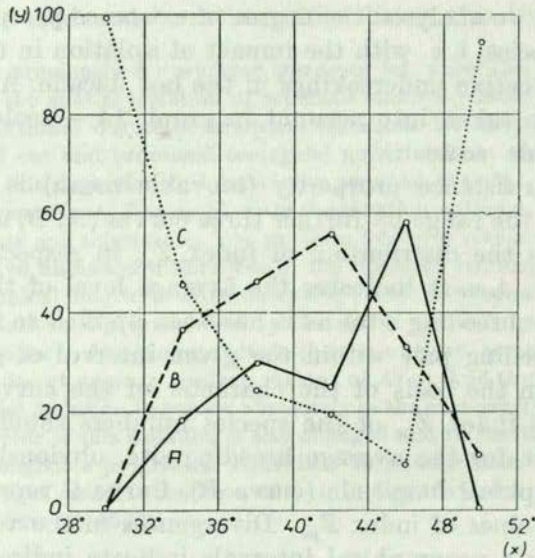
The degree of existence prosperity (movable mean) is represented along the parallel axis of the range by further three curves (*A*, *B*, and *C* — graph 14). Curve *A* illustrates the distribution of index  $Z_{pe}$  in respect of the numerical state of the species, i. e. it indicates the average level of this measure not in relation to separate breeding sites as it has been applied so far, but in relation to the average breeding pair within the given interval of geographical longitude. Concluding on the basis of the character of the curve of concentration (cf. JÓZEFIK, 1970) index  $Z_{pe}$  of the species numbers should exceed the level of  $Z_{pe}$  characteristic for the average breeding site, obviously within the same intervals of geographical longitude (curve *B*). Curve *C* represents the average of the maximum values of index  $Z_{pe}$ . Divergences in the values of the curves discussed in separate geographical intervals indicate indirectly and relatively the level of the degree of concentration (cf. JÓZEFIK, 1970).

We can also assume that the character of the distribution of curves *A*, *B*, and *C* is sufficiently evident and we shall not discuss it here at large. However we should concentrate our attention on the divergence between curves *A*, *B*, and *C*, on the one hand, and curve *D* on the other, as it gives an idea of the potential possibility of the species existence in the case of a permanent deterioration of conditions under which this species exists. These possibilities are more limited in the eastern regions of the range.

The level of index  $Z_{pe} = 2$  *prexes* forms a limit below which the balance birth rate — mortality rate becomes negative. This level (after taking into account the correction) comprises western, central, and some eastern regions of the range. Following the level of curve *B* it reaches the 52° line of eastern longitude, i. e. almost exactly up to the meridian marking out the eastern boundary of the range in the XXth century. This fact requires no commentaries.

### Zones in the meridian cross-section of the range

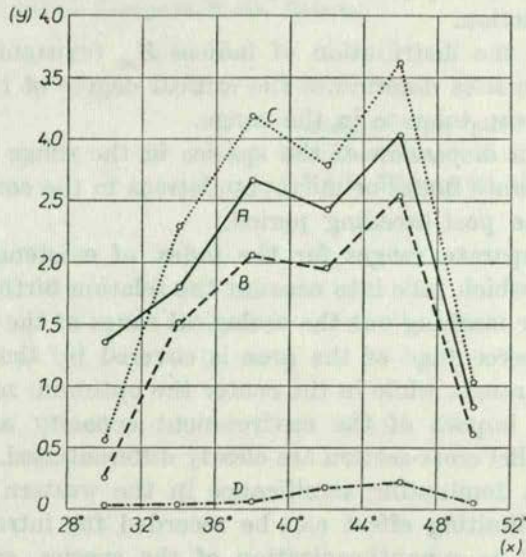
The composition of ecological zones in the meridian cross-section of the range (Graph 15) does not require any further explanations. The compensation of the optimum zone by the transitional one is most effective in mountainous and highland areas. The vertical distribution of the species is here highly differentiated (e. g. certain breeding sites in the Transcaucasian region are situated at an altitude higher than 1,000 meters above sea level). At the southern as well as at the northern ends of the range there occurs a classical and very sudden disappearance of the optimum and transitional zones (suboptimum) under the impact of the encroachments of the extreme zone. The meridian distribution of index  $Z_{pe}$  (Graph 16) is also so simple and evident that I shall limit here myself to a discussion concern-



Graph 15. Percentage distribution of breeding sites situated in different ecological zones — the meridian cross-section (the XIXth and the XXth centuries treated jointly).  $x$  — geographical latitude,  $y$  — number of sites in per cent within separate classes of geographical latitude,  $A$  — sites in the optimum zone,  $B$  — sites in the transitional (suboptimum) zone,  $C$  — sites in the extreme zone.

ing the average value of index  $Z_{pe}$  for the critical values of all the breeding sites in the range (curve  $D$ ). Along a long section it does not differ much from the zero level (28°–40°). Curve  $D$  rises maximally up to 0.2 *prex* in the belt of the maximum concentration of the species. At such small differences the problem of the meridian correction of index  $Z_{pe}$  has no practical significance — the character of isolation impact is very uniform in the meridian cross-section. We should also take into account that average values of index  $Z_{pe}$  calculated separately for the species numbers (curve  $A$ ), and separately for breeding sites (curve  $B$ ), and the average maximum values of index  $Z_{pe}$  calculated for the latitudes of 36°–40° are very high. A comparison with the previously discussed graphs inclines us to suppose that the environment capacity assumes particular significance in the southern regions of the range. This capacity is, in turn, strongly limited by the impact of human activity (cf. JÓZEFIK, 1970). This might suggest a practical conclusion that the species under investigation requires at present that energetic protective activities are undertaken at the southern end of the

palaearctic part of the range which would have as their purpose to protect its environment and the species itself over the entire annual circle. Most probably the species is still being reduced by man, particularly so in regions outside the boundaries of Europe which ought to be considered as a main stumbling block on the way to its successful synanthropization. The initiation of protective activities in Turkey has already taken place. Let us earnestly hope that the same will soon happen in Tunisia, Algeria and Morocco in the nearest future.



Graph 16. Degree of the species existence prosperity in the meridian cross-section (the XIXth and the XXth centuries treated jointly).  $x$  — geographical latitude,  $y$  — scale of index  $Z_{pe}$  in *prexes*,  $A$  — distribution of  $Z_{pe}$  in relation to the species numbers,  $B$  — distribution of  $Z_{pe}$  in relation to breeding sites,  $C$  — in relation to maximum values of  $Z_{pe}$ ,  $D$  — in relation to minimum values of  $Z_{pe}$ .

#### CONCLUSIONS

1) Intraspecific isolation (temporal-spatial isolation between separate flocks, micropopulations), beside its speciological aspect, ought to be treated as one of real ecological factors, limiting in their character, affect decisively the formation of ecological zones as well as the area (its shape) of the range.

2) Spatial isolation, as one the more important limiting factors, exerts its impact on the social species distributed in an island-like pattern over the range. The mechanism of the impact effected in the post breeding period assumes the form of temporal isolation. An increase in spatial isolation in an arithmetic progress coincides with an increase in its impact according to an exponential function.

3) The existence prosperity of a given micropopulation, outside the combination of local ecological conditions, depends on the degree of isolation. The critical values of the degree of existence prosperity limit the spatial distribution of the species. An index of the degree of existence prosperity can be the

ratio between the size of breeding sites (micropopulations) and the degree of their isolation in respect of other breeding sites in the nearest vicinity (average distances).

4) Under the impact of the arithmetically increasing isolation, the degree of existence prosperity enjoyed by separate micropopulations is lowered in a logarithmical function.

5) The mode of the distribution of indices  $Z_{pe}$  (existence prosperity) for regular and sporadic sites determines the critical degree of the maximum dispersion the species can tolerate in the range.

6) The maximum dispersion of the species in the range is limited by the survival rate of separate flocks or micropopulations in the course of their absolute isolation in the post-breeding period.

7) Izolines of separate ranges for the index of existence prosperity, the so-called izoprexes, which take into account the relation birth rate — mortality rate, can be used for marking out the ecological zones of the range.

8) The largest percentage of the area is covered by the extreme zone at the outskirts of the range, while in the center the optimum zone is dominating.

9) The limiting impact of the environment capacity and the degree of isolation in the parallel cross-section are clearly differentiated. The environment capacity assumes a dominating significance in the western regions, while in the east a greater limiting effect can be recorded for intraspecific isolation.

10) Such factors as synanthropization of the species, specific protection, reduction of predators, counteract the limiting impact of isolation, lower the critical values of the parameters of the distribution structure.

11) The limiting impact of isolation in the meridian cross-section of the range is more prominent in the northern regions. In the south the environment capacity assumes the role of the more limiting factor.

---

#### REFERENCES

- CHAPMAN R. N. 1931. Animal ecology. New York.
- GÉROUDET P. 1958. Garzettes, Crabiers, Echasses et Guifettes moustacs au printemps 1958 en Suisse. Nos Oiseaux, Neuchâtel, 263: 49-52.
- GÉROUDET P. 1960. Les migrations du printemps 1959. Nos Oiseaux, Neuchâtel, 269: 230-233
- GÉROUDET P. 1961. Les migrations du printemps 1960. Nos Oiseaux, Neuchâtel, 275: 53-55.
- HUXLEY J. S. 1945. Evolution, the modern synthesis. London.
- JÓZEFIK M. 1969a. Studies on the Squacco Heron, *Ardeola ralloides* (SCOP.). Part I. History of research. Acta orn., Warszawa, 11, 6: 103-134.
- JÓZEFIK M. 1969b. Studies on the Squacco Heron, *Ardeola ralloides* (SCOP.). Part II. Secular changes in the numbers and distribution in the Palearctic range. Acta orn., Warszawa, 11, 7: 135-262.
- JÓZEFIK M. 1970a. Studies on the Squacco Heron, *Ardeola ralloides* (SCOP.). Part III. Geographical variability in the critical and mean micropopulation size. Acta orn., Warszawa, 12, 3: 57-102.

- JÓZEFIK M. 1970b. Studies on the Squacco Heron, *Ardeola ralloides* (SCOP.). Part IV. Spatial organization and mechanisms integrating the species. Acta orn., Warszawa, 12, 10: 393-444.
- MAYR E. 1965. Animal species and evolution. Cambridge, Mass.
- PONUGAYEVA A. G. 1951. Izučeniye stadnykh reflektsov na teploobmen kak metod ekologo-fiziologičeskoj charakteristiki mlekopitajuščich. Sborn. „II Ekol. konf. cast' 3”, Kijev.
- VOOUS K. H. 1960. Atlas of European Birds. Nelson.

---

Accepted for publication: 24 III 1970.  
 Author's address: Instytut Zoologiczny  
 PAN, Warszawa, ul. Wilcza 64, Poland.

## Appendix I.

Table of corrections for calculating index  $Z_{pe}$  according to formula (4) (explanations cf. page 18).

$x$	10	20	30	40	50	60	70	80	90	100	200	300	400	500	600	700	800	900	1000	$Z$
$b$	0.72	0.66	0.60	0.57	0.56	0.57	0.57	0.58	0.68	0.97	1.42	1.77								10.00
$c$	+0.003	0.006	0.009	0.010	0.012	0.015	0.016	0.017	0.025	0.040	0.061	0.075								5.00
$b$	0.69	0.60	0.51	0.47	0.44	0.42	0.41	0.41	0.43	0.57	0.81	1.02	1.13							1.00
$c$	+0.026	0.028	0.032	0.040	0.038	0.038	0.040	0.042	0.050	0.082	0.132	0.172	0.186							0.10
$b$	0.56	0.46	0.35	0.27	0.25	0.21	0.20	0.18	0.16	0.15	0.16	0.20	0.28	0.59	0.97					0.01
$c$		-0.69	-0.58	-0.53	-0.47	-0.43	-0.39	-0.36	-0.32	-0.25	-0.18	-0.14	-0.10	-0.02	+0.27	+0.60				0.01
$b$		1.15	0.93	0.80	0.72	0.66	0.60	0.56	0.50	0.41	0.33	0.30	0.30	0.30	0.32	0.37	0.46	0.81		0.01
$c$				-52.4	-43.4	-38.0	-32.1	-27.9	-22.2	-13.9	-8.0	-5.6	-4.1	-3.4	-2.8	-2.2	-0.9	+0.6		0.01
$b$				6.04	5.06	4.46	3.81	3.35	2.72	1.79	1.13	0.86	0.71	0.64	0.60	0.59	0.55	0.87		0.01



## Appendix II.

Characteristics of certain features of *A. ralloides* breeding range (Palearctic part).

Explanations: 1 — name of the region of the range, 2–5 — directed distances, 6 — average distances in separate centuries, 7 — average size of sites, 8 — mean value of average distances for the last two centuries treated jointly, 9 — average value of index  $Z_{pe}$  for the last two centuries treated jointly (the upper number in prexes, in parenthesis one — nonlogarithmic form of  $Z_{pe}$ ).

Century	XIXth		XXth		XIXth		XXth		XIXth		XXth	
1	12°W 40° N	Iberian Peninsula (Portugal)	8°W 40° N	8°W 40° N	Iberian Peninsula (Spain)	4°W 40° N	4°W 40° N	Iberian Peninsula (Spain)	0° 40° N			
2	—	(WN)	—	—	(WN)	325	—	(WN)	—			
3	—	(NE)	1145	1290	(NE)	375	—	(NE)	525			
4	—	(ES)	335	260	(ES)	195	—	(ES)	915			
5	—	(SW)	—	370	(SW)	370	—	(SW)	375			
6	—		740	640		316	—		605			
7	—		5	35		75	—		5			
8	—		—	473			—					
9	12°W 36° N	0.0569 <i>prex</i> (0.0114)	8°W 36° N	8°W 36° N	1.6439 <i>prex</i> (0.4405)	4°W 36° N	4°W 36° N	0.1398 <i>prex</i> (0.0138)	0° 36° N			
1	8°W 36° N	North Western Africa (Morocco)	4°W 36° N	4°E 40° N	Northern Africa (Algeria)	8°E 40° N	4°E 36° N	Northern Africa (Algeria)	8°E 36° N			
2	265	(WN)	230	1160	(WN)	480	610	(WN)	485			
3	105	(NE)	240	205	(NE)	205	150	(NE)	120			
4	—	(ES)	1080	140	(ES)	140	230	(ES)	1610			
5	140	(SW)	100	120	(SW)	120	1120	(SW)	1115			
6	149		253	406		236	528		832			
7	75		32	150		75	55		15			
8	—	201	—	321			680					
9	8°W 32° N	2.1408 <i>prex</i> (1.3852)	4°W 32° N	4°E 36° N	2.1781 <i>prex</i> (1.5075)	8°E 36° N	4°E 32° N	1.0314 <i>prex</i> (0.1075)	8°E 32° N			

(appendix II)

Century	XIXth			XXth			XIXth			XXth		
1	8°E 40°N	Northern Africa (Tunisia)	12°E 40°N	8°E 36°N	Northern Africa (Tunisia)	12°E 36°N	0° 40°N	Balearic Isles (Mallorca)	4°E 40°N			
2	265	(WN)	377	110	(WN)	120	—	(WN)	—			
3	475	(NE)	185	932	(NE)	330	—	(NE)	415			
4	127	(ES)	127	1090	(ES)	2310	—	(ES)	490			
5	152	(SW)	152	347	(SW)	305	—	(SW)	535			
6	254		210	617		766	—		480			
7	75		45	40		25	—		5			
8		235			693			—				
9	8°E 36°N	2.1370 <i>prex</i> (1.3713)	12°E 36°N	8°E 32°N	1.2081 <i>prex</i> (0.1615)	12°E 32°N	0° 36°N	0.2355 <i>prex</i> (0.0172)	4°E 36°N			
1	8°E 44°N	Sardinia	12°E 44°N	12°E 40°N	Sicily	16°E 40°N	24°E 36°N	Crete	28°E 36°N			
2	455	(WN)	—	—	(WN)	460	—	(WN)	500			
3	425	(NE)	—	—	(NE)	640	—	(NE)	320			
4	395	(ES)	—	—	(ES)	1140	—	(ES)	905			
5	440	(SW)	—	—	(SW)	290	—	(SW)	1410			
6	429		—	—		632	—		784			
7	5		—	—		5	—		5			
8		—	—	—	—	—	—	—	—			
9	8°E 40°N	0.2455 <i>prex</i> (0.0176)	12°E 40°N	12°E 36°N	0.1205 <i>prex</i> (0.0132)	16°E 36°N	24°E 32°N	0.0334 <i>prex</i> (0.0108)	28°E 32°N			

(appendix II)

Century	XIXth		XXth	XIXth		XXth	XIXth		XXth
1	4°E 48°N	France	8°E 48°N	4°E 44°N	France	8°E 44°N	8°E 48°N	Apenine Peninsula (Northern Italy)	12°E 48°N
2	—	(WN)	—	—	(WN)	240	308	(WN)	111
3	—	(NE)	910	—	(NE)	290	196	(NE)	214
4	—	(ES)	240	—	(ES)	645	127	(ES)	115
5	—	(SW)	225	—	(SW)	420	228	(SW)	153
6	—		458	—		399	215		148
7	—		5	—		20	11		12
8	—		—	—		—	180		—
9	4°E 44°N	0.2148 <i>prex</i> (0.0164)	8°E 44°N	4°E 40°N	0.9370 <i>prex</i> (0.0865)	8°E 40°N	8°E 44°N	1.3334 <i>prex</i> (0.2155)	12°E 44°N
1	12°E 44°N	Apenine Peninsula (Central Italy)	16°E 44°N	16°E 48°N	Hungary, Yugoslavia	20°E 48°N	16°E 44°N	Yugoslavia, Albania	20°E 44°N
2	—	(WN)	260	86	(WN)	67	98	(WN)	225
3	—	(NE)	385	89	(NE)	87	244	(NE)	175
4	—	(ES)	730	69	(ES)	67	125	(ES)	137
5	—	(SW)	460	186	(SW)	221	827	(SW)	597
6	—		459	111		117	323		308
7	—		15	222		70	35		52
8	—		—	—	109	—	303		—
9	12°E 40°N	0.5658 <i>prex</i> (0.0568)	16°E 40°N	16°E 44°N	3.0951 <i>prex</i> (12.4505)	20°E 44°N	16°E 40°N	1.8808 <i>prex</i> (0.7605)	20°E 40°N

(appendix II)

Century	XIXth		XXth		XIXth		XXth		XIXth		XXth	
1	20°E 52°N	Hungary	24°E 52°N	20°E 48°N	Hungary, Roumania, Yugoslavia	24°E 48°N	20°E 44°N	Yugoslavia, Bulgaria	24°E 44°N			
2	—	(WN)	—	61	(WN)	66	125	(WN)	169			
3	420	(NE)	700	117	(NE)	128	223	(NE)	231			
4	70	(ES)	70	89	(ES)	94	227	(ES)	186			
5	30	(SW)	75	79	(SW)	94	275	(SW)	262			
6	173		282	87		92	237		223			
7	15		15	64		25	80		45			
8		227			90			212				
9	20°E 48°N	1.0406 <i>prex</i> (0.1098)	24°E 48°N	20°E 44°N	3.1010 <i>prex</i> (12.6217)	24°E 44°N	20°E 40°N	2.1872 <i>prex</i> (1.5397)	24°E 40°N			
1	20°E 40°N	Greece	24°E 40°N	24°E 48°N	Roumania, Bulgaria	28°E 48°N	24°E 44°N	Bulgaria	28°E 44°N			
2	305	(WN)	305	198	(WN)	174	110	(WN)	154			
3	280	(NE)	280	54	(NE)	41	80	(NE)	217			
4	620	(ES)	500	292	(ES)	112	560	(ES)	182			
5	1040	(SW)	760	58	(SW)	62	410	(SW)	265			
6	561		461	150		97	290		512			
7	15		15	45		35	30		13			
8		511			124			247				
9	20°E 36°N	0.7348 <i>prex</i> (0.0543)	24°E 36°N	24°E 44°N	2.2748 <i>prex</i> (1.8838)	28°E 44°N	24°E 40°N	1.1789 <i>prex</i> (0.1515)	28°E 40°N			

(appendix II)

Century	XIXth			XXth			XIXth			XXth		
1	24°E 52°N	USSR (the Ukraine)	28°E 52°N	28°E 52°N	USSR (the Ukraine)	32°E 52°N	32°E 52°N	USSR (the Ukraine)	36°E 52°N			
2	637	(WN)	—	—	(WN)	—	165	(WN)	—			
3	410	(NE)	—	—	(NE)	—	1420	(NE)	—			
4	270	(ES)	—	105	(ES)	355	267	(ES)	—			
5	520	(SW)	—	350	(SW)	350	222	(SW)	—			
6	480	—	—	227	—	352	518	—	—			
7	5	—	—	5	—	5	10	—	—			
8	—	—	—	290	—	—	—	—	—			
9	24°E 48°N	0.2121 <i>prex</i> (0.0163)	28°E 48°N	28°E 48°N	0.2405 <i>prex</i> (0.0174)	32°E 48°N	32°E 48°N	0.6483 <i>prex</i> (0.0445)	36°E 48°N			
1	28°E 48°N	USSR (the Ukraine, Moldavia), Roumania	32°E 48°N	32°E 48°N	USSR (the Ukraine)	36°E 48°N	36°E 48°N	USSR (Krasnodar Region)	40°E 48°N			
2	116	(WN)	198	275	(WN)	318	324	(WN)	323			
3	128	(NE)	104	159	(NE)	170	294	(NE)	118			
4	186	(ES)	148	344	(ES)	344	432	(ES)	538			
5	74	(SW)	61	210	(SW)	210	457	(SW)	553			
6	128	—	155	232	—	268	389	—	374			
7	306	—	152	111	—	96	59	—	55			
8	—	127	—	—	253	—	—	379	—			
9	28°E 44°N	3.1701 <i>prex</i> (15.1447)	32°E 44°N	32°E 44°N	2.3872 <i>prex</i> (2.4393)	36°E 44°N	36°E 44°N	1.9044 <i>prex</i> (0.8025)	40°E 44°N			

(appendix II)

Century	XIXth		XXth		XIXth		XXth		XIXth		XXth	
1	28°E 44°N	Turkey	32°E 44°N	24°E 40°N	Turkey	28°E 40°N	32°E 40°N	Turkey	36°E 40°N			
2	490	(WN)	275	357	(WN)	—		(WN)	215			
3	1145	(NE)	1145	332	(NE)	—	539	(NE)	541			
4	325	(ES)	325	347	(ES)	—	261	(ES)	261			
5	215	(SW)	820	1130	(SW)	—	589	(SW)	598			
6	544		640	544		—	401		403			
7	200		150	25		—	15		11			
8		592			—			402				
9	28°E 40°N	1.9340 <i>prex</i> (0.8591)	32°E 40°N	24°E 36°N	1.3729 <i>prex</i> (0.2360)	28°E 36°N	32°E 36°N	0.7986 <i>prex</i> (0.0629)	36°N 36°N			
1	36°E 40°N	Turkey	40°E 40°N	32°E 36°N	Israel	36°E 36°N	32°E 32°N	Israel	36°E 32°N			
2	90	(WN)	90	535	(WN)	535	530	(WN)	530			
3	720	(NE)	720	350	(NE)	350	60	(NE)	60			
4	760	(ES)	760	1140	(ES)	1140	1150	(ES)	1150			
5	100	(SW)	100	120	(SW)	120	630	(SW)	1750			
6	417		417	536		536	592		872			
7	75		75	5		5	15		15			
8		417			536			732				
9	36°E 36°N	1.8032 <i>prex</i> (0.6357)	40°E 40°E	32°E 32°E	0.1643 <i>prex</i> (0.0146)	36°E 32°N	32°E 28°N	0.5751 <i>prex</i> (0.0376)	36°E 28°N			

(appendix II)

Century	XIXth		XXth	XIXth		XXth	XIXth		XXth
1	40°E 48°N	USSR (Krasnodar Region)	44°E 48°N	44°E 48°N	USSR (Caspian Plain)	48°E 48°N	48°E 48°N	USSR (Caspian Plain)	52°E 48°N
2	115	(WN)	450	445	(WN)	1080	110	(WN)	215
3	330	(NE)	1030	300	(NE)	50	358	(NE)	358
4	590	(ES)	590	332	(ES)	750	750	(ES)	750
5	255	(SW)	255	333	(SW)	230	53	(SW)	53
6	322		581	363		527	317		344
7	100		75	233		100	233		66
8		451			441			331	
9	40°E 44°N	1.7994 <i>prex</i> (0.6392)	44°E 44°N	44°E 44°N	2.6207 <i>prex</i> (4.1766)	48°E 44°N	48°E 44°N	2.4795 <i>prex</i> (3.0173)	52°E 44°N
1	52°E 48°N	USSR (Caspian Plain)	56°E 48°N	40°E 44°N	USSR (Transcaucasian region), Turkey	44°E 44°N	44°E 44°N	USSR (Dagestan, Transcaucasian region)	48°E 44°N
2	305	(WN)	1720	427	(WN)	427	152	(WN)	174
3	—	(NE)	—	187	(NE)	187	223	(NE)	205
4	370	(ES)	790	128	(ES)	128	106	(ES)	100
5	615	(SW)	270	670	(SW)	670	241	(SW)	221
6	328		926	358		358	180		176
7	212		100	18		18	117		70
8		678			358			178	
9	52°E 44°N	2.0492 <i>prex</i> (1.1200)	56°E 44°N	40°E 44°N	1.4255 <i>prex</i> (0.2664)	44°E 44°N	44°E 40°N	2.6101 <i>prex</i> (4.0750)	48°E 40°N

(appendix II)

Century	XIXth		XXth	XIXth		XXth	XIXth		XXth
1	48°E 44°N	USSR (Transcaucasian region)	52°E 44°N	44°E 40°N	USSR (Transcaucasian region), Iran	48°E 40°N	48°E 40°N	USSR (Transcaucasian region), Iran	52°E 40°N
2	97	(WN)	97	35	(WN)	35	65	(WN)	65
3	360	(NE)	360	95	(NE)	95	224	(NE)	256
4	55	(ES)	62	192	(ES)	192	288	(ES)	347
5	162	(SW)	162	1100	(SW)	1100	463	(SW)	534
6	169		170	355		355	264		305
7	100		80	100		92	434		147
8		169			355			280	
9	48°E 40°N	2.2815 <i>prex</i> (1.9578)	52°E 40°N	44°E 36°N	2.1232 <i>prex</i> (1.3286)	48°E 36°N	48°E 36°N	2.8535 <i>prex</i> (7.1387)	52°E 36°N
1	52°E 40°N	USSR (Turkmenia)	56°E 40°N	44°E 36°N	Iraq	48°E 36°N	44°E 32°N	Iraq, Kuwait	48°E 32°N
2	977	(WN)	1015	605	(WN)	605	180	(WN)	180
3	367	(NE)	367	625	(NE)	625	576	(NE)	576
4	522	(ES)	977	240	(ES)	240	165	(ES)	165
5	495	(SW)	495	875	(SW)	875	1160	(SW)	1160
6	590		713	586		586	559		559
7	15		15	5		5	5		5
8		652			586			559	
9	52°E 36°N	0.6532 <i>prex</i> (0.0450)	56°E 36°N	44°E 32°N	0.1238 <i>prex</i> (0.0133)	48°E 32°N	44°E 28°N	0.0969 <i>prex</i> (0.0125)	48°E 28°N



## (appendix II)

Century	XIXth		XXth	XIXth	XXth	XIXth	XXth		
1	56°E 44°N	USSR (Uzbekistan)	60°E 44°N	60°E 40°N	USSR (Turkmenia)	64°E 40°N	60°E 36°N	USSR (Turkmenia)	64°E 36°N
2	355	(WN)	790	407	(WN)	—	135	(WN)	—
3	552	(NE)	585	104	(NE)	—	280	(NE)	—
4	250	(ES)	430	166	(ES)	—	—	(ES)	—
5	615	(SW)	595	603	(SW)	—	1475	(SW)	—
6	443		600	319		—	472		—
7	20		5	40		—	15		—
8		600			—				—
9	56°E 40°N	1.2271 <i>prex</i> (0.1687)	60°E 40°N	60°E 36°N	1.8190 <i>prex</i> (0.6592)	64°E 36°N	60°E 32°N	0.7379 <i>prex</i> (0.0547)	64°E 32°N
1	64°E 48°N	USSR (Kazachstan)	68°E 48°N	64°E 40°N	USSR (Turkmenia, Uzbekistan)	68°E 40°N			
2	975	(WN)	1065	258	(WN)	595			
3	—	(NE)	—	622	(NE)	565			
4	—	(ES)	—	177	(ES)	350			
5	520	(SW)	585	187	(SW)	1267			
6	747		825	288		897			
7	15		15	28		25			
8		786			502				
9	64°E 44°N	0.5403 <i>prex</i> (0.0347)	68°E 44°N	64°E 36°N	1.3306 <i>prex</i> (0.2141)	68°E 36°N			

## STRESZCZENIE

W części V cyklu poświęconego badaniom nad strukturą rozmieszczenia przestrzennego czapli modronosej, *Ardeola ralloides* (SCOP.) autor koncentruje uwagę na kluczowym zagadnieniu tego problemu — mechanizmach oddziaływania izolacji wewnątrzgatunkowej (międzymikropopulacyjnej) i jej ekologiczno-ewolucyjnych konsekwencjach. Izolacja wewnątrzgatunkowa jest więc traktowana jako: a) realny ekologiczny czynnik ograniczający i wpływający na kształtowanie się stref ekologicznych zasięgu, b) czynnik ewolucyjny odgrywający istotną rolę w procesach dywergencyjnych.

Wychodząc z udokumentowanych w poprzednich częściach cyklu współzależności stopnia izolacji oraz wielkości i stopnia ustabilizowania mikropopulacji, dla określenia jej sytuacji biologicznej, a ściślej ekologicznego prosperity, autor wprowadza tzw. „wskaźnik powodzenia egzystencji”  $Z_{pe}$  (wzory (1)–(5) na stronach: 2, 18, 29). Precyzując jego definicję, określa go autor jako ogólny względny, w sensie porównywalności jego wartości w obrębie jednego tylko gatunku, miernik stopnia ustabilizowania i ostatecznego bilansu przebiegu wszelkich przejawów życiowych określonej mikropopulacji zasiedlającej dane stanowisko lęgowe w układzie warunków oferowanych przez środowisko. Wskaźnik ten, po wprowadzeniu poprawki na krzywoliniowość współzależności jego elementów składowych (str. 18, appendix I) i przetransponowaniu go w postać logarytmiczną proponuje autor stosować jako dogodny miernik stopnia powodzenia egzystencji poszczególnych mikropopulacji w aspekcie badań porównawczych różnych części zasięgu. Podstawową jednostką miernika jest 1 *prex* (od łac. (*pr*) *osperitas* (*ex*) *istentiae*). Dokonywana przy jego zastosowaniu ocena sytuacji biologicznej mikropopulacji, populacji czy większej części gatunku uwzględniać musi co najmniej roczne lub kilkuletnie odcinki czasu.

W dalszej części pracy autor analizuje zmienność parametrów składowych  $Z_{pe}$ , teoretyczny model oscylacji jego wartości, jak również dokonuje ekologicznej oceny zakresu jego zmienności. Wyznacza też wartość progową  $Z_{pe}$ , którą stanowi dominanta rozkładu ogólnego tego wskaźnika. Na podstawie znanych wartości progowych wielkości mikropopulacji oraz wskaźnika  $Z_{pe}$  autor oblicza wartość progową maksymalnie tolerowanego przez gatunek stopnia izolacji, tj. próg maksymalnego w zasięgu lęgowym rozproszenia.

Na podstawie danych: a) wstępnego ekologicznego wartościowania rozkładu  $Z_{pe}$ , b) analizy krzywej koncentracji gatunku, c) analizy ekologicznej poszczególnych stanowisk lęgowych w palearktycznej części zasięgu autor oblicza niektóre charakterystyki strefy ekstremalnej i optymalnej zasięgu *A. ralloides*. W strefie ekstremalnej rozmieszczonych jest średnio 53,58 % stanowisk lęgowych (głównie sporadycznych i niestabilizowanych) oraz tylko 6,72 % liczebności gatunku.

Istotnym momentem omawianym w kolejnym rozdziale jest analiza współzależności podstawowych parametrów rozmieszczenia przestrzennego gatunku, rozkłady których zestawiono na zbiorczym wykresie (wykr. 5). Podane są też obszary krytycznych wartości niektórych parametrów rozmieszczenia.

W rozdziale dotyczącym biologicznych mechanizmów oddziaływania izolacji autor omawia zagadnienie stopnia redukcji poszczególnych mikropopulacji w zależności od wielkości ich izolacji względem siebie — redukcja (ograniczający wpływ izolacji) wzrasta wykładniczo w stosunku do arytmetycznego zwiększania się stopnia izolacji. Integracja małych stad z odległych względem siebie stanowisk w okresie pozalegowym ma więc dla przeżywalności gatunku znaczenie pierwszorzędne. Szanse łączenia się małych stad, bądź pojedynczych osobników, w miarę wzrastania dystansów między stanowiskami lęgowymi gwałtownie maleją. Maksymalne rozproszenie gatunku w zasięgu, limitowane jest więc przez przeżywalność poszczególnych stad względnie mikropopulacji podczas ich absolutnej izolacji w okresie pozalegowym. Pod wpływem arytmetycznie narastającej izolacji obniża się w funkcji logarytmicznej stopień powodzenia egzystencji poszczególnych mikropopulacji. Przedstawione zależności autor ujmuje w postać równań wykładniczych.

W osobnym rozdziale przeprowadza autor dyskusję konfrontując pojęcia: „powodzenie egzystencji”, „przeżywalność”, „opór środowiska”. Wprowadzenie terminu „powodzenie egzystencji” podyktowane zostało koniecznością uwzględnienia, prócz sfery „klasycznych” środowiskowych czynników ograniczających, nowo odkrytego czynnika — ograniczającego wykładniczo wpływu izolacji międzymikropopulacyjnej (wewnątrzgatunkowej), a który jak udowadnia autor, w znacznej mierze kształtuje wymiar przestrzenny gatunku.

W rozdziale poświęconym gradacji ekologicznej poszczególnych poziomów wskaźnika  $Z_{pe}$  autor omawiając relację: rozrodczość — śmiertelność podkreśla, że wpływ izolacji na wielkość mikropopulacji przy wysokich wartościach tego wskaźnika sprowadza się niemal do zera. Przy niskich wartościach wpływ ten potężniejąc urasta do rozmiarów bariery ekologicznej. Autor udokumentował że: a) w mikropopulacjach charakteryzujących się  $Z_{pe} > 5$  rozrodczość znacznie przewyższa śmiertelność, pod wpływem przegęszczenia odpływa z nich stale część osobników do stanowisk o niższych wartościach  $Z_{pe}$ ; b) przy  $1 \leq Z_{pe} \leq 5$  rozrodczość — śmiertelność utrzymują się w stanie równowagi dynamicznej, odpływ — przyływ osobników równoważą się; c) przy  $Z_{pe} < 1$  bilans: rozrodczość — śmiertelność jest stale ujemny, stanowiska rozmieszczone w znacznej mierze w strefie ekstremalnej mogą utrzymywać się jedynie w warunkach stałego dopływu nowych osobników ze strefy optymalnej (przegęszczenie).

Posługując się wskaźnikiem  $Z_{pe}$  w przetransponowanej, logarytmicznej postaci, autor dokonuje charakterystyki stref ekologicznych zasięgu. Strefę ekstremalną charakteryzuje zakres  $Z_{pe} = 0-1,7$  *prex*, strefę przejściową (suboptymalną) = 1,7-2,0 *prex*, strefę optymalną = 2,0-4,0 *prex*. Posługując się skalą

prex'ów wyznaczył on w obrębie zasięgu tzw. obszary izoprexów (mapa 1), które dają obraz ekologicznej charakterystyki poszczególnych stref w ich układzie geograficznym.

Na podstawie profilowej analizy rozkładów  $Z_{pe}$  autor stwierdza, że w zachodnich regionach zasięgu strefa ekstremalna obejmuje większość stanowisk, tam też najintensywniej przebiega przekształcanie przez człowieka środowiska i najbardziej zaawansowany jest proces synantropizacji czapli modronosej. Dominującym czynnikiem ograniczającym na zachodzie jest wydolność środowiska. W kierunku wschodnim coraz większego znaczenia, jako czynnik limitujący, nabiera izolacja międzymikropopulacyjna. Wraz z postępującą synantropizacją ograniczający wpływ izolacji znacznie maleje. Według prognozy autora, w przyszłości w warunkach znacznego zredukowania przez człowieka ograniczającego wpływu izolacji (ograniczenie wrogów naturalnych, ochrona, synantropizacja) możliwe będzie utrzymanie nawet małych izolowanych populacji socjalnych gatunków wędrownych. Ewolucyjne konsekwencje tego stanu znajdą odbicie w intensyfikacji procesów dywergencyjnych. Wśród gatunków socjalnych zaniknie prawdopodobnie instynkt stadny — nastąpi gnieźdzenie się w pojedynczych parach, znacznie zmaleje wartość progowa rozproszenia, rozszerzą się zasięgi geograficzne.

W profilu południkowym oddziaływanie izolacji ma charakter bardziej wyrównany, jakkolwiek w północnych regionach jest ono bardziej uwidocznione, niż w południowych, gdzie z kolei wyraźnie wzrasta ograniczający wpływ wydolności środowiska.

W części VI rozpatrywane będą wszelkie typy przemieszczeń (migracje, dyspersje itd.) w cyklu rocznym i wieloletnim z punktu widzenia zmian struktury przestrzennej gatunku w okresie pozalęgowym.

Objaśnienia do map, wykresów i tabel:

Mapa 1. Strefy ekologiczne palearktycznej części zasięgu *A. ralloides* — obszary izoprex'ów. 1 — strefa optymalna, izoprex'y w zakresie 3.0–4.0; 2 — strefa optymalna, zakres 1.7–3.0 prex; 3 — strefa przejściowa (suboptymalna), zakres 1.0–1.7 prex; 4 — strefa ekstremalna, zakres 0.5–1.0 prex; 5 — strefa ekstremalna, zakres 0.0–0.5 prex; 6 — granice zasięgu.

Wykr. 1. Korelacja wielkości stanowisk i wskaźnika  $Z$ .  $y$  — wielkość stanowiska wyrażona w parach łęgowych,  $x$  — skala wartości wskaźnika  $Z$ , krzywe regresji: — przeciętnej wartości  $Z$  względem stanowisk różnej wielkości,  $B$  — przeciętnej wielkości stanowisk względem skali wskaźnika  $Z$ ;  $C$  — odchylenie od krzywej  $A$ , jeśli przyjąć prostoliniową zależność  $Z$  od wielkości stanowisk.

Wykr. 2. Teoretyczna zmienność wskaźnika  $Z$  podczas stopniowego wzrastania i obniżania się wielkości stanowiska (zgodnie z prawidłowościami wynikającymi z równań regresji:  $x = 560 - 2,95y$ ;  $y = 165 - 0,24x$ ).  $x$  — wielkość stanowiska wyrażona w liczbie par łęgowych,  $y$  — skala wartości  $Z$ ,  $A$  — krzywa zmienności  $Z$  przy wzrastaniu wielkości stanowiska (przy początkowej odległości 600 km),  $B$  — krzywa zmienności  $Z$  przy obniżaniu się wielkości stanowiska (przy początkowej odległości 70 km).

Wykr. 3. Rozkład wskaźnika  $Z$  w odniesieniu do przeciętnej liczby stanowisk łęgowych.  $x$  — logarytmiczna skala wartości  $Z$ ,  $y$  — liczba stanowisk wyrażona w  $\%_{000}$ ,  $A$  — stanowiska

sporadyczne,  $B$  — stanowiska regularne,  $D_s$  — dominanta rozkładu stanowisk sporadycznych,  $D_{rs}$  — dominanta rozkładu ogólnego wszystkich stanowisk (krzywą tego rozkładu nie uwidoczniiono na wykresie),  $D_r$  — dominanta rozkładu stanowisk regularnych.

Wykr. 4. Rozkład wskaźnika  $Z$  w odniesieniu do przeciętnego poziomu liczebności gatunku.  $x$  — logarytmiczna skala wartości  $Z$ ,  $y$  — liczebność gatunku wyrażona w liczbie par lęgowych przedstawiona w ‰,  $A$  — liczebność gatunku zasiedlająca stanowiska sporadyczne,  $B$  — liczebność gatunku zasiedlająca stanowiska regularne.

Wykr. 5. Schemat obszaru zmienności wskaźnika  $Z$  oraz współzależności ważniejszych parametrów struktury palearktycznej części zasięgu lęgowego *A. ralloides*.  $y$  — wielkość stanowisk (liczba par),  $x$  — odległości przeciętne — stopień izolacji (km),  $z$  — procentowy stosunek liczebności stanowisk lęgowych i liczebności gatunku w poszczególnych przedziałach klasowych odległości przeciętnych; krzywe średnich wartości wskaźnika  $Z$ :  $A$  — stanowisk strefy optymalnej,  $B$  — stanowisk regularnych,  $C$  — stanowisk sporadycznych i regularnych łącznie,  $D$  — stanowisk strefy ekstremalnej,  $E$  — stanowisk sporadycznych; teoretyczne krzywe progowych wartości stosunku  $y : x$  — krzywe zamykające obszar zmienności  $Z$ :  $a_1$  — progowe wartości  $Z$  uzależnione od wydolności środowiska i stopnia zagęszczenia gatunku,  $a_2$  — odcinek maksymalnych wartości  $Z$  ukazujący obszar maksymalnego zagęszczenia gatunku,  $b_1$  — odcinek minimalnych wartości  $Z$  oraz progowych wartości maksymalnego rozproszenia gatunku,  $b_2$  — najniższy krytyczny poziom  $Z$  egzystencji stanowisk regularnych,  $c_1$  — progowe wartości parametrów  $Z$ , przy których może być zachowana autonomia stanowisk,  $c_2$  — krzywa progowych wartości parametrów  $Z$  przy mieszanym wpływie wydolności środowiska i izolacji; pozostałe symbole:  $F$  — krzywa przeciętnego stopnia izolacji stanowisk wg poszczególnych klas wielkości,  $G$  — obszar zmienności  $Z$  w strefie przejściowej między optymalną a strefą ekstremalną,  $H$  — obszar zmienności  $Z$  w strefie optymalnej,  $I$  — obszar zmienności  $Z$  w strefie ekstremalnej,  $J$  — krzywa procentowego rozkładu liczebności stanowisk w zależności od stopnia izolacji (wielkość przedziału klasowego = 10 km),  $K$  — krzywa rozkładu liczebności gatunku w zależności od stopnia izolacji (wielkość przedziału klasowego = 10 km); linie ukośne określają odpowiednie poziomy wartości  $Z$ , kółkami oznakowano momenty przelomowe zmienności  $Z$  poszczególnych stanowisk, oto ich symbole:  $\bigcirc$  — stanowiska regularne w XIX wieku,  $\oplus$  — stanowiska regularne w XX wieku,  $\bullet$  — stanowiska sporadyczne w XIX w.,  $\ominus$  — stanowiska sporadyczne w XX wieku, kółko z trójkącikiem u góry oznacza uplasowanie stanowiska w strefie optymalnej, z trójkącikiem u dołu — w strefie przejściowej, nie oznaczone trójkącikiem — w strefie ekstremalnej.

Wykr. 6. Współzależność wielkości stanowiska i odległości przeciętnych przy wykładniczym wpływie izolacji.  $x$  — odległości przeciętne,  $y$  — wielkość stanowiska; linie cieńsze — współzależność prostoliniowa przy pierwotnej (roboczej) koncepcji wskaźnika  $Z$  (równania typu:  $y = ax$ ); linie grubsze — wykryta rzeczywista współzależność krzywoliniowa (wyrażająca się równaniami wykładniczymi typu:  $y = kb^x$ ) (na wykresie przedstawiono równania poszczególnych krzywych).

Wykr. 7. Ogólny rozkład wskaźnika  $Z_{pe}$  w zależności od stopnia izolacji.  $x$  — odległości przeciętne (km) — stopień izolacji,  $y$  — logarytmiczna skala  $Z_{pe}$  (na wykresie podano równanie krzywej rozkładu).

Wykr. 8. Uproszczony schemat współzależności powodzenia egzystencji i oporu środowiska.  $x$  — skala (czasowo)-przestrzenna egzystencji mikropopulacji (populacji, gatunku),  $y$  — skala względnego odniesienia  $Z_{pe}$  i potencjału realizowanego,  $z$  — skala względnego odniesienia oporu środowiska,  $A$  — (czasowo)-przestrzenna zmienność względnych wartości  $Z_{pe}$  oraz różnicy: potencjał biotyczny — potencjał realizowany oraz (czasowo)-przestrzenna zmienność oporu środowiska,  $B$  — sumaryczne oddziaływanie wszystkich czynników ograniczających środowiska,  $C$  — efektywność walki o byt,  $D$  — poziom potencjału biotycznego.

Wykr. 9. Regresja liczebności gatunku (ujęta procentowo) i stopnia izolacji.  $x$  — odległości przeciętne (km) — stopień izolacji,  $y$  — liczebność gatunku w stosunku procentowym,  $z$  — liczebność gatunku według ugrupowań koncentracji (wielkości stanowisk),  $A$  — regresja stopnia izolacji względem ugrupowań koncentracji liczebności  $B$  — regresja liczebności względem stopnia izolacji.

Wykr. 10. Rozkład wielkości stanowisk *A. ralloides* w zależności od ich przeciętnych odległości względem siebie (w stosunku procentowym do ogólnej liczby stanowisk w danym zakresie odległości).  $x$  — przedziały klasowe wielkości stanowisk,  $y$  — liczba stanowisk w danym zakresie odległości w ‰, krzywe rozkładu w zakresie:  $A$  — do 50 km,  $B$  — 50 — 200 km,  $C$  — 200 — 500 km,  $D$  — < 500 km.

Wykr. 11. Diagram procentowego stosunku przeciętnych odległości w obrębie poszczególnych przedziałów klasowych wielkości stanowisk.  $x$  — wielkość stanowisk,  $y$  = liczba stanowisk w poszczególnych zakresach odległości wyrażona w ‰, zakresy odległości:  $a$  — do 50 km,  $b$  — 50 — 200 km,  $c$  — 200 — 500 km,  $d$  — < 500 km.

Wykr. 12. Rozkłady  $Z_{pe}$  stanowisk różnych kategorii.  $x$  — logarymiczna skala wartości  $Z_{pe}$ ,  $y$  — liczba stanowisk,  $A$  — stanowiska sporadyczne efemeryczne,  $B$  — sporadyczne ustabilizowane,  $C$  — regularne ze znaczną oscylacją liczebności,  $D$  — regularne o umiarkowanym stopniu oscylacji,  $E$  — regularne o dodatnim bilansie rozrodczość — śmiertelność, o dobrym prosperity ekologicznym,  $F$  — regularne o dodatnim bilansie rozrodczość — śmiertelność, o doskonałym prosperity ekologicznym, przegęszczone. W górnej części wykresu zamieszczono nomogram przełożenia bezwzględnych wartości  $Z_{pe}$  na skalę prexów.

Wykr. 13. Rozkład procentowy stanowisk lęgowych rozmieszczonych w poszczególnych strefach ekologicznych — profil równoleżnikowy (XIX i XX wiek łącznie; średnie ruchome).  $x$  — długość geograficzna,  $y$  — liczba stanowisk w stosunku procentowym w poszczególnych przedziałach długości geograficznej,  $A$  — stanowiska w strefie optymalnej,  $B$  — w strefie przejściowej (suboptymalnej),  $C$  — w strefie ekstremalnej.

Wykr. 14. Stopień powodzenia egzystencji gatunku w profilu równoleżnikowym zasięgu (XIX i XX wiek łącznie).  $x$  — długość geograficzna,  $y$  — skala  $Z_{pe}$  w prex'ach,  $z$  — skorygowana względem długości geograficznej skala  $Z_{pe}$  w prex'ach,  $A$  — rozkład  $Z_{pe}$  w odniesieniu do liczebności gatunku,  $B$  — rozkład  $Z_{pe}$  w odniesieniu do stanowisk lęgowych,  $C$  — rozkład  $Z_{pe}$  w odniesieniu do maksymalnych ich odchyżeń,  $D$  — rozkład  $Z_{pe}$  w odniesieniu do minimalnych wartości tego wskaźnika.

Wykr. 15. Rozkład procentowy stanowisk lęgowych rozmieszczonych w poszczególnych strefach ekologicznych w profilu południkowym (XIX i XX wiek łącznie).  $x$  — szerokość geograficzna,  $y$  — liczba stanowisk w stosunku procentowym w poszczególnych przedziałach szerokości geograficznej,  $A$  — stanowiska w strefie optymalnej,  $B$  — w strefie przejściowej (suboptymalnej),  $C$  — w strefie ekstremalnej.

Wykr. 16. Stopień powodzenia egzystencji w profilu południkowym (XIX i XX wiek łącznie).  $x$  — szerokość geograficzna,  $y$  — skala  $Z_{pe}$  w prex'ach,  $A$  — rozkład  $Z_{pe}$  w odniesieniu do liczebności  $B$  — w odniesieniu do stanowisk lęgowych,  $C$  — w odniesieniu do maksymalnych wartości  $Z_{pe}$ ,  $D$  — w odniesieniu do minimalnych wartości  $Z_{pe}$ .

Tabela 1. Charakterystyka statystyczna wskaźnika  $Z_{pe}$ . (1) — charakterystyka  $Z$  w odniesieniu do stanowisk, (2) — średnia, (3) — dominanta, (4) — zakres zmienności, (5) — uwagi, (6) — w strefie ekstremalnej, (7) — w strefie optymalnej, (8) — regularne, (9) — sporadyczne, (10) — rozpatrywane łącznie, (11) — przedziały klasowe = 0,01, (12) — przedziały klasowe = 0,001, (13) — przedziały klasowe = 0,01.

Tabela 2. Zestawienie obliczonych różnymi metodami niektórych charakterystyk strefy ekstremalnej i optymalnej palearktycznej części zasięgu *Ardeola ralloides*. (1) — metoda obliczeń, (2) — strefy, (3) — ekstremalna, (4) — optymalna, (5) — wskaźnik  $Z$ , (6) — liczba stanowisk, (7) — liczebność gatunku, (8) — wskaźnik  $Z$ , (9) — liczba stanowisk, (10) — liczebność gatunku, (11) — na podstawie ekologicznej analizy poszczególnych stanowisk,

(12) na podstawie danych krzywej koncentracji (JÓZEFIK, 1970), (13) — na podstawie rozkładu wskaźnika  $Z$ , (14) — średnio.

Tabela 3. Charakterystyki statystyczne rozkładu wskaźnika  $Z_{pe}$  w zależności od ekologicznej gradacji. (1) kategoria stanowisk, (2) — przedziały klasowe  $Z_{pe}$ , (13) — rozkład procentowy w stosunku do poszczególnych przedziałów klasowych, (4) — stanowiska w strefie ekstremalnej, (5) — stanowiska w strefie przejściowej, (6) — stanowiska w strefie optymalnej, (A) — efemeryczne, sporadyczne, (B) — ustabilizowane, sporadyczne, (C) — regularne ze znaczną oscylacją liczebności, (D) — regularne o umiarkowanej oscylacji, (E) — regularne, o dobrym prosperity ekologicznym, (F) — regularne o doskonałym prosperity ekologicznym, przegęszczone.

Tabela 4. Charakterystyka stref ekologicznych zasięgu *A. ralloides* w zależności od gradacji wskaźnika powodzenia egzystencji ( $Z_{pe}$ ) wyrażonego w preksach (w nawiasach podano zakresy  $Z_{pe}$  w nieprzetransponowanej postaci). (1) — strefy, (2) — zakresy  $Z_{pe}$  w preksach, (3) — wskaźnik  $Z_{pe}$  w nieprzetransponowanej postaci, średnia ( $\bar{x}$ )  $Z_{pe}$  w preksach, (5) — ekstremalna, (6) — przejściowa (suboptymalna), (7) — optymalna.

Appendix I. Tabela poprawek dla obliczania wskaźnika  $Z_{pe}$  według wzoru (4) (str. 18).  $x$  — wielkość stanowisk (przedziały klasowe),  $b$  — współczynnik krzywoliniowości wpływu izolacji przy danym poziomie wskaźnika  $Z$ ,  $c$  — poprawka interpolacyjna dla obliczenia  $b$ ,  $Z$  — poprzedni niepoprawiony wskaźnik powodzenia egzystencji obliczany według wzoru (1) (str. 2).

Appendix II. Charakterystyka niektórych cech zasięgu lęgowego *A. ralloides* (palearktyczna część). Objasnienia: 1 — nazwa regionu zasięgu, 2 — 5 — dystanse ukierunkowane, 6 — przeciętne dystanse w poszczególnych stuleciach, 7 — przeciętna wielkość stanowisk, 8 — średnia dystansów przeciętnych dla obydwu ostatnich stuleci, 9 — średnia wskaźnika  $Z_{pe}$  dla obydwu ostatnich stuleci (dolna liczba podaje wartość w preksach), w nawiasach — niezlogarytmowana postać wskaźnika  $Z_{pe}$ , „century” — stulecie.

## РЕЗЮМЕ

В V части цикла посвященного исследованиям по пространственной структуре ареала желтой цапли автор сосредоточивается на основном вопросе этой проблемы — механизмах воздействия внутривидовой (межмикропопуляционной) изоляции и ее эколого-эволюционных последствиях. Таким образом, внутривидовую изоляцию следует рассматривать как: а) действительно воздействующий ограничивающий фактор, влияющий на формирование экологических зон ареала, б) эволюционный фактор играющий существенную роль в дивергентных процессах.

На основании документированных в предыдущих частях цикла данных по взаимозависимости степени изоляции, величины и степени стабилизации микропопуляции, с целью определения ее биологической ситуации, а более точно, экологического процветания, автором предлагается так называемый „индекс успеха существования” (формулы (1) — (5) стр. 2, 18, 29). Автор уточняя формулировку этого индекса, определяет его как общий, относительный (в смысле возможности сравнения его численных показаний в пределах одного только вида) показатель степени стабилизации и окончательного баланса всех жизненных процессов данной микропопуляции, заселяющей определенное место гнездования, в условиях созданных внешней средой.

После введения поправки на криволинейный характер взаимозависимости составных элементов этого показателя (стр. 18, аппендикс I), и перевода его в логарифмическую форму, автором дается предложение применять этот показатель в качестве измерителя величины успеха существования соответственных микропопуляций в аспекте сравнительных исследований в различных частях ареала. Основной единицей этого измерителя является 1 *прекс* (от латинского сокращения (*pr*)*osperitas* (*ex*)*istentiae*). Производимая при его использовании оценка биологической ситуации микропопуляции, популяции или же более значительной части вида, должна охватывать по крайней мере одногодичные или многолетние отрезки времени.

В последующих частях работы автором дается анализ изменчивости составных параметров показателя  $Z_{pe}$ , рассматривается теоретическая модель осцилляции его величины, а также производится экологическая оценка диапазона его изменчивости. Автор определяет также критическую величину  $Z_{pe}$ , которой является мода общего распределения этого показателя. На основании известных, имеющихся критических числовых данных по величине микропопуляции и показателя  $Z_{pe}$  автор вычисляет критическую величину максимально терпимого видом рассеяния особей в пределах ареала т. е. критического порога изоляции.

Исходя из следующих данных: а) предварительной экологической оценки распределения  $Z_{pe}$ , б) анализа кривой концентрации вида, в) экологического анализа соответственных гнездовок в палеарктической части ареала желтой цапли, автор вычисляет некоторые характеристики экстремальной и оптимальной зоны ее ареала. В экстремальной зоне имеется в среднем 53,58% всех мест гнездования (главным образом спорадических и с неустойчивой численностью) и только лишь 6,72% численности вида.

Существенным вопросом, рассматриваемым в очередной главе является анализ основных параметров распространения вида. Распределения этих параметров сопоставил автор на сводном графике (граф. 5), где также учитываются критические величины некоторых параметров.

В главе касающейся биологических механизмов воздействия изоляции, автором рассматривается вопрос степени редукции отдельных микропопуляции в зависимости от расстояний между ними. Ограничивающее влияние изоляции (редукция) по отношению к ее арифметическому увеличиванию возрастает экспоненциально. Объединение малых стад, происходящих из очень отдаленных друг от друга мест гнездования, в послегнездовом периоде имеет для выживаемости вида существенное значение. Шансы соединения малых стад, или отдельных особей, по мере возрастания расстояний между гнездовками, очень резко уменьшаются. Максимальная дисперсия вида по ареалу лимитируется выживаемостью отдельных стад или микропопуляций в период их абсолютной изоляции в течение послегнездового периода. Под влиянием арифметически нарастающей изоляции снижается логарифмически степень успеха существования соответственных микропопуляций. Выявленные связи автор представляет в форме экспоненциальных уравнений.

В отдельной главе автором производится обсуждение терминов: „успех существования”, „выживаемость”, „сопротивление внешней среды”. Введение нового



термина „успех существования” обуславливается необходимостью учета, кроме „классических” ограничивающих факторов, обнаруженного автором нового фактора — ограничивающего экспоненциально влияния межмикрораспространенной (внутривидовой) изоляции. Как доказывает автор, этот фактор в значительной степени сказывается на пространственной картине вида.

В главе посвященной экологической градации соответственных уровней показателя  $Z_{pe}$ , автором анализируется соотношение: размножаемость — смертность. Он подчеркивает, что при высоких показателях  $Z_{pe}$  влияние изоляции падает почти к нулю, но при незначительных показателях этого показателя, оно усиливаясь, принимает размеры экологического барьера. Автором доказывается, что: а) в микрораспространенных характеризующихся  $Z_{pe} > 5$  размножаемость значительно превышает смертность, в условиях перенаселенности постоянно уходит из них часть особей к местам гнездовок о более низких показателях  $Z_{pe}$ ; б) при  $1 \leq Z_{pe} \leq 5$  размножаемость — смертность уравниваются динамически, приплыв — отлив особей удерживаются на одном уровне; в) при  $Z_{pe} < 1$  баланс размножаемость — смертность постоянно отрицательный, места гнездовок в значительной степени расположены в экстремальной зоне могут удерживаться единственно в условиях постоянного притока новых особей из оптимальной зоны ареала (где существует перенаселенность).

Пользуясь показателем  $Z_{pe}$  в его логарифмической форме, автор дает характеристику экологических зон ареала. Для экстремальной зоны характерным является  $Z_{pe}$  в пределах 0–1,7 *прексов*, переходную (субоптимальную) зону характеризует  $Z_{pe}$  в границах 1,7–2,0 *прексы*, оптимальную зону — 2,0–4,0 *прексы*. Пользуясь шкалой *прексов*, автор подразделил палеарктическую часть ареала на так называемые площади *изопрексов* (карта 1), которые складываются на экологическую характеристику соответственных зон в их географическом расположении.

На основании профильного анализа распределений  $Z_{pe}$  автор констатирует, что в западных частях ареала экстремальная зона охватывает большинство гнездовий, там же происходит наиболее интенсивное преобразование естественных биотопов производимое человеком, а также наиболее интенсивно протекают процессы синантропизации желтой цапли. Господствующим, ограничивающим фактором в западных регионах ареала является экологическая вместительность биотопа, в то время как по направлению к востоку все больше в этом отношении возрастает роль межмикрораспространенной изоляции. Совместно с прогрессирующей синантропизацией вида ограничивающее влияние изоляции значительно уменьшается. Согласно выдвигаемому автором прогнозу, в будущем, в условиях значительной, производимой человеком редукции ограничивающего влияния изоляции (ограничение хищников, охранительные мероприятия, синантропизация), будет возможным существование даже незначительных количественно, изолированных популяций среди колониально гнездящихся мигрантных видов. Эволюционные последствия такого рода обстоятельств найдут свое отражение в более интенсивном продвижении формообразовательных процессов. Среди колониальных видов исчезнет, по всей вероятности, стадный инстинкт — они станут гнездиться отдельными па-

рами, значительно понизиться критические величины максимальной по ареалу дисперсии, возрастет поверхность географических ареалов.

В меридиональном разрезе ареала (профильный анализ) влияние изоляции имеет более выровненный характер, хотя в северных регионах оно проявляется более четко чем на юге, где в свою очередь возрастает ограничивающее влияние экологической вместительности биотопов.

В VI части автор преднамерен анализировать различные типы пространственных передвижений (миграции, дисперсия итд.) рассматриваемые в аспекте изменений пространственной структуры вида с учетом одногодичных и многолетних циклов.

Объяснения к карте, графикам и таблицам:

Карта 1. Экологические зоны палеарктической части ареала желтой цапли — районы изопреков. 1 — оптимальная зона, изопрексы в пределах 3,0–4,0; 2 — оптимальная зона, изопрексы 1,7–3,0; 3 — переходная зона (субоптимальная), пределы 1,0–1,7 преков; 4 — экстремальная зона, изопрексы в пределах 0,5–1,0 преков; 6 — экстремальная зона, пределы 0,0–0,5 преков; 6 — границы ареала.

График 1. Корреляция величины гнездовок и показателя  $Z$ .  $y$  — величина гнездовки выражающаяся количеством гнездовых пар,  $x$  — шкала показателя  $Z$ , кривые регрессии:  $A$  — средняя величина  $Z$  по величине гнездовок,  $B$  — средней величины гнездовок по величине показателя  $Z$ ;  $C$  — отклонение от кривой  $A$ , если принять прямолинейную зависимость от величины гнездовок.

График 2. Теоретическая изменчивость показателя  $Z$  при возрастающей и обнижающейся величине гнездовок (согласно правилам вытекающим из уравнений регрессии:  $x = 560 - 2,95y$ ;  $y = 165 - 0,24x$ ).  $x$  — величина гнездовок выражающаяся количеством гнездовых пар,  $y$  — показатель  $Z$ ,  $A$  — кривая изменчивости  $Z$  при возрастании величины гнездовки (при первоначальном расстоянии 600 км),  $B$  — изменчивость  $Z$  при снижении величины гнездовки (при первоначальном расстоянии 70 км).

График 3. Распределение величины показателя  $Z$ .  $x$  — логарифмическая шкала  $Z$ ,  $y$  — численность гнездовок в ‰,  $A$  — спорадические гнездовки,  $B$  — регулярные гнездовки,  $D_s$  — мода распределения спорадических гнездовок,  $D_{rs}$  — мода общего распределения всех мест гнездования (кривая этого распределения не учитывается на графике),  $D_r$  — мода распределения регулярных мест гнездования.

График 4. Распределение показателя  $Z$  по отношению к среднему уровню численности вида.  $x$  — логарифмическая шкала показателя  $Z$ ,  $y$  — численность вида выраженная количеством гнездовых пар (в ‰),  $A$  — численность вида в спорадических местах гнездования,  $B$  — численность вида в регулярных местах гнездования.

График 5. Сводный график изменчивости показателя  $Z$  и взаимозависимости более существенных параметров структуры палеарктической части ареала желтой цапли.  $y$  — величина мест гнездования (количество гнездовых пар),  $x$  — средние расстояния — степень изоляции (км),  $z$  — процентное соотношение численности гнездовок и численности вида в пределах соответственных классов по средним расстояниям; кривые средних величин показателя  $Z$ :  $A$  — гнездовки оптимальной зоны,  $B$  — регулярные гнездовки,  $C$  — совместно спорадические и регулярные гнездовки,  $D$  — гнездовки экстремальной зоны,  $E$  — спорадические гнездовки; теоретические кривые критических величин соотношения  $y : x$  — кривые охватывающие пределы изменчивости показателя  $Z$ :  $a_1$  — критические величины  $Z$  в зависимости от экологической вместительности биотопа и степени густоты заселения вида,  $a_2$  — отрезок максимальных величин  $Z$  указывающий пределы максимальной перенаселенности вида,  $b_1$  — отрезок минимальных величин  $Z$  а также критических величин максимальной дисперсии вида,  $b_2$  — наиболее низкий критический уровень  $Z$  существования регулярных гнездовок,  $c_1$  — критические величины составных параметров  $Z$ , при котором может еще удерживаться автономия мест гнездования,  $c_2$  — кривые критических величин составных параметров  $Z$  при смешанном влиянии экологической вместительности биотопа и изоляции; остальные обозначения:  $F$  — кривая средней величины изоляции между гнездовками по отдельным классам их величины,

$G$  — пределы изменчивости  $Z$  в промежуточной (субоптимальной) зоне,  $H$  — пределы изменчивости  $Z$  в оптимальной зоне,  $I$  — пределы изменчивости  $Z$  в экстремальной зоне,  $J$  — процентное распределение численности мест гнездования в зависимости от степени изоляции (величина классовых пределов = 10 км),  $K$  — распределение численности вида в зависимости от степени изоляции (классовые пределы = 10 км); линии по диагонали обозначают соответственные уровни  $Z$ , кружками обозначены переломные моменты изменчивости  $Z$  соответственных мест гнездования а их символы следующие:  $\circ$  — регулярные места гнездовок в XIX веке,  $\odot$  — регулярные места гнездовок в XX веке,  $\bullet$  — спорадические места гнездовок в XIX веке,  $\ominus$  — спорадические в XX веке, кружочки с треугольником в верхней части обозначают расположение в оптимальной зоне, с треугольниками внизу — в переходной (субоптимальной) зоне, без треугольников — в экстремальной зоне.

График 6. Взаимозависимость величины гнездовок и средних дистанции при экспоненциальном влиянии изоляции.  $x$  — средние дистанции,  $y$  — величина гнездовок; тонкой линией обозначена прямолинейная взаимозависимость при первоначальной (рабочей) концепции показателя  $Z$  (уравнения типа:  $y = ax$ ); жирной линией обозначена действительная, обнаруженная автором криволинейная взаимозависимость (уравнение типа:  $y = kl^x$ ), на графике обозначены кривые соответственных уравнений.

График 7. Общее распределение показателя  $Z_{pe}$  в зависимости от степени изоляции.  $x$  — средние дистанции (км) — степень изоляции,  $y$  — логарифмическая шкала  $Z_{pe}$  (на графике обозначены уравнения кривой распределения).

График 8. Упрощенная схема взаимозависимости успеха существования и сопротивляемости внешней среды.  $x$  — шкала по времени пространству существования микропопуляции (популяции, вида),  $y$  — относительная шкала показателя  $Z_{pe}$  и реализованного потенциала,  $z$  — относительная шкала сопротивляемости внешней среды,  $A$  — изменчивость во времени и пространстве относительных величин  $Z_{pe}$  а также разницы: биотический потенциал — реализованный потенциал, кривая  $A$  показывает также изменчивость во времени и пространстве сопротивляемости внешней среды,  $B$  — суммарное воздействие всех ограничивающих факторов в биоценозе,  $C$  — эффективность борьбы за существование,  $D$  — уровень биотического потенциала.

График 9. Регрессия численности вида (в процентных соотношениях) и степени изоляции.  $x$  — средние дистанции (км) — степень изоляции,  $y$  — численность вида в процентных соотношениях,  $z$  — численность вида в аспекте группировок концентрации (величины гнездовок),  $A$  — регрессия степени изоляции по группировкам концентрации численности вида,  $B$  — регрессия численности вида по степени изоляции.

График 10. Распределение величины мест гнездования желтой цапли в зависимости от расстояний между ними (в процентных соотношениях к общему числу гнездовий в данном классе расстояний).  $x$  — классовые интервалы по величине гнездовок,  $y$  — численность (в процентах) гнездовок в данном классе расстояний, распределение величин гнездовок в пределах:  $A$  — до 50 км,  $B$  — 50–200 км,  $C$  — 200–500 км,  $D$  — <500 км.

График 11. Диаграмма процентных соотношений средних расстояний в пределах соответственных классовых промежутков по величине гнездовок.  $x$  — величина гнездовок,  $y$  — численность гнездовок (в процентах) в соответственных категориях расстояний, категории расстояний:  $a$  — до 50 км,  $b$  — 50–200 км,  $c$  — 200–500 км,  $d$  — 500 км.

График 12. Распределения  $Z_{pe}$  гнездовок различных категории.  $x$  — логарифмическая шкала  $Z_{pe}$ ,  $y$  — число гнездовок,  $A$  — спорадические эфемерные места гнездования,  $B$  — спорадические стабилизированные,  $C$  — регулярные характеризующиеся значительной осцилляцией численности,  $D$  — регулярные с умеренно выраженной осцилляцией,  $E$  — регулярные с положительным балансом размножаемость — смертность, характеризующиеся благоприятной экологической обстановкой,  $F$  — регулярные с положительным балансом размножаемость — смертность, экологически процветающие с признаками перенаселенности. В верхней части графика помещается номограмма трансформации абсолютных величин показателя  $Z_{pe}$  на величины выраженные в прекасах.

График 13. Процентные распределения мест гнездования согласно их расположению в соответственных экологических зонах — в параллельном разрезе ареала (XIX и XX век совместно; подвижные средние).  $y$  — численность гнездовок (в процентах) в соответственных классах географической

долготы,  $x$  — географическая долгота,  $A$  — гнездовки в оптимальной зоне,  $B$  — в переходной (субоптимальной) зоне,  $C$  — в экстремальной зоне.

График 14. Степень успеха существования в параллельном разрезе ареала (XIX и XX век совместно).  $x$  — географическая долгота,  $y$  — шкала  $Z_{pe}$  в преках,  $z$  — прокорректированная по отношению к географической долготы шкала  $Z_{pe}$  в преках,  $A$  — распределение  $Z_{pe}$  по отношению к численности вида,  $B$  — распределение  $Z_{pe}$  по отношению к численности мест гнездовок,  $C$  — распределение максимальных величин  $Z_{pe}$ ,  $D$  — распределение минимальных величин  $Z_{pe}$ .

График 15. Процентное распределение численности мест гнездования расположенных в соответственных экологических зонах в меридиональном разрезе ареала (XIX и XX век совместно),  $x$  — географическая широта,  $y$  — численность гнездовок (в процентных соотношениях) в соответственных пределах географической широты,  $A$  — гнездовки в оптимальной зоне,  $B$  — переходной (субоптимальной) зоне,  $C$  — в экстремальной зоне.

График 16. Степень успеха существования в меридиональном разрезе ареала (XIX и XX век совместно).  $x$  — географическая широта,  $y$  — шкала,  $Z_{pe}$  в преках,  $A$  — распределение  $Z_{pe}$  по отношению к численности вида,  $B$  — по отношению к численности мест гнездовок,  $C$  — по отношению к максимальным величинам  $Z_{pe}$ ,  $D$  — по отношению к минимальным величинам  $Z_{pe}$ .

Таблица 1. Статистическая характеристика показателя  $Z_{pe}$ . (1) — характеристика  $Z$  по отношению к гнездовкам, (2) — среднее число, (3) — мода, (4) — пределы изменчивости, (5) — замечания, (6) — в экстремальной зоне, (7) — в оптимальной зоне, (8) — регулярные, (9) — спорадические, (10) — рассматриваемые совместно, (11) — классовые интервалы = 0,01, (12) — классовые интервалы = 0,001, (13) — классовые интервалы = 0,01.

Таблица 2. Сопоставление вычисленных различными методами некоторых характеристик экстремальной и оптимальной зоны в палеарктической части ареала желтой цапли. (1) — метод подсчета, (2) — зоны, (3) — экстремальная, (4) — оптимальная, (5) — показатель  $Z$ , (6) — число гнездовок, (7) — численность вида, (8) — показатель  $Z$ , (9) — число гнездовок, (10) — численность вида, (11) — на основании экологического анализа соответственных мест гнездования, (12) — на основании данных кривой концентрации (JÓZEFIK, 1970), (13) — на основании распределения показателя  $Z$ , (14) — в среднем.

Таблица 3. Статистические характеристики распределения показателя  $Z_{pe}$  в зависимости от экологической градации. (1) — категория гнездовок, (2) — классовые интервалы  $Z_{pe}$ , (3) — процентное распределение по отношению к отдельным классовым промежуткам, (4) — места гнездовок в экстремальной зоне, (5) — гнездовки в переходной (субоптимальной) зоне, (6) — гнездовки в оптимальной зоне, (A) — эфемерные, спорадические, (B) — стабилизированные, спорадические, (C) — регулярные со значительной осцилляцией численности, (D) — регулярные с умеренно выраженной осцилляцией, (E) — регулярные, экологически процветающие, (F) — регулярные характеризующиеся превосходном экологическим состоянием, перенаселенные.

Таблица 4. Характеристика экологических зон ареала желтой цапли в зависимости от градации показателя успеха существования ( $Z_{pe}$ ) выраженного в преках (в скобках подаются пределы  $Z_{pe}$  в нелогарифмической форме). (1) — зоны, (2) — пределы  $Z_{pe}$  в преках, (3) — показатель  $Z_{pe}$  в нелогарифмической форме, среднее число ( $\bar{x}$ )  $Z_{pe}$  в преках, (5) — экстремальная, (6) — переходная (субоптимальная), (7) — оптимальная.

Аппендикс I. Таблица поправок для вычисления показателя  $Z_{pe}$  по формуле (4) (стр. 18).  $x$  — величина мест гнездования (классовые промежутки,  $b$  — коэффициент криволинейности воздействия изоляции при данном уровне показателя  $Z$ ,  $c$  — интерполяционная поправка для подсчета  $b$ ,  $Z$  — прежний без коррективы показатель успеха существования вычисляемый согласно формуле (1) (стр. 2).

Аппендикс II. Характеристика некоторых признаков гнездового ареала желтой цапли (палеарктическая часть). Обозначения: 1 — название региона ареала, 2–5 — направленные расстояния, 6 — средние расстояния в соответственных столетиях, 7 — величина гнездовок в среднем, 8 — среднее число средних расстояний характерных для двух последних столетий, 9 — среднее число показателя  $Z_{pe}$  характерное для двух последних столетий (нижнее число выражается в преках, в скобках подается величина показателя  $Z_{pe}$  в нелогарифмической форме, „century” — столетие.

Redaktor pracy — mgr Z. Swirski

---

Państwowe Wydawnictwo Naukowe — Warszawa 1971  
Nakład 1030+90 egz. Ark. wyd. 5,5; druk. 3<sup>7</sup>/<sub>8</sub>. Papier druk. sat. kl. III 80 g B. Cena zł 18, —  
Nr zam. 1255/70 — Wrocławska Drukarnia Naukowa