ACTA ORNITHOLOGICA

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Studies on the Squacco Heron, *Ardeola ralloides* (Scop.). Part IV.
Spatial organization and mechanisms integrating the species

Studia nad czaplą modronosą, *Ardeola ralloides* (Scop.). Część IV.
Organizacja przestrzenna i mechanizmy integrujące gatunek

Исследования по желтой цапле, *Ardeola ralloides* (Scop.). Часть IV.
Пространственная организация и механизмы интегрирующие вид

[with 9 tables and 17 graphs in the text]

INTRODUCTION

The aim of the present study, as part of the cycle devoted to *Ardeola ral-loides* (Scop.), is to analyse the structure of spatial distribution recorded for the Squacco Heron, mechanisms integrating the species in space, the effect of isolation between separate micropopulations on their size and the general configuration of the range. Of secondary importance will be problems also

connected with the main topic and discussed in the body of the paper, such as: territorial preference of the micropulation, pulsations of the boundaries of the range, formation of disjunction, mechanisms of territorial expansion and regression, as well as certain other zoogeographical phenomena. There will also be a continuation of research after critical values of factors limiting the spreading of the species.

I have already shown ample evidence that the spatial distribution of the species is closely dependent on the geographical position of marshland habitats, degree of their transformation, ecological capacity (evidently within the limits of the gradient of environmental factors proper for the species), and also on the character of the anthropogenic factor's effect (JÓZEFIK, 1969, 1970). An answer to the recurrent question whether intraspecific factors (such as populational organization and a tendency to live in larger communities) also affect the spatial distribution of the species, beside the sphere of biogeophysical factors mentioned above, will be attempted in the first place.

AGGREGATIONS OF BREEDING SITES

Assuming that the distribution of separate micropopulations habitating breeding sites in their range does not occur in a random way, but that it displays diverse tendencies, the author has checked with test χ^2 differences between theoretical and empirical distributions of site occurence in separate squares of the range*) in order to supply convincing evidence for his thesis. For the sake of comparison the distribution characteristic for the 2nd half of the XIXth century, for the 1st half of the XXth century, and for the period 1950–1960 was taken, as well as the respective theoretical distribution according to POISSON'S probability:

$$\frac{N\bar{x}^x}{x!\,(e^x)}. \tag{1}$$

The results are presented in Table 1.

And thus, irrespective of considerable secular numerical oscillations, changes in the character of environmental factors limiting the species reveal a clear-cut tendency to clumped distribution of breeding sites which can be unequivocally interpreted as an attempt to overcome isolation between separate micropopulations and to maintain the optimum level of density over the area occupied.

INTERRELATIONS BETWEEN THE SIZE OF SITES AND THE DEGREE OF THEIR ISOLATION

When discussing aggregations we are faced, first of all, by the problem of the isolation of breeding sites in relation to each other. As we are confined to

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*) The palearctic part of the range has been broken down into squares with sides of 4° of longitude and 4° of latitude (cf. JÓZEFIK, 1969b).

Table 1. Characteristics of theoretical and empirical distributions of *A. ralloides* breeding sites in the palearctic part of the range.

Statistical characteristics (2) / Periods	$\bar{x}$	$\sigma_{\bar{x}}^2$	P (according to Poisson)	χ^2 of the difference between theoretical and empirical distributions
(1)	(3)	(4)	(5)	(6)
XIXth century (7)	1.305	6.316	0.01106	1817
1st half of the XXth century (8)	1.237	6.525	0.01048	2531
period 1950 — — 1960 (9)	0.589	3.145	0.00108	947
total (10)	1.010	5.296	0.00856	1904

the possibility of using an objective and not very complicated measure of the degree of isolation, the choice of the right parameter is decisive for the course of further research. However, this choice is limited anyway. We have to reject straightaway all areal indices (density per unit of area). In the case of a mosaic--like pattern of distribution with a tendency to form aggregations it is most effective to measure distances between separate sites in kilometres. It ought to be remarked that indices and measures used in phytosociology to determine the degree of isolation (CLARK, EVANS, 1964; DICE, 1952; THOMPSON, 1956), mainly for purposes of determining isolation between individuals, do not seem particularly useful when applied to studies on animal micropopulations.

The following scheme of calculating the index of isolation for each of the breeding sites has been used in this paper: a) the area around the given sites was divided, on a detailed map, into quarters WN, NE, ES, SW; b) within each quarter distances to the nearest sites were measured along straight lines. In such a way the so called directed distances were obtained, measured separately for the situation of the species in the XIXth and in the XXth century. In any further operations all counts were calculated on the basis of balanced means obtained from measurements of distances.

Leaving aside the previously shown tendency to form crowded communities and assuming that the average site size depends entirely on biogeophysical factors, we are in a position to accept that distances between them should not affect their size (it ought to be remembered that in view of the heterogeneity of the environment the enormous majority of the sites are isolated in relation to each other by areas biologically alien for the species). Let us consider this thesis applying an analysis of the coefficient of correlation ratio:

$$\eta_{xy} = \sqrt{1 - \frac{\sigma^2 y\,(x)}{\sigma^2 y}} \qquad (2)$$

which occurs between the size of the site (y) and the distance (x) (Table 2).
The explanation why a curvilinear correlation has been applied here will be
given in the ensuing part of the present paper.

Table 2. Indices of the correlation between the size of breeding sites (y) and distances
between them (x) (XIXth and XXth centuries are considered together).

Sites	Correla-tion (3) Distances	Coefficients of the correlation ratio		Coefficient of cor-relation	Coefficient of curvilinear reg-ression
		η_{yx}	η_{xy}	r_{xy}	$\eta_{xy}^2 - r_{xy}^2$
(1)	(2)	(4)	(5)	(6)	(7)
Regular and sporadic toge-ther (8)	maximum (9)	0.776	0.813	−0.274	0.586
	minimum (10)	0.819	0.712	−0.687	0.035
	average (11)	0.710	0.849	−0.846	0.005
Sporadic (12)	maximum (13)	0.747	0.718	−0.029	0.515
	minimum (14)	0.533	0.586	−0.151	0.321

Distances between both sporadic and regular sites have been treated in
three separate variants: maximum and minimum distances, irrespective of
their direction, have been decided as one of the four measurements charac-
terizing each of the sites, while average distances have been treated as the mean
value for all directed distances which can be measured for the given site.

Co-efficient η_{yx} for all the three variants is relatively high and it indicates
that the size of the site depends, to a large extent, on the degree of isolation.
Let us consider in turn the correlation and problems connected with it.

POSITION OF THE SITE IN THE AGGREGATION

When we consider that maximum distances, irrespective of their position
in one of the quarters of directed distances, reveal to what an extent the given
site is removed from the community center of other sites, or whether it is
situated at one of such centers, then we can accept the category of distances
as an index of the position of the given site in relation to other sites. In propor-
tion to the increase in maximum distances the given site will be either in an
outlying position, or, inasmuch as the value of maximum distances does not
differ much from average distances, i.e. the resultant values of all the direc-
ted distances, we can be sure that the given site is situated at the center of the
aggregation. Thus an analysis of the correlation between the size of sites and

the maximum distances will reveal the connection between the size of the site and its position in relation to other sites. This connection, in the aspect of the effect of the extreme zone on the distribution and numerical state of sporadic sites, was already discussed in part III of the cycle (JÓZEFIK, 1970).

The little differentiated and relatively high value of the correlation for regular and sporadic sites considered together ($\eta_{yx} = 0.776$), just as the one for sporadic sites treated separately ($\eta_{yx} = 0.747$) indicates not only an increasing resistance of the habitat outside the centers of aggregations, but it also signals the tendency of the species to concentrate in aggregations. This is also indicated by the course of the curve presenting maximum distances (graph 1, curve A) — the values are highest for small sites of fewer than 20 pairs. In cases of more
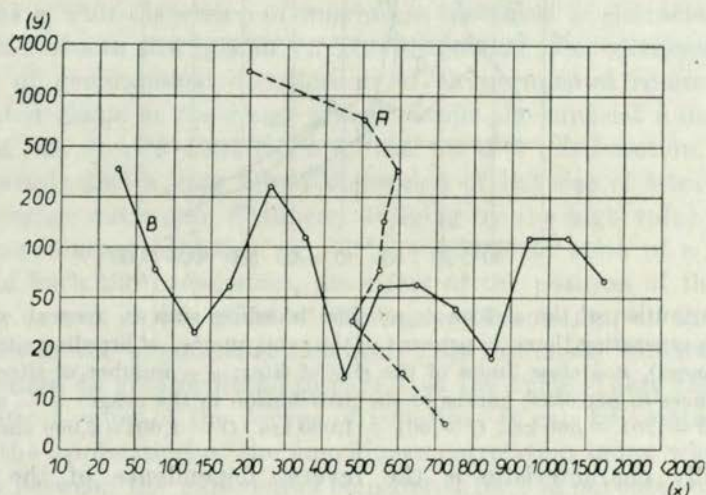

Graph 1. Correlation between the size of *A. ralloides* breeding sites and the maximum distances separating them (the XIXth and the XXth centuries are treated together). x — class limits of maximum distances (in km); y — class limits of the size of breeding sites; curves of regression: A — average maximum distances characteristic for separate classes of site size, B — average site size characteristic for separate classes of maximum distances.

than 500 pairs the average for these distances rapidly falls down. The average size of sites situated at distances shorter than 500 km is also summarily higher (graph 1, curve B). This is much more evident in the percentage distribution of maximum distances taken in four ranges within separate classes of site size (graph 2). And thus sites of more than 10 pairs are characterized by only 20% of cases of distances up to 200 km and slightly more than 40% up to 500 km. Distances up to 500 km in the case of sites of 20 pairs made up more than 50% of the total, while sites of more than 1,000 pairs — 100%.

It follows evidently from graph 1 that the average value of maximum distances, for the great majority of sites, oscillates between 450 and 600 km. Sporadic sites fall below this value while above that we have large sites of more

than 500 pairs. The following conclusion can be drawn on the basis of these data: the size of a site depends, to a large extent, on its position in relation to the groups of other sites in the range. The farther is the given site situated from the center of the aggregation, i. e. the relatively nearer the border of the range, the smaller is its average size. The majority of sites are concentrated to form groups of sites.
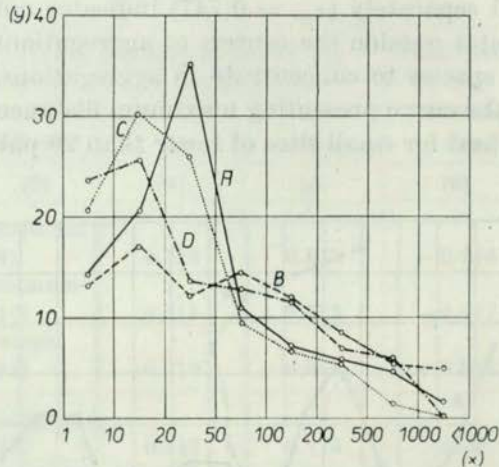
Graph 2. Distribution of the size of *A. ralloides* breeding sites in respect of their maximum distances separating them (in per cent of the total number of breeding sites in the given range of distances). x — class limits of the size of sites; y — number of sites in the given range of distances in per cent; curves of the distribution in the range: A — up to 200 km, B — 201 — 500 km, C — 501 — 1,000 km, D — 1,001 – 2,000 km.

Specifically characteristic is the reverse dependence of the parameters discussed (η_{xy}), i. e. dependence between maximum distances and the size of sites. It seems apparent that this dependence is devoid of any real significance. None the less, it reveals that at least in a majority of cases we can determine the maximum degree of isolation at which the given site can function normally. In order to make this concept more precise the following should be taken into account: the maximum degree of isolation tolerated by the micropopulation habitating the given small and isolated site. In relation to separate sites this can be only partial spatial isolation, i. e. encompassing 90–180° and only rarely 270° of the area around the given site.

Maximum distances can also be treated as an index of isolation between separate groups of sites, even of a complete isolation within the radius of 360°.

Let us compare indices η_{xy} calculated jointly for regular and sporadic sites, as well as separately for sporadic ones (Table 2). A considerably higher value of η_{xy} ($= 0.813$) for the former suggests a close correlation between the size of sites, and the degree of isolation and the spatial distribution of environmental resources. The higher value of η_{xy} ($= 0.718$) for sporadic sites is the result of the effect of various extreme environmental factors clearly discernible here.

What is the character of dependence η_{xy}? If we went only as far as calculating the co-efficients of correlation (Table 2), then we should conclude that the degree of the isolation of sporadic sites remains unaffected by the size of neighbouring sites ($r_{xy} = -0.029$), and that there is no correlation in relation to all the breeding sites in the entire range ($r_{xy} = -0.274$). In our case the co-efficients of correlation will help to determine the value of curvilinear regression:

$$c = \eta_{xy}^2 - r_{xy}^2. \tag{3}$$

It is unusually high (Table 2) and this inclines us to devote more attention to the character of this connection.

And thus a wide dispersion of maximum distances is characteristic for separate classes of site size (graph 1). This dispersion is conditioned by the heterogeneity of geographical distribution of environmental resourses, a paralelly elongated shape of the range which entails the unusual numerical diversification of the species occurrence in the parallel cross-section. And consequently, there is also a very broad dispersion of the size of sites for separate values of average maximum distances. Judging by the high value of the co-efficient of curvilinear regression ($\eta_{xy}^2 - r_{xy}^2 = 0.586$), in spite of a considerable dispersion of both the parameters, the effect of the position of the site in the aggregation, as well as the effect of the degree of isolation, on the size of this site increases in the exponential function. This extremely important problem will be discussed in greater detail in part V of the cycle. There the author will give the critical value of the degree of isolation. It can be treated as a justification of the application of the curvilinear correlation index when analysing connections between the parameters considered for the purposes of the present study.

Summing up, it should be stressed that the position of the site in relation to others in the range and its size are interrelated with each other. When we consider maximum distances as a measure of the degree of isolation and dispersion of separate groups of sites, or single sites, then this dependence assumes the character of a negative curvilinear correlation, i. e. an increasing linear dispersion is accompanied by a logarithmic decrease in the size of breeding sites. In comparison with the previously mentioned tendency of the species to form aggregations of separate micropopulations, i. e. to form more spatially compact groups of breeding sites, this fact assumes a deep general biological meaning.

CHANCES OF CONTACTS BETWEEN MICROPOPULATIONS

Minimum distances assume a different character. They are a sort of an index showing what the chances of direct contacts between neighbouring micropopulations are. Such contacts boil down in the breeding season to an impro-

vement of the situation in temporarily overcrowded sites. In the case of local disasters (reeds destroyed by fire, breeding colonies destroyed by poachers, etc.) at one of the sites Herons can, at least partially, move quickly to one of the neighbouring sites and then go through another breeding cycle. This sort of thing happened in 1955 when a heronry and a breeding colony of Cormorants in the region of Vilkovo in the Danube delta were destroyed by artillery barrage in the course of military manouvres and the birds removed in the same breeding season to the Dniester delta and successfully carried out the process of having the second brood (NAZARENKO, JÓZEFIK, 1957). In the post-breeding period individuals from small neighbouring sites often join in common flocks. As a result close neighbouring of breeding sites provides a larger chance of survival for the entire population within an aggregation. And thus both the indices of the correlation of maximum and minimum distances reflect, in different aspects, one and the same dependence of the size of a given site on its position in relation to other sites in the area.

It follows from graphs 3 and 4 that the largest sites of more than 1,000 pairs are accompanied by minimum distances not exceeding 20 km. Breeding
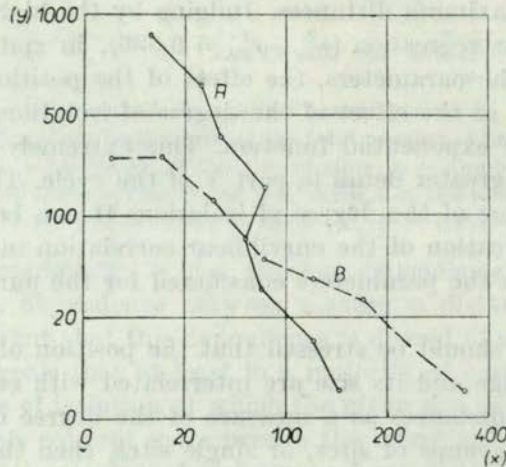
Graph 3. Correlation between the size of sites and their minimum distances separating them (the XIXth and XXth centuries treated together). x — class limits of minimum distances (in km); y — class limits of the size of sites; curves of regression: A — average minimum distances characteristic for separate classes of site size, B — average size of sites characteristic for separate classes of minimum distances.

sites of 500–1,000 pairs neighbour in 54% of cases upon other sites which are nearer than 20 km. Minimum distances never exceed 700 km. A large majority of sites (90%) neighbour upon each other within distances of up to 200 km. Separated by distances longer than 200 km there are 28% of the smallest sites (up to 10 pairs), and 6% of sites of 10–20 pairs. None of the sites of more than 50 pairs were characterized by minimum distances shorter than 200 km

(graph 4). The distribution of the size of sites in separate classes of minimum distances is very significant here (cf. graph 3). An analysis of these graphs enables us to draw the following conclusion: separate sites are grouped in the range in such a way that irrespective of other circumstances micropopulations habitating it could keep up contacts with at least one more other breeding site. This trend is supported by the characteristics of the dispersion of minimum distances (cf. Table 6). And thus, leaving aside a small number of exceptions, all micropopulations within the breeding range are connected by "bridges" of minimum distances.
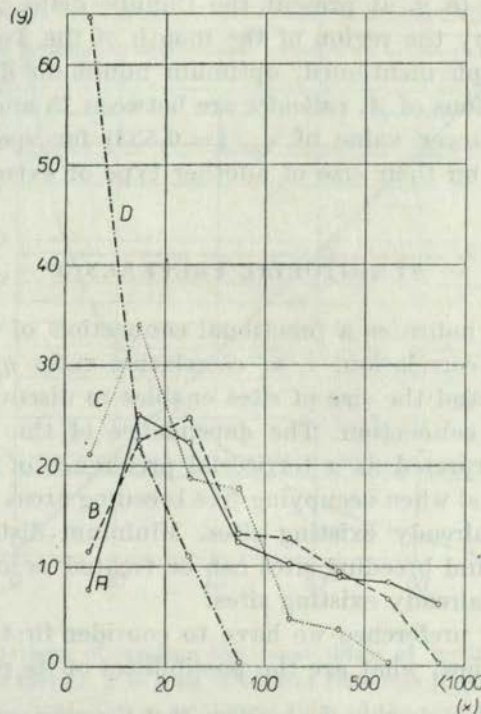
Graph 4. Distribution of the size of *A. ralloides* breeding sites in respect of their minimum distances separating them (in per cent of the total number of breeding sites in the given range of distances). *x* — class limits of the size of sites; *y* — number of sites in the given range of size in per cent; curves of the distribution in the range: *A* — up to 20 km, *B* — 21 to 50 km, *C* — 51 to 200 km, *D* — 201 to 700 km.

Coefficient η_{yx} (= 0.819) seems to signal a close correlation between the size of sites and minimum distances. And really the regression of sites of small size (graph 3, curve *B*) in relation to distances is relatively even in its character. And thus it is reasonable to remark that, when we assume that the intensity of contacts between neighbouring micropopulations is in proportion to distances separating them, then it follows that it also depends on the size of these micropopulations.

The initial section of curve *B* in graph 3 is extremely interesting. It indicates that as the distances grow smaller, the size of sites increases only to a certain limit, and when it is overstepped the correlation is reversed from negative to positive. This supports statistically the fact that the species displays a tendency to maitain only optimum minimum distances in separate aggregations, any shorter distances lead to overcrowding which would prevent neighbouring micropopulations from increasing their numbers. Such a situation can be observed in the case of larger aggregations, individual breeding sites of which are not separated from each other by larger areas of habitats alien for the species (e. g. at present the Danube delta, Lenkoran Plain, and in the XIXth century the region of the mouth of the Teiss, the Drave, etc.). Judging by the graph mentioned, optimum minimum distances between separate micropopulations of *A. ralloides* are between 15 and 35 km long.

A considerably lower value of η_{yx} ($= 0.533$) for sporadic sites indicates an increasing effect on their size of another type of extreme factors.
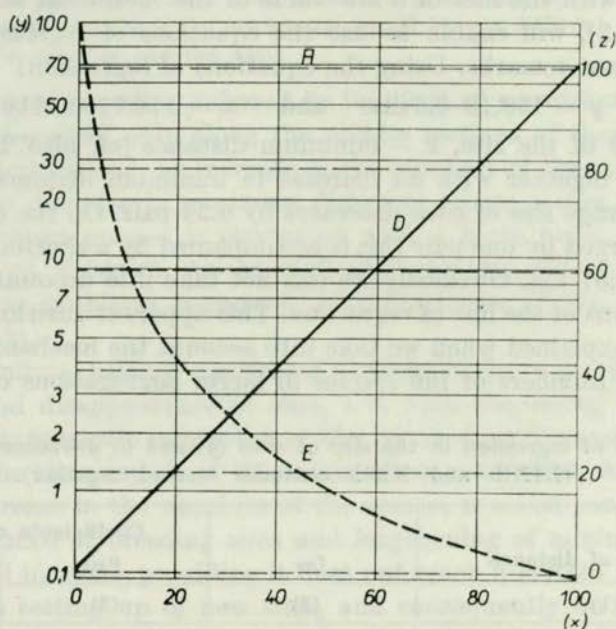
TERRITORIAL PREFERENCE

Inasmuch as η_{yx} indicates a functional connection of the values discussed, then their reverse correlation, i. e. correlation ratio η_{xy} occurring between minimum distances and the size of sites enables to discover the real biological significance of this connection. The dependence of the distance on the size of sites can be interpreted as a territorial preference of newly settled micropopulations (or flocks) when occupying free breeding areas in relation to the position and size of already existing sites. Minimum distances between these latter and newly found breeding sites can be treated as an index of this preference in relation to already existing sites.

When discussing preference we have to consider first of all, at least from a general point of view, what are the possibilities of its realization.

Assuming, in order to simplify the problem, that the resources of habitats suitable for the species are limited and that their total amounts $= 100\%$, then we shall take the numbers of the species as 100% when it reaches the highest carrying capacity of the resources mentioned. In the case of such an assumption any numerical level expressed in per cent would coincide with the same per cent of the occupied habitat which means that a rectilinear correlation would occur (graph 5, straight *D*). The ratio of the area of the occupied habitat (*a*) to the reserves (*b*) could then be expressed by the course of curve *E* along a vertical axis plotted in the logarithmic scale. And thus $E = \frac{a}{b}$. Leaving aside the degree of environment resistance encountered by each individual settling in the reserve part of the environment resources, co-efficient *E* indicates the degree of possibility to choose the breeding site between occupied and free habitats which would be enjoyed by each of newly arriving flocks, or each of newly arriving individuals. And if the numbers of 20% coincide with the possibility of choosing between an occupied or a free habitat in the ratio of 1 : 4, then an increase in the numbers to 60% alters the possibility of preference to 1 : 0.66, while at 90% it rapidly decreases ($E = 1 : 0.11$).

On the basis of long field observations and an analysis of materials derived from the literature on the subject (JÓZEFIK, 1957, 1969) the author has found out that the choice of place for setting up a new colony (or a site) is limited in a large number of cases to settling in a most suitable for the species habitat in the close neighbourhood for the existing sites. The power of social attraction, a tendency to territorial integration contribute to the fact that territorial preferences of separate micropopulations are motivated by the intraspecific factors mentioned to at least the same extent as by the ecological

Graph 5. A simplified pattern of relating the possibilities of territorial preference to the numerical increase of the species. x — area of habitat resources (breeding habitat); y — $100°$ logarithmic scale of co-efficient E; z — numerical state of the species in per cent; A — carrying capacity of the habitat, D — curve presenting the increase in the species numbers, E — curve presenting the coefficient of preference possibility.

attractiveness of the given habitat. And here we have sufficient evidence for explaining the fact, so far not explained satisfactorily either by zoogeography or by applied biology (particularly evident in protective activities, hunting, and acclimatization), that in spite of the existence, in certain parts of the range, of a relatively artificial production of considerable, ecologically attractive habitat resources, they were not properly used up by the species. The existence of unused habitat reserves has been proved by a drastic increase in the numbers of *A. ralloides* in the years 1960–1968 in the palearctic part of the range (JÓZEFIK, 1969).

Judging by the relatively high value of η_{xy} ($= 0.712$), the possibility of choosing from the entire range was quite considerable, although there were also evident influences of other environmental factors (probably the biocenotic composition of breeding mutuants).

NUMERICAL OSCILLATIONS AND THE DEGREE OF ISOLATION

Concluding from the distribution of data in the preparatory correlative table, the dispersion of the parameters discussed is quite moderate, and this, when coupled with the fact of a low value of the coefficient of curvilinear regression (Table 2), will enable to use the equations of regressions for making several important remarks. Using the equations of regression:

$$y = 159.19 - 0.542x \quad \text{and} \quad x = 178.77 - 0.871y,$$

where y — size of the site, x — minimum distance (cf. also Table 3), we can conclude that together with an increase in minimum distances by each kilometer, the average size of sites decreases by 0.54 pair. On the other hand when the site is enlarged by one pair this is accompanied by a shortening of minimum distances by 0.87 km. Obviously we can not take into account here the initial and final sections of the line of regression. This apparent „arithmetical paradox" will be easily explained when we take into account the mechanism of numerical changes in the numbers of the species in larger aggregations of breeding sites.

Table 3. Indices of regression in the size of sites (y) and in distances between them (x) (XIXth and XXth centuries treated together).

Category of distance	r_{xy}	Coefficients of regression	
		$a_{x(y)}$	$a_{y(x)}$
(1)	(2)	(3)	(4)
Maximum (5)	− 0.274	− 1.374	− 0.055
Minimum (6)	− 0.687	− 0.871	− 0.542
Average (7)	− 0.846	− 2.958	− 0.243

I shall start from the second case, i.e. from the increase in the numbers of the species in the group of sites in the sphere affected tby the factor contributing to this phenomenon. Theoretically this increase is possible only to the limit of the habitat carrying capacity within the given site. Observations ought to be started at the moment when the numbers of the sites are sufficiently high (we are to observe not the formation of aggregations but their growth). Only when the numbers constantly increase can there occur an overcrowding in the aggregation leading to the setting up of a new breeding site, while the distances remain intact. After the new site has been founded its position is, as a rule, fixed in the outlying parts of the grouping and thus it only insignicantly affects the average value of minimum distances (this average value could be more seriously affected only in the case of locating the newly founded sites inside the aggregation). Hence, a considerable numerical increase can be accompanied by a twice smaller decrease in minimum distances.

A reverse process, i.e. a general decrease in the number of breeding pairs in the aggregation and a disappearance of breeding sites occur somewhat differently. I shall discuss here

a theoretical variant of situations typical for the Squacco Heron in the last few decades. A disappearance of a site (cf. Józefik, 1969; 1970) is not necessarily connected with a gradual decrease in the number of breeding pairs and it need not take place centripetally inside the aggregation. It is predominantly caused by destructive activities of man and it includes, as a rule, sites in the center of the aggregation. A disappearance of even one single site in the center is connected with a sudden increase in the average value of minimum distances, while there is no certainty that the numbers start decreasing straightaway — the birds can remove to the remaining sites or they can form a new site at the edge of the aggregation. Hence a slow decrease in the numbers is accompanied by a more drastic decrease in the average value of minimum distances. The pattern drawn above is directly connected with human activities limiting the species. In cases when other factors affecting the situation of the species occur (e.g. climatic changes), the mechanism would have a different character but its effect would remain more or less the same.

Both the mechanisms when referred to the lines of regression act according to the pattern described only along the middle sections of these lines. It can be briefly stated as follows: an increase in the numbers of the species is accompanied by a slow decrease in minimum distances (there occurs a spatial overcrowding). A reverse process is connected with a more rapid lengthening of these distances (cf. Table 6). As we shall see later this will be important for explaining certain problems connected with pulsations of the borders of the range (cf. page 21).

As in a definitive balance numerical oscillations have to correspond with the setting up and disappearance of sites, i. e. with shortening or lengthening of minimum distances, the regression of the parameters discussed here throws some light on the time aspect of the mechanisms mentioned. And thus, when almost each decrease in the numbers of the species is accompanied by an adequate disappearance of breeding sites and lengthening of minimum distances, then a numerical increase, providing it does not reach a certain level, will have no effect on the setting up of new sites, and consequently on the shortening of minimum distances. This level is exceeded when the ecological carrying capacity of sepaate sites is reached. This is followed by a relatively intensive territorial expansion, i. e. the setting up of new breeding sites and changes in the composition of minimum distances. As expansion here consists not only in an increase in the area of the range, but mainly in an increase in the number of sites within the aggregation, this has ist bearing on a general decrease in minimum distances.

The mechanisms discussed enable us to learn more about the essence of sporadic sites. Obviously I am not referring here to sites which appeared as a result of the removal of a given micropopulation caused by the persecution of the birds. Each culminating numerical increase in the cycle of long (many years) oscillations and the territorial expansion of the species are connected with the formation of numerous small dependent sites situated in the outlying regions of larger aggregations and in the border zone of the range. The ensuing, up to the next culmination, case of a decrease in the numbers of the species is connected with the disappearance of these sites. A few years long periods

of the functioning of those sites are quite characteristic, as well as breaks last-
ing many years.

Considering the problem from the point of view of secular changes in the
numbers and taking into accout the fact that they were very considerable
(Józefik, 1969), we come to the conclusion that there are no statistically signi-
ficant differences either between average values of separate categories of
distances calculated only for the XIXth century and then for the XXth century,
or between standard deviations characteristic for these average values
(Table 4). A similar conclusion follows from the comparison of the distribution of
these distances set up separately for the XIXth and the XXth centuries (graphs
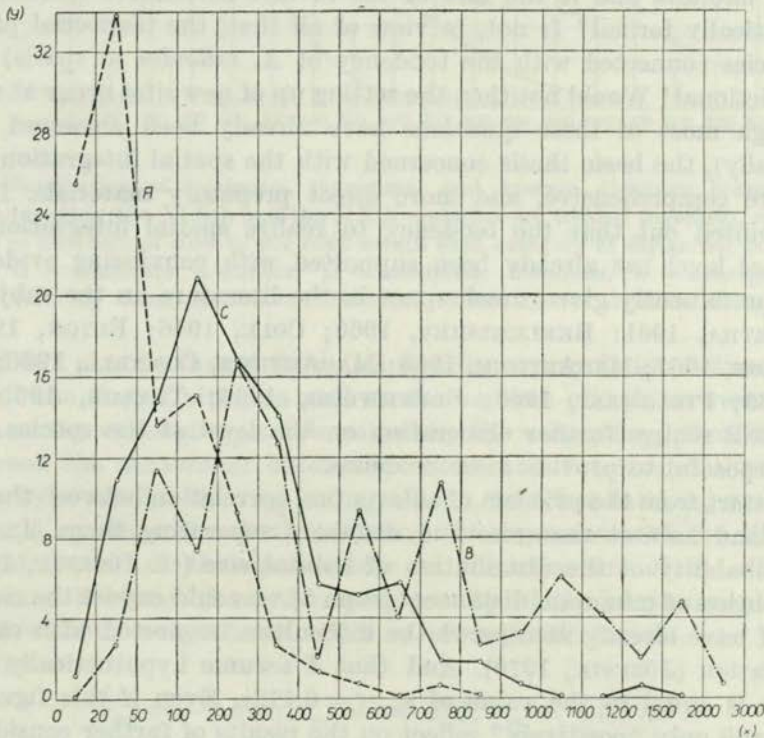6 and 7).
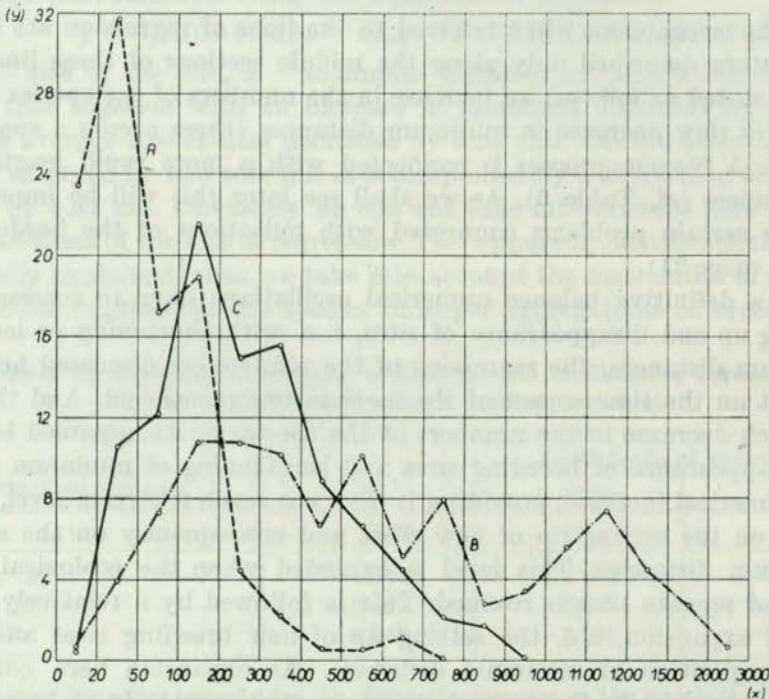
Graph 6. Distribution of minimum, maximum, and average distances between *A. ral-
loides* breeding sites in the XIXth century irrespective of their direction. *x* — distance
(in km); *y* — number of sites in per cent within each category of distances; curves of distri-
bution: *A* — minimum distances, *B* — maximum distances, *C* — average distances.

Summing up, it should be stressed that irrespective of considerable secular
changes and cyclic numerical oscillations, the species maintains the same,
not exceeded (in the meaning of the highest tolerated dispersion) density within
the range. As the acceptance of a given degree of isolation depends on the size
of separate micropopulations (cf. page 3), a drop in the numbers of the spe-
cies is always connected with the disappearance of small sites (sporadic ones),
and moreover it is connected with territorial regression.

Table 4. Characteristic features of distances between breeding sites of *A. ralloides* (in km).

Statistical characteristics (2) Distances (1)	Century (3)	n (4)	$\bar{x}$ (5)	t of the difference (6)	$\sigma_{\bar{x}}$ (7)	t of the difference (8)	D (9)
Maximum (10)	XIX	176	518	0.451	384	0.034	183
	XX	160	499		383		280
Minimum (11)	XIX	176	86	0.168	105	0.948	29
	XX	160	88		113		24
Average (12)	XIX	176	243	—	396	0.418	131
	XX	160	243		409		123

Graph 7. Distribution of minimum, maximum, and average distances between *A. ralloides* breeding sites in the XXth century irrespective of their direction. x — distance (in km); y — number of sites in per cent within each category of distances; curves of distribution: A — minimum distances, B — maximum distances, C — average distances.

SPATIAL INTEGRATION OF THE SPECIES

Irrespective of the evidence discussed above and concerned with the spatial integration of the species (tendency to combine groups in aggregations, dependence of the size of micropopulations on the degree of their isolation, mechanisms realizing the territorial preference of the species, maintenance of certain density in the range irrespective of numerical changes), we are still faced with certain doubts. And thus, if a relatively high value of η_{xy} (minimum distances) indicates the tendency of the species to reach its optimum density and shows the existence of considerable possibilities to realize the territorial preference of the species, then how this is connected with the eventual correlation of the size (meaning by that rather area) of marsh-land habitats unevenly distributed in the range, occupied by *A. ralloides* or still unoccupied, and minimum distances separating those habitats? Are we to look for the causes of correlation η_{yx} just here? Is co-efficient η_{yx} a reflection of the dependence of the size of marsh-land habitats on the gradient of minimum distances separating these habitats and is the fact of the reverse correlative relationship η_{xy} only statistically formal? Is not, in view of all that, the territorial preference of the species connected with the tendency of *A. ralloides* to spatial integration only fictional? Would not then the setting up of new sites occur at random?

Although most of these questions have already been answered (even if only partially), the basic thesis concerned with the spatial integration requires fuller, more comprehensive, and more direct prepatory materials. It should also be pointed out that the tendency to realize spatial integration on the populational level has already been supported with convincing evidence and has been prominently given much space in the literature on the subject (e. g. ANDREWARTHA, 1961: BEKLEMISHEV, 1960; COLE, 1946; ELTON, 1966; LEWIS, TAYLOR, 1967; MACARTHUR, 1966; MACARTHUR, CONNELL, 1966; MACFADYEN, 1963; PIELOWSKI, 1966; SOUTHWOOD, 1966; TAYLOR, 1965; WATT, 1966), it still reqires further elaboration on the level of the species. Thus it will be purposeful to provide more evidence.

I shall start from the problem of an eventual correlation between the amount of marsh-land habitat resources and distances separating them. Judging by a high probability of the distribution of habitat size (cf. JÓZEFIK, 1970) and the distribution of minimum distances (graph 8) we could expect the correlation to occur. I have already mentioned the difficulties connected with calculating this correlation (JÓZEFIK, 1970). And thus I assume hypothetically that the correlation is equal to the value of η_{yx} ($= 0.712$). Even if this figure is too high, this will only "positively" reflect on the results of further considerations. As r_{xy} differs only insignificantly from η_{xy} (cf. Table 2), in further calculations I shall use the multiple correlation, it will be more convinient to operate only with coefficient r. I shall only mention that the evidence is based on the measurement of minimum distances between separate sites.

According to the hypothetically assumed equality of the correlation between distances (x) and the size of sites (y), and the amount of habitat resources at separate points of the range (z) we shall have: $r_{xy} = r_{xz} = -0.687$ (cf. Table 2).
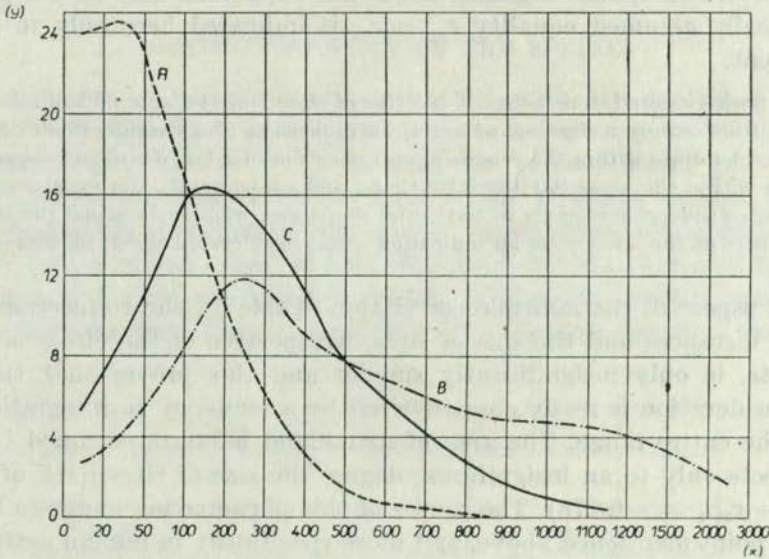
Graph 8. Distribution of minimum, maximum, and average distances between *A. ralloides* breeding sites (the XIXth and the XXth centuries are treated together). x — distance (in km); y — numbers of sites in per cent within each category of distances; curves of distribution: A — minimum distances, B — maximum distances, C — average distances (moving mean of directed distances calculated for separate sites).

I shall still assume that if there is a significant correlation between the distances and the size of sites, as well as the amount of habitat resources, and inasmuch as the value of r_{xy} is determined by the value of r_{xz}, then the correlation between the amount of habitat resources and the size of sites, i. e. r_{yz}, ought not to be smaller than r_{xy} and r_{xz}. If, on the other hand, r_{yz} really differs from r_{xy} and r_{xz}, then the thesis assuming the dependence of the structure of spatial distribution of the species only on the structure of the distribution of marsh-land habitats, (i. e.) the heterogeneity of the environment, will not be proved without a significant effect of intraspecific factors.

And thus:

$$r_{xy} = -0.678; \quad r_{xz} = -0.678; \quad r_{yz} = +0.378$$

The last value has been arrived at in the following way: on the basis of data from the literature on the subject (JÓZEFIK, 1969), and on the basis of precise maps I have calculated the area of marshland habitats in square kilometres of 45 breeding sites. These sites were chosen with the help of the table of ran-

dom numbers out of the number of 211 sites recorded in the palearctic part of the range (cf. Józefik, 1969). These values were taken for calculating the value of r_{yz}.

The low value of r_{yz} indicates that the thesis rejecting the effect of intraspecific factors on spatial organization is not supported here as the previously hypothetically assumed equality $r_{xy} = r_{xz}$ is indicated here only to a certain small extent.

A low positive correlation between the size of sites and the area of habitats should be interpreted (this is only a digression) as: a) an indication of a considerable differentiation of marshland habitats within the range; b) an indication of a low density of separate micropopulations within the areas habitated by them, and consequently the existence of habitat reserves and considerable chances of territorial preference with an eventual further increase in the numbers of the species; c) an indication of a considerable effect of factors limiting the species.

In the aspect of the multiple correlation (Table 5), the connection between minimum distances and the size of sites, irrespective of the effect of the area of habitats, is only insignificantly smaller and this proves that the species under consideration is really characterized by a tendency to integration in the scale of the entire range. The area of marshland habitats occupied by *A. ralloides* affects only to an insignificant degree the size of sites (lack of any correlation — $r_{23\cdot1} = -0.178$). The causes of this phenomenon ought to be looked for in the point mentioned above, and more specifically in human activity comprehensively limiting the species (cf. Józefik, 1969; 1970).

Table 5. Multiple correlation between minimum distances (x), the size of sites (y) and the area of marshland habitats (z) on which the sites are situated.

Correlation of features (1)	Coefficients of correlation (2)	
	total (3)	partial (4)
$x(1) - y(2)$	$r_{12} = -0.687$	$r_{12\cdot3} = -0.635$
$x(1) - z(3)$	$r_{13} = -0.686$	$r_{13\cdot2} = -0.635$
$y(2) - z(3)$	$r_{23} = +0.378$	$r_{23\cdot1} = -0.178$

There is no satisfactory answer to the question in what specific relation (e. g. a relation expressed by a definite function) remain to each other: size of sites, degree of isolation (or intensity of contacts between micropopulations), and the specific spatial composition of habitat resources. The problem seems to be quite complicated as we have to take into account also other biogeophysical factors determining the size of sites and which are normally not very prominent when we operate with calculations of the total correlation. This connection can be discussed in a more detailed way when we include in the course of our considerations also data on basic environmental factors, when having at our disposal characteristic features of their changeability (particularly in space) we shall be able to obtain seaparate characteristics of their partial cor-

relation. As this will be realized only in the ensuing parts of the cycle, I shall have to restrict myself here to draw only some conclusions based on less accurate premises which will lead only to an initial presentation of the tendencies and connections revealed.

OPTIMUM DENSITY OF THE SPECIES

The arguments quoted here and concerned with the spatial integration of the species testify that *A. ralloides* displays a tendency to try and reach the optimum density (optimum in the meaning of overcoming the effects of isolation between micropopulations). Theoretically it would be such a density at which the combined effects of intraspecific competition and isolation would reach their lowest values. This is well illustrated by the curves of regression for minimum distances presented in graph 3, and for average distances in graph 9. It follows from these graphs that for excessive densities the correla-

Graph 9. Correlation between the size of sites and average distances separating them (the XIXth and the XXth centuries are treated together). x — class limits of average distances; y — class limits of the size of sites; curves of regression: A — mean values of average distances characteristic for separate classes of the size of sites, B — average site size characteristic for separate classes of average distances.

tion between the size of sites and distances between them is changed from a negative to a positive one. Obviously when considering overcrowding I use not a direct index of the number of pairs per square kilometer, but an indirect one — distances between sites, as in the case of an irregular, mosaic-like pattern of the occurrence of marshland habitats, and especially in the case of their considerable ecological diversification, a direct index would not reflect spatial relations between micropopulations.

As to minimum distances the problem of optimum density has already been discussed (cf. page 10) and I have stated that optimum distances turned out to be between 15 and 35 km. Average distances, those representing a more proper relation of density in the range, are, judging by graph 9, distances between 30 and 50 km, although even sites situated at a distance of 130 km often reach considerable size. For dissipating any possible doubts I want to stress once again that the criterium of an optimum density is to be looked for in the highest values of site size occurring together with the shortest distances between them.

And here are certain facts from the history of *A. ralloides* in the light of the regularities presented. As I have mentioned already (JÓZEFIK, 1969) the numerical level of sites in the range continued decreasing in the period 1940–1960 in spite of an absolute increase in the number of breeding pairs. This apparent contradiction will be easily explained when we consider the numerical dynamics of the species and the sites in which it occurs from the point of view which takes into account the fact that the species displays a tendency to form aggregation with optimum density and when we know the factors limiting the species. And thus in certain regions of the Transcaspian area or of the Hungarian Plain where small sites were dispersed, the disappearance of even a few of them (land-reclamation) resulted in the extinction of many others in these areas, as this led to overstepping the critical value of the highest dispersion of the species. In the same period there also occurred a relaxation in direct persecution and reduction of the Squacco Heron in the region of larger sites or even in entire aggregations, and this evidently led to an absolute increase in the numbers up to the full use of the ecological capacity of the habitats there and the occurrence of overcrowding (cf. Józefik, 1970). Thus there was an increase in the number of breeding pairs in the scale of the entire range with a simultanous decrease in the number of breeding sites.

In the period mentioned there was also a transformation of a large part of the area of habitats typical for *A. ralloides*, but mostly within the limits enabling the species to adapt themselves to the altered conditions. And here we are faced with a very important problem necessary for understanding the mechanisms of changes in the range of most species habitating in colonies distributed in a mosaic-like pattern. I have assumed, to simplify the problem, that the habitat transformation as far as the numerical state of the population is concerned, occurred proportionally within the entire range. Thus in regions characterized by a low density of breeding sites or points in habitats typical for the species, the lengthening of average distances between micropopulations when certain such points are done away with (a high degree of transformation) is much more intensive than in the case of areas with a high level of density. The process of getting adapted to moderately transformed habitats is accompanied by a general decrease in the numbers (cf. JÓZEFIK, 1970) which in regions with a low level of density is connected with overstepping the critical value of the highest possible dispersion by the population habitating there and leading in cõnsequence to the disappearence of the species. In the regions where there is a considerable concentration of habitat resources all the aboriginal habitats are occupied in which the increasing intraspecific and interspecific competition acquires great importance and this forces part of the individuals to adapt themselves to the transformed habitat and this enables the population to maintain a level of density approximating the optimum one. Social attractiveness stimulates this process and prevents the formation of čonsiderably isolated new sites, as well as hampers the use of non-transformed but dispersed resources of breeding habitats. We can easily imagine that social connections, forcing separate micropopulations to maintain the necessary density in the range, leave the species no other way but to adapt themselves to the transformed habitat in the area of larger groups of sites, and thus they intensify the process of the synanthropization of the species.

PULSATION MECHANISMS OF THE BOUNDARIES OF THE RANGE

On the basis of the equations of regression:

$$y = 165 - 0.243x \quad \text{and} \quad x = 560 - 2.954y$$

we can detect, similarly as in the case of minimum distances (cf. page 12), the phenomenon of a more rapid lengthening of average distances when the size of sites decreases as compared with the shortening of these distances when the sites become larger (cf. Table 6). Differences in the rate of changes are here, however, smaller — distances lengthen 2.13 times faster, together with a decrease in the size of sites, in comparison with the rate of shortening when the size of sites increases, which could be observed in relation to minimum distances, but still it amounts to 1.41 (Table 6). How will the regularity described reflect on the pulsation mechanism of the boundaries of the range (cf. JÓZE-FIK, 1969)?

When the numbers of the species start increasing, distances between sites are shortened more slowly — there comes the phase of numerical cumulation. The borders of the range remain in this period intact. An increase in the size of sites can proceed until the limits of the ecological capacity of the given breeding area are reached. When this limit is overstepped, the intraspecific competition is drasically intensified and its pressure forces part of the micropopulation to resettle outside the boundaries of the range. Thus there occurs a restitution of the species in the regions of the previous regression (e. g. the present situation of *A. ralloides* in the Transcaspian part of the range).

When there is a further eventual increase in the numbers of the species and the habitat reserves are exhausted, the vagility of separate populations is intensified. If even in more distant regions far from the initial range there are habitat sthe occupation of which will not be connected with considerable adaptative efforts, or which will depend on the overcoming of a natural geographical barrier, a territorial expansion connected with population explosion of the species will follow (a classicial example of this phenomenon is at present the world--wide expansion of *Ardeola ibis*). Cases of the latter type, far exceeding the usual, in the case of many years long cycles, pulsations of boundaries of the range, belong to relatively rare phenomena.

The phase of numerical cumulation, which is followed by a relatively rapid changes in the boundaries and an increase in the area of the range (phase of expansion), is characterized generally by a disproportion between the rapid rate of numerical increase and a gradual shortening of distances between separate sites. In the phase of expansion, when around the larger overcrowded sites we can record the appearance of numerous small dependent sites (mainly sporadic), such distances are drastically shortened, although only in the central parts of the range as the border distances will be lengthened due to the appearance of new sporadic sites.

The second possibility, i. e. a decrease in the numbers of the species, as it follows from Table 6 (set up the basis of the equations of regression)

is connected with an unproportionally more intensive, as compared with this numerical decrease, lengthening of distances between breeding sites. This phenomenon indicates that even when the numbers of the species decrease only insignificantly in the depth of the range, the pressure of intraspecific competition will be relieved. This will spark off a sudden outflow from the extreme zone in the outlying districts of the range of a part of micropopulations into the central regions until the competitional tension is levelled off. Thus most of small sites will disappear, and consequently distances between larger ones will automatically increase. This will be additionally accompanied by a limiting effect of the increased degree of isolation. Inasmuch as in certain regions the density of sites was not very high, then they will probably disappear there completely in a relatively short period of time, while the area of the range will shrink.

Recapitulating, an increase in the area of the range as part of the pulsations of its boundaries and also the expansion of the species is preceded by the phase of numerical cumulation. And thus not each apogee of numerical oscillations (cyclical fluctuations) is connected in time with an adequate increase in the area of the range, while each numerical drop results in a clear-cut retraction of the boudaries of the range. Hence the centrifugal shifting of the boundaries is much more drastic and sudden, while the centripetal one takes place more slowly and gradually. It can be supposed that the course of the curves presenting numerical oscillations and pulsations of the range (meaning here the size of the its area), although they can be similar, can coincide in time only in the phase of falling down.

Table 6. Average interrelationship between the size of *A. ralloides* breeding sites and distances between them.

Distances (1)	Changes in the size of sites (2)		Differences in the rate of changes in the numbers of the species and distances (5)
	increase by ... (number of pairs) (3)	decrease by ... (number of pairs) (4)	
	↓	↓	
Minimum (6)	1.00 − 0.87	1.00 − 1.85	→ 2.13 ←
	1.15 − 1.00	0.54 − 1.00	
Average (7)	1.00 − 2.95	1.00 − 4.16	→ 1.41 ←
	0.34 − 1.00	0.24 − 1.00	
	↑	↑	
	decrease by ... (number of km) (8)	increase by ... (number of km) (9)	
Changes in distances between breeding sites (10)			

To what an extent this dependence is close in the case of *A. ralloides* is impossible to determine at present in view of the lack of sufficiently accurate materials. This problem has been touched upon here because changes in the boundaries used to be connected, in a simplified way, predominantly with numerical oscillations and the effect of external factors determining this oscillation. The pattern described here, although based on indirect premises, indicates that the mechanism of changes in the boundaries of the range is closely connected, among others, with the social peculiarities of the species, with its tendency to maintain their optimum density.

MECHANISM OF DISJUNCTION FORMATION

There is still relatively little information on various conditions contributing to the formation of disjunction, and because of that it might be useful to devote more attention to this problem, at least within the limits of the correlation discussed above (cf. page 4). I have stated before, when discussing η_{xy}, that newly settled flocks limit their choice of breeding site to places in the nearest neighbourhood of the existing sites. And thus increasing ranges are, as a rule, compact. I have also discussed previously (cf. page 22) the mechanism connected with a decrease in the numbers of the species and the retraction of the boundaries of the range — the tendency of the species to form aggregations prevents the occurrence of disjunction. A classical example here is the withdrawal of *A. ralloides* from its sites in the drainage area of the Aral Sea, Persian Gulf, and some other regions in the Middle East in the period of regression between 1880 and 1920 when the eastern boundary of the range was shifted, on average, by about 1,200 km to the west (JÓZEFIK, 1969). The disappearance of the species investigated within the area mentioned was undoubtedly caused by a numerical decrease in its central regions (JÓZEFIK, 1969), and it can not be explained by either the stepping up of human interference or climatic changes, or even by the pressure of other factors, as just in this part of the range the factors mentioned were relatively stable at the turn of the century. If the Transcaspian population had previously been so numerous and if it had reached a suitable level of density so that irrespective of a drop in the numbers of the Caspiana nd Caucasian populations it could maintain itself independently in its winter ranges outside the breeding period, then it would have had chances to realize a classical disjunction. Most probably then not only a geographical isolation but also genetical one would follow in its turn.

It is important to clear up the problem of a "directional" revealment of the features integrating the species in order to gain a more comprehensive understanding of the spatial structure, and consequently of the conditions conducive to the formation of disjuctions. The term "directional" revealment should be here interpreted in the following two aspects: 1) as an interrelationship of the previously considered pecularities of micropopulations neighbouring

upon each other in the parallel cross-section, i. e. in direction W — E; 2) of micropopulations neighbouring upon each other in the meridian cross-section, i. e. in direction S — N. We are concerned here with the problem to what an extent, in connection with the spreading of the range in the parallel direction, separate micropopulations can maintain autonomy in respect of changes taking place in their surrounding at the sites neighbouring upon them to the east and to the west, and also those situated to the north and the south.

If the average distances are an exponent of the combined effect of the geographical distribution of habitat resources, the degree of isolation, and the territorial preference of separate micropopulations, then the correlation of these distances calculated separately for the parallel cross-section of the range and its meridian profile in respect of: a) average number of sites (r_{xa}), b) average size of sites (r_{xb}), c) average numerical state of the species (r_{xc}), will enable to determine directionally the dependences mentioned.

Table 7. Correlation of average distances between breeding sites (x) in respect of the average number of sites (a), average size of sites (b), average numerical state of the species (c) in the parallel and meridian cross-section of the range (material calculated for the XIXth and the XXth centuries jointly; the value of class limits in the two cross-sections = 4° of latitude and longitude).

Coefficient of correlation (1)	Cross-section of the range	
	meridian (N—S) (2)	parallel (W—E) (3)
r_{xa}	—0.572	—0.648
r_{xb}	—0.647	—0.384
r_{xc}	—0.533	—0.533

The data for the parameters mentioned were calculated here for each part of the range encompassed in a square 4° of latitude by 4° of longitude. Thus in the parallel cross-section the squares include breeding sites between parallels separated by 4° of longitude, while in the meridian cross-section they include sites between meridians separated by 4° of latitude. It should be mentioned that the palearctic part of the range of the Squacco Heron stretches from east to west along 80° of longitude (on average 6,500 km), while from south to north along 20° (on average 2,200 km) (JÓZEFIK, 1969).

The correlation between average distances and values a, b, c is obviously negative and not very high. The low values of r are the result of the curvilinear character of the correlation (cf. page 4), here they are only for the sake of comparison.

In the case of r_{xa} the highest correlation is in the parallel cross-section (r_{xa} = —0.648) and somewhat lower in the meridian cross-section (r_{xa} = —0.572)

— the difference is statistically significant. This indicates that the number of sites in the given region depends, to a larger extent, on the presence of other sites neighbouring upon them to the west and to the east, than on the presence of sites to the south or to the north. And thus the possibility of the formation of disjunction largely depends on the parallel density of breeding sites. The Sahara disjunction, levelled off in recent years by the settling of the Squacco Heron in the valley of the Lower Nile, forms here an obvious exception*).

What determines in the two cross-sections the average size of sites? Coefficient r_{xb} reaches its highest value in the meridian cross-section (-0.647) and is almost twice as high as r_{xb} in the parallel cross-section (-0.384). It is known to what extent the size of sites is connected with distances between them (cf. page 7). Distances along the line of W — E are considerably longer than along the line of N — S, and consequently in the cases of overcrowding it is most probably eased meridionally, i. e. in the direction of migrations, although the birds are provided with better chances of preference parallelly. It should also be remarked that the preference is realized in the final phase of spring migrations and thus there are more chances that, for instance, young birds will settle in a new breeding area more to the north or to the south in respect of their primary breeding site, than to the east or to the west. The trek of *A. ralloides* in western or eastern directions is well known but only along such sections of the range where the spatial distribution of habitat resources prevents any other movements (e. g. recent situation along the northern coast of the Black Sea). Only at a very low index of the possibility of territorial preference (probably when $E < 0.5$–0.2; graph 5) the resettling is carried out not in the direction of migrations but parallelly and is expansive in its character.

In the latter case (r_{xc}), when we take into account the hierarchy of interrlationships, then the size of sites depends on environmental factors and on the social structure of the species, while the number of breeding sites partly depends on their size, while the numbers of the species are indirectly determined by these two parameters. In consequence, the correlation between average distances and the numbers of the species, i.e. r_{xc}, is only indirect and functionally determined. From a logical point of view, it should be expressed in more or less the same way in the two cross-sections, and this is really so as the value of r_{xc} is the same in the two cases (it amounts to -0.533; cf. Table 7).

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*) Formally, as it has been pointed out the majority of faunistic works, that this disjunction stretched over the area of about 2,000 km, while de facto, starting from the 40° line of northern latitude, it amounted, up to the sixties of the present century, to 2,600 km. Although the palearctic and central African populations contact with each other in the course of winter, we have at our disposal no facts which would indicate the occurrence of a genetical exchange between them. As it will be shown in the ensuing parts of the cycle, the two populations are isolated not only phenologically but they also differ ecologically. It is not excluded that they can form two separate subspecies. A taxonomical processing of materials from the two parts of the range belongs to the nearest future. At present the most interesting seems the population occupying the lower courses of the Nile.

Thus we are in a position to put forward an important conclusion: connections integrating the species are much more prominent in the meridian direction, i. e. in the direction of the most intensive physical contacts between separate micropopulations. Parallelly separate micropopulations maintain more autonomy which probably disappears with the occurrence of overcrowding (cf. Table 8). This autonomy ought to be treated as a potential possibility of disjunction. This enables to draw several conclusions, partly hypothetical in their nature, and concerned with causal connections occurring between the structure of the spatial distribution of the species and its evolutional destiny:

1) In the conditions of the optimum environment the numbers of the species increase and the parallel autonomy of the population disappears. The genetical flow is intensified, while the chances of fixing the directed variability of separate populations are decreased; the rate of microevolutional changes is a minimum one. This state, characteristic for the cumulative phase, is changed when the species enters its expansive phase.

2) In the case of a tendencious deterioration of environmental conditions over the entire range (c. g. pressure of the anthropogenic factor, cf. JÓZEFIK, 1969) when the numbers of the species considerable decrease, the autonomy of separate populations or micropopulations increases parallelly (they still remain closely integrated in the meridian cross-section), which leads, as the numbers of the species continue to fall down, to disjunction and genetical isolation between some of them. The deepening stress of the environment leads to the critical numerical state, increases mutability and sharpens selection. New features spread more quickly when numbers of the population are low. The rate of microevolutional processes is increased. The populations which survived are characterized by the divergence of features — these are the initial stages of speciation.

Ant thus the processes of speciation can occur more intensively not only as a result of an increase in the numbers of the species, its expansiveness over the new areas, and in consequence of geographical isolation and the formation of divergent forms. It seems that this phenomenon occurs more often in the conditions of profound environmental changes connected with the formation of the ecological pessimum according to the pattern described above.

To put it more generally, all profound secular changes in the numbers of the species, that is the state of imbalance in the homeostasis of the species, lead to the intensification of microevolutional processes, which has been proved in the case of *A. ralloides*, taking as an example synanthropization, in the previous part of the cycle (JÓZEFIK, 1969).

SPATIAL ISOLATION IN THE CROSS-SECTION ANALYSIS

I have used so far the concept of complete isolation, i. e. when the site is isolated in the radius of 360°. The measure of this type of isolation were ave-

rage distances, as average values of directed distances, which can play a certain role in the determination of directions for postbreeding noma- dic movements. Late summer nomadic movements, and later on migra- tions which are specifically directed, play a considerable role in the joining of flocks in larger groups, the birds of which are derived from various small breeding sites. Postbreeding nomadic movements form an extremely important period for the species in their annual cycle. Separate flocks look for each other
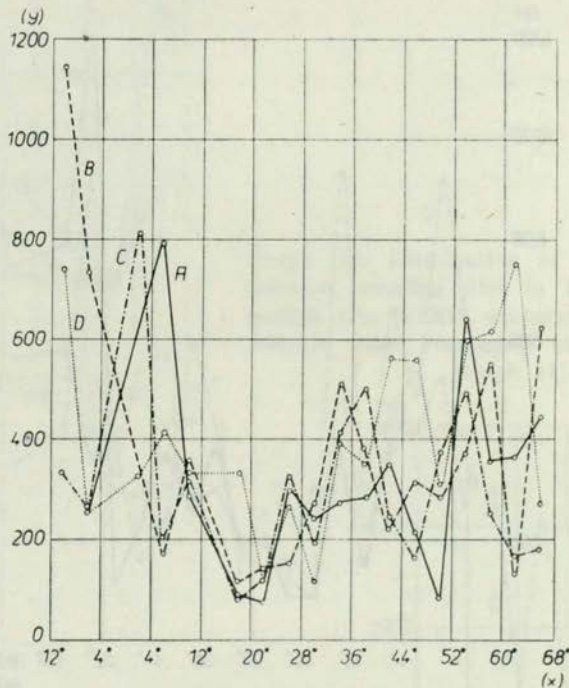
Graph 10. Distribution of directed distances between breeding sites in the parallel cross-section (the XIXth century). x — geographical longitude; y — distance (in km); A — directed distances WN, B — NE, C — SE, D — SW.

very actively in this period, and they take up the most "economical" direction of flight. As it follows from graphs 10—13 the shortest distances both in the previous and in the present century were WN. And really this direction of no- madic movements, not only in the case of *A. ralloides* but also among other Heron species, has been very popular. Migrations in the south-western di- rection are particularly preferred by populations occupying the central regions of the range (cf. curves D in graphs 10 and 11). In the period of spring migrations distances NE assume particular importance. They also belong to the relatively shortest distances (curves B in graphs 10 and 11). I shall return to the problems only touched upon here in one of the next parts of the cycle which will be de- voted to migrations.

The fact that directed distances are balanced is characteristic for the area of the highest concentration of the species. This is particularly evident in the meridian cross-section (graphs 12 and 13). It is easy to realize how the situation of the species changed in the last 100 years in the western and eastern regions of the range when we consider separate directed distances. In the present century, all the directed distances, except those in the central part of
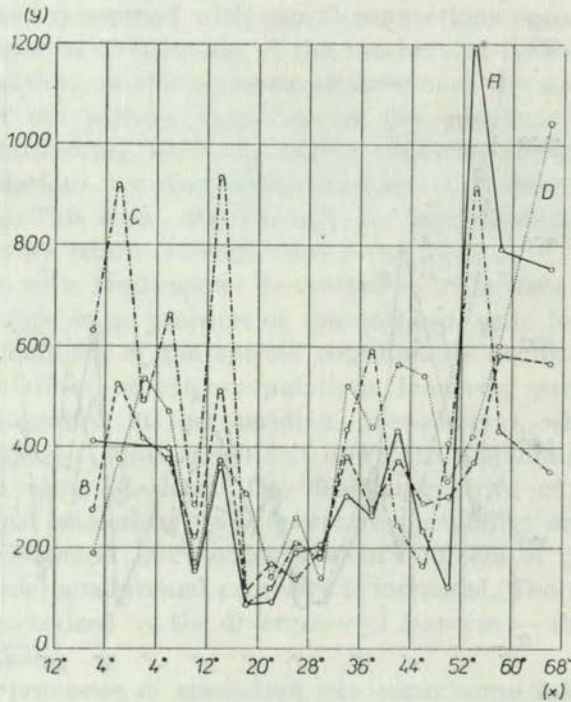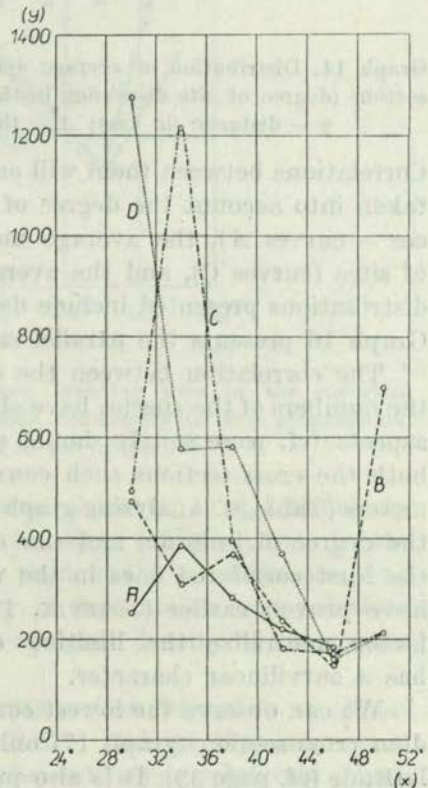

Graph 11. Distribution of directed distances between breeding sites in the parallel cross-section (the XXth century). x — geographical longitude; y — distances (in km); A — distances in direction NW, B — NE, C — SE, D — SW.

the range, were considerably lengthened, particularly in the eastern parts. This is clearly seen in graph 14 which represents the distribution of average distances calculated separately for the XIXth century (curve A) and separately for the present century (curve B). The course of the two curves characterizes the degree of site dispersion in the range. Inasmuch as this dispersion, analysed in the parallel cross-section, was altered only insignificantly in the central parts of the range, and even decreased in the western outlying districts in the XXth century, then the eastern distances were lengthened, on average, by 200–400 km.

The degree of site dispersion in the meridian cross-section is presented in graph 15. It remained almost unchanged in the zone of highest concentration,
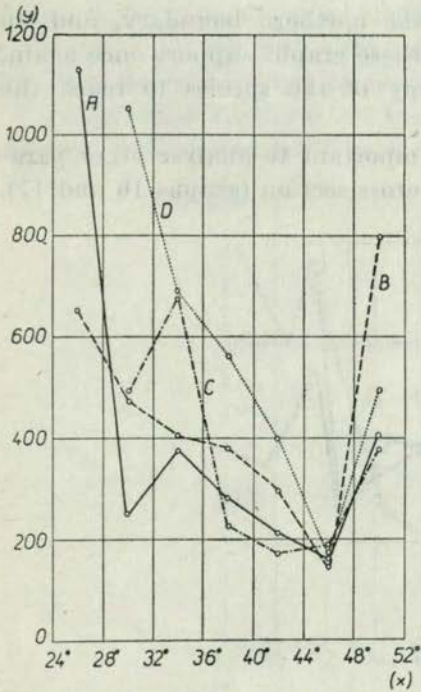
Graph 12. Distribution of directed distances between breeding sites in the meridian cross-section (the XIXth century). x — geographical latitude (the remaining explanations as for Graph 11).

Graph 13. Distribution of directed distance between breeding sites in the meridian cross-section (the XXth century); (explanations as for Graph 12).

while it increased quite considerably along the northern boundary, and, to a lesser extent, along the southern one. Both these graphs support once again, proved already at other levels, the tendency of the species to reach the optimum concentration of breeding sites.

Beside those directed ditances, it is very important to analyse other parameters considered in the meridian or parallel cross-section (graphs 16 and 17).
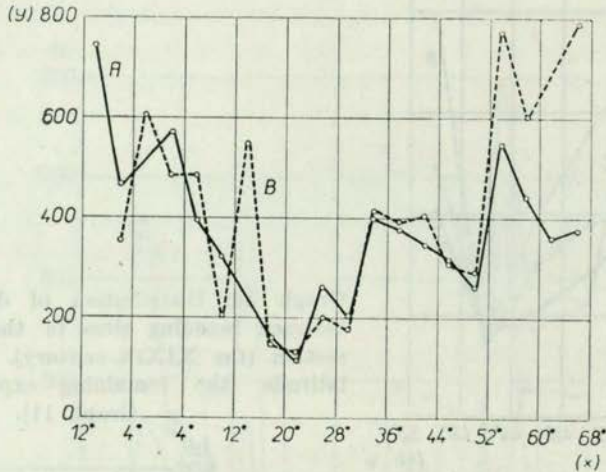
Graph 14. Distribution of average distances between breeding sites in the parallel cross-section (degree of site dispersion in the parallel cross-section). x — geographical longitude; y — distance (in km); A — the XIXth century; B — the XXth century.

Correlations between them will enable to reveal new dependences. Thus I have taken into account the degree of isolation (balanced means of average distances — curves A), the average numbers of sites (curves B), the average size of sites (curves C), and the average numbers of the species (curves D). The distributions presented include data calculated for the two centuries together. Graph 16 presents the parallel cross-section, graph 17 the meridian one.

The correlation between the degree of isolation and the size of sites, and the numbers of the species have already been discussed here previously in certain aspects (cf. page 24). It should only be added now that it does not reach in both the cross-sections such considerable values as correlations of other parameters (Table 8). Analysing graph 16 we can instantly find out that, for instance, the degree of isolation and size of sites (r_{AC}) in the parallel cross-section are the least correlated ones in the western regions of the range. It follows, as I have proved earlier (JÓZEFIK, 1970) from the fact that the anthropogenic factor neutralize the limiting effect of izolation and that the correlation has a curvilinear character.

We can observe the lowest correlation between curves A and C in the meridian cross-section (graph 17) only between the 36° and 40° lines of northern latitude (cf. page 33). It is also purposeful to point out that as the synanthrop-

ization of the species gets gradually more complete, the value of r_{AC} will undoubtedly be lowered yet again. The same can be applied to the correlation between the degree of isolation and other parameters.

As the numerical state of sites, the degree of isolation, and the size of sites are closely connected with each other, the correlation between the numerical
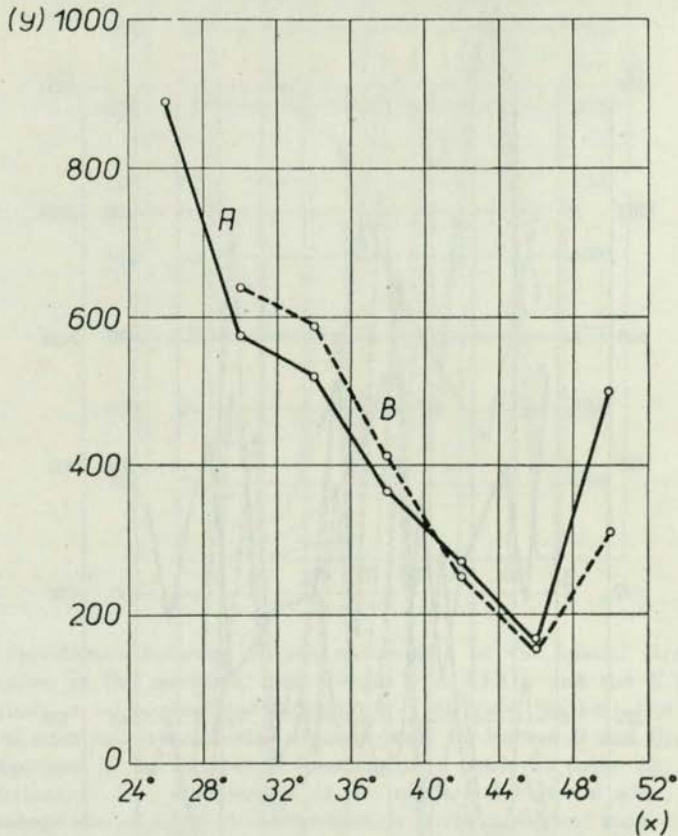
Graph 15. Distribution of average distances between breeding sites in the meridian cross-section (degree of site dispersion in the meridian cross-section). x — geographica latitude; the remaining explanations as for Graph 14).

state of sites and their size (r_{BC}) assumes the same character as r_{AC} (obviously taking into account here the change of algebraic sign) (cf. page. 34). In the parallel cross-section r_{BC} is considerably lower than in the meridian one, and this once again indicates the higher autonomy of separate micropopulations along the parallel (cf. page 25) and testifies to a higher density of the species in the meridian cross-section.

The numbers of the species in the parallel cross-section depend in an almost equal measure, on the size of sites ($r_{CD} = +0.825$) and on their numerical state ($r_{BD} = +0.801$). In the two cases the dependence is relatively consi-

derable. Differences between the values of r_{BD} and of r_{CD} are significant in the meridian cross-section (Table 8). And thus at $r_{BD} = +0.997$ the dependence is almost linear, while at $r_{CD} = +0.767$ the correlation is lower and the difference is statistically significant. This undoubtedly indicates a higher density of the species along the meridians, which is also evident for the reasons discussed below.
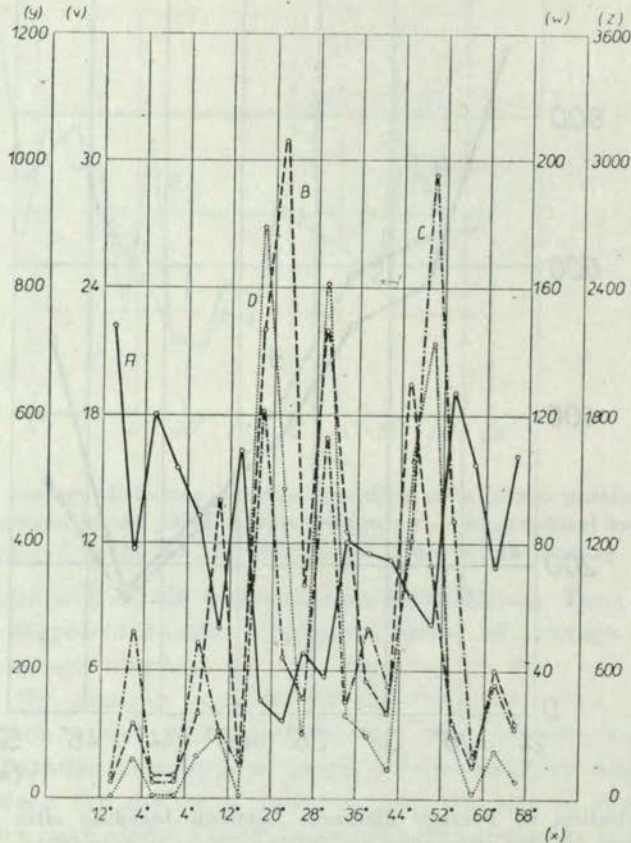
Graph 16. Dependences between certain parameters of the spatial structure of *A. ralloides* distribution in the parallel cross-section of the range (the XIXth and the XXth centuries are treated together). *x* — geographical longitude; *y* — distance (in km) (scale for curve *A*); *v* — number of breeding sites (scale for curve *B*); *w* — size of sites expressed in the number of breeding pairs (scale for curve *C*); *z* — numerical state of the species expressed in the number of breeding pairs (scale for curve *D*); *A* — average distances; *B* — distribution of the numerical state of sites; *C* — distribution of the average size of sites; *D* — distribution of the numerical state of the species.

In the zone of the species concentration, in view of the fact that there are a large number of dependent breeding sites there, i. e. small in reality, the average site size remains relatively insignificant and only in a small degree
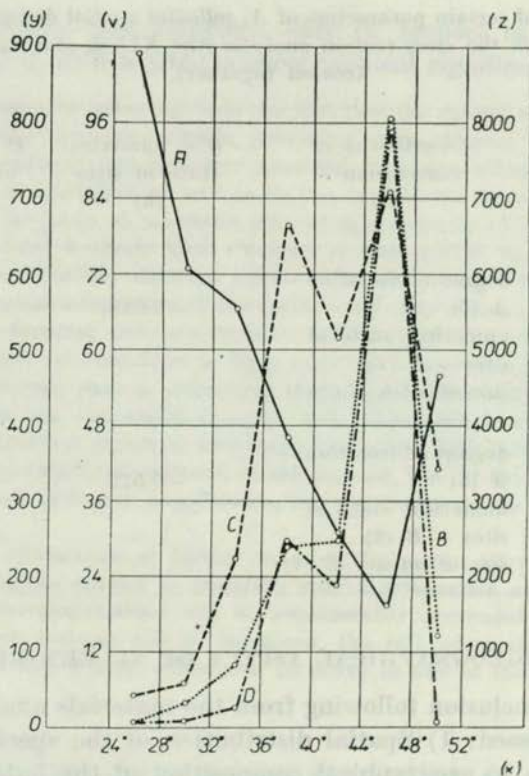
Graph 17. Dependences between certain parameters of the spatial structure of *A. ral-loides* distribution in the meridian cross-section (the XIXth and the XXth centuries are treated together). *x* — geographical latitude; *y* — distance (in km) (scale for curve *A*); *v* — number of sites and average size of sites (scale for curves *B* and *C*); *z* — numbers of the species expressed in the number of breeding pairs (scale for curve *D*); *A* — distribution of average distances; *B* — distribution of the numerical state of sites; *C* — distribution of the average size of sites; *D* — distribution of the numerical state of the species.

it exceeds the averege size between the 36° and 40° lines of northern latitude. The numerical state of sites, in its turn, between the parallels mentioned, is relatively limited, but as I have mentioned before (JÓZEFIK, 1969) those sites are relatively large. Hence, not each class of geographical latitude in respect of the size of sites is characterized by the proportional numbers of the species, while r_{CD} is lower than r_{BD} (Table 8). The lack of overcrowding within the area of separate micropopulations prevents the occurrence of dependent sites between the 36° and 40° lines of northern latitude, and this is caused by an excessive degree of isolation and an unusually intensified effect of the anthropogenic factor (JÓZEFIK, 1969). It should also be stressed here that sites along the latitude discussed here, even in the meridian cross-section, due to their relatively considerable size, retain certain autonomy.

Table 8. Correlation of certain parameters of *A. ralloides* spatial distribution in the palearctic part of the range in the cross-section analysis (the XIXth and the XXth centuries are treated together).

Cross-section of the range (1)	Co-efficient of correlation r (2)	B — numerical state of sites (6)	C — size of sites (7)	D — numbers of the species (8)
Parallel (2)	degree of isolation — A (5)	− 0.648	− 0.384	− 0.533
	numerical state of sites — B (6)	—	+ 0.467	+ 0.801
	size of sites — C (7)	—	—	+ 0.825
Meridian (3)	degree of isolation — A (5)	− 0.572	− 0.647	− 0.533
	numerical state of sites — B (6)	—	+ 0.764	+ 0.997
	size of sites — C (7)	—	—	+ 0.767

ZOOGEOGRAPHICAL ASPECT OF ALLEE'S RULE

In a general conclusion following from the materials analysed the following points can be stressed: 1) Spatial distribution of the species in the breeding range depends on: a) geographical composition of the habitat resources proper for the species, b) its numerical state, c) tendency to maintain the optimum density over the maximum area of the range. 2) Degree of integrational tendency to form aggregations, i. e. to overcome isolation, is revealed more intensively when the species is threatened and its numbers low, although there are still unused reserves of the habitats (cf. JÓZEFIK, 1970). 3) As the numbers of the species gradually increase the tendencies to form aggregations are to a large extent levelled off (although not hindered), in the proximity of the upper limit of the carrying capacity of the habitat, by the effect of the increasing intraspecific competition whose consequence is dispersion and expansiveness.

From the point of view of ALLEE's rule (ALLEE, EMERSON et all., 1958), worked out on the basis of studies on interrelationships between the degree of clumping and the survival of populations, the biological meaning of the tendency to integration displayed by the species as a biological unit is identical. The species reveals its tendency to reach such a relation between the pressure of intraspecific competition and its efforts to form aggregations (the overcoming of isolation and attempts to reach the maximum effect of gregariousness) which can ensure the maximum degree of survival in the long run (e. g. annual cycle). In our case ALLEE's rule has been statistically proved on the basis

of historical materials, and although only in respect of one species, even that fact imparted it with a wide zoogeographical significance.

Also other consequences following from the fact that the species tends to form optimum groupings deserve more attention. Beside providing more chances for survival, aggregations secure better conditions for intensive genetical exchange, which has in its turn quite an effect on the rate of speciation as well as on the evolutionary direction of the species as a whole. Judging on the basis of materials presented previously (JÓZEFIK, 1970), it seems reasonable to put forward a thesis that chances of the species to maintain a uniform genetical structure and definitely directed microevolutional changes increase proportionally to the degree of the spatial integration of the species and they remain inversly proportional to the possibility of forming interpopulational isolation, leading in its turn to further divergencies. Taking into account that a large number of species, mainly social in their character, have enormous ranges stretching parallely, whose differences between the extremes are enormous, we can easily imagine how impossible it would be for them to preserve a relatively uniform genetical structure, how often disjunctions would be formed in their ranges, and how rapidly divergence would proceed, but for the social connections not only within the structure of flocks, populations, but just being visible on a large scale of the entire species.

Together with the elimination of factors reducing the species (birds and beasts of prey) by man, factors forcing the species to maintain spatial integration and social connections, the critical size of micropopulations will be considerably decreased (cf. JÓZEFIK, 1970), the possibilities to form isolates will be enhanced, the rate of speciational processes will be rendered faster. All this I shall endeavour to prove in one of the ensuing parts of the cycle.

CHANGES IN THE DISTRIBUTION STRUCTURE AS AFFECTED BY THE ANTHROPOGENIC FACTOR

As I have proved previously in the case of *A. ralloides* synanthropization, we can discuss the effect of the anthropogenic factor on the species investigated when comparing individual parameters calculated separately for periods singled out in the history of the species under consideration. I shall remind here that both the 2nd half of the XIXth century and the 1st half of the XXth century ought to be treated as periods of direct and indirect reduction in the numbers of the Squacco Heron, while the period after 1950 has been characterized, to a large extent, by a favourable effect of the anthropogenic factor, which can be presented in a simplified way thus: a) *A. ralloides* is now under specific protection, b) a pattern of natural reserves has been set up, c) new transformed habitats are available for the Squacco Heron (rice fields in Europe, water canals, retentional reservoirs), d) natural enemies of *A. ralloides* have been considerably reduced (JÓZEFIK, 1969). The positive effect of this factor increases from east to west and that found its reflection, even before 1950, in a considerable decrease in the critical size of micropopulations in the western parts of the range and in a general synanthropization of the species. After 1960 it had its bearing on the sudden increase in the numbers of the species in the central and eastern regions of the range (JÓZEFIK, 1969).

I have proved earlier that irrespective of considerable secular oscillations in the numbers of the species, the density of sites in the XIXth century and in the 1st half of the XXth century did not reveal any significant differences (cf. Table 1). Judging by the character of the effect of limiting factors the species was forced to keep up close spatial integration, i. e. close social connections. After 1950, the character of previous limiting factors has changed completely — the species can now exist even in the form of even small micropopulations (cf. JÓZEFIK, 1969), and thus it can use more fully its habitat resources. Judging by the data presented in Table 1 ($\bar{x}$ and $\sigma_{\bar{x}}^{2}$) the species can now maintain in the range a lower density of breeding sites.

In order to make sure whether changes in the effect of the anthropogenic factor have significantly influenced the so far permanent structural features of the distribution (cf. page 3), and in the first place the density of breeding sites in the range, I have tested with χ^2 empirical distribution of the numerical state of sites in squares 4° of geographical longitude by 4° of geographical latitude characteristic for the 2nd half of the XIXth century, the 1st half of the XXth century, and the period after 1950 (Table 9).

Table 9. Secular changes in the density of *A. ralloides* breeding sites in the palearctic part of the range.

Periods compared (1)	χ^2 of differences between empirical distributions of the numbers of sites in squares 4° of longitude by 4° of latitude (2)	$P\,(df = 5)$ (3)
2nd half of the XIXth and 1st half of the XXth cent. (4)	4.58	0.52
2nd half of the XIXth cent. — state after 1950 (5)	14.77	0.02
1st half of the XXth cent. — state after 1950 (6)	13.05	0.02

As it follows from Table 9, there are no significant diferences between the 2nd half of the XIXth century and the 1st half of the XXth century, although, as it is well known (JÓZEFIK, 1969), numerical changes of the species reached 85% in this period. Significant are here differences between the periods mentioned and the state after 1950 which is a period with a different effect of the anthropogenic factor.

And thus the final thesis from the previous chapter (cf. page 34) can be accepted now as a conclusion with sufficient evidence to support it.

CONCLUSIONS

1. The distribution of *A. ralloides* breeding sites in the range is not a random one but it reveals, irrespective of considerable secular oscillations of the species and a change in the effect of limiting factors, a decisive tendency to form aggregations.

2. The species as a whole reveals a tendency to attempt at spatial integration, i. e. it shows a tendency to overcome any excessive isolation between micropopulations and to maintain such a level of density in the range which would not exceed a definite critical value.

3. Separate breeding sites are grouped in the range in such a way that, irrespective of other circumstances, micropulations habitating them can get in touch with each other, each site with at least one more site. Thus there are formed "bridges" of minimum distances connecting, with only a small number of exceptions, all the micropopulations within the breeding range.

4. The species endeavours to maintain only optimum minimum distances in separate aggregations below which overcowding occurs which prevents any further increase in the size of micropopulations closely neighboring upon each other. It should be interpreted as an attempt to reach such a relation between the pressure of intraspecific competition and the overcoming of isolation and reaching the highest social effect which would ensure the highest degree of survival in the annual cycle.

5. The force of social attraction and the tendency to realize territorial integration contribute to the fact that the preference of a breeding habitat at a given point of the range displayed by separate flocks and micropopulations is motivated by these factors not less than by the ecological attractiveness of the habitat at this point.

6. Irrespective of considerable historical secular changes and cyclic oscillations of the numbers of the species, it maintained up to 1950 the same, not exceeded (in the meaning of the highest tolerated dispersion), density within the breeding range.

7. The tendency to form aggregations is diplayed more intensively when the species is threatened, when it is reduced, and when its numbers are low. Together with the elimination, or at least with the curtailment by man, of the reducing factors and with the protection of the species (the period after 1950) the connections integrating the species became loose and the critical size of micropopulations was lowered, as well as the occurrence of significant changes characteristics of basic parameters of the spatial structure (e. g. the maximum critical value of dispersion is lowered). This leads to an increase in the possibility of the frequent formation of isolates and of an intensified rate of the process of speciation.

8. A general increase in the numbers of the species is accompanied by a slower decrease in the degree of isolation between separate micropopulations.

This is characteristic for the cumulative phase which is followed by the expansive one connected with an increase in the area of the range and a simultaneous decrease in the degree of isolation (the appearance of a larger number of dependent and sporadic sites). When the numbers of the species decrease, the increase in the degree of isolation between separate sites is relatively intensified (the disappearance of small dependent and sporadic sites as well as the territorial regression). Not each apogee in numerical oscillations is accompanied by an adequate, in time, increase in the area of the range, while each decrease in the numbers of the species leads to the retraction of its boundaries. Hence the centrifugal progress (pulsation of the boundaries) is carried out by leaps and bounds while the centripetal one is gradual.

9. The possibility of disjunctions to occur (in the case of *A. ralloides*) is determined by the parallel crowding of sites in the range. Connections cementing the species are more prominent in the southern direction, i. e. in the direction of the most intensive contacts between separate micropopulations. They preserve greater autonomy along the parallels, i. e. they are less susceptible to the limiting effect of spatial isolation. This autonomy, being the potential initiation of eventual disjunctions, is deepened together with a decrease in the numerical state of the species.

10. All the profound secular changes in the numbers of the species (lack of homeostasis) contribute to the intensification of microevolutional processes. It seems that the processes of speciation occur more rapidly in the conditions of ecological pessimum connected with a considerable decrease in the numbers of the species and the formation of diverging isolates, than in the case of a numerical increase, and in consequence its expansiveness and a delayed formation of populations which are also isolated.

11. The size of the micropopulation habitating a given breeding site is correlated with the degree of spatial isolation in respect of other sites in the closest neighbourhood. This correlation has a curvilinear character. The further is a site situated from the center of the aggregation, the larger is the micropopulation habitating this site. The smallest sites are in the outlying parts of the breeding range and also near the borders separating individual aggregations. The effect of the degree of isolation on the size of micropopulations increases in an exponential function, i.e. the increasing linear dispersion is accompanied by a logarithmic decrease in the size of micropopulations.

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STRESZCZENIE

Część IV cyklu stanowi kontynuację prac dotyczących struktury rozmieszczenia przestrzennego *Ardeola ralloides* (SCOP.) w palearktycznej części zasięgu i poświęcona jest badaniom nad organizacją przestrzenną i mechanizmami integrującymi gatunek.

Autor udokumentowuje tezę, iż rozmieszczenie stanowisk lęgowych w zasięgu nie jest losowe, a poza sferą czynników biogeofizycznych na ukształtowanie przestrzenne gatunku w znacznej mierze wpływają też czynniki wewnątrzgatunkowe. W tym celu przebadano testem χ^2 różnice rozkładów teoretycznych według prawdopodobieństwa POISSONA i empirycznych występowania sta-

nowisk lęgowych w poszczególnych kwadratach zasięgu o boku 4° szerokości
i 4° długości geograficznej ujmowanych w trzech wariantach: a) oddzielnie dla
II połowy XIX wieku, b) I połowy XX wieku, c) dla okresu 1950–1960 (tab. 1).
Niezależnie od znacznych sekularnych wahań ilościowych, zmiany charakteru
oddziaływania środowiskowych czynników ograniczających gatunek, jako
całość, wykazuje zdecydowaną tendencję do tworzenia skupisk (agregacje
stanowisk lęgowych), tj. pokonywania nadmiernej izolacji między poszcze-
gólnymi mikropopulacjami i utrzymywania w zasięgu zagęszczenia nie prze-
kraczającego określonej wartości krytycznej. Jako miernika izolacji stosuje
autor mierzenie tzw. odległości kierunkowych, tj. dystansów dzielących dane
stanowisko od innych najbliższych, leżących w kierunkach NW, NE, SW, SE.
Badając za pomocą współczynników stosunku korelacyjnego η_{yx} i η_{xy} współza-
leżność między wielkością stanowiska lęgowego (wielkością mikropopulacji)
(y — liczba par lęgowych zasiedlających dane stanowisko) a stopniem izolacji
(x — odległość w km) wyrażonym jako: a) kierunkowe odległości maksymalne,
b) minimalne oraz c) przeciętne (wypadkowa wszystkich odległości kierunko-
wych) (tab. 2) autor dochodzi do wniosku, że wielkość mikropopulacji zasiedla-
jącej dane stanowisko skorelowana jest ze stopniem izolacji przestrzennej
względem innych najbliższych w zasięgu stanowisk. Korelacja ta ma charakter
krzywoliniowy. Im dane stanowisko położone jest bliżej centrum agregacji,
tym wielkość zasiedlającej go mikropopulacji jest większa. Stanowiska w stre-
fie peryferyjnej zasięgu a także na pograniczach agregacji są najmniejsze.
Wpływ stopnia izolacji na wielkość mikropopulacji wzrasta w funkcji wykład-
niczej, tj. wzrastającemu liniowo rozproszeniu towarzyszy logarytmiczne
zmniejszanie się wielkości mikropopulacji.

Badając korelację odległości minimalnych i wielkości stanowisk, autor
stwierdza, iż poszczególne stanowiska grupują się w zasięgu w taki sposób,
aby niezależnie od innych okoliczności mikropopulacje je zasiedlające mogły
kontaktować się każda przynajmniej z jednym innym stanowiskiem lęgowym.
"Pomosty" dystansów minimalnych wiążą w ten sposób prawie wszystkie
populacje w obrębie zasięgu lęgowego. W miarę zmniejszania się odległości
minimalnych między stanowiskami ich wielkość wzrasta tylko do określonej
granicy (15–35 km), po przekroczeniu której korelacja z ujemnej przechodzi
na dodatnią. Jest to dowodem zmierzania gatunku do utrzymywania jedynie
optymalnych dystansów minimalnych w poszczególnych agregacjach stano-
wisk, poniżej których następuje przegęszczenie ograniczające dalsze wzrastanie
blisko sąsiadujących mikropopulacji.

Interpretując η_{xy} dla dystansów minimalnych autor wysnuwa następujący
wniosek: siła socjalnego przyciągania i dążność do integracji terytorialnej
sprawiają, iż preferencja biotopu lęgowego nowo osiedlających się stad w okre-
ślonym punkcie zasięgu motywowana jest tymi czynnikami w stopniu prawdo-
podobnie nie mniejszym, niż atrakcyjnością ekologiczną środowiska tego punk-
tu. Wspomniane czynniki wewnątrzgatunkowe zmuszają niektóre populacje

do przystosowywania się do środowiska przekształconego i bynajmniej nie
optymalnego ekologicznie oraz przyśpieszają synantropizację gatunku.

Posługując się równaniami regresji autor dochodzi do przekonania, że
ogólnemu zwiększaniu się liczebności gatunku towarzyszy wolniejsze obniżanie
się stopnia izolacji między mikropopulacjami. Charakterystyczne to jest dla
fazy kumulacyjnej, po której może dopiero nastąpić faza ekspansywna zwią-
zana ze zwiększeniem się powierzchni zasięgu i równocześnie zmniejszaniem
stopnia izolacji (powstawanie większej liczby stanowisk satelitarnych i spora-
dycznych). Przy spadku liczebności gatunku, zwiększanie się stopnia izolacji
między stanowiskami w stosunku względnym odbywa się szybciej (zanik drob-
nych stanowisk satelitarnych i sporadycznych oraz regresja terytorialna).
Autor omawia też mechanizmy: kumulacyjnej fazy wzrastania liczebności
gatunku w zasięgu, jego ekspansji i regresji terytorialnej, tworzenia się i zaniku
sporadycznych stanowisk lęgowych. Niezależnie od znacznych historycznych
zmian sekularnych oraz krótszych cyklicznych wahań liczebności gatunek
utrzymywał jednakowe, nieprzekraczalne (w sensie maksymalnie tolerowanego
rozproszenia) zagęszczenie w obrębie zasięgu. Dopiero po znacznym zsynantro-
pizowaniu się większości populacji czapli modronosej w ostatnich dwóch dzie-
sięcioleciach, gatunek ten mógł egzystować już w warunkach zwiększonego
rozproszenia.

Prócz poprzednio przytoczonych dowodów dążenia gatunku do integracji
przestrzennej (grupowanie się stanowisk lęgowych w agregacje, zależność wiel-
kości mikropopulacji od stopnia jej izolacji, mechanizmy preferencji teryto-
rialnej, utrzymywanie niezależnie od znacznych wahań sekularnych liczebności
określonego zagęszczenia w zasięgu) autor udokumentowuje tezę, iż struktura
rozmieszczenia przestrzennego gatunku w słabym stopniu skorelowana jest
z przestrzennym rozmieszczeniem biotopów wodno-błotnych i w znacznej
mierze zależy od czynników wewnątrzgatunkowych, scalających gatunek jako
realną jednostkę biologiczną. Gatunek zmierza do takiego zagęszczenia w za-
sięgu, przy którym sumujące się negatywne wpływy konkurencji wewnątrz-
gatunkowej oraz izolacji osiągają najniższe wartości.

W dalszej części pracy autor analizuje mechanizmy pulsacji granic zasięgu
A. ralloides. Zwiększanie powierzchni zasięgu poprzedzane jest przez fazę ku-
mulacji liczebności. Nie każdemu przeto szczytowi wzrostu liczebności, zwłasz-
cza gdy chodzi o kilkuletnie fluktuacje, towarzyszą adekwatne przesunięcia
granicy zasięgu.   Natomiast każdy spadek liczebności powoduje cofanie się
jego granicy. Stąd odśrodkowe przesuwanie się (pulsacja granicy) następuje
gwałtowniej większymi skokami, dośrodkowe odbywa się stopniowo i łagodnie.

W kolejnym rozdziale rozważany jest mechanizm tworzenia się dysjunkcji
w zasięgu. W przypadku A. ralloides, jak udowadnia autor, o możliwości wytwo-
rzenia się dysjunkcji decyduje równoleżnikowe zagęszczenie stanowisk w zasięgu.
Więzi scalające gatunek są bardziej uwydatnione w kierunku południkowym,
tj. w kierunku najbardziej intensywnych bezpośrednich kontaktów między

poszczególnymi mikropopulacjami. Równoleżnikowo zachowują one większą
autonomię, tzn. są mniej podatne na ograniczający wpływ izolacji przestrzen-
nej. Autonomia ta, będąc potencjalnym zaczątkiem ewentualnych dysjunkcji,
pogłębia się między agregacjami wraz ze spadkiem ilościowym gatunku. Autor
jest też zdania, że wszelkie głębokie zmiany sekularne liczebności (zachwianie
homeostazy gatunku) powodują intensyfikację procesów mikroewolucyjnych.
Wydaje się, iż procesy specjacyjne przebiegają prawdopodobnie znacznie
częściej i szybciej w warunkach pessimum ekologicznego, połączonego ze znacz-
nym obniżeniem się liczebności gatunku i wytworzeniem się dywergujących izo-
latów, niż w przypadku wzrastania liczebności a w konsekwencji jego ekspan-
sywności i późniejszego wytworzenia się również izolowanych populacji.

W kolejnym rozdziale omawia autor izolację przestrzenną w ujęciu profilo-
wej analizy zasięgu.

Rozpatrując w zoogeograficznym aspekcie prawidłowości przestrzennej
organizacji gatunku autor podkreśla, iż sens tendencji integracyjnych gatunku
jako jednostki biologicznej jest identyczny z wykrytym przez ALLEEGO w od-
niesieniu do populacji (skupiskowość — przeżywalność). Gatunek zmierza
do osiągnięcia takiej relacji między parciem konkurencji wewnątrzgatunkowej
a dążnością do skupiskowości (pokonanie izolacji i osiągnięcie maksymalnego
efektu stadnego), która to relacja z perspektywy dłuższego czasu zapewni mu
maksymalny stopień przeżywalności. W oparciu o przykład *A. ralloides* autor
nadaje zasadzie ALLEEGO szersze ramy reguły zoogeograficznej. Na podstawie
przeanalizowanych materiałów wysuwa tezę, iż dążność gatunku do określo-
nej optymalnej skupiskowości, poza większą szansą przeżycia, stwarza lepsze
warunki do bardziej wzmożonej wymiany genetycznej, co nie może pozostawać
bez wpływu na tempo procesów specjacyjnych, jak również ukierunkowane
ewoluowanie gatunku jako całości. Autor sądzi, iż proporcjonalnie do stopnia in-
tegracji przestrzennej gatunku wzrastają jego szanse do zachowania jednolitej
struktury genetycznej i ściśle ukierunkowanych zmian mikroewolucyjnych.

W końcowym rozdziale autor omawia wpływ czynnika antropogenicznego
na zmiany struktury rozmieszczenia. Dochodzi do konkluzji, iż dążność do
tworzenia skupisk przejawia się intensywniej, gdy gatunek jest bardziej zagro-
żony i redukowany, a jego liczebność niska. Wraz z wyeliminowaniem, bądź
znacznym ograniczeniem przez człowieka czynników redukujących i objęciem
gatunku ochroną (okres po 1950 roku) rozluźniły się więzi integrujące gatunek
przestrzennie, obniżyła się wielkość progowa mikropopulacji, jak również
zaszły istotne zmiany w charakterystykach podstawowych parametrów struk-
tury przestrzennej (np. obniżenie się progu maksymalnie tolerowanego rozpro-
szenia gatunku). Zwiększyły się w związku z tym możliwości częstszego tworze-
nia się izolatów oraz przyśpieszenia procesów specjacyjnych.

Część V cyklu poświęcona będzie analizie stref ekologicznych zasięgu
z punktu widzenia badań nad strukturą przestrzenną gatunku.

Objaśnienia do wykresów i tabel:

Wykres 1. Korelacja wielkości stanowisk lęgowych *A. ralloides* i ich maksymalnych względem siebie odległości (XIX i XX wiek łącznie). x — przedziały klasowe odległości maksymalnych (km); y — przedziały klasowe wielkości stanowisk lęgowych; krzywe regresji: A — średnie maksymalnych odległości charakterystyczne dla poszczególnych klas wielkości stanowisk, B — średnie wielkości stanowisk właściwe dla poszczególnych klas odległości maksymalnych.

Wykres 2. Rozkład wielkości stanowisk lęgowych *A. ralloides* w zależności od ich maksymalnych 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 200 km, B — 201–500 km, C — 501–1000 km, D — 1001–2000 km.

Wykres 3. Korelacja wielkości stanowisk i ich minimalnych odległości względem siebie (XIX i XX wiek łącznie). x — przedziały klasowe odległości minimalnych (km); y — przedziały klasowe wielkości stanowisk; krzywe regresji: A — średnie minimalnych odległości charakterystyczne dla poszczególnych klas wielkości stanowisk, G — średnie wielkości stanowisk właściwe dla poszczególnych klas odległości minimalnych.

Wykres 4. Rozkład wielkości stanowisk lęgowych *A. ralloides* w zależności od ich minimalnych 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 wielkości w %%; krzywe rozkładu w zakresie: A — do 20 km, B — 21–50 km, C — 51–200 km, D–201–700 km.

Wykres. 5. Uproszczony schemat uzależnienia możliwości preferencji terytorialnej od wzrostu liczebności gatunku. x — powierzchnia zasobów środowiska (biotopu lęgowego); y — 100-stopniowa logarytmiczna skala współczynnika E; z — liczebność gatunku w %%; A — asymptota wydolności środowiska; D — krzywa wzrastania liczebności gatunku; E — krzywa współczynnika możliwości preferencji.

Wykres 6. Rozkład minimalnych, maksymalnych, i przeciętnych odległości między stanowiskami lęgowymi *A. ralloides* w XIX wieku niezależnie od ich ukierunkowania. x — odległość (km); y — liczba stanowisk w stosunku procentowym w obrębie każdej kategorii odległości; krzywe rozkładu: A — odległości minimalne, B — maksymalne, C — przeciętne.

Wykres 7. Rozkład minimalnych, maksymalnych i przeciętnych odległości między stanowiskami lęgowymi *A. ralloides* w XX wieku niezależnie od ich ukierunkowania. x — odległość (km); y — liczba stanowisk w stosunku procentowym w obrębie każdej kategorii odległości; krzywe rozkładu: A — odległości minimalne, B — maksymalne, C — przeciętne.

Wykres 8. Rozkład minimalnych, maksymalnych i przeciętnych odległości między stanowiskami lęgowymi *A. ralloides* (XIX i XX wiek łącznie). x — odległość (km); y — liczba stanowisk w stosunku procentowym w obrębie każdej kategorii odległości; krzywe rozkładu: A — odległości minimalne, B — maksymalne, C — przeciętne (średnia ruchoma wypadkowych odległości kierunkowych obliczanych dla poszczególnych stanowisk).

Wykres 9. Korelacja wielkości stanowisk i ich przeciętnych względem siebie odległości (XIX i XX wiek łącznie). x — przedziały klasowe przeciętnych odległości; y — przedziały klasowe wielkości stanowisk; krzywe regresji: A —średnie przeciętnych odległości charakterystyczne dla poszczególnych klas wielkości stanowisk, B — średnie wielkości stanowisk właściwe dla poszczególnych klas odległości przeciętnych.

Wykres 10. Rozkłady ukierunkowanych odległości między stanowiskami w profilu równoleżnikowym (XIX wiek). x — długość geograficzna; y — odległość (km); A — odległości kierunkowe WN; B — NE; C — SE; D — SW.

Wykres 11. Rozkłady ukierunkowanych odległości między stanowiskami w profilu równoleżnikowym (XX wiek). x — długość geograficzna; y — odległość (km); A — odległości w kierunku NW; B — NE; C — SE; D — SW.

Wykres 12. Rozkłady ukierunkowanych odległości między stanowiskami w profilu południkowym (XIX wiek). x — szerokość geograficzna (pozostałe oznaczenia — jak na wykr. 11).

Wykres 13. Rozkłady ukierunkowanych odległości między stanowiskami w profilu południkowym (XX wiek), (oznaczenia — jak na wykr. 11).

Wykres 14. Rozkłady odległości przeciętnych między stanowiskami lęgowymi w profilu równoleżnikowym (stopień rozproszenia stanowisk w profilu równoleżnikowym). x — długość geograficzna; y — odległość (km); A — XIX wiek; B — XX wiek.

Wykres 15. Rozkłady odległości przeciętnych między stanowiskami lęgowymi w profilu południkowym (stopień rozproszenia stanowisk w profilu południkowym) x — szerokość geograficzna (pozostałe oznaczenia — jak na wykr. 14).

Wykres 16. Zależności między niektórymi parametrami struktury przestrzennej rozmieszczenia *A. ralloides* w profilu równoleżnikowym zasięgu (XIX i XX wiek łącznie). x — długość geograficzna; y — odległość (km) (skala dla krzywej A); v — liczba stanowisk lęgowych (skala dla krzywej B); w — wielkość stanowisk wyrażona w liczbie par lęgowych (skala dla krzywej C); z — liczebność gatunku wyrażona w liczbie par lęgowych (skala dla krzywej D); A — odległości przeciętne; B — rozkład liczebności stanowisk; C — rozkład przeciętnej wielkości stanowisk; D — rozkład liczebności gatunku.

Wykres 17. Zależności między niektórymi parametrami struktury przestrzennej rozmieszczenia *A. ralloides* w profilu południkowym zasięgu (XIX i XX wiek łącznie). x — szerokość geograficzna; y — odległość (km) (skala dla krzywej A); v — liczba stanowisk i przeciętna wiekość stanowisk (skala dla krzywych B, C); z — liczebność gatunku wyrażona w liczbie par lęgowych (skala dla krzywej D); A — rozkład odległości przeciętnych; B — rozkład liczebności stanowisk; C — rozkład przeciętnej wielkości stanowisk; D — rozkład liczebności gatunku.

Tabela 1. Charakterystyka rozkładów teoretycznych i empirycznych rozmieszczenia stanowisk lęgowych *A. ralloides* w palearktycznej części zasięgu. (1) — okresy, (2) — charakterystyka statystyczna, (3) — średnia $\bar{x}$, (4) — wariancja $\sigma_{\bar{x}}^2$, (5) — prawdopodobieństwo (według Poissona), (6) — x^2 różnicy rozkładów teoretycznych i empirycznych, (7) — XIX wiek, (8) — I połowa XX wieku, (9) — okres 1959–1960, (10) — ogólnie.

Tabela 2. Wskaźniki stosunku korelacyjnego między wielkością stanowisk lęgowych (y) a odległością między nimi (x) (XIX i XX wiek łącznie). (1) — kategoria stanowiska, (2) — odległości, (3) — korelacja, (4) współczynnik stosunku korelacyjnego η_{yx}, (5) — współczynnik stosunku korelacyjnego η_{xy}, (6) — współczynnik korelacji r_{xy}, (7) — współczynnik krzywoliniowości regresji $\eta_{xy}^2 - r_{xy}^2$, (8) — regularne i sporadyczne łącznie, (9) — (13) — maksymalne, (10) — (14) — minimalne, (11) — przeciętne, (12) — sporadyczne.

Tabela 3. Wskaźniki regresji wielkości stanowisk (y) i odległości między nimi (x) (XIX XX wiek łącznie). (1) — kategoria odległości, (2) — współczynnik korelacji r_{xy}, (3) — współczynnik regresji $a_{x(y)}$, (4) — współczynnik regresji $a_{y(x)}$, (5) — maksymalne, (6) — minimalne, (7) — przeciętne.

Tabela 4. Charakterystyka odległości między stanowiskami lęgowymi *A. ralloides* (w km). (1) — odległości, (2) — charakterystyka statystyczna, (3) — stulecie, (4) — liczba pomiarów n, (5) — średnia $\bar{x}$, (6) — t różnicy, (7) — odchylenie standardowe $\sigma_{\bar{x}}$, (8) — t różnicy, (9) — dominanta D, (10) — maksymalne, (11) — minimalne, (12) — przeciętne.

Tabela 5. Korelacja wieloraka odległości minimalnych (x), wielkości stanowisk (y) i wielkości biotopów wodno-błotnych (z), na których te stanowiska są usytuowane. (1) — korelacja cech, (2) — współczynnik korelacji, (3) — całkowitej, (4) — cząstkowej.

Tabela 6. Współzależność wielkości stanowisk lęgowych *A. ralloides* i odległości między nimi. (1) — odległość, (2) — zmiany wielkości stanowisk, (3) — wzrost o... liczbę par, (4) — spadek o liczbę ... par, (5) — różnice tempa postępujących zmian liczebności gatunku i odległości, (6) — minimalne, przeciętne, (7) — spadek o liczbę... km, (8) — wzrost o liczbę ... km, (9) — zmiany odległości między stanowiskami.

Tabela 7. Korelacja przeciętnych odległości między stanowiskami (x) względem: przeciętnej liczby stanowisk (a), przeciętnej wielkości stanowisk (b), przeciętnej liczebności gatunku (c) w profilu południkowym i równoleżnikowym zasięgu (materiał wypośrodkowany dla XIX i XX wieku łącznie; wielkość przedziałów klasowych w obydwu profilach = 4° długości i 4° szerokości geograficznej). (1) — współczynnik korelacji, (2) — profil południkowy zasięgu (N — S), (3) — profil równoleżnikowy zasięgu (W — E).

Tabela 8. Korelacja niektórych parametrów struktury rozmieszczenia przestrzennego *A. ralloides* w palearktycznej części zasięgu w ujęciu analizy profilowej (XIX i XX wiek łącznie). (1) — profil zasięgu, (2) — równoleżnikowy, (3) — południkowy, (4) — współczynnik korelacji r, (5) — stopień izolacji — A, (6) — liczebność stanowisk — B, (7) — wielkość stanowisk — C, (8) — liczebność gatunku — D.

Tabela 9. Zmiany sekularne zagęszczenia stanowisk lęgowych *A. ralloides* w palearktycznej części zasięgu. (1) — porównywane okresy, (2) — χ^2 różnic rozkładów empirycznych liczby stanowisk w kwadratach 4° dług. geogr. x 4° szer. geograficznej, (3) — $P_{(df=5)}$ prawdopodobieństwo przy 5 stopniach swobody, (4) — II połowa XIX wieku — I połowa XX wieku, (5) — II połowa XIX wieku — stan po 1950 r., (6) — I połowa XX wieku — stan po 1950 r.

РЕЗЮМЕ

Четвертая часть цикла является продолжением исследований по структуре пространственного распределения желтой цапли в палеарктической части ареала. В частности посвящается она изучению пространственной организации вида и механизмам обуславливающим его интеграцию.

Автор доказывает, что распределение мест гнездования лишено черт случайности. Распределение мест гнездования в ареале, кроме факторов биогеофизического характера, в значительной мере зависит от внутривидовых факторов определяющих пространственные параметры вида. Этот тезис проверяется автором критерием χ^2 — по этому критерию сравнивались теоретические распределения вероятностей по Пуассону и эмпирические распределения встречаемости мест гнездования желтой цапли в квадратах гнездового ареала о боках 4° географической широты и 4° географической долготы. Сравнивались распределения в трех вариантах: а) характерные для II половины XIX века, б) I половины XX столетия, в) характерные для периода 1950–1960 гг. (таб. 1). Независимо от значительных вековых колебаний численности вида, независимо от характера влияния ограничивающих факторов внешней среды, вид как целое проявляет решительно тенденцию к образованию скоплений (аггрегации мест гнездования). Следует это понимать, как стремление к преодолению чрезмерной изоляции между отдельными микропопуляциями и удерживания по всему ареалу плотности не переходящей определенной критической величины. В качестве измерителя степени изоляции автором применяется измерение так называемых направляющих дистанций, т. е. расстояний между соответственными местами гнездовок измеряемых в четырех вариантах согласно четвертям розы ветров (NW, NE, SW, SE). Пользуясь коэффициентами корреляционного отношения η_{yx} и η_{xy} автором изучалась взаимозависимость между величиной места гнездования (величиной микропопуляции заселяющей определенное место гнездования) выраженной числом гнездовых пар (y) и степению изоляции (расстояние в киломе-

трах — x). Рассматривались 3 варианта: максимальные направляющие дистанции, минимальные дистанции и дистанции в среднем (среднее число 4-х промеров направляющих дистанции) — см. таблица 2. Автор приходит к выводу, что величина микропопуляции заселяющих отдельные места гнездовок коррелирует со степенью пространственной изоляции между этими микропопуляциями (отрицательная, криволинейная корреляция). Чем ближе к центру аггрегации находится определенное место гнездования, тем больше величина заселяющей его микропопуляции. Места гнездовок расположенные в периферийной части ареала, а также на окраинах более крупных аггрегаций характеризуются самыми незначительными величинами. Влияние изоляции на величину микропопуляции возрастает в показательной функции, т. е. возрастающему в линейной функции рассеиванию вида соответствует уменьшение величины микропопуляции в логарифмической функции.

Анализируя корреляцию между минимальными дистанциями и величиной мест гнездовок автор констатирует, что отдельные микропопуляции группируются в ареале таким образом, чтобы независимо от всех других обстоятельств они могли между собой иметь контакт по крайней мере хотя бы с одной стороны. Возникают, таким образом, связывающие звенья минимальных дистанций связывающие в пределах гнездового ареала почти все микропопуляции. В меру уменьшения минимальных дистанции величина микропопуляции возрастает только до определенного предела (15–35 км), затем при дальнейшем сокращении дистанции корреляция с отрицательной становится положительной, что свидетельствует о стремлении вида к поддерживанию единственно оптимальных расстояний между гнездящимися микропопуляциями среди соответственных аггрегации мест гнездования. Слишком близкое соседство между микропопуляциями ограничивает их дальнейшее возрастание — создается картина перенаселенности.

Интерпретируя величину η_{xy} минимальных дистанций автор приходит к выводу, что сила социального притягивания и стремление вида к территориальной интеграции являются не менее существенным фактором в преферировании определенных территории новопоселяющимися стадами чем экологическая атракционность биотопа в пределах этой территории. Этот внутривидовой фактор заставляет некоторые микропопуляции приспосабливаться к видоизмененным человеком и отнюдь в экологическом отношении не оптимальным биотопам и ускоряет процессы синантропизации вида.

Пользуясь уравнениями регрессии автор приходит к выводу, что возрастание численности вида сопровождается медленным снижением степени изоляции между микропопуляциями. Это явление следует считать характерным для кумулятивной фазы, после которой может следовать фаза экспансивная, сопровождающаяся увеличением поверхности ареала и одновременно уменьшением степени изоляции (возникновение значительного числа спорадических мест гнездовок). В случае падения численности вида увеличение степени изоляции между микропопуляциями происходит более быстро (конечно в относительных масштабах). Имеет тогда место исчезновение сателлитарных и спорадических мест гнездования, а также территориальная регрессия вида. Автором рассматриваются механизмы кумулятивной

фазы возрастания численности вида, его экспансии и регрессии, возникания и исчезания спорадических мест гнездования. Независимо от значительных исторических вековых изменений, а также более коротких периодических колебаний численности, вид в целом, удерживает в пределах своего ареала одинаковую, в смысле допустимо толерантной, густоту заселения. Только после синантропизации большинства популяции желтой цапли в течение двух последних десятилетий исследуемый вид мог проживать в условиях более значительной дисперсии.

Кроме выше приведенных доказательств стремления вида к пространственной интеграции (группировка гнездовок в более крупные аггрегации, зависимость величины микропопуляции от степени изоляции, механизмы территориальной преференции, удерживание в ареале независимо от значительных вековых колебаний численности определенной плотности заселения), автором доказывается тезис, что структура пространственного распределения вида лишь в незначительной степени коррелирует с пространственным распределением болотных биотопов, и в значительной мере зависит от внутривидовых факторов, интегрирующих вид как естественную биологическую единицу. Вид проявляет стремление лишь к такой плотности заселения по ареалу, при которой суммирующееся отрицательное влияние внутривидовой конкуренции и изоляции между микропопуляциями достигают самых незначительных величин.

В последующей части работы автором анализируются механизмы пульсации границ ареала желтой цапли. Увеличению поверхности ареала предшествует фаза кумуляции численности. Поэтому не всякому апогею возрастания численности соответствует адекватное передвижение границы ареала и особенно, когда речь идет о колебаниях, охватывающих короткие периоды времени (например, несколько лет). Однако всякое снижение численности ведет за собой отступление вида из окраин ареала к его центру. Отсюда центробежное передвижение границ ареала наступает большими скачками и более быстро, в то время, как центростремительно границы передвигаются постепенно и более мягко.

В очередной главе автором рассматривается механизм возникновения в ареале разрыва. Имея в виду пример ареала желтой цапли, автор полагает, что о возможности возникновения разрыва решает плотность расположения мест гнездовок в параллельном разрезе ареала. Связи объединяющие вид более заметно проявляются в меридиональном направлении, т. е. согласно с направлением наиболее интенсивных непосредственных связей между отдельными микропопуляциями. По мере количественного снижения численности вида проявляется более четко автономия отдельных микропопуляций, которая является зачатком увеличивающегося потом разобщения между отдельными аггрегациями мест гнездовок. Автор считает, что всякие глубокие вековые изменения численности и нарушение гомеостаза вида приводят к усилению микроэволюционных процессов. Формообразование осуществляется, по всей вероятности, в более частых случаях и в более быстрых темпах именно тогда, когда вид, находясь в пессимальных экологических условиях, претерпевает значительное снижение численности, а в пределах его ареала возникают географически разобщенные изоляты. В противоположных случаях (территориальная экспан-

сия и возникновение изолированных популяций вне пределов прежнего ареала) формообразование проходит, быть может, не так быстро.

В следующей главе автором рассматривается вопрос пространственной изоляции в аспекте профильного анализа ареала. С точки зрения зоогеографических законов пространственной организации вида, биологический смысл его направленности к интеграции тот же, что и обнаруженная Аллим (ALLEE) по отношению к популяции тенденция к образованию всякого типа группировок и скоплений обеспечивающих более высокий уровень переживаемости. По автору, вид в целом стремится достичь такого соотношения между напором внутривидовой конкуренции и устремленностью к интеграции (преодоление изоляции и осуществление максимального стадного эффекта), которое в перспективе более продолжительного времени сможет обеспечить наиболее высокий уровень переживаемости. Основываясь на материале касающемся желтой цапли, автор придает правилу Алли более широкое значение зоогеографического закона. Он утверждает, что устремленность вида к образованию скоплений характеризующихся определенной (оптимальной) плотностью заселения, кроме потенциальной возможности более значительной переживаемости, обеспечивает виду более благоприятствующие условия для генетического обмена. Этот факт в свою очередь не может не оказывать влияния на ход процессов видообразования а также направленность эволюции вида в целом. Автор полагает, что пропорционально степени пространственной интеграции вида возрастают его шансы удержать однородную генетическую структуру, а также сохранять определенную направленность микроэволюционных изменений.

В последней главе автором анализируется влияние антропогенного фактора на структуру пространственного распределения вида. Устремленность вида к образованию скоплений проявляется более ярко в моментах, когда он находится под угрозой, а его численность резко снижается. Одновременно с устранением или же значительным ограничением человеком редуцирующих факторов и принятием мер охраны вида (период после 1950 года), стали ослабевать связи пространственной интеграции вида, снизилась критическая величина микропопуляции, а также были отмечены существенные изменения в характеристике основных параметров пространственной структуры вида (например снижение порога максимально толерантной дисперсии вида). По той же причине возросли шансы более ускоренного возникновения географических изолятов и более быстрого хода формообразовательных процессов.

В пятой части цикла будет рассматриваться вопрос экологических зон ареала в аспекте исследований по пространственной струкруре вида.

Объяснения к графикам и таблицам:

График 1. Корреляция величины гнездовий желтой цапли и максимальных расстояний между ними (XIX и XX столетия рассматриваются совместно). x — классовые интервалы максимальных расстояний (км); y — классовые интервалы величины гнездовий; кривые регрессии: A — средняя регрессия максимальных расстояний по отношению к величине гнездовий, B — регрессия величины гнездовок по максимальным расстояниям.

График 2. Распределение величины гнездовий желтой цапли в зависимости от максимальных расстояний между ними (в процентах к общему числу гнездовий данной категории расстояний). x — классовые интервалы величины гнездовий; y — численность гнездовий в %%; распределение расстояний в пределах до: A — 200 км, B — 201–500 км, C — 501–1000 км, D — 1001–2000 км.

График 3. Корреляция величины гнездовий и минимальных расстояний между ними (XIX и XX век совместно). x — классовые интервалы минимальных расстояний (км); y — классовые интервалы величины гнездовий; кривые регрессии: A — регрессия минимальных расстояний по величине гнездовий, B — регрессия величины гнездовий по минимальным расстояниям.

График 4. Распределение величины гнездовий желтой цапли в зависимости от минимальных расстояний между ними (в процентных соотношениях в пределах данной категории расстояний). x — классовые интервалы величины гнездовий; y — численность гнездовий в %%; кривые распределения: A — до 20 км, B — 21–50 км, C — 51–200 км, D — 201–700 км.

График 5. Упрощенная схема обусловленности территориальной преференции от количественного возрастания вида. x — поверхность ресурсов гнездового биотопа; y — 100-бальная логарифмическая шкала коэффициента E; z — численность вида в процентах; A — асимптота вместительности экологической среды; D — кривая численного возрастания вида; E — кривая коэффициента шансов преференции.

График 6. Распределение минимальных, максимальных и средней величины дистанций между местами гнездования желтой цапли в XIX веке независимо от их направленности. x — расстояние (км); y — численность гнездовий в процентах в пределах каждой категории расстояний; кривые распределения: A — минимальные расстояния, B — максимальные, C — в среднем.

График 7. Распределение минимальных, максимальных и средних расстояний между гнездовками желтой цапли в XX веке независимо от их направленности. x — расстояние (км); y — число гнездовий в процентах в пределах каждой категории расстояний; кривые: A — минимальные расстояния, B — максимальные, C — в среднем.

График 8. Распределение минимальных, максимальных и средних расстояний между гнездовками желтой цапли (XIX и XX век рассматривается совместно). x — расстояния (км), y — численность гнездовок в процентах в пределах каждой категории расстояний; кривые: A — минимальные расстояния, B — максимальные, C — в среднем (подвижная средняя всех направленных дистанции высчитываемых для каждого места гнездовок).

График 9. Корреляция между величиной гнездовок и средних между ними расстояний (XIX и XX век совместно). x — расстояния (км); y — классовые интервалы величины гнездовок; кривые регрессии: A — регрессия средних расстояний по величине гнездовок, B — регрессия величины гнездовок по средним расстояниям.

График 10. Распределение направленных расстояний между гнездовками в параллельном разрезе ареала (XIX век). x — географическая долгота; y — расстояние (км); A — дистанция WN; B — NE; C — SE; D — SW.

График 11. Распределения направленных расстояний между гнездовками желтой цапли в параллельном разрезе ареала (XX век). x — географическая долгота; y — расстояние (км); A — дистанция NW; B — NE; C — SE; D — SW.

График 12. Распределения направленных расстояний между нездовками желтой цапли в меридиональном разрезе ареала (XIX век). x — географическая широта (остальные обозначения — как на графике 11).

График 13. Распределение направленных расстояний между местами гнездовок в меридиональном разрезе ареала (XX век). Все обозначения — как на графике 11.

График 14. Распределени средних расстояний между местами гнездования в широтном разрезе ареала (степень дисперсии гнездовок). x — географическая долгота; y — расстояние (км); A — XIX век; B — XX век.

График 15. Распределение средних расстояний между местами гнездовок в меридиональном разрезе ареала (степень дисперсии гнездовок). x — географическая широта (остальные обозначения — как на графике 14).

График 16. Взаимозависимость между некоторыми параметрами пространственной структуры распространения желтой цапли в широтном разрезе ареала (XIX и XX век совместно). *x* — географическая долгота; *y* — расстояние (км) (шкала для кривой *A*); *v* — число мест гнездования (шкала для *B*); *w* — величина гнездовок выраженная количеством гнездовых пар (шкала для кривой *C*); *z* — численность вида выраженная числом гнездовых пар (шкала для *D*); *A* — средние расстояния; *B* — распределение численности гнездовок; *C* — распределение средней величины гнездовок; *D* — распределение численности вида.

График 17. Взаимозависимость между некоторыми параметрами пространственной структуры распространения желтой цапли в меридиональном разрезе ареала (XIX и XX век совместно). *x* — географическая широта; *y* — расстояния (км) (шкала для кривой *A*); *v* — число гнездовок и средняя величина места гнездования (шкала для кривых *B*, *C*); *z* — численность вида выраженная числом гнездовых пар (шкала для *D*); *A* — распределение средних расстояний; *B* — распределение численности гнездовок: *C* — распределение средней величины гнездовок; *D* — распределение численности вида.

Таблица 1. Характеристика теоретических и змпирических распределений распространения гнездовок желтой цапли в палеарктической части ареала. (1) — период, (2) — статистическая характеристика, (3) — в среднем, (4) — дисперсия, (5) — вероятности (по Пуассону), (6) — χ^2 разницы между теоретическими и эмпирическими распределениями, (7) — XIX век, (8) — I половина XX века, (9) — период 1951 – 1960 гг. (10) — в общем.

Таблица 2. Коэффициенты корреляционных отношений между величиной гнездовок (*y*) и расстояниями между ними (*x*), (XIX и XX век совместно). (1) — категория гнездовки, (2) — расстояния, (3) — корреляция, (4) — коэффициент корреляционного отношения η_{yx}, (5) — коэффициент корреляционного отношения η_{xy}, (6) — коэффициент корреляции r_{xy}, (7) — коэффициент криволинейности регрессии $\eta_{xy}^2 - r_{xy}^2$ (8) — совместно регулярные и спорадические, (9)—(13) — максимальные, (10)–(14) — минимальные, (11) — в среднем, (12) — спорадические.

Таблица 3. Коэффициенты регрессии по величине гнездовок (*y*) и расстояниям между ними (*x*) (XIX и XX век совместно). (1) — категория расстояний, (2) — коэффициент корреляции r_{xy}, (3) — коэффициент регрессии $a_{x(y)}$, (4) — коэффициент регрессии $a_{y(x)}$, (5) — максимальные, (6) — минимальные, (7) — в среднем.

Таблица 4. Характеристика расстояний между гнездовками желтой цапли (км). (1) — расстояния, (2) — статистическая характеристика, (3) — столетие, (4) — число промеров *n*, (5) — средняя величина, (6) — *t* разницы, (7) — стандартное отклонение, (8) — *t* разницы, (9) — мода, (10) — максимальные, (11) — минимальные, (12) — в среднем.

Таблица 5. Множественная корреляция по минимальным расстояниям (*x*), величине гнездовок (*y*) и величине болотных биотопов (*z*) в пределах которых они расположены. (1) — корреляция признаков, (2) — коэффициент корреляции, (3) — полной, (4) — частной.

Таблица 6. Зависимость между величиной гнездовок и расстояниями между ними. (1) — расстояние, (2) — изменения величины гнездовок, (3) — увеличение на ... число гнездовых пар, (4) — снижение на... число гнездовых пар, (5) — разница темпов происходящих изменений по численности вида и расстояниям между гнездовками, (6) — минимальные, в среднем, (7) — снижение на число... км, (8) — увеличение на число ... км, (9) — изменения расстояний между гнездовками.

Таблица 7. Корреляция средних расстояний между гнездовками и их численностью (*a*), величиной гнездовок (*b*), численностью вида (*c*) рассматриваемой в широтном и меридиональном разрезе ареала (данные из XIX и XX века рассматриваются совместно; величина классовых промежутков в обоих разрезах равна 4° географической долготы и 4° геогр. широты). (1) — коэффициент корреляции, (2) — меридиональный разрез ареала (*N—S*), (3) — широтный разрез ареала (*W—E*).

Таблица 8. Корреляция некоторых параметров структуры распространения желтой цапли в палеарктической части ареала в аспекте профильного анализа (XIX и XX век совместно). (1)— разрез ареала, (2) — широтный, (3) — меридиональный, (4) —коэффициент корреляции, (5)—степень изоляции *A*, (6) — численность гнездовок *B*, (7) — величина гнездовок *C*, (8) — численность вида *D*.

Таблица 9. Вековые изменения распределения гнездовок желтой цапли в палеарктической части ареала. (1) — сравниваемые периоды, (2) — χ^2 разницы между распределениями эмпирическими численности гнездовок в квадратах ареала 4° геогр. долготы х 4° геогр. ширины, (3) — $P_{(df\,=\,5)}$ вероятность, (4) — II половина XIX века — I половина XX века, (5) — II половина XIX века — период 1950–1960 гг., (6) — I половина XX века — период 1950–1960 гг.