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**Studies on the Squacco Heron, *Ardeola ralloides* (SCOP.).  
Part III. Geographical variability in the critical and mean micropopulation size**

**Studia nad czapłą modronosą, *Ardeola ralloides* (SCOP.).  
Część III. Zmienność geograficzna progowej i przeciętnej wielkości mikro-  
populacji**

**Исследования по желтой цапле, *Ardeola ralloides* (SCOP.).  
Часть III. Географическая изменчивость критической и средней величины  
микронуляции**

[with 13 graphs and one table in the text]

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#### INTRODUCTION

##### Basic assumptions

The present paper is a continuation of studies on the spatial distribution of the Squacco Heron, *Ardeola ralloides* (SCOP.) in the palearctic part of its range. In the preceding publication (JÓZEFIK, 1969) the author analysed secular changes in the numbers and spatial distribution as they were affected

historically by the anthropogenic factor. Less attention was devoted to structural interrelationships of the species spatial distribution. Here the author will concentrate on the elementary population inhabiting a breeding site, i.e. the micropopulation. By discovering basic interrelationships occurring within the micropopulation (critical values of the minimal size, mean size, geographical variability of these parameters, relationships connected with concentration and dispersion of the species) we shall be able to discern ecological zones (optimum and extreme) in the range investigated as well as throw some light on certain microevolutional mechanisms and genetical diffusion. This obviously will not cover all the problems of spatial distribution, and the basic problem, the structure of the species spatial distribution, will be discussed in Part IV, while the effect of isolation on the micropopulation size and spatial distribution of the species, together with the ecological aspects of spatial distribution will be dealt with in Part V.

Characterization of the material, terminology and methodological assumptions have already been discussed (JÓZEFIK, 1969a, b). Here I shall only mention that the concept "spatial structure of a species" is here comprised in measurable interrelationships which: (a) follow from the spatial situation of elementary populations, (b) are connected with homeostatic mechanisms forming and integrating the species spatially; (c) enable to discern general evolutionary trends of the spatial organization of the species. The concept of the spatial structure of the species includes also the sphere of intraspecific factors which determine the spatial character of the species.

Both the composition of historical and environmental factors, and the intraspecific problems (structure of the flock, of the micropopulation, inter-population relations) in studies on the spatial distribution of *A. ralloides* will be dealt with later, but the ranges of their action will always be discussed in such a way that their separateness is analysed in the context of the interdependences. Retaining the idea of functional and historical integrity of the species, all the phenomena and their interrelationships will be discussed, (a) on the descriptive level — a study of functional connections, (b) with a view to discover causal relations — an analysis of the mechanisms displayed by separate phenomena and their interrelationships.

The concept of the spatial structure of the species regarded from the dynamic point of view covers quite a wide range of problems. The basic question seems to be the "essence of intraspecific organization" which provides the species with the best chances, all over its area, in the struggle for existence. Thus the essence of the organization comprises all the social spatial adaptations enhancing the chances of survival, mechanisms facilitating the flow of genes, the maintenance of the species numbers at a level which can contribute to its stability and resistance in adverse circumstances. We should include here also mechanisms regulating the spatial distribution of numbers.



## Review of the history of investigations

As the problem under consideration is closely connected with the question of the spatial organization of biological units both above the level of species (polyspecific communities, higher taxonomic units), as well as below that level (populations, micropopulations), I shall have to take into account both these aspects when discussing the present state of investigations.

DE CANDOLLE (1855) was the first to point out some structural features of the range — the relative size of plant ranges, while WALLACE (1876) shed some light on the correlation between the size of the range and the variability of the species.

Until the populational studies got well under way, and more particularly until the populational conception of polytypic species strengthened its position in biological investigations, there had not been much interest displayed, and attention paid, to the problems of the spatial organization of organism communities. Advances in phytosociology and classical zoogeography are connected with a more careful and detailed analysis of the spatial structure of polyspecific communities. At the outset there were mathematical formulas which determined the relation between the number of species and the size of the study area (ARRHENIUS, 1921; GLEASON, 1922, 1925; WILLIAMS, 1943; VESTAL, 1949); next the investigators concentrated on the interrelationships between the phylogenetic age of the species and the area occupied (WRIGHT, 1941). Gradually there came out more general publications presenting regularities in the distribution of the range sizes of species habitating larger areas of the globe (HOPKINS, 1955; TERENTYEV, 1958), in the distribution of numbers within separate species in polyspecific communities (FISHER, CORBET, WILLIAMS, 1943; MACARTHUR, 1957; GLADKOV, 1958), in the distribution of the number of species, types etc., and the area of their range on the level of the higher taxonomic units, so perfectly and accurately analysed by PRESTON (1948, 1956, 1960, 1962a, b). He has introduced the principle of lognormal distribution of separate parameters on the basis of structural dependences, and he has drawn some far-reaching conclusions concerned with general zoogeographic phenomena and the evolution of the animal world.

Inasmuch as studies on the spatial structure of polyspecific communities, the best synthesis of which has been provided by PRESTON (1962b), can have their bearing only on some aspects of the spatial distribution of the species (e.g. the so called canonical distribution), then studies on the spatial structure of the population can be used as a starting point for more comprehensive studies. The crucial point in any investigation carried out on the level of the population is the structure of the spatial distribution of individuals, while in the case of studies on the level of the species the basic unit is the micropopulation and the population.

COLE (1946) was the first who proved that there is a tendency to spatial integration of individuals on the population level, and who found out that random occurrence is very rare. The works of WADLEY (1950), DICE (1952), CLARK and EVANS (1954, 1964), THOMPSON (1956), and TAYLOR (1965) also deal with random occurrence. In a short space of time there have been published numerous attempts to describe mathematically the spatial structure of the population, and to interpret this structure from the point of view of biological functionality (BEKLEMISHEV, 1960; ANDREWARTHA, 1961; MACFADYEN, 1963; ODUM, 1963; KERSHAW, 1964; ELTON, 1966; LEVINS, 1966; MACARTHUR, 1966; MACARTHUR, CONNELL, 1966; NOVOZHENOV, 1966; PIELOWSKI, 1966; SOUTHWOOD, 1966; WATT, 1966; LEWIS, TAYLOR, 1967; ZYKOV and SAPETIN, 1967). Much new material for the analysis of the spatial organization of the population has been furnished by works dealing with the essence of populational phenomena (LACK, 1954, 1966; POLIVANOV, 1957; DERAMOND, 1959; SOUTHERN, 1959; WYNNE-EDWARDS, 1959; HOVARD, 1960; MEUNIER, 1960; CRAGG, 1962; SLOBODKIN,



1962; BREWER, 1965; CLARK, EVANS, 1964; SHVARTS, 1965; DUBININ, 1966; SYROYETSCH-KOVSKIY, 1966; DUBININ, GLEMBOTSKIY, 1967).

A point of signal importance in the studies on the spatial distribution of the population, and the species in particular, is the analysis of the structure of the flock and of the micro-population. The results obtained so far in this field enable us to determine quite precisely the character of groups below the populational level (ISAKOV, 1949, 1957; MIKHEYEV, 1950; WERTH, 1960; VORONTOV, 1960; NAUMOV, 1965; PAYUSOVA, 1965; JÓZEFIK, 1962, 1969).

And thus, both above and particularly below the level of the species the structure of spatial distribution has been analysed relatively sufficiently, especially in relation to vertebrates. A synthesis of problems connected with the populational and spatial structure of the species has been put forward by MAYR in his recent work (1963). Although, as it was stressed by PETRUSEWICZ and TROJAN (1964), the conception of polytypic species which is characterized by spatial measurements is completely dominating at present in various fields of biology, there has not been done much, especially when considered against the background of the achievements mentioned above, in the way of clarifying empirically the interrelations of the species distribution as well as the mechanisms integrating it in space, so that we could proceed beyond laboratory experiments in these studies, support them statistically and describe them in mathematical functions. There is no lack of general hypotheses in this field. They are known in a variety versions from most of manuals on zoogeography (vide — references). ARNOLDI (1957) put forward a not very optimistic question in connection with this state of things — how much are our views on the spatial structure of the species based on factual material? After all this problem is utterly important for the clarification of basic evolutionary questions. But let us go back in time. 30 years ago the well known zoogeographer HEPTNER (1936) commented not without an undertone of pessimism when discussing the general theory of range: "The question of the species distribution within its area ..... has almost never been approached by investigators." Twenty years later the excellent investigator of the structure of distribution within the range mentioned already above, ARNOLDI, thus summed up the situation in 1957: "Even at present the deep knowledge of both the populational structure and the real picture of the distribution of any biological species within a more or less large area still remains an unattainable ideal." It should be pointed out here that ARNOLDI considered as an ideal not the knowledge of the entire range but only its large section. Discussing further the achievements in this field he stressed that, "as a whole, there can be no doubt that the material quoted here marks only the first step in the necessary direction and the existence of these works does not contradict the pessimistic estimate discussed above and concerned with the state of our knowledge in relation to one of the most important questions of ecology and speciation." (ARNOLDI, 1957). This quotation characterizes quite clearly the situation prevailing in the fifties. There has been further progress in the last decade (ANDRUSHKO, 1957; ARNOLDI, 1957; ZAVADSKIY, 1961; VORONOV, 1963; ARTEMYEV, 1964; JÓZEFIK, 1969) and, what is most important — it has been realized that there is a necessity to fill the gaps, the more so that tendencies to systematize and synthesize the knowledge on the species, in spite of repeated attempts in the past, are more and more urgently required by the needs of the present age. The problem of spatial structure not only lies at the base of the theoretical knowledge of the species but is also a key to the methodological profile of practical problems, such as those concerned with the organization of the best ecological environment for man and the most rational utilization of natural resources (hunting, acclimatization, pest control). One of the pressing evolutionary problems requiring a modern approach as pointed out by OLENOV (1961), ER-LICH and HOLM (1963), MAYR (1963), SAVAGE (1963), HANSON (1966), and FORD (1967), is the analysis of the mechanism of genetic flow on the interpopulational level. The basic link which can lead to the explanation of this problem is just the knowledge of the spatial structure of the species. It must be spatial not only as to the distribution and relations



within the breeding area but also within the entire range. Some questions have been tersely and succinctly formulated by ISAKOV (1963a, b) and ROKITSKIY (1965) in connection with the need to solve practically a number of economic tasks serving wide social requirements. ISAKOV also stressed that in the present stage we should pass from the observations of frontiers and the area of ranges to detailed studies on their structure. The enormous amount of material collected enables to venture some general conclusions and should be used to put through some syntheses. Other weighty arguments, revealing vital connections with economic utility, have been put forward by VORONOV (1858) and many other investigators of the Soviet school (ARTEMYEV, 1964; ISAKOV, 1963a, b; KIZYAKIN, 1963; KOROVITSYN, 1963; LYUBISHTSHEV, 1958, and others).

A number of problems faced by the modern knowledge of the species and difficult to solve in view of the lack of links which would help to learn about mechanisms regulating its numbers, ensuring the genetic flow, deciding the degree of vagility (ability of the species to expand in space), affecting the populational structure and interpopulational relations, producing a differentiated type of isolation, bearing on the history of range alterations, etc., stressed by numerous authors (ALLEE and SCHMIDT, 1951; ARNOLDI, 1957; BEKLEMISHEV, 1960; CRAGG, 1962; DARLINGTON, 1957; DERAMOND, 1959; FORD, 1964; GLADKOV, 1958; 1960; ISAKOV 1949, 1957; KALELA, 1957; KURAZHNSKOVSKIY, 1957; LACK, 1954; MAYR, 1963; MEUNIER, 1960; PETRUSEWICZ, 1959; POLIVANOV, 1957; SLOBODKIN, 1962; TERENTIEV, 1958; VORONTOV, 1964; VORONOV, 1958; WERTH, 1960; WYNNE-EDWARDS, 1959; ZAVADSKIY, 1961), undoubtedly could be solved satisfactorily, providing we studied more comprehensively the spatial parameters of the species.

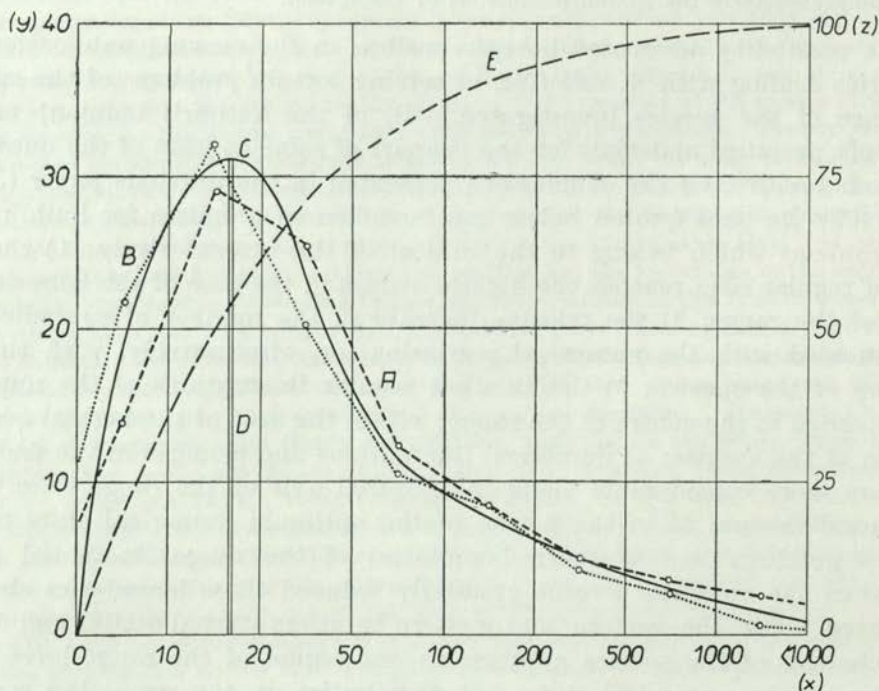
The possibility advocated here, as well as in the ensuing publications of the series dealing with *A. ralloides*, of solving certain problems of the spatial structure of the species investigated will, in the author's opinion, enable to supply practical materials for the support of some at least of the questions mentioned above. Of the conclusions presented in the previous paper (JÓZSEFIK, 1969) the ones quoted below can be taken as premises for building up the problems which belong to the subject of the present study: 1) the per cent of regular sites reaches the highest values in the case of the homeostatic state of the range; 2) the relative increase in the number of sporadic sites is connected with the numerical regression, or, alternatively, with the expansion of the species; 3) the smallest secular fluctuations of the numbers are recorded in the centre of the range, within the area of the highest concentration of the species; 4) numerical fluctuations and changes in the distribution are more considerable along the parallel axis of the range than along the meridian one; 5) in the period of the optimum numerical state of the species northern and southern boundaries of the range fluctuated most, but when the numbers became gradually reduced these boundaries steadily stabilized while the eastern and western frontiers started oscillating; 6) secular changes of the species numbers in one region of the range have some bearing on the numerical state and distribution in the remaining regions; 7) a decrease in the numbers is accompanied by a territorial regression. Territorial expansion is preceded, on the other hand, by a certain period when the numbers increase. This is a cumulative phase which is followed by the proper expansion of the species.

I would like to mention in passing that I shall discuss here only the basic structural point of distribution, namely its characteristics in the first phase of the breeding period (this concerns, first of all, the measurable features of the micropopulation). Problems connected with the spatial distribution of *A. ralloides* in other periods of the annual cycle will be discussed only marginally, and more space will be devoted to them in the IVth and Vth parts of the series.

#### GEOGRAPHICAL VARIABILITY IN THE MICROPOPULATION SIZE

##### Distribution of breeding sites

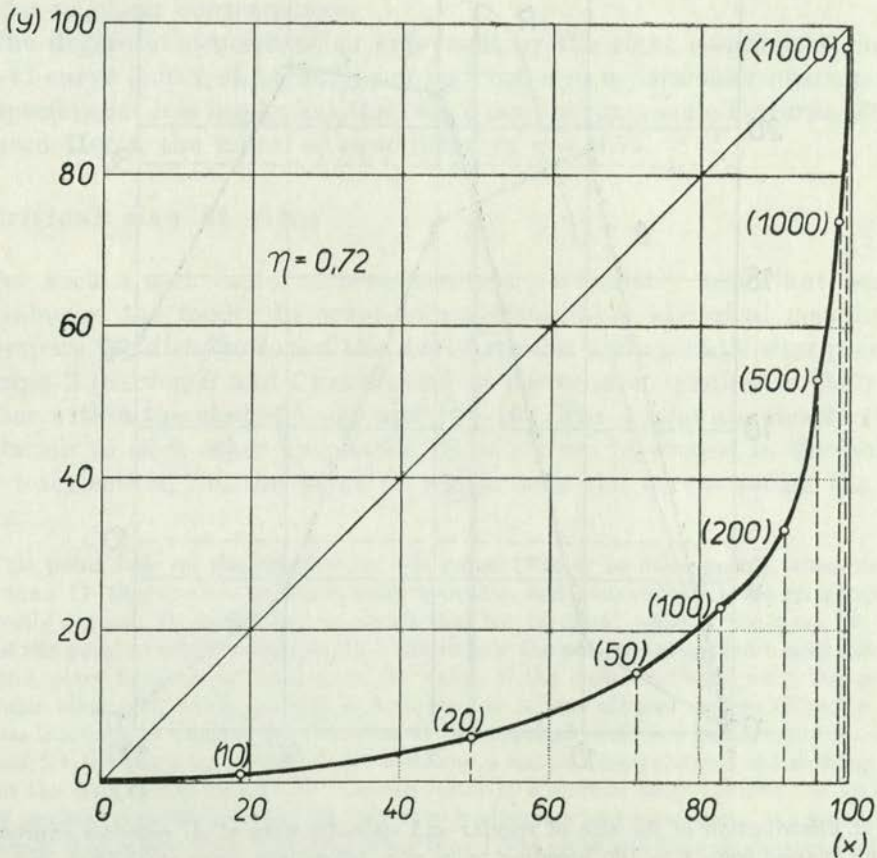
A study of geographical variability in the micropopulation size (breeding site) of *A. ralloides* is a key problem in this third part of the series. Before I attack this problem, I shall discuss general characteristic types of the distribution of site sizes, and both sporadic and regular sites will be taken



Graph 1. Distribution of the size of *A. ralloides* breeding sites expressed in per cent.  $x$  — class intervals of the size of sites;  $y$  — per cent of sites in relation to their total number (scale for curves A, B, C);  $z$  — the same as  $y$  (scale for curve E); A — XIXth century; B — XXth century; C — resultant for the XIXth and XXth centuries; D — mode of curve C; E — ogive of the cumulative series (XIXth and XXth centuries together).



together. The distribution mentioned for the XIXth century is represented in graph 1 by curve *A*, and for the XXth century by curve *B*. Curve *C* is the resultant of the two previous curves. The course of curves *B* and *A* is closely intercorrelated although the secular changes discussed previously (JÓZEFIK, 1969) for low as well as high values of classes are here stressed. Curve *C* is here a characteristic parameter of the species. Thus the general distribution is decidedly right-skewed (skewness  $+0.59$ ) with mode = 17.5 pairs, average =  $108 \pm 10.6$ ,  $\sigma = 154$ . It is evident that for this type of distribution the indices quoted give an incomplete picture. This also concerns the

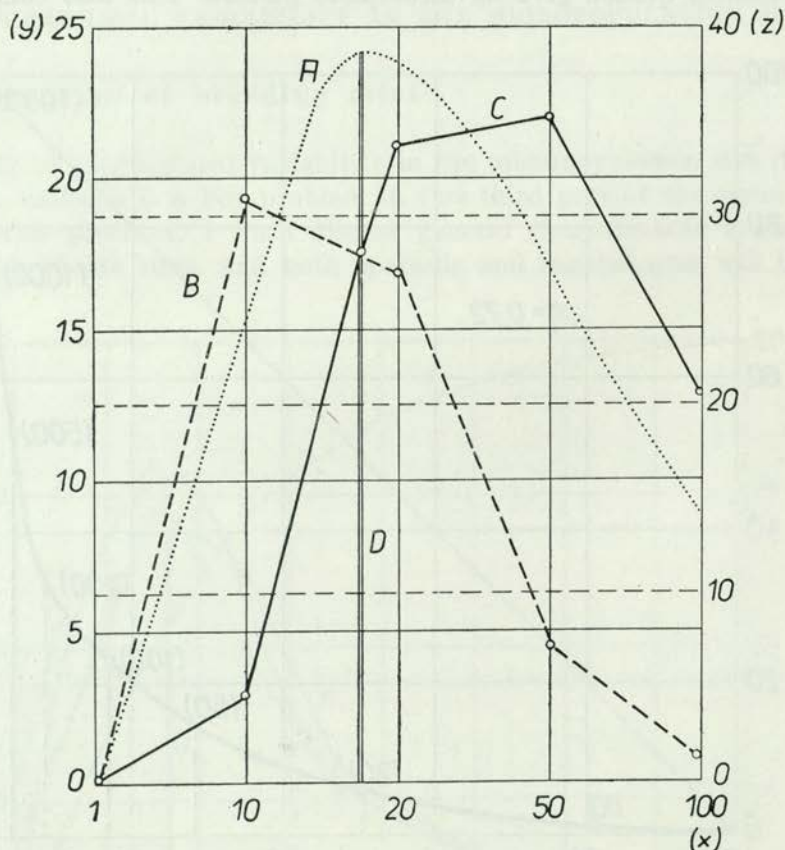


Graph 2. Curve of *A. valloides* concentration in the palearctic part of the range (XIXth and XXth centuries together). *x* — number of sites expressed in per cent; *y* — number of breeding pairs expressed in per cent.

course of curve *C* which also apparently falsifies the picture in the conditions of an increase in the values of class intervals. Apart from the difficulties of characterization in the case of treating the frequency distribution as a

normal distribution, the mode is the most valuable index\*). As it will be shown later its value in comparison with the course of curve *C* and the course of the curve presenting the concentration of the species numbers (graph 2) provides the most objective estimate of dispersion.

Let us characterize briefly the curve of concentration (graph 2). It gives quite objective information which does not depend on the increasing values of the class intervals of the distribution discussed above. Thus only 1.02% of the species numbers concentrate in sites including up to 10 breeding pairs.



Graph 3. Distribution of the size of regular and sporadic sites of *A. ralloides* expressed in per cent (classes from 1 to 100 breeding pairs were taken into account; XIXth and XXth centuries together). *x* – class intervals of the size of sites; *y* – number of breeding sites (scale for curves *B* and *C*); *z* – the same as *y* (scale for curve *A*); *A* – distribution of regular and sporadic sites together; *B* – distribution of sporadic sites; *C* – distribution of regular sites; *D* – mode of curve *A*.

\*) As a matter of fact, it is the so called “lognormal curve”, i.e. the normal Gaussian distribution with the logarithmic scale on the abscissa which, as it was proved by PRESTON (1948, 1958, 1962a, b), enables to characterize a number of phenomena in zoogeography.



Sites of such size mostly belong to the category of sporadic sites (curve *B* — graph 3). The value of the mode exceeds only 5.3% of the total numbers of the species. As it will be shown later, it is a very significant statement. More than half of all the sites are inhabited by only 6.06% of the species numbers; in 80% of the sites approximately 20% are concentrated, while 50% of the total number occupy as many as 95% of all the sites. This suggests a conclusion that seems to have significant practical importance — such a type of social species as *A. ralloides* is concentrated only in a few (!) main centers of its enormous palearctic range (cf. also — JÓZEFIK, 1969). For the purposes of control and rational use of natural resources this has great and far-reaching consequences.

The degree of concentration expressed by the right co-efficient, for this type of curve (curve of Lorenz), can be treated as a parameter characterizing the species, not less important than for example taxonomic features. For the Squacco Heron the index of concentration  $\eta = 0.72$ .

#### Critical size of sites

For such a high index of concentration particularly important becomes the value of the mode. In order to understand its biological meaning, let us compare the distribution of the size of regular and sporadic sites presented in graph 3 (curves *B* and *C*) expressed in per cent in relation to their total number within the classes 1—10 and 50—100. The curves are clearly shifted in relation to each other by phases, while we are interested in the point of their intersection, i.e. the point at which both the curves attain the same values.

This point falls on the abscissa for the value 17.5, or in other words, sites including fewer than 17–18 pairs are predominantly sporadic, and conversely — more numerous sites are mostly regular. It should also be added that the terminal value of the class, 20, is just beyond the point of intersection. Graph 3 shows how the per cent of sporadic sites falls down from this place towards an increase in the value of the class intervals, while the per cent of regular sites goes down towards a decrease. As it was stressed before (JÓZEFIK, 1969) the class intervals in view of the character of the material could not be narrower from those accepted for the purposes of the study. Even by a simple interpolation, the shifting of the limit of the class down from 20 to 17.5 will result in a sudden drop towards the right and a more gradual increase towards the left of sporadic sites and away from the regular ones. This means that regular sites including fewer than 17–18 pairs lose their character and become sporadic, or disappear altogether.

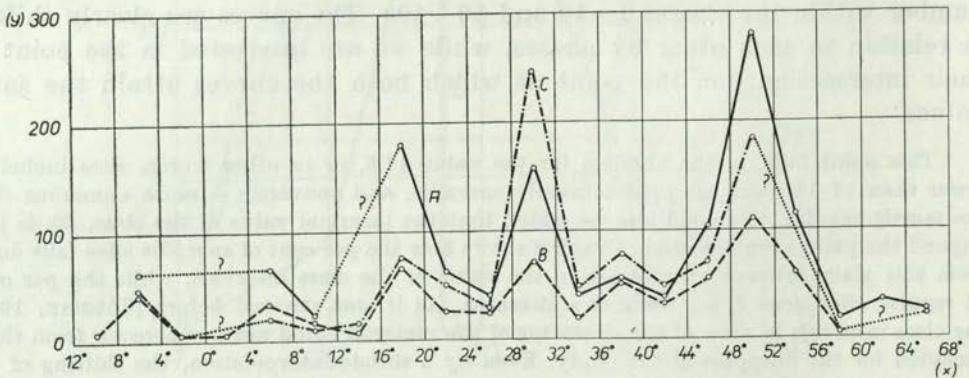
Thus an important conclusion can be drawn: the critical size of regular sites of *A. ralloides* is 17–18 pairs (17.5). This value occurs here naturally as an average calculated on the basis of materials for the last two centuries and covering the entire range investigated.

It is evident even at the first glance that the point at which the curves presenting the distribution of sporadic (*B*) and regular (*C*) sites intersect is

de facto the mode of the general distribution of their values (cf. graph 3). This provides ground for another conclusion with practical implications: the surest way of determining the critical size of breeding sites inhabited by social species distributed in an island-like pattern is to calculate the mode of the general distribution of their values. This mode calculated in relation to the given part or to the entire range, is the value needed. As I have shown earlier the same result can be obtained in a more graphic way, i.e. like in the case of curves *C* and *D* in graph 3 by plotting on the same grid the distribution of sporadic and regular sites. The point at which the two curves have the same value determines the critical value, as well as the mode of the general distribution. To clear the thing up, I shall add that by the minimum critical size of sites (micropopulation) within the area studied I understand such a size below which their existence, or more precisely their ability to reproduce, will be disturbed (regular sites become sporadic, or even disappear altogether).

#### The size of sites in the parallel cross-section

The elementary rules of the cross-section analysis of the range were presented in the II<sup>nd</sup> part of the series dealing with *A. ralloides* (JÓZEFIK, 1969). I discussed then secular oscillations in the number of sites and in the



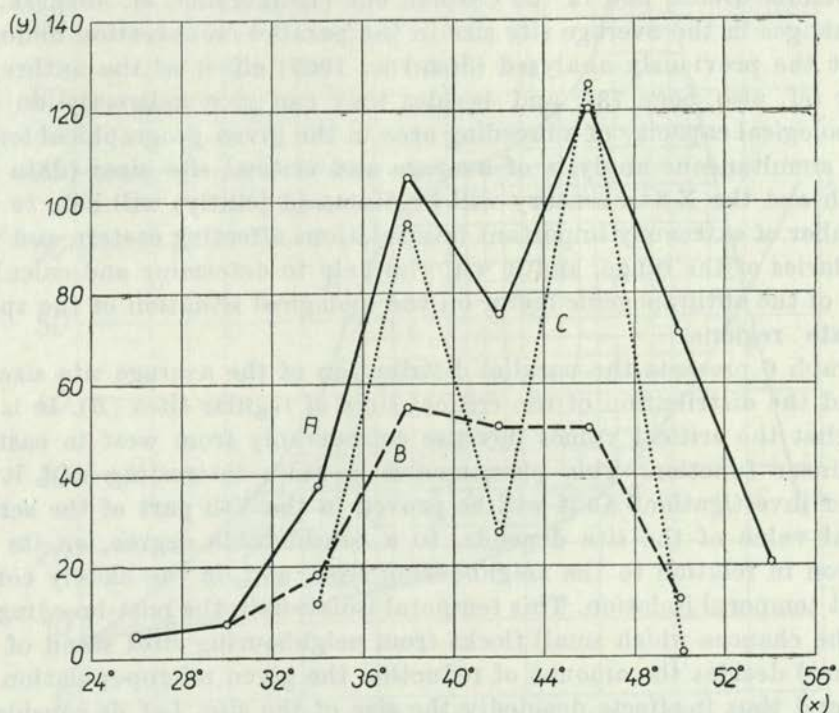
Graph 4. Size of sites in the parallel cross-section.  $x$  — geographical longitude;  $y$  — size of sites expressed by the number of breeding pairs; *A* — 2<sup>nd</sup> half of the XIX<sup>th</sup> century; *B* — 1<sup>st</sup> half of the XX<sup>th</sup> century; *C* — period 1950-1960.

number of breeding pairs in both parallel and meridian cross-section, as well as relations recorded between sporadic and regular sites. The statistical characteristics presented there (cf. page 63) seemed to indicate a considerable variability in the size of sites. And indeed, graphs 4 and 5 which presented the average site size in the two types of cross-section characteristic for second half of the XIX<sup>th</sup> century (curves *A*), for the first half of the XX<sup>th</sup>



century (*B*), and for the years 1950–60 (*C*), suggested that the value underwent considerable fluctuations in time, and moreover changes as to the geographical position.

As compared with the second half of the XIXth century, with the exception of the northern Black Sea center, the average site size in the present century in the parallel cross-section displayed a general decrease (graph 4).



Graph 5. Size of sites in the meridian cross-section.  $x$  – geographical latitude;  $y$  – size of sites expressed by the number of breeding pairs; *A* – 2nd half of the XIXth century; *B* – 1st half of the XXth century; *C* – period 1950–1960.

This decrease was particularly evident in the middle Danube and the Caspian centers, i.e. in those regions where until the 1st World War the landscape had been exceptionally intensively transformed, while the population inhabiting these areas had not been able to synanthropize. This is also valid in the case of the North Italian center.

In the entire range the average size of sites after 1950, as compared with the twenties and the thirties of the present century is higher. The only exception is here the North Italian center. This seems to be closely connected with the termination of direct destruction carried out on a mass scale by man (JÓZEFÍK, 1969). When the vogue for egret feathers reached its culmination

(beginning of the XXth century) the species became dispersed all over the entire range, with the exception of the Caspian center, and the size of sites did not exceed, on average, 50–75 pairs. Only owing to the fact that there was carried out a simultaneous and not less intensive reduction of the natural enemies of *A. ralloides*, such as for example birds of prey, the situation did not turn out to be disastrous for the entire species. At present the highest average size of sites can be recorded in the northern Black Sea center (mainly the Danube Delta) and in the Caspian one (Lenkorania, cf. JÓZEFIK, 1969).

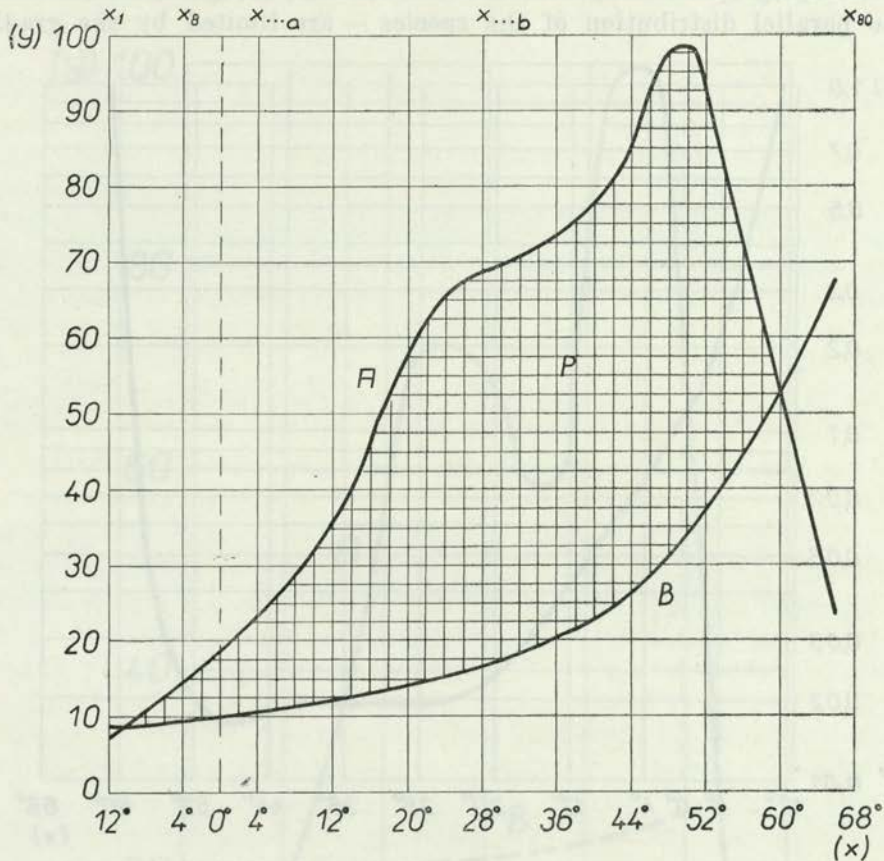
Changes in the average site size in the parallel cross-section undoubtedly reflect the previously analysed (JÓZEFIK, 1969) effect of the anthropogenic factor (cf. also page 73), and besides they can give indirectly an idea of the ecological capacity of a breeding area in the given geographical longitude.

A simultaneous analysis of average and critical site sizes (data for the XIXth and the XXth century will be discussed jointly) will help to explain a number of extremely important interrelations affecting eastern and western boundaries of the range, and it will also help to determine and calculate the effect of the anthropogenic factor on the biological situation of the species in separate regions.

Graph 6 presents the parallel distribution of the average site size (curve A) and the distribution of the critical sizes of regular sites (B). It is clearly seen that the critical values increase considerably from west to east in the curvilinear function. This phenomenon is quite interesting and it merits further investigation. As it will be proved in the Vth part of the series, the critical value of the site depends, to a considerable degree, on its spatial isolation in relation to the neighbouring sites, and on the closely correlated with it temporal isolation. This temporal isolation in the post-breeding period (i.e. the chances which small flocks from neighbouring sites stand of joining together) decides the amount of reduction the given micropopulation undergoes, and thus it affects decidedly the size of the site. Let us consider now: what are the factors affecting indirectly the reduction of passing flocks and those carrying out nomadic movements. I shall take here into account the effect of birds of prey and the intensification of the anthropogenic factor. Both these factors eliminate in the course of migration a considerable part of migrating birds, but their effect is completely different (man can notice and reduce as a rule individuals staying in large and easily spotted flocks, while birds of prey attack usually either small flocks or single individuals). As it was pointed out by FERGUSON-LEES (1963), in the last 100 years 26 species of European birds of prey, out of the total number of 37, were reduced due to the action of man. Thus it is evident that the gradient of the reducing effect of the anthropogenic factor, measured in absolute values, remains inversely proportional to the gradient of the effect of birds of prey. The action of man in the pre- and post-breeding periods is relatively most intensive in the western parts of the range and it displays a tendency to a decrease



towards the east and then it is taken over by birds of prey. The course of curve *B* in graph 6 supports indirectly this conclusion and at the same time indicates the adaptability of the species as to the spatial distribution and the intensity of the factors discussed. We have to take here into account also

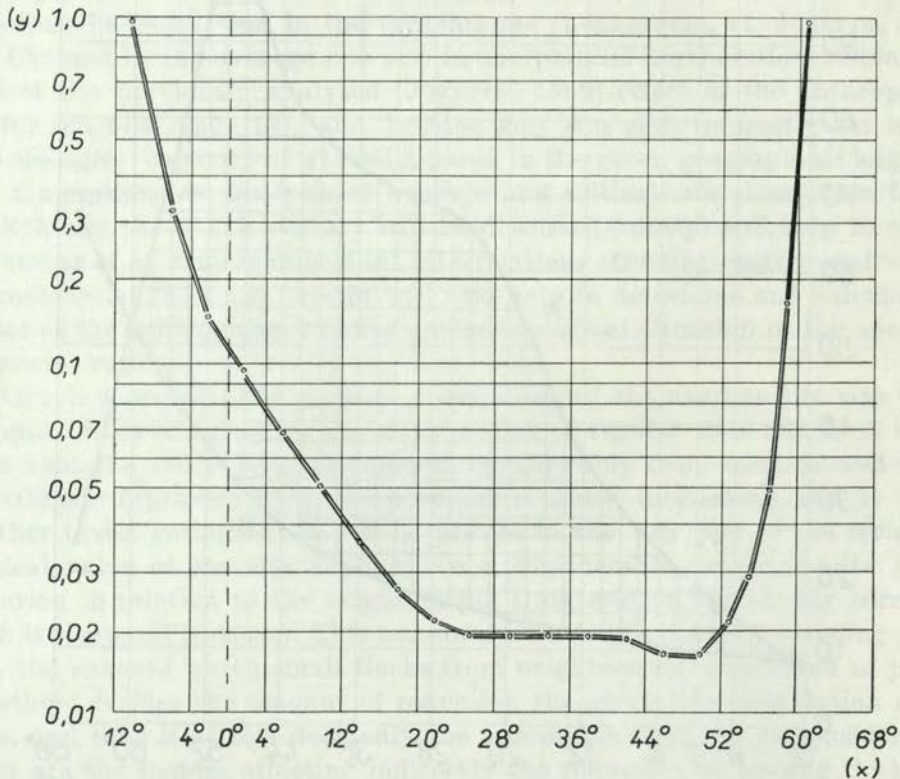


Graph 6. Variability of the critical size of regular breeding sites and the average size of all the sites in the parallel cross-section of the range (XIXth and XXth centuries together; movable average values).  $x$  — geographical longitude;  $y$  — size of sites in absolute figures; *A* — average size of sites; *B* — critical size of regular sites; *P* — area between curves *A* and *B* =  $V$  (index of ecological vitality).

the period of the absolute isolation of separate micropopulations which increases considerably towards the east. The winter ranges of *A. ralloides* include also the tropical part of Africa. Ample evidence will be presented in the ensuing parts of the series to show that migration routes of western populations are shorter and much "safer" than those of eastern populations. As a result, low critical site sizes in western regions enable the species to habitate even smaller water bodies and marshy stretches, and the further

we go towards the east, the larger is the area of breeding spaces. Thus smaller breeding areas are occupied there only sporadically by the species, or even never at all.

Summing up I should say that one of the most important structural parametrs of the spatial distribution — critical sizes of regular sites determining the parallel distribution of the species — are limited by the gradient



Graph 7. Anthropogenic stress in the parallel cross-section (XIXth and XXth centuries together).  $x$  — geographical latitude;  $y$  — logarithmic scale of index  $S_a$ .

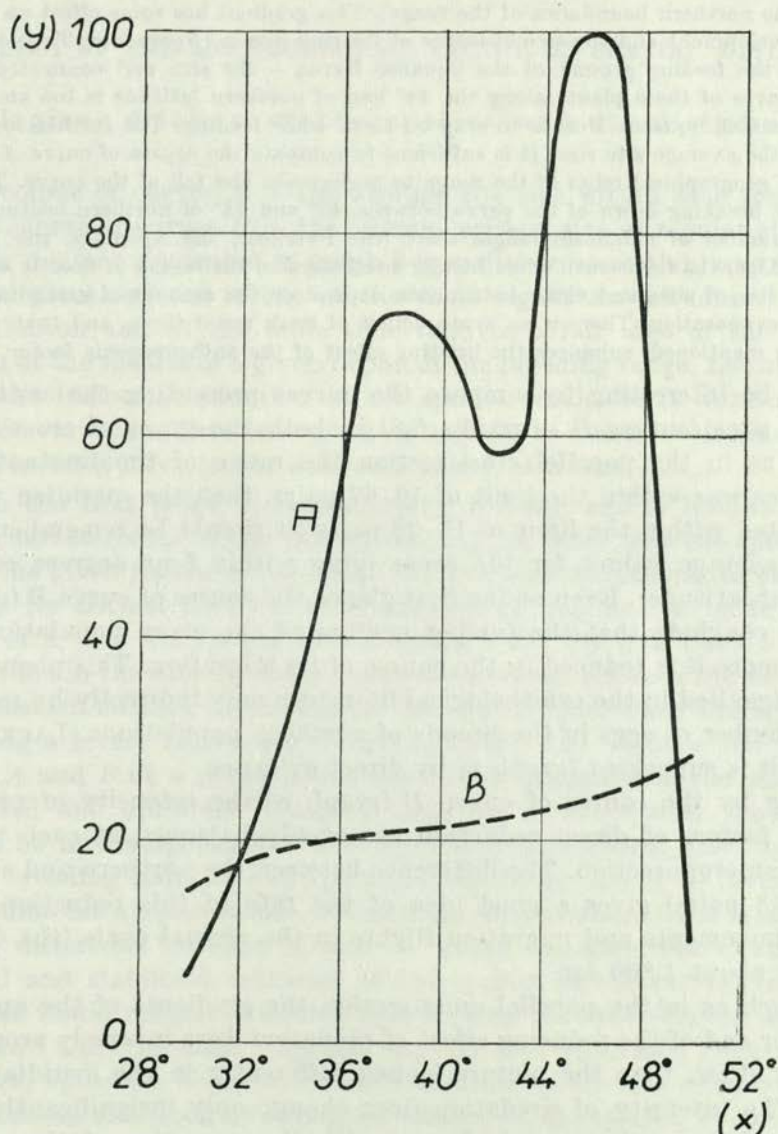
and the character of limiting factors which affect strongly the species in the postbreeding period (temporal isolation between the micropopulations). Among these factors the following are particularly important: man (hunting, poaching) and predators.

#### The size of sites in the meridian cross-section

Functional interrelations of the parameters discussed, although they are analogous to those in the parallel cross-section analysis, in many cases acquire different qualitative features. And thus, for example, in the parallel cross-section the level of the curve presenting the size of sites reflected in the first



place the effect of the anthropogenic factor, while here it was evident in the "southern" section of the curve (graph 8). The largest sites are grouped along the latitude of their highest concentration, i.e. between  $44^\circ$  and  $48^\circ$  of northern latitude, which becomes particularly obvious when we take into account the resultant for the last two centuries (curve *A* — graph 8). This



Graph 8. Variability of the critical size of regular sites and of the average size of all the sites in the meridian crosssection of the range (XIXth and XXth centuries together). *x* — geographical latitude; *y* — size of sites in absolute figures; *A* — average size of sites; *B* — critical size of regular sites.

can lead to certain reflections connected with the gradient of environmental factors and ecological requirements of *A. ralloides*.

Thus the left-skewed distribution is undoubtedly caused here by the lack of sufficiently capacious breeding habitats in the southern regions of the palearctic part of the range. It should also be mentioned here that the northern border of the range is limited only directly by the thermal gradient (the highest concentration of the species takes place just in the vicinity of the northern boundaries of the range). This gradient has some effect on the phenology of development and the size of leaves of floating plants (*Nymphaea*, *Trapa*) forming the basis of the feeding ground of the Squacco Heron — the size and connected with it the lift of leaves of these plants along the 48° line of northern latitude is too small, even in June, to enable Squacco Herons to stay on them while feeding. The further southward, the lower is the average site size. It is sufficient to compare the course of curve *A* with the physical and geographical relief of the range to understand the fall of the curve. Thus the characteristic breaking down of the curve between 40° and 44° of northern latitude is the result of a number of mountain ranges there (the Pyrenees, the Apennines, the Balkans, the Dinaric Alps, the Caucasus), while further southward in the region of deserts and semi-deserts the size of sites and their distribution depend on the amount of precipitation and intensity of evaporation. There is an acute deficit of fresh water there, and that, as it has already been mentioned, enhances the limiting effect of the anthropogenic factor.

It will be interesting to compare the curves presenting the critical size of regular sites (curves *B* — graphs 6,8) in both the types of cross-section. Inasmuch as in the parallel cross-section the range of the fluctuations of critical sizes was within the limit of 10-67 pairs, then the meridian variability oscillated within the limit of 15-28 pairs (it should be remembered that these are average values for the areas lying within four degrees of either longitude or latitude). Even at the first glance the course of curve *B* (graph 8) enables to conclude that the further northward the given population habitats, the more it is reduced in the course of its migration. This phenomenon has been signalled in the ornithological literature only indirectly by recording a larger number of eggs in the broods of northern populations (LACK, 1954). This time it is supported (graph 8) by direct evidence.

Judging by the course of curve *B* (graph 8) the intensity of predation and other factors of direct reduction are evenly balanced at each place in the meridian cross-section. The difference between the northern and southern sections (13 pairs) gives a good idea of the rate of this reduction during nomadic movements and migration flights in the annual cycle (the distance covered is about 1,800 km.).

Inasmuch as in the parallel cross-section the gradients of the anthropogenic factor and of the reducing effect of predators were inversely proportional to each other, then the picture looked differently in the meridian cross-section: the intensity of predation does change only insignificantly, while the effect of the anthropogenic factor, with the exception of the phase of direct reduction at the turn of the century (JÓZEFIK, 1969), gradually increases southward while the deficit of fresh water supplies gets more acute (cf. curve *B* — graph 5). The combined limiting effect of these two factors



in the region of deserts and semi-deserts resulted in the occurrence of a wide disjunction between the palearctic and Ethiopian parts of the range of *A. ralloides*. However the progressing synanthropisation of the Squacco Heron in the south across the Nile valley seems to diminish gradually this disjunction.

#### THE EFFECT OF THE ANTHROPOGENIC FACTOR ON SPATIAL DISTRIBUTION

##### Ecological vitality of the species and its distribution

The course of curves *A* — the average site size within each four degrees, and the course of curves *B* — the average critical size of regular sites within each four degrees, presented in graph 6 (parallel cross-section) and in graph 8 (meridian cross-section) is one of the most significant structural moments of distribution and at the same time it gives a fair idea of the biological situation of the species in a given region of the breeding range. Let us consider a) how the biological situation of the species would be in various circumstances of variations between values *A* and *B*; b) which environmental factors and in what form decide the combination of *A* and *B*.

As to the first point, it seems pretty obvious, and it follows from the general characteristics of the two curves, that in order that the species could exist in the given region of the range the average site size has to exceed permanently its critical size, i.e. the condition  $A > B$  has to be fulfilled. In the case of  $A = B$  the species would undoubtedly die out. Such a situation was recorded in the eastern Asiatic part of the range between the  $60^\circ$  and  $68^\circ$  lines of eastern latitude at the turn of the century just when the species was undergoing a severe regression (JÓZEFIK, 1969). The wider is the difference between *A* and *B* at a given point, the better grounded is the certainty of a stabilized and optimum biological situation of the species. Theoretically it would be advantageous for the species if *B* (critical size) equalled 2 (i.e. one breeding pair) at each point of the range and if *A* (average size) could assume the highest values. Considering the question in the long run, the widening difference between *A* and *B* would enhance the chances of a successful and stabilized existence of the species in the future. In a word, the species would remain in a state approaching the optimum one and would be "secure" and "immune" against any dangers (natural), such as freaks of weather, epizootic diseases, climatic extremes, etc. The complex of such features can be described as ecological vitality of the species. From the point of view of nature protection, applied ecology, etc., the determination of the index of ecological vitality, which would reflect on the stability or dangers threatening the species, would be extremely practical, and this explains why I have devoted so much space to it although it is only a digression in



relation to the basic subject of the paper. In the case of the Squacco Heron the degree of ecological vitality ( $V$ ) can be relatively determined by the area within a given class ( $x_a - x_b$ ) of geographical longitude contained between the respective sections of curves  $A$  and  $B$  (graph 6). And thus:

$$V = \frac{1}{n} \int_{x_a}^{x_b} [f_A(x) - f_B(x)] dx, \quad (1)$$

where:  $x_a$  and  $x_b$  restrict the area of the range investigated and for which value  $V$ , i.e. the index of ecological vitality, is calculated;  $n$  = number of geographical degrees;  $f_A(x)$  and  $f_B(x)$  are integral functions of curves  $A$  and  $B$ ;  $dx$  is component of the integral equation.  $V$  calculated for the entire range is a relatively stable parameter characterizing the species. For *A. ralloides*  $V = 34.09$ . In the case of more complicated functions of both the curves it is possible to introduce a somewhat simplified version of index  $V$  (cf. page 76).

Let us have a look at graph 6. The critical size of sites ( $B$ ) increases very regularly (at an exponential rate) from west to east. It is easy to conclude that it is just this parameter which restricts the spreading of the species in the east. The average site size ( $A$ ) increases in a more complicated function. The points where the two curves intersect determine the eastern and western boundaries of the range. In their region the ecological vitality of the species is lowest. It reaches the highest values in the central parts of the range. The biological situation of the western population is not very favourable — their ecological vitality there is very low indeed.

When we know the distribution of  $V$  in the parallel cross-section (graph 7), it is not difficult to draw practical, and very weighty, conclusions concerned with attempts at protective measures and generally based on the scientific principles of the utilization of natural resources. It is a truism to state that if we had at our disposal, at the right time, the distribution of the degree of vitality and other materials of the type analysed here above (although the way to obtain them may be a hard one) then undoubtedly we were able to keep a number of species from dying out, to say nothing of a sensible solution provided for other problems which are a result of the so far unbalanced relation: man — nature.

### Anthropogenic stress

Let us state precisely the effect of the anthropogenic factor on the character of the parallel distribution. The level of curve  $B$  is affected, beside the already analysed direct numerical reduction (JÓZEFIK, 1969), by the reduction of the Squacco Heron's natural enemies carried out by man (cf. page 68) as well as by protective measures. Thus we can record the effect twofold in



its character: a) negative, restraining the spreading of the species by forcing it to increase the critical size of the micropopulation and rendering impossible the use of habitats with a low ecological capacity, b) positive, leading to a decrease in the minimum critical size of the micropopulation which enables the use of habitats with a low ecological capacity, and thus it renders possible wide spreading of the species. The relation of the two types of effect in their historical aspect has already been discussed (JÓZEFIK, 1969), and I would like to point out here that in the last two phases of the action of the anthropogenic factor on the critical size of the micropopulation ( $B$ ) positive elements gain the upper hand. Only by the restriction of natural enemies of *A. ralloides* and by specific protection did the critical size of regular sites decreased in the western parts of the palearctic range (cf. graph 6), and this enabled the species to exist there when the habitat had been transformed. Generally, it can be accepted that a decrease in  $B$  is connected with a beneficial influence of man.

The level of curve  $A$  (average micropopulation size) also depends on the factors determining the critical size, although the anthropogenic factor acts here differently — reduction and transformation of breeding habitats. The average value of curve  $A$  within separate sectors of the range situated between meridian lines indicates the capacity of the sites being at the disposal of the species. In western regions of the range the capacity is lowest and it gradually increases towards the center, while it decreases sharply in the east. Assuming that a) in the prehistoric times the ecological capacity of sites along the parallel axis of the range was little differentiated, b) resources of breeding habitats in relation to the general area of separate parts of the range before man entered the ecological arena had been maintained in permanent proportions (e.g. enormous marshes in the middle courses of the Danube, in the Caucasus, in northern Africa, etc., in former times), c) western and eastern reaches of the range were formed by the gradient of environment resistance without interference of civilization — the present, differentiated from west to east, size of sites (cf. curve  $A$ , graph 6) should be accepted as restrained by the effect of man and his historical influence. This effect is undoubtedly negative and only insufficiently set off by the synanthropization of the species. Thus the anthropogenic stress increases together with a decrease in the value of  $A$ . I shall reiterate here that the intensive reduction of primary habitats in the zone of Khara-Kum (the Tedzhen, the Murghab, and other rivers) carried out at the beginning of the present century, with the simultaneous high level of the critical size of sites, inevitably led to regression — the frontier of the range was shifted westward by about 1,200 km (JÓZEFIK, 1969).

On the basis of the arguments given above, we can express the effect of the anthropogenic factor on the parallel distribution by the ratio  $A/B$ , and when the absolute value of the ratio goes down, the anthropogenic

stress increases. In the case of  $\frac{A}{B} \geq 1$  the species disappears in the given region. Theoretically, in the conditions of a complete mastery of man over nature (in the sense of a complete control of biocenotic relations) the species could exist even in the case of  $\frac{A}{B} = 1$ , i. e. in a situation when the degree of ecological vitality ( $V$ ) would be insignificantly small. The application of the formula  $\frac{A}{B}$  could be useful in the case of a necessity to determine without delay the effect of man on the biological situation of the species. This formula can also be a simplified index of the ecological vitality of the species (cf. page 74).

As the effect of man within the boundaries of the potential range is a dominating factor limiting the numbers and distribution of the species, the relative value of this effect is at the same time an index of the anthropogenic stress. The ecological vitality of the species is invertly proportional to the value of stress, i.e. an intensification of stress results in a decrease in the ecological vitality and in consequence it leads to the disappearance of the species, or to its synanthropization. Let us present the dependency discussed in the form of the following formula:

$$S_a = V^{-1}, \quad (2)$$

where  $S_a$  = index of anthropogenic stress,  $V$  = ecological vitality of the species (cf. formula (1) on page 74). It follows from the dependency above that when  $V \approx 0$ , then  $S_a \approx 1$ , and thus when the species disappears from the area the stress reaches the highest maximum relative intensity = 1. Calculating  $S_a$  for a certain part of the range (obviously in the aspect of the cross-section analysis), formula (2) will be transformed:

$$S_a = \frac{n}{\sum_{x_a}^{x_b} V}, \quad (3)$$

where:  $n$  = number of geographical degrees between  $x_a$  and  $x_b$  (cf. graph 6),  $\sum_{x_a}^{x_b} V$  = ecological vitality of the species in a given area of the range.

Graph 7 presents distribution  $S_a$  in the parallel cross-section. It is in a surprising agreement with the degree of transformation of marshland habitats by man in prehistoric times. In the areas where there is an acute shortage of fresh water (north-western parts of Africa, the Iberian peninsula, the Transcaspian areas) index  $S_a$  approaches 1. The density of population and the degree of transformation of the primary landscape also seem to be well correlated with the course of the curve discussed above. As I have



already mentioned (cf. page 67) the intensification of the anthropogenic stress corresponds, on the basis of counteraction, with an increase in the processes of *A. ralloides* synanthropization. It should be stated generally that processes of synanthropization spread particularly early over the western regions of the area (JÓZEFIK, 1969). Only recently has this phenomenon been recorded in the eastern regions. It is responsible for the restitution of the species in the Transcaspiian part of the range (cf. page 75).

Interpreting the course of curve (graph 7) we should remember that the degree of  $S_a$  is relative, i.e. it is expressed mainly by the results of the action of the anthropogenic factor. This means that if its effect could be expressed by any absolute measure, then the same type of action and of the same intensity (e.g. equally intensive measures of land reclamation, the same number of individuals reduced, etc.) carried out in different parts of the range would vary considerably in their effects. And thus, for example, the reduction of the same area, proportionally to the existing resources of breeding areas in the outlying eastern parts of the range, where the critical size of sites is largest, and in the central regions, will turn out to be disastrous for the eastern population while in the center it will cause only insignificant changes in the biological situation of the species. It should also be taken into consideration that the relative value of  $S_a$  depends, to a considerable extent, on the intensity of the anthropogenic factor along the migration routes and in the winter ranges as well. This problem will be discussed in greater detail in one the ensuing publications belonging to the present series.

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The index of ecological vitality ( $V$ ) acquires a different significance when it is analysed in the meridian cross-section as compared with the parallel approach. If, for example, we accept the distance which the range stretches along a meridian ( $16^\circ$  of latitude) as a certain proof of the species adaptation and tolerance in relation to the climatic gradient, index  $V$  will not only give us an idea of the potential abilities of the species to resist the anthropogenic stress and predation, but it can also reveal the potential possibilities of existence in the conditions of the given geographical latitude.

Similarly as in the parallel cross-section (graphs 6 and 7), also in the case of parameters presented in graph 8 we can draw certain practical conclusions with the view to strengthen protective measures. For example, it is evident straightaway that protective measures in the east should include in the first place restitution and protection of the habitat (mainly an increase in the ecological capacity — level of curve  $A$  ought to be raised), and not only specific protection (the lowering of the level of curve  $B$ ).



## CONCENTRATION OF THE SPECIES AND ITS RANGE ZONES

## Extrapolation of the species numbers

Let us consider which of the structural elements of the distribution are of a permanent character being the non-oscillating feature of the species. If we assumed the relative permanence of such elements, we could use them to carry out specified extrapolations which might shed some light on the history of the species. We can not include here the critical and average size of sites analysed in the two types of cross-section. On the other hand, the general distribution of the size of sites, and consequently the curve of concentration, are more constant. As I have proved earlier, in spite of considerable numerical differences of the species in the XIXth and XXth centuries (JÓZEFIK, 1969), we can detect striking similarities when the distributions for the two centuries are compared (cf. graph 1). The permanence is definitely not accidental.

Below I shall present evidence, based on analogy, which indicates that in the case of small secular changes in the numbers the distribution of micropopulation size corresponds with (and in certain cases is also formed by) a general regularity in the distribution of geographical units, such as flowing waters, bodies of standing water, etc.

If we classified resources of marshland habitats within the range according to the increasing size (area in hectares) then we would probably arrive at the distribution skewed to the right monotonically decreasing in the right-hand side part (probably approaching lognormal or binomial) which, except the initial section, would be correlated with the course of curve *C* in graph 1, the one presenting the general distribution of the size of breeding sites. Obviously the drawing of such a distribution was impossible for the author in view of the lack of a sufficient amount of data\*. Thus we have to limit ourselves to a hypothetical model (curve *A* — graph 9), and mainly to be restrained to the use of premises based on direct field observations, data from the literature on the subject, and on detailed analyses of maps. Thus within the breeding range there are mostly small, isolated water bodies and marshes, ponds and flood waters, usually seasonal in character and rarely exceeding 10 hectares in area. As a rule, they are used only in the course of migrations and while carrying out nomadic movements. A much smaller part is made up of water bodies medium in size such as lakes, old river beds, and complexes of marshes 500–1,000 hectares in area. There were fewer water bodies and deltas of medium size rivers approaching the area of 50,000 hectares, and there was only a very small per cent of marshland habitats between 100 and 200 thousand hectares.

As a social species having a distinct critical micropopulation size, *A. ralloides* can inhabit only areas which exceed a certain specified ecological capacity. This critical area probably varies for different parts of the range. And thus there remains an enormous per cent of smaller water bodies not used in the breeding period, or only inhabited sporadically. Judging by the hypothetical distribution of habitats (graph 9) the per cent of larger areas suitable for the species decreases although not as sharply as in the initial section of the curve (we have to take into account the logarithmic scale). If there were a possibility to plot, in adequate proportions, the distribution of the size of sites and a real (and not

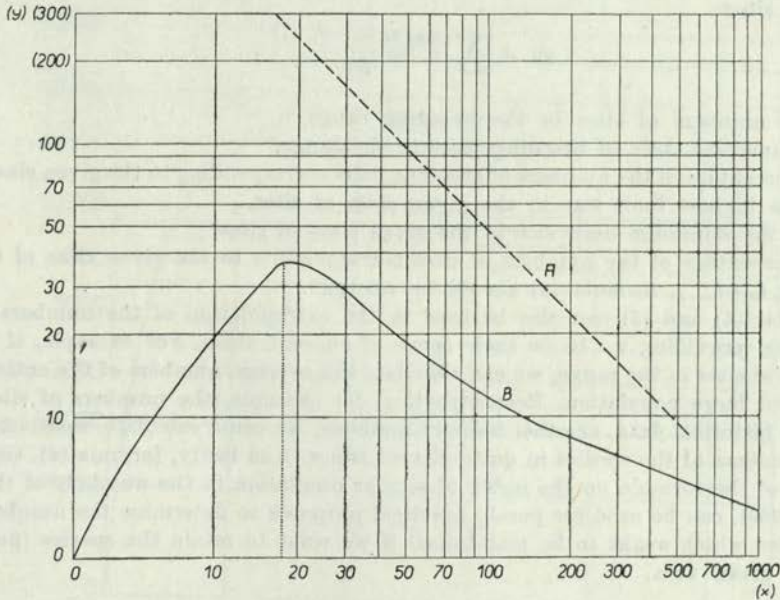
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\* By the analogy with the distribution of the size (in km) of flowing waters from the smallest streams to large rivers within the given geographical unit, we could build a hypothetical model of the distribution of standing waters characterized by the suitable, for *A. ralloides*, habitat formation. A simplified model of such a curve would have the shape of a hyperbola whose asymptotes would be co-ordinates *x* and *y*, while the centre of symmetry would be the point where the co-ordinates intersect — point 0 (the equation would look as follows:  $2\ Bxy = F$ ). It is not excluded that it could also be a binomial distribution.



hypothetic like in graph 9) distribution of breeding habitat areas, on a grid, then we would most probably arrive at two well correlated curves (or even possibly covering each other). This correlation would reach the point determined by the mode of the distribution of the size of sites (critical size). This point would also determine the critical area (e.g. in hectares) of marshland habitats below which the functioning of a regular site, and consequently the existence of the micropopulation, could not be stabilized (cf. graph 9).

As the structural features of the distribution of habitats are a result of the physical and geographical properties of the countryside, they are stable and have a bearing (at least to a certain extent) on the general distribution of the size of sites. It should be assumed that the concentration of the



Graph 9. Hypothetical distribution of the amount of resources recorded in the breeding habitats of *A. ralloides* against the distribution of the size of breeding sites.  $x$  — class intervals of the size of breeding sites and the relative amount of resources in the breeding habitats;  $y$  — number of sites expressed in per cent and the relative number of sites in the breeding habitats;  $A$  — hypothetic distribution of resources in the breeding habitats;  $B$  — distribution of the size of breeding sites.

species (graph 2) is one of its constant properties (cf. page 65). Hence the curve of concentration can serve to extrapolate the numbers of the species in the past, forecast for the future, as well as it helps to model certain situations of the species. It should also be added that the effect of the anthropogenic factor on the structure of the concentration curve can, up till now, be reflected in its initial section (change in the critical size), and also in the final section (considerable reduction of the species).

Summing up, the percentage relation of separate classes of micropopulation size and the corresponding ratio of the species numbers, disregarding

here the absolute state, is relatively constant (Table 1). As we shall see later this is possible down to a certain limit when the absolute numbers of the species steadily decline, but below this limit the proportions will be very seriously affected.

Without going into details I suggest the following equations for the extrapolation of the numbers of sites ( $x_{st}$ ) at a given level of the number of breeding pairs:

$$x_{st} = \sum \frac{2y_b p_n}{100(l_n + l_{n-1})} \quad (4)$$

and for the extrapolation of the level of species numbers ( $y_b$ ) at a given (or known) number of breeding sites:

$$y_b = \sum \frac{x_{st} q_n (l_n + l_{n-1})}{200}, \quad (5)$$

where  $x_{st}$  = numbers of sites in the breeding range,

$y_b$  = numerical state of breeding pairs in the range,

$p_n$  = percentage of the numbers of breeding pairs corresponding to the given class of sites,

$l_n$  = the highest limit size in the given class of sites,

$l_{n-1}$  = the minimum limit size in the given class of sites,

$q_n$  = percentage of the numbers of sites corresponding to the given class of their size.

If  $y_b < l_n + l_{n-1}$ , formula (4) should be altered\*.

Formulas (4) and (5) can also be used in the extrapolation of the numbers of other social species, providing we know their curve of concentration. For example, if we know the number of sites in the range, we can calculate the average numbers of the entire species, or a specified large population. Reconstructing, for example, the numbers of sites on the basis of the historical data, or other indirect methods, we could calculate, relatively accurately, the numbers of the species in quite distant times. And lastly, formula (4), similarly as in the case of the formula on the index of secular oscillation in the numbers of the species (JÓZEFIK, 1969), can be used for purely practical purposes to determine the number of sites and their size which ought to be maintained if we want to retain the species (population) within the given area.

Starting from the characteristics of concentration (Table 1) and using formula (5), let us now analyse how the numbers of the species will increase theoretically together with an increase in the number of sites (graph 10).

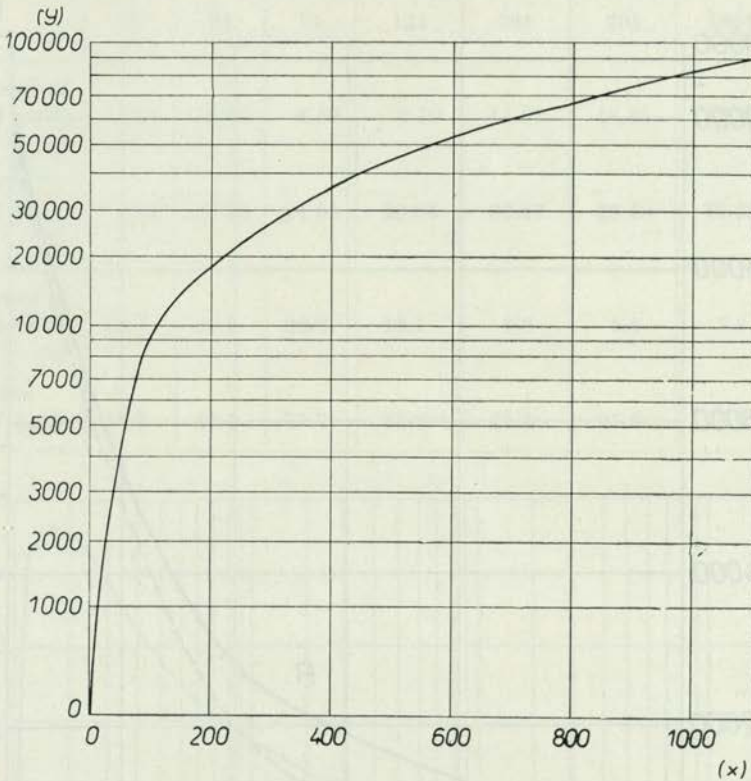
\* This alteration boils down to the necessity to accept as 100 such a value of the cumulative series  $p_n$ , which is in the class with a sum of its limiting values  $l_n + l_{n-1}$  smaller than  $y_b$ , and on this basis a corresponding recalculation of all  $p_n$  values in the lower classes, however together with the class whose value of the cumulative series was accepted as 100 (Table 1). A correction has to be introduced into formula (5) if  $x_{st} < 100$ . This consists in:

a) picking in series  $q_n$  such a value which divided by  $\frac{100}{x_{st}}$  would give a quotient within

1—2; b) in a class in which this condition is met, the value of the cumulative series is accepted as 100, and similarly as in the correction to formula (4) we have to recalculate all the values of  $q_n$  from the beginning of the series to the class whose value of the cumulative series was accepted as 100. The new values of  $q_n$  will be inserted into formula (5). It is obvious that in both these cases  $\Sigma$  includes only the left side of the series from the class in which values  $p_n$  or  $q_n$  of cumulative series were accepted as 100.



This extrapolation is important for the determination of certain momentous periods in the history of the species (e.g. knowing the numerical level we can conclude on the rate of genetic flow, role of the species in the paleobiocenoses, possibilities of spreading, etc.), and thus it is possible to obtain some premises as to the evolution of the species studied.

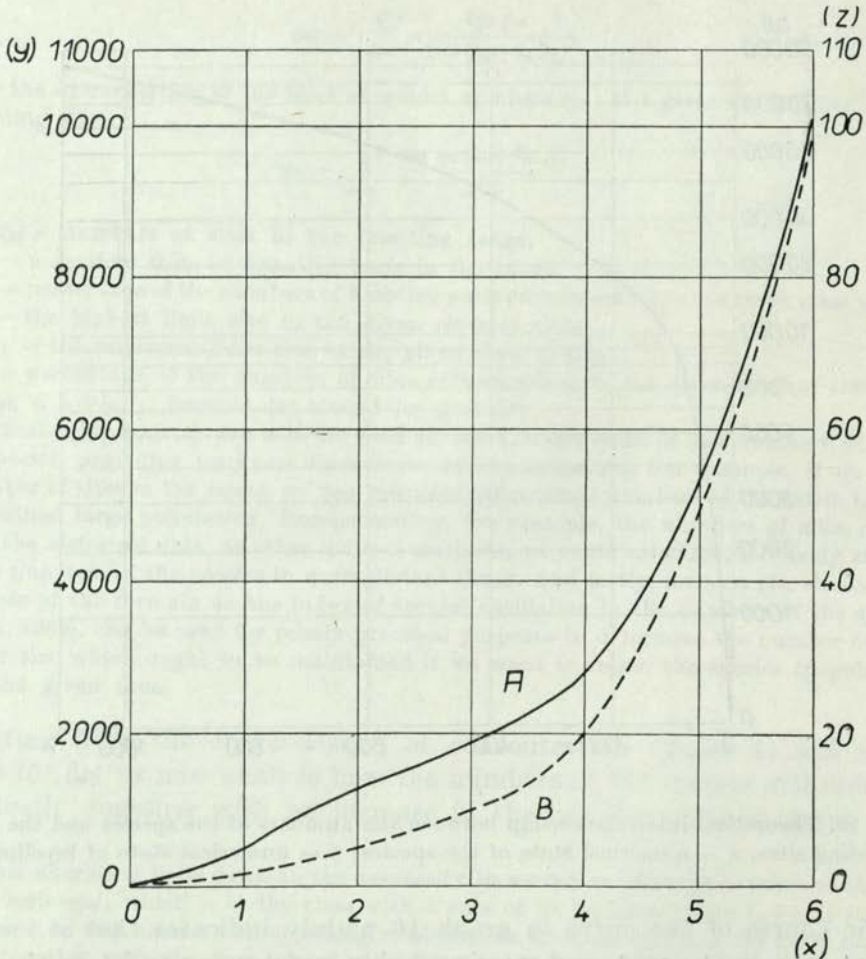


Graph 10. Theoretical interrelationship between the numbers of the species and the number of breeding sites.  $x$  — numerical state of the species;  $y$  — numerical state of breeding pairs.

The course of the curve in graph 10 plainly indicates that *A. ralloides* has not been in the past, and most probably is not going to be, in the future a very numerous species, for example not having hundreds of thousands of individuals. Even assuming that the number of sites in the Palearctic exceeded 1,000 in the so called climatic maximum after the latest freeze-up, while the total numbers of the species, providing that it did not differ substantially in its biological aspect from the present state, were probably maintained at a level of 100-120 thousand pairs.

Graph 11 presents a theoretical interrelationship of a decrease or an increase in the number of sites and of breeding pairs in the range. Only above

the level of 5,000 pairs the proportions of the two parameters are stabilized which is particularly well borne out by graph 12. It illustrates the theoretical variability of the percentage proportions of the two parameters. A numerical decline of the species below the level of 5,000 pairs disturbs the structure of the concentration of the species, and this in turn sparks off changes in the mechanism of numerical regulation and disturbs the structure of



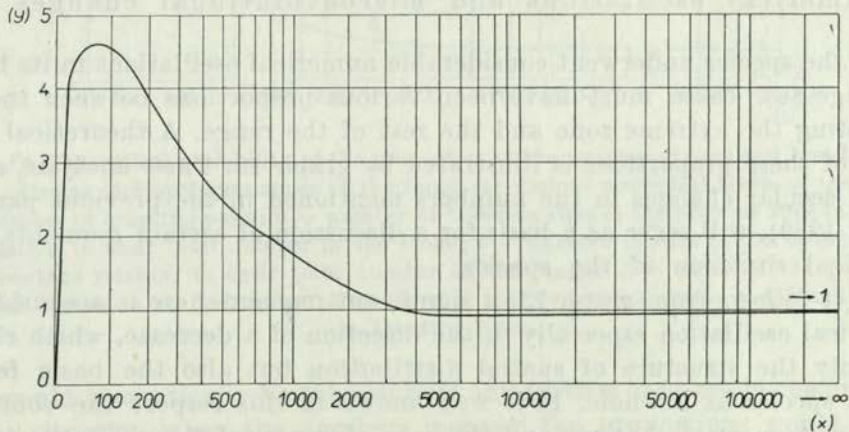
Graph 11. Theoretical interrelationship between an increase in the number of sites (A) and in the number of breeding pairs (B).  $x$  — relative units of time;  $y$  — numerical state of breeding pairs;  $z$  — numerical state of breeding sites.

genetical exchange, interpopulational relations, and it also frees the self-protective mechanisms of the species. Before I touch upon some of these, I shall discuss the micropopulational ecological zone system of the range which is connected with the concentration of the species and its structure.



Table 1. Numerical concentration of *A. ralloides* breeding pairs according to the number of breeding sites and their size (calculated for the palearctic part of range on the basis of data for the last 100 years)

Class intervals of site size (1)	1-10	11-20	21-50	51-100	101-200	201-500	501-1000	<1000 (2000)
$l_n + l_{n-1}$	11	31	71	151	301	701	1501	3000
$p_n$ (per cent of breeding pairs) (2)	1.02	5.04	8.49	9.10	14.02	16.81	22.75	(22.75)
cumulative series of $p_n$ (3)	1.02	6.06	14.55	23.65	36.67	53.48	76.23	98.98
$q_n$ (per cent of breeding sites) (4)	18.7	30.8	22.2	11.1	8.6	4.4	2.8	(1.4)
cumulative series of $q_n$ (5)	18.7	49.5	71.7	82.8	91.4	95.8	98.6	(100.0)



Graph 12. Theoretical variability of percentage proportions in the number of sites and the numerical state of *A. ralloides* breeding pairs in relation to the numerical level of the species.  $x$  — number of breeding pairs;  $y$  — quotient of percentage proportions in the number of sites and in the number of pairs.

### Ecological zones of the range

The map presenting the numerical distribution of sites and breeding pairs, which was included in Part II of the present series (JÓZEFIK, 1969), showed clearly that the size of sites is smallest in the outlying parts of the

range. They are mostly sporadic sites, or alternatively smaller regular ones, but undergoing considerable numerical oscillations. This lack of stability is a result, beside intraspecific reasons, of habitat extremes limiting the spreading of the species. The distribution of this type of sites can be used to determine the extreme zone (ecological pessimum) of the range. The ecological criteria of this zone will be determined more precisely in the ensuing parts of the series, here we shall use the critical size mainly as a simplified indirect index. I have used the expression "mainly" because in the case of considerable oscillations displayed by regular sites they will also determine the extreme zone. Generally, sites of more than 20 pairs should be treated as signalling an extreme area. I shall put off the discussion of the criteria of suboptimum and optimum zones for the moment — they will be given much space in Part V of the present series, and here I shall call tentatively all the parts of the range with the distribution of larger and stabilized sites as an "optimum zone".

The curve of concentration (graph 2) indicates that when we take the average numerical state for the last 100 years, more than 60% of the general population stayed in the extreme area and nearly half of the total amount of sites (48%) were situated there.

#### Numerical oscillations and microevolutional changes

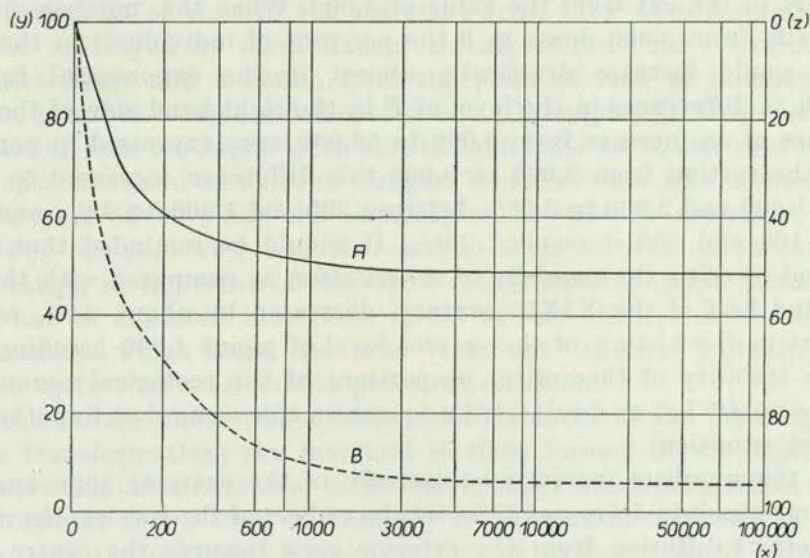
As the species underwent considerable numerical oscillations in its history (cf. page 86), there must have been various proportions between the part habitating the extreme zone and the rest of the range. A theoretical variability of these proportions is illustrated by graph 13. Their analysis, as well as the secular changes in the numbers mentioned in the previous part (JÓZEFIK, 1969), will serve as a basis for a discussion of certain moments of the biological situation of the species.

As it follows from graph 13, a significant moment here is a considerable numerical oscillation especially in the direction of a decrease, which changes not only the structure of spatial distribution but also the basic features of the species as a whole. It is well known in this respect the connection between numerical changes and the rate of genetical flow and the progress of evolution (FORD, 1967; MACFADYEN, 1963; WRIGHT, 1948). Causal relations between the spatial structure and microevolutional processes are feedback as it will be shown later.

Judging by the characteristics of sites, the balance of fertility and reduction in the extreme zone is permanently negative — this area is constantly supplied from the centre. The genetical flow towards the central parts is probably negligible, although the population habitating the extreme zone being quite exposed to the habitat pessimum suffers the most intensive selection, however it also displays the highest degree of adaptation which is not fixed genetic-



ally in view of the negative balance mentioned above. This state is characteristic for the stabilized situation of the species (homeostasis). The 6% of the general population habitating the extreme zone remains at a more or less stable level. In the case of the parameters extrapolated here (graph 13), such a state would theoretically correspond with the numbers of the general population in the region of 5,000 breeding pairs, i.e. until the moment when the proportions between the extreme and optimum zones are disturbed.



Graph 13. Theoretical variability of the proportion of the number of sites and breeding pairs in the extreme and optimum zones of the range for various numerical levels of the species.  $x$  — number of breeding pairs;  $y$  — number of breeding sites in the extreme zone in percentage relation to their total number in the range;  $z$  — number of sites in the optimum zone in percentage relation to their total number in the range;  $A$  — curve of the percentage relations of sites in the two zones;  $B$  — curve of the percentage relations of breeding pairs in the two zones.

This would theoretically be the result of any further decrease in the numbers. In the situation when the numbers increase the proportions would change very little (within a few per mille — cf. graph 13). The following conclusion can be drawn: at the homeostatic state of the species the extreme zone is habitated by a permanent per cent of individuals. And then genetical material only insignificantly penetrates inside the range, and the rate of microevolutional changes is very small in the scale of the entire species. It should be remembered that *A. ralloides* never achieved the homeostatic state in the period under consideration (cf. JÓZEFIK, 1969).

Let us consider now changes occurring in the conditions of a considerable decrease in the numbers of the species. We are mainly concerned with

the problem of how the self-protective mechanisms, potentially concealed in the part of the species habitating the extreme zone and bearing in consequence on the situation of the entire species, really work.

Such a situation was analysed (mainly in the aspect of functional connections) when discussing the crisis of the Squacco Heron in the years 1900-1920 (JÓZEFIK, 1969). The effect of human civilization was considered as a factor disturbing the state of homeostasis — the extreme zone began to increase relatively. In graph 13 such a situation is illustrated by a section of curve *B* to the left from the value of 5,000. When the numbers decrease theoretically from 5,000 down to 0 the per cent of individuals in the extreme zone would increase drastically almost in the exponential function. Inasmuch as differences in the level of *B* in the right-hand side of the graph in the case of an increase from 5,000 to 50,000 were expressed in per mille, then in the section from 2,000 to 5,000 this difference increased to 1.5‰, between 1,000 and 2,000 to 3.5‰, between 500 and 1,000 to 4‰, and lastly between 100 and 500 it reached 26‰. It should be reminded that during this period of crisis the numbers of *A. ralloides*, as compared with the state for the 2nd half of the XIXth century, decreased by about 84‰ reaching the lowest in the history of the species level of about 4,000 breeding pairs. Thus the stability of theoretical proportions of the ecological zones of the range was upset. Let us dwell a little longer on this somewhat hypothetically considered situation.

With the numbers increasing relatively in the extreme zone and a simultaneous absolute decrease in the total numbers of the species, the chances of a genetical diffusion from the extreme zone towards the centre of the the range become more and more pronounced. Theoretically, the degree of diffusion would increase even at a small drop in the absolute numbers of the species (exponential dependence). We are not able to express this relationship in mathematical terms although it would be of prime importance. Consequently I am going to devote more attention to the mechanism of exchange between the zones (rotation — cf. JÓZEFIK, 1969) in the condition of a danger threatening the species (crisis in the years 1900-1920) which can have a bearing on the dependence mentioned.

In the situation of a natural deterioration of habitat conditions (e.g. climatic factors), an increase in the extreme zone, as it should be expected, would be a concentric one. If, on the other hand, the anthropogenic factor is the limiting factor, the zone, beside its natural place in the outlying parts of the range, spreads in a mosaic-like pattern into the centre of the range. The problem is complicated by the fact that the differentiated character of the natural part of this zone and the one formed by man has, as a consequence, a different effect on the mechanisms of diffusion.

We have now to refer to the previously discussed (JÓZEFIK, 1969) two phases of regression connected with the anthropogenic factor: a) until 1920 —



the phase of a direct reduction of the species, b) period between 1921 and 1940 — the phase of an indirect reduction characterized by the transformation of the habitat.

In the first of the two phases as a result of a strong dispersion of the species an inflow of micropopulations from the outlying districts to the central regions of the range could be expected. As the destruction of the species assumed a regular character in the regions where the concentration of breeding sites was highest, the effect was reversed. Once there were formed larger groupings of sites in the marginal area, they were instantly discovered and destroyed by man. Except certain sections the rotation covered the entire range and it could, from the point of view of microevolutional changes, result in a rapid development of anthropophobia. However the rate of reduction was too rapid to be able to contribute to it, and thus the future of the species was in an extreme danger. When we take into account that in the course of 50-60 years the numbers of *A. ralloides* decreased by more than 84% (cf. page 76), and the extreme zone covered an enormous part of the range, in the sense of the effect of the anthropogenic factor, then it should not be expected that there would be any chances of the occurrence of mechanisms which would enable to "work out" and fix "suitable" adaptations, in spite of a considerable genetical diffusion.

In the second phase (reduction of the resources of the breeding habitat and its transformation) the marginal sections formed in the depths of the range were similar in character to habitat changes which occurred in a natural way (JÓZEFIK, 1969). Thus the density of population increased in separate centres, and the outflow of some individuals to transformed habitats was constantly intensified. As most of the habitat resources became modified, the balance of rotation could not remain onesidedly positive or negative, the diffusion of genetical material from the extreme zone (transformed habitat) most probably intensified its rate especially that until the forties the numerical level of the species remained low. The result, and at the same time the evidence, of this state of things is: a) the occupation of some of the transformed habitats (rice cultures, fish-ponds, land-reclamation canals), b) a general increase in the years 1941-1960 in the numbers of the species by more than 30%, c) the occurrence of certain expansive tendencies in the western, and recently in the eastern, regions of the range, which were rendered possible only when new abilities to adapt to the transformed habitat had been acquired, d) changes (genetically, to a certain extent, already fixed) in a number of ethological features contributed to the possibility of existing in the habitat (including those already transformed) in the nearest proximity to human settlements and the products of civilization encroachments, i.e. synanthropization.

Microevolutional changes, among which synanthropization should be included, have not taken the species to the optimum state (homeostasis) and pro-



bably, in view of the increasing rate of civilization progress, it will never be reached. The extreme zone, in its various variations, will make up a considerable per cent of living space within the range. Even if the unchanged reserves are retained, it will probably be impossible to keep the Squacco Heron in its "primeval" state, together with the species which do not easily yield to synanthropization. In view of that the course of the curves in graph 13, calculated as derivatives of the curve of concentration, can only supply us with approximate information on the future of the species and even that only in respect of short periods of time. Taking into account the numerical state of the species in the years 1941-1960 (about 10,000 breeding pairs — JÓZEFIK, 1969), while now (1968) it far exceeds 100,000 pairs (!), and relating it to the course of curve *B*, we could expect a stabilized situation of the species. Whether this will be supported by facts only future studies can answer.

Thus here there is some additional evidence in support of the theory (cf. page 84) which correlates the rate of genetical flow and microevolutional changes with the general numerical state of the species. Only a thesis should be added here (treated hypothetically) that the rate of these changes increases probably logistically in relation to the decrease in the numbers, which however does not exceed a certain specified critical level.

This phenomenon can be treated as one of the more important self-preservation and compensating mechanisms of the species in the periods of considerable secular oscillations in the numbers. Probably at one of the points of decent of curve *B* there exists a "zone of the critical level" within which the general effects of individual variability (mutations) and selection coupled with the rate of genetical exchange and of fixing the newly acquired features enable the species to get out of the crisis in a relatively short time. Depending on the character and intensity of the limiting factor (group of factors), the "critical zone" can be exceeded and even if the effectiveness of this factor is considerably reduced, the species may be faced with total destruction. In the case of *A. ralloides* the "critical zone" (as well as the critical size of the general population) lies probably below the level of 1,000 breeding pairs.

#### CONCLUSIONS

1. The point where the curves presenting the distribution of the size of sporadic and regular sites intersect, coincides with the mode of the general distribution of the size of sites — they determine the critical size of regular sites.

2. The critical size of sites in the parallel cross-section of the range increases from west to east in a curvilinear function. This increase is determined by an intensification of isolation in time and space, towards the eastern ends of the range, between micropopulations in the post-breeding period and the gradient of the effect of reducing factors (beasts of prey, hunting).



3. In the meridian cross-section the critical size of sites increases from south to north which can give us an idea of the average rate of reduction in the period of nomadic movements and migrations in the annual cycle along the route between northern and southern regions of the range.

4. The distribution of the critical and average size of sites in the parallel cross-section provides ground for concluding on the ecological vitality of the species. This distribution depends to a large extent on the effect of the anthropogenic factor. The anthropogenic stress and ecological vitality are intercorrelated with each other — it is an inversely proportional correlation.

5. The average size of sites in the cross-section analysis considered from the point of view of dynamics displayed a considerable geographical variability.

6. The general distribution of the size of sites and the curve of concentration show considerable stability as compared with the secular oscillations in the numbers of the species. They are a reflection of general regularities of the distribution of separate categories of habitats in nature. They can help to carry out the extrapolation of the species numbers in the past.

7. The numerical concentration of *A. ralloides* is very high ( $\eta = 0.72$ ), while its main potential in the Palearctic range is concentrated in several large sites which make up only a small per cent of the total number of breeding sites in the entire range.

8. In the case of the homeostatic state of the range the extreme zone is inhabited by a very small per cent of individuals. The diffusion of genetical material towards the centre of the range is minimal, and the same is true about the rate of microevolutional changes.

9. When there occurs a considerable (critical) decrease in the numbers of the species, the structure of the species concentration becomes disturbed, the per cent of individuals in the extreme zone increases at exponential rate, the genetical flow is intensified towards the centre, and the rate of microevolutional changes increases as well.

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## STRESZCZENIE

W rozdziale wstępnym autor definiuje ogólną koncepcję badań nad strukturą przestrzenną gatunku, która na przykładzie rozmieszczenia *Ardeola ralloides* (SCOP.) w palearktycznej części zasięgu będzie przedmiotem analizy w częściach III-V kontynuowanego cyklu. W krótkim zarysie uwypukla autor poważne luki w badaniach nad przestrzenną strukturą gatunku, zaznacza, iż na tle badań nad strukturą przestrzenną populacji (przeważnie owadziach) dziedzina ta ledwie została zapoczątkowana, chociaż znaczenie jej dla rozwoju teorii ewolucji, a szczególnie zastosowania w gospodarce zasobami przyrody ma pierwszorzędne znaczenie. Część III dotyczy zmienności wielkości progowej (krytycznej) i przeciętnej populacji elementarnych (mikropopulacji) zasiedlających poszczególne stanowiska lęgowe. Autor koncentruje się więc na wyjawianiu: a) podstawowych prawidłowości warunkujących zmienność geograficzną wspomnianych parametrów, b) wpływu na nie czynnika antropogenicznego oraz c) ich współzależności z innymi cechami struktury przestrzennej.

W rozdziale drugim podana jest charakterystyka statystyczna rozkładu wielkości mikropopulacji. Krzywe charakteryzujące rozkłady dla XIX i XX wieku (wykr. 1) są ściśle skorelowane, stąd rozkład ten autor uznaje za względnie stałą cechę gatunku, jak również pozostającą w zależności od niego krzywą koncentracji gatunku (wykr. 2) oraz wskaźnik koncentracji ( $\eta = 0,72$ ).

Koncentracja liczebności *A. ralloides* jest bardzo wysoka — główny jej potencjał w stosunku do olbrzymiej powierzchni zasięgu skupia się w kilkunastu dużych stanowiskach. Większość więc stanowią w zasięgu małe stanowiska (np. ponad 50% stanowisk skupia zaledwie 6% liczebności gatunku).

Nakładając na siebie rozkłady wielkości stanowisk regularnych i sporadycznych (wykr. 3), autor udowadnia, iż punkt przecięcia się obydwu krzywych pokrywa się z dominantą rozkładu ogólnego, a równocześnie wyznacza próg-minimum wielkości stanowiska regularnego. Progiem minimum (wielkością krytyczną) określa on taką wielkość stanowiska, poniżej której zdolność samoreprodukcji zasiedlającej go mikropopulacji istotnie zostaje zakłócona — stanowisko regularne przeistacza się w sporadyczne, bądź zanika. Praktycznym sposobem wyznaczania progum-minimum jest obliczenie dominanty rozkładu ogólnego wielkości stanowisk.

Analizując w profilu równoleżnikowym przeciętną wielkość stanowiska autor stwierdza, w odróżnieniu od stałości rozkładu ogólnego, znaczną (ujmowaną dynamicznie) zmienność geograficzną. W I połowie XX wieku uległa ona w porównaniu z XIX wiekiem ogólnemu obniżeniu (wykr. 4), zaś w okresie 1950-1960 znowu się zwiększyła, co pozostaje w ścisłym związku z charakterem oddziaływania czynnika antropogenicznego.

Wielkość progowa stanowisk wypośredkowana dla obydwu stuleci (wykr. 6) wzrasta z zachodu na wschód w funkeji krzywoliniowej. Wartość prog-



-minimum uwarunkowana jest izolacją czaso-przestrzenną poszczególnych mikropopulacji względem siebie, wielkością i charakterem ich redukcji w okresie pozalegowym (koczowiska, wędrowki, zimowiska). Na redukcję w profilu równoleżnikowym składają się pozostające względem siebie w stosunku odwrotnie proporcjonalnym działanie drapieźników — większe na wschodzie — i odstrzał (łowiectwo, kłusownictwo) — przeważający na zachodzie. Okres izolacji między mikropopulacjami jest większy na wschodzie, dłuższa i bardziej niebezpieczna jest też trasa wędrowek mikropopulacji wschodnich. Stąd różnica wartości progowych wielkości stanowisk między krańcem wschodnim a zachodnim jest bardzo znaczna (ponad 50 par), stąd też we wschodnich regionach zasięgu zasiedlone są tylko większe kompleksy biotopów wodno-błotnych o znacznej pojemności ekologicznej.

O rozmieszczeniu w profilu południkowym liczebności gatunku gradient termiczny decyduje pośrednio — największe stanowiska koncentrują się w pobliżu granicy północnej zasięgu (wykr. 8). W kierunku południowym, wraz z deficytem zasobów słodkowodnych, wzmagają się ograniczający wpływ człowieka. Progowa wielkość stanowisk wzrasta ku północnej granicy (różnica 13 par). Daje to pogląd o wielkości redukcji mikropopulacji podczas koczowisk i przelotów w cyklu rocznym na odcinku trasy między północnymi a południowymi regionami zasięgu (odległość około 1800 km).

W kolejnym rozdziale analizowany jest wpływ czynnika antropogenicznego na wielkość rozpatrywanych parametrów. Układ krzywych progumimum i wielkości przeciętnej stanowiska (wykresy: 6, 8), według autora, jest jednym z bardziej istotnych momentów struktury rozmieszczenia, dającym pogląd na ogólną sytuację biologiczną gatunku. Im bowiem wyższą wartość w danym punkcie zasięgu w profilu równoleżnikowym osiąga różnica między tymi krzywymi, tym większa jest szansa dalszej ustabilizowanej, niezagrożonej egzystencji gatunku, tym większa jest jego odporność na klęski losowe, tym większa witalność ekologiczna charakteryzuje gatunek. Ze zmniejszeniem się różnicy do zera (krzyżowanie się krzywych A, B na zachodnim i wschodnim krańcu zasięgu) obniża się również witalność i gatunek w danym regionie zanika. Sytuacja taka została opisana wcześniej w zakaspijskiej części zasięgu (JÓZEFIK, 1969), gdzie zanik tamtejszej populacji spowodował przesunięcie się granicy wschodniej ku zachodowi o ok. 1200 km.

Autor proponuje przyjęcie powierzchni pola zawartego między krzywymi A, B jako wskaźnika witalności ekologicznej gatunku ( $V$ ) — patrz wzór (1) str. 74, porównaj wykr. 6. Uproszczonym wskaźnikiem  $V$  może też być stosunek przeciętnej ( $A$ ) do progowej wielkości ( $B$ ). Następnie analizuje on historycznie wpływ na poziom i przebieg obydwu krzywych czynnika antropogenicznego, ujawniając jego złożony charakter. Autor udowadnia, iż obniżanie się przeciętnej wielkości stanowisk jest wyrazem negatywnego oddziaływania tego czynnika, natomiast obniżanie się progowej wielkości jest efektem korzystnego dla gatunku wpływu człowieka. Stąd stosunek  $A/B$  przyjąć można jako ogólny wy-



raz wpływu wspomnianego czynnika. Wraz z obniżaniem się wartości  $A/B$  maleje witalność i narasta stress antropogeniczny. Autor udowadnia, iż odwrotność wyrażenia (1), tj.  $V^{-1}$ , przyjęć można jako wskaźnik stressu antropogenicznego ( $S_a$ ) — patrz wyrażenie (2) str. 76. Stąd wyprowadza on ogólny wzór na obliczenie  $S_a$  w stosunku do danego w profilu równoleżnikowym sektora zasięgu — patrz wyrażenie (3) str. 76. Nasilenie stressu antropogenicznego we wspomnianym profilu (wykr. 7) jest najwyższe na krańcach zasięgu ( $S_a \approx 1$ ).

W przedostatnim z rozdziałów autor dowodzi, iż lewostronna asymetria rozkładu ogólnego wielkości mikropopulacji oraz zarys krzywej koncentracji w pewnej mierze są odbiciem ogólnych prawidłowości rozkładu poszczególnych kategorii biotopów w przyrodzie. Stąd, mimo oscylującej w określonych granicach liczebności gatunku obydwa parametry są dość ustabilizowane i posłużyć mogą do ekstrapolacji liczebności gatunku w przeszłości, jak również teoretycznego modelowania niektórych sytuacji. W tym celu autor posługując się tabelarycznym zestawieniem (tab. 1) koncentracji gatunku oraz wzorami na ekstrapolację liczebności par łęgowych (wyrażenie (4)) oraz stanowisk (wyrażenie (5)), dochodzi do wniosku, iż *A. ralloides* nawet przy przypuszczalnym zajmowaniu w przeszłości do 1000 stanowisk nie mogła być gatunkiem dość liczny (wykr. 10). Proporcje między liczbą stanowisk a liczebnością par łęgowych są dość stałe (wykresy: 11, 12); ulegają one przesunięciu po obniżeniu się liczebności poniżej 5000 par.

Na podstawie rozmieszczenia stanowisk małych z nie ustabilizowanymi mikropopulacjami (sporadyczne, ze znacznie oscylującą liczebnością) autor wydziela w zasięgu obok strefy optymalnej, strefę ekstremalną (pessimum ekologiczne). Przy homeostatycznym stanie zasięgu strefę tę zasiedla minimalny stały odsetek osobników (6% populacji generalnej).

W dalszej części pracy, w oparciu o modele teoretyczne (wykresy 10-13) i materiał dotyczący sekularnych oscylacji liczebności przedstawiono hipotetycznie mechanizmy przepływu genetycznego i przebieg niektórych procesów mikroewolucyjnych. Przy ustabilizowanym stanie zasięgu minimalne jest przenikanie ze strefy ekstremalnej materiału genetycznego w głąb zasięgu, minimalne jest też tempo zachodzących zmian mikroewolucyjnych (np. procesów synantropizacji). Przy znacznym obniżeniu się liczebności odsetek osobników w strefie ekstremalnej zwiększa się wykładniczo, następuje też intensywniejsza wymiana genetyczna, co w zmniejszonej populacji generalnej w warunkach ostrej selekcji ułatwia szybkie rozprzodzenie korzystnych mutacji. Autor analizuje następnie sytuację kryzysową *A. ralloides* w latach 1900-1920 i stwierdza, że wobec znacznego tempa obniżania się liczebności gatunku genetyczne utrwalenie odpowiednich adaptacji było niemożliwe. Dopiero w ostatnich dziesięcioleciach ujawniła się wyraźniej synantropizacja, będąca wyrazem zmian mikroewolucyjnych, pozwalających opanować przekształcone środowisko, zwiększyć liczebność oraz zrestytuować populacje w regionach poprzedniej regresji.



W zakończeniu autor wysuwa hipotezę, iż tempo przepływu genetycznego i zmian mikroewolucyjnych w stosunku do pewnego odcinka obniżania się liczebności gatunku (strefa krytyczna) wzrasta w funkcji logistycznej. Faza logarytmiczna tego wzrastania jest prawdopodobnie najistotniejszym mechanizmem samozachowawczym w sytuacjach krytycznych u progu totalnego wyginięcia gatunku.

Objaśnienia do wykresów i tabeli:

Wykr. 1. Rozkład wielkości stanowisk łęgowych *A. ralloides* w ujęciu procentowym.  $x$  — przedziały klasowe wielkości stanowisk,  $y$  — odsetek stanowisk w stosunku do ich ogólnej liczby (skala dla krzywych  $A, B, C$ ),  $z$  — znaczenie — jak  $y$  (skala dla krzywej  $E$ ),  $A$  — XIX wiek,  $B$  — XX wiek,  $C$  — wypadkowa dla XIX i XX wieku,  $D$  — dominanta krzywej  $C$ ,  $E$  — ogniwa szeregu kumulacyjnego (XIX i XX wiek łącznie).

Wykr. 2. Krzywa koncentracji *A. ralloides* w palearktycznej części zasięgu (XIX i XX wiek łącznie).  $x$  — liczebność stanowisk w ujęciu procentowym,  $y$  — liczebność par łęgowych w ujęciu procentowym.

Wykr. 3. Rozkład wielkości stanowisk regularnych i sporadycznych *A. ralloides* w ujęciu procentowym (pod uwagę wzięto klasy od 1 do 100 par; XIX i XX wiek łącznie).  $x$  — przedziały klasowe wielkości stanowisk,  $y$  — liczebność stanowisk (skala dla krzywych  $B, C$ ),  $z$  — znaczenie — jak  $y$  (skala dla krzywej  $A$ ),  $A$  — rozkład stanowisk regularnych i sporadycznych łącznie,  $B$  — rozkład stanowisk sporadycznych,  $C$  — rozkład stanowisk regularnych,  $D$  — dominanta krzywej  $A$ .

Wykr. 4. Wielkość stanowiska w profilu równoleżnikowym.  $x$  — długość geograficzna,  $y$  — wielkość stanowiska wyrażona liczbą par łęgowych,  $A$  — II połowa XIX wieku,  $B$  — I połowa XX wieku,  $C$  — okres 1950–1960.

Wykr. 5. Wielkość stanowiska w profilu południkowym.  $x$  — szerokość geograficzna,  $y$  — wielkość stanowiska wyrażona liczbą par łęgowych,  $A$  — II połowa XIX wieku,  $B$  — I połowa XX wieku,  $C$  — okres 1950–1960.

Wykr. 6. Zmienność wielkości progowych stanowisk regularnych i przeciętnych wielkości wszystkich stanowisk w profilu równoleżnikowym zasięgu (XIX i XX wiek łącznie; średnie ruchome).  $x$  — długość geograficzna,  $y$  — wielkość stanowisk w liczbach bezwzględnych,  $A$  — przeciętna wielkość stanowisk,  $B$  — wielkość progowa stanowisk regularnych,  $P$  — pole między krzywymi  $A, B = V$  — wskaźnik witalności ekologicznej.

Wykr. 7. Stress antropogeniczny w profilu równoleżnikowym (XIX i XX wiek łącznie).  $x$  — długość geograficzna,  $y$  — logarytmiczna skala wskaźnika  $S_a$ .

Wykr. 8. Zmienność wielkości progowych stanowisk regularnych i przeciętnych wielkości ogółu stanowisk w profilu południkowym zasięgu (XIX i XX wiek łącznie).  $x$  — szerokość geograficzna,  $y$  — wielkość stanowisk w liczbach bezwzględnych,  $A$  — przeciętna wielkość stanowisk,  $B$  — wielkość progowa stanowisk regularnych.

Wykr. 9. Hipotetyczny rozkład wielkości zasobów biotopów łęgowych *A. ralloides* na tle rozkładu wielkości jej stanowisk łęgowych.  $x$  — przedziały klasowe wielkości stanowisk łęgowych.  $x$  — przedziały klasowe wielkości stanowisk łęgowych oraz względnej wielkości zasobów biotopów łęgowych,  $y$  — liczebność stanowisk w ujęciu procentowym oraz względna liczebność stanowisk biotopów łęgowych,  $A$  — hipotetyczny rozkład zasobów biotopów łęgowych,  $B$  — rozkład wielkości stanowisk łęgowych.

Wykr. 10. Teoretyczna zależność liczebności gatunku od liczby stanowisk łęgowych.  $x$  — liczebność stanowisk,  $y$  — liczebność par łęgowych.



Wykr. 11. Teoretyczna współzależność wzrastania liczby stanowisk ( $A$ ) i liczebności par lęgowych ( $B$ ).  $x$  — względne jednostki czasu,  $y$  — liczebność par lęgowych,  $z$  — liczebność stanowisk lęgowych.

Wykr. 12. Teoretyczna zmienność procentowych proporcji liczby stanowisk i liczebności par lęgowych *A. ralloides* w zależności od poziomu liczebności gatunku.  $x$  — liczebność par lęgowych,  $y$  — iloraz procentowych proporcji liczby stanowisk i liczebności par.

Wykr. 13. Teoretyczna zmienność proporcji liczebności stanowisk i liczebności par lęgowych w ekstremalnej i optymalnej strefie zasięgu przy różnym poziomie liczebności gatunku,  $x$  — liczebność par lęgowych,  $y$  — liczebność stanowisk w strefie ekstremalnej w stosunku procentowym do ogólnej ich liczby w zasięgu,  $z$  — liczebność stanowisk w strefie optymalnej w stosunku procentowym do ogólnej ich liczby w zasięgu,  $A$  — krzywa stosunku procentowego stanowisk w obydwu strefach,  $B$  — krzywa stosunku procentowego liczebności par lęgowych w obydwu strefach.

Tab. 1. Koncentracja liczebności par lęgowych *A. ralloides* w zależności od liczebności stanowisk lęgowych i ich wielkości (obliczone dla palearktycznej części zasięgu na podstawie 100-letnich danych). (1) — przedziały klasowe wielkości stanowisk, (2) —  $p_n$  odsetek liczebności par lęgowych, (3) — szereg kumulacyjny  $p_n$ , (4) —  $q_n$  odsetek liczebności stanowisk, (5) — szereg kumulacyjny  $q_n$ .

#### РЕЗЮМЕ

Во вступительной главе автором формулируется общая концепция исследований по пространственной структуре вида, которую на примере распространения желтой цапли, *Ardeola ralloides* (Scop.) в палеарктической части ее ареала будет он анализировать в III–V частях продолжаемого цикла. В кратком очерке автор, указывая на значительные пробелы в исследованиях по пространственной структуре вида, подчеркивает, что по сравнению с изучением пространственной структуры популяции (главным образом насекомые) эта область едва начата, хотя ее значение для развития теории эволюции и особенно для применения ее в практике природохозяйственных мероприятий имеет первостепенное значение. Настоящая III часть цикла охватывает вопросы изменчивости критической и средней величины элементарных популяций (микрораспространения) заселяющих соответственные места гнездования. Автор сосредотачивается на следующих вопросах: а) основные закономерности обуславливающие географическую изменчивость рассматриваемых параметров, б) воздействия на них антропогенного фактора, в) их взаимозависимости с другими параметрами пространственной структуры.

Во второй главе автором подается статистическая характеристика распределения величины микрораспространения. Кривые характеризующие распределение в XIX и XX веке (граф. 1) строго между собой коррелируют, поэтому автор считает их относительно постоянным признаком вида так, как и построенную непосредственно на их основе кривую концентрации вида (граф. 2) и коэффициент концентрации ( $\eta = 0,72$ ).



Концентрация численности желтой цапли весьма значительна — по отношению к огромной поверхности гнездового ареала концентрируется она лишь в нескольких больших местах гнездования. Таким образом большинство разбросанных по ареалу мест гнездования это небольшие гнездовья — в свыше 50% мест гнездования скопляется лишь только 6% численности исследуемого вида.

Сопоставляя вместе распределение величины регулярных и спорадических мест гнездования (граф. 3) автор удокументировал, что в точке пересечения обеих кривых находится также мода общего распределения величины мест гнездования, а также этот пункт определяет критическую величину регулярного места гнездования. Критической величиной (порог-минимум) называет автор такой численный уровень определенного места гнездования, ниже которого заселяющая это место микропопуляция утрачивает способность к самовоспроизведению; регулярное место гнездования переходит к разряду спорадических или полностью исчезает. Практическим способом определения критической величины микропопуляции является вычисление моды общего распределения величины мест гнездования.

Автор, анализируя в широтном разрезе ареала среднюю величину мест гнездования, приходит к выводу, что в отличии от постоянного характера общего распределения этого параметра, характеризуется она (рассматриваемая динамически) значительной географической изменчивостью. В первой половине XX века, по сравнению с XIX столетием, подверглась она в общем масштабе снижению (граф. 4), а в течение 1950–1960 гг. она опять возрасла, что тесным образом было связано с характером воздействия антропогенного фактора.

Критическая величина микропопуляции, рассматриваемая в среднем для обеих столетий (граф. 6), возрастает в криволинейной функции с запада на восток. Ее уровень обуславливается рассматриваемой во времени и в пространстве изоляцией отдельных микропопуляции по отношению друг к другу, степенью и характером редукции этих микропопуляции в негнездовое время (пред- и послездовой период, кочевки, период миграций и зимовок). В широтном разрезе ареала на редукцию вида складываются факторы остающиеся по отношению друг к другу в обратной пропорциональности — доминирующее на западе влияние антропогенного фактора (охотники, браконеры) к востоку постепенно замещается ограничивающим воздействием хищников, которых численность к востоку возрастает. Как указывает автор, продолжительность временной изоляции между микропопуляциями, на востоке больше, а также более длинные и более опасные миграционные пути восточных микропопуляций. Поэтому разница между критической величиной микропопуляции на западе и востоке достигает свыше 50 пар, вследствие чего в восточных районах ареала желтая цапля заселяет единственно более значительные по поверхности комплексы водно-болотных биотопов о большой экологической вместительности.

О распределении численности вида в меридианном разрезе термический градиент играет посредственную роль — наиболее крупные места гнездования вида скопляются в близости северной границы ареала (граф. 8). К югу, совместно с нарастанием дефицита пресноводных ресурсов усиливается ограничивающее влияние человека. Критическая величина микропопуляции возрастает к северу (разница



13 пар), что образует наглядно, в какой степени подвергаются редукции во время кочевок и миграционных перелетов в годичном цикле микропопуляции на пути между северными и южными окраинами ареала (расстояние около 1800 км).

В очередной главе автором анализируется влияние на величину рассматриваемых параметров антропогенного фактора. Соотношение кривых критической и средней величины микропопуляции (графики 6,8), как подчеркивает автор, является одним из более существенных моментов пространственной структуры распределения вида внутри ареала. Это соотношение позволяет сделать общую оценку биологической ситуации вида. Чем более высокую разницу в данном пункте ареала достигнут эти кривые, тем больше шанс на дальнейшую, стабилизированную, безопасную продолжительность существования вида, тем больше его устойчивость против стихийных бедствий, тем больше его экологическая витальность. Одновременно с уменьшением этой разницы и снижением ее к нулю (пересечение кривых *A*, *B* на западных и восточных окраинах ареала — см. граф. 6) подвергнется также снижению экологическая витальность вида, который в данном районе может даже полностью исчезнуть. Такого рода ситуация была раньше описана автором по отношению к каспийской части ареала (JÓZSEFİK, 1969), где исчезновение местной популяции (территориальная регрессия) было причиной передвижения границы ареала на около 1200 км к западу.

Автор предлагает считать поверхность поля между кривыми *A*, *B* в качестве показателя экологической витальности вида (*V*) — см. формулу (1) стр. 74, граф. 6. Упрощенным показателем *V* может быть также частное из *A* : *B* (соотношение средней величины к критической величине микропопуляции). Автором исторически анализируется влияние на уровень обеих кривых антропогенного фактора, вскрывается его сложность. Он доказывает, что снижение средней величины микропопуляции наступает вследствие отрицательного воздействия этого фактора, в то время как снижение критической величины микропопуляции является результатом благоприятного для вида влияния человека. Отсюда соотношение  $\frac{A}{B}$  можно считать общим показателем воздействия антропогенного фактора. Одновременно, со снижением величины  $\frac{A}{B}$  уменьшается экологическая витальность вида и увеличивается давление (stress) антропогенного фактора. Автором доказывается, что обратное число выражения (1), т. е.  $V^{-1}$  можно принять в качестве показателя степени давления антропогенного фактора ( $S_a$ ) — см. формулу (2) стр. 76. Отсюда выводит он общую формулу для вычисления величины  $S_a$  по отношению к данному сектору ареала рассматриваемого в широтном разрезе — см. формулу (3) стр. 76. Величина давления антропогенного фактора в широтном разрезе ареала (граф. 7) наиболее велика на западных и восточных рубежах ареала ( $S_a \approx 1$ ).

В предпоследней главе автором констатируется, что левосторонняя асимметрия общего распределения средней величины микропопуляции, а также ход кривой концентрации отображают в известной мере общие правила распределений соответ-



ственных типов биотопов в природе. Отсюда, независимо от колебаний численности вида оба параметра характеризуются довольно хорошо выраженной стабильностью и можно ими воспользоваться для экстраполяции численности исследуемого вида в прошлом, а также для теоретического моделирования некоторых ситуаций в его истории. С этой целью автор, пользуясь табличным сопоставлением данных концентрации вида (таб. 1) и формулами экстраполяции численности гнездовых пар (формула (4)) и численности мест гнездования (формула (5)) приходит к выводу, что желтая цапля, если предположить, что в прошлом заселяла до 1000 мест гнездования, то однако не могла она быть очень многочисленным видом (граф. 10). Пропорции между численностью мест гнездования и числом гнездовых пар являются довольно постоянными (граф. 11, 12); заметные сдвиги наступают после снижения численности вида ниже 5000 пар.

Автор принимая за основу распределение по ареалу малых мест гнездования с неуравновешенными колебаниями численности заселяющих их микропопуляции (спорадические места гнездования), кроме оптимальной экологической зоны выделяет в пределах ареала зону экологического пессимума (экстремальная зона). При динамически уравновешенном состоянии численности вида в ареале (гомеостазис) зону экологического пессимума заселяет минимальный и постоянный процент численности вида (6% общей численности).

В последующих частях работы, основываясь на теоретических моделях (граф. 10-13) и на данных касающихся вековых колебаний численности автором представляются гипотетические механизмы генетического потока и хода некоторых процессов микроэволюции. При динамически уравновешенном состоянии ареала и численности вида диффузия генетического материала из зоны экологического пессимума вглубь ареала является очень незначительной, в минимальном темпе проходят также микроэволюционные изменения вида (например минимальное продвижение процессов синантропизации). В случае значительного снижения численности вида процент особей заселяющих зону экологического пессимума возрастет экспоненциально, усиливается значительно генетический обмен между зонами, что в условиях общей низкой численности вида, и при остром естественном отборе благоприятствует быстрому распространению полезных мутаций. Автором анализируется кризисная ситуация вида в период 1900-1920 гг. — при тогдашнем снижении численности вида и особенно при значительных темпах этого снижения генетическое закрепление соответственных адаптации не представлялось возможным. Только в период последних десятилетий четко определились признаки связанные с синантропизацией вида, благодаря которой желтая цапля смогла приспособиться к преобразованным биотопам, значительно увеличить свою численность и восстановить ее в районах, где прежде исчезла.

В заключении автором выдвигается гипотеза, что скорость генетического потока и темпы микроэволюционных изменений по отношению к определенным границам снижения численности вида (на кривой снижения численности критический отрезок) возрастают в логистической функции. Логарифмическая фаза этого возрастания, как предполагает автор, является одним из более существенных механизмов



змов самосохранения вида, который находясь в критической ситуации, оказался на грани тотального вымирания.

Объяснения к графикам и таблице:

Граф. 1. Распределение величины микропопуляции желтой цапли в процентных соотношениях.  $x$  — классы по величине микропопуляции,  $y$  — процент мест гнездования по отношению к общему их числу (шкала для кривых  $A, B, C$ ),  $z$  — значение, как  $y$  (шкала для  $E$ );  $A$  — XIX век,  $B$  — XX век,  $C$  — средняя для XIX и XX столетия,  $D$  — мода кривой  $C$ ,  $E$  — огиба кумулятивного ряда (XIX и XX век вместе).

Граф. 2. Кривая концентрации численности желтой цапли в палеарктической части ареала.  $x$  — численность мест гнездования в процентах,  $y$  — численность гнездовых пар в процентах.

Граф. 3. Распределение величин регулярных и спорадических мест гнездования в процентных соотношениях (принимались во внимание классы I до 100 пар; XIX и XX век вместе).  $x$  — классы по величине мест гнездования,  $y$  — численность мест гнездования (шкала для кривых  $B, C$ ),  $z$  — значение, как  $y$  (шкала для  $A$ ),  $A$  — распределение регулярных и спорадических мест гнездования,  $B$  — распределение спорадических гнездовок,  $C$  — регулярных,  $D$  — мода кривой  $A$ .

Граф. 4. Величина мест гнездования в широтном разрезе ареала.  $x$  — геогр. долгота,  $y$  — величина мест гнездования (микропопуляции) в парах,  $A$  — II половина XIX века,  $B$  — I половина XX века,  $C$  — 1950—1960 гг.

Граф. 5. Величина мест гнездования в меридиональном разрезе ареала.  $x$  — геогр. широта,  $y$  — величина мест гнездования (микропопуляции) выражена числом гнездовых пар,  $A$  — II половина XIX века,  $B$  — I половина XX века,  $C$  — 1950—1960 гг.

Граф. 6. Изменчивость критической величины регулярных мест гнездования и средней величины всех гнездовок в широтном разрезе ареала (XIX и XX век вместе).  $x$  — геогр. долгота,  $y$  — величина мест гнездования (микропопуляции) выражена числом гнездовых пар,  $A$  — средняя величина гнездовок,  $B$  — критическая величина регулярных гнездовок,  $P$  — поле между кривыми  $A, B = V$  — показатель экологической витальности вида.

Граф. 7. Давление антропогенного фактора в широтном разрезе ареала (XIX и XX век вместе).  $x$  — геогр. долгота,  $y$  — логарифмическая шкала показателя  $S_a$ .

Граф. 8. Изменчивость критической величины регулярных мест гнездования и средней величины всех гнездовок в меридиональном разрезе ареала (XIX и XX век вместе).  $x$  — геогр. широта,  $y$  — величина мест гнездования выражена числом гнездовых пар,  $A$  — средняя величина гнездовок,  $B$  — критическая величина регулярных гнездовок.

Граф. 9. Гипотетическое распределение величины ресурсов гнездовых биотопов желтой цапли в сопоставлении с общим распределением величины мест гнездования.  $x$  — классы по величине мест гнездования а также по относительной величине ресурсов гнездовых биотопов,  $y$  — численность мест гнездования в процентных соотношениях и относительная численность мест нахождения гнездовых биотопов,  $A$  — гипотетическое распределение ресурсов гнездовых биотопов,  $B$  — распределение величины мест гнездования.

Граф. 10. Теоретическая зависимость численности вида от числа мест гнездования.  $x$  — число мест гнездования,  $y$  — численность гнездовых пар.

Граф. 11. Теоретическая взаимозависимость увеличения численности мест гнездования ( $A$ ) и числа гнездовых пар ( $B$ ).  $x$  — относительные единицы времени,  $y$  — число гнездовых пар,  $z$  — численность мест гнездования.

Граф. 12. Теоретическая изменчивость процентных соотношений числа мест гнездования и численности гнездовых пар желтой цапли в зависимости от численного уровня вида.  $x$  — численность гнездовых пар,  $y$  — частное из процентных соотношений численности мест гнездования и числа гнездовых пар.

Граф. 13. Теоретическая изменчивость пропорции численности мест гнездования и числа гнездовых пар в зоне экологического пессимум и оптимум ареала при различном численном уровне вида.  $x$  — численность гнездовых пар,  $y$  — число мест гнездования в зоне экологического пессимум в процентном соотношении к общей их численности по всему ареалу,  $z$  — численность мест гнездования в зоне экологического оптимум в процентном соотношении к общему их числу в ареале,  $A$  — кривая процентных соотношений мест гнездования в обеих зонах,  $B$  — кривая процентных соотношений численности гнездовых пар в обеих зонах.

Таб. 1. Концентрация численности гнездовых пар желтой цапли в зависимости от численного уровня мест гнездования и их величины (величины микропопуляции), (данные вычисленные для палеарктической части ареала на основании материалов из XIX и XX столетия). (1) — классы по величине мест гнездования (по величине микропопуляции), (2) —  $p_n$  процент по отношению к численности гнездовых пар, (3) — кумулятивный ряд  $p_n$ , (4) —  $q_n$  процент по отношению к числу мест гнездования, (5) — кумулятивный ряд  $q_n$ .

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