

ACTA ORNITHOLOGICA

Tom XI

Warszawa, 15 III 1969

Nr 6

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Studies on the Squacco Heron, *Ardeola ralloides* (SCOP.)

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INTRODUCTION

This paper initiates a series of studies dealing with the biology and evolution of Squacco Heron, *Ardeola ralloides* (SCOPOLI, 1769), in the Palearctic part of its range. The individual papers will also use material originating from the Ethiopian part of the range but its value is considerably less important than that from the European part of the range.

Ardeola ralloides belongs to a not numerous but zoogeographically very interesting group of species inhabiting simultaneously the Palearctic and the Ethiopian regions and, in spite of the fact that both parts of the range are isolated from each other, it does not form differentiated geographical sub-species.

In the European fauna *A. ralloides* is one of the few representants of a typically African element (according to VOOUS, 1960, one of four) which makes it theoretically a very interesting species deserving a more detailed study.

As regards its evolution *A. ralloides* similarly to the whole genus *Ardeola* BOIE, 1822, is a young species and although highly specialised shows a wide range of adaptiveness. It is one of the seven species of genus *Ardeola* and taxonomically occupies a central position connecting the extremely divergent *Ardeola ibis* (L.) and *Ardeola rufiventris* (SHARPE). These two species were in the past allotted to the genera *Bubulcus* BONAPARTE, 1855 (*ibis*) and *Erythocnus* SHARPE, 1894 (*rufiventris*) (BOCK, 1956).

It is necessary to underline that the genus *Ardeola* inhabited until the first decades of our century the Old World exclusively. A quick expansion of *Ardeola ibis* to both parts of America and Australia in the 1930s made it a cosmopolitan genus*. Similarly to *A. ibis* but on a considerably smaller scale *A. ralloides* and the remaining species: *Ardeola idae* (HARTB.), *Ardeola bacchus* (BP.), *Ardeola grayii* (SYKES), *Ardeola speciosa* (HORSF.) and *Ardeola rufiventris* (SHARPE) which with a few exceptions cover in relation to each other the allopatric ranges, also show the progressive features of adaptational plasticity. This manifests itself in synanthropisation process different in degree. Due to a violent transformation of the environment by man it is possible to expect their further successful evolution.

In the genus *Ardeola* the species *A. ralloides* is nearest in relation to *A. idae*, occupying with the latter a common area in Madagascar and also with *A. grayii* with which it borders probably until quite recently in areas in south-western Asia (Persian Gulf).

The Squacco Heron appears in the Palearctic not very uniformly, occupying insular sites isolated from each other by tens and hundreds of kilometers of biologically strange regions. It is a scarce species but in individual breeding places it may be numerous. It breeds exclusively in colonies with high organisation of social life and is characterised by mutual interrelation of coexistence with its main symbiont the Night Heron, *Nycticorax nycticorax* (L.) (JÓZEFIK, 1957).

Undertaking a study of the ecology of *A. ralloides* twelve years ago, I aimed only to investigate the biology of its breeding period. Later on, as new problems arose the range of my interest became wider. Observing considerable deficiencies in the knowledge of the biology of this species I commenced to gather material in a very broad aspect. A young evolutionarily species was for me an exceptionally interesting theme for studying. Due to its specifical biology and insular occurrence it was a very grateful object of research and all-biological theoretical considerations. It was possible to take it in a very strict control and to gather a copious material for characteristics of peculiar parameters on the ground of many tens of other similarly rare and interesting but dispersed in range bird species.

* It is the only case, I guess, known in historical times of a transatlantic migration of a bird species from the eastern to the western hemisphere connected with its overall range expansion and not connected with the interference of man.

This series of papers aims to show in the fullest manner possible the ecology of the Squacco Heron in its year round cycle, the analysis of the distribution structure in the breeding area, the study of the history of this species during the last two centuries and its evolution. A more general intention was to build on the example of *A. ralloides* a model of a species which, being sufficiently representative for a wide group of migratory colonial birds of the temperate zone, would allow a critical review of some problems of the theory of species. The influence of human civilisation and the synanthropisation processes were in my studies an especially accented point because one of the most important tasks of these papers is to prepare the methodical basis for the protection of *A. ralloides* and allied species.

The individual parts of this series, irrespectively of their manifold interrelations, have been dealt in such a manner that the all-biological problems form an isolated entity. The general concept of the series is therefore twofold:

1. a recognition in all its aspects of the biology and evolution of one of the less examined species of Old World (ornithological aspect), and
2. on the basis of obtained facts and their interconnections to form a sufficiently precise model of a biological species, a model enabling to confront it with some still not fully confirmed hypotheses concerning the laws governing the species (all-biological evolutional aspect).

This series although of monographical character does not pretend to be an exhaustive one. But I hope it will satisfy the present need for a general synthesis and summary of a secular achievement in this field of world ornithology.

I take this opportunity to express my gratitude and thanks to Professor I. I. PUZANOV for his heart care and scientific guidance in the first stage of my studies, to Doc. L. F. NAZARENKO and Cand. Biol. Sci. M. F. POPOVA for their help in working out a part of the analyses of digestive tracts. For devoted help in the field work I wish to express my thanks to H. ROLIK, M. Sc., Dr. F. KOSIBA, Cand. Biol. Sci. W. KHAMAGUSHKIN, Cand. Biol. Sci. A. E. LUGOVY, Z. SWIRSKI, M. Sc., Dr. A. PAPADOPOL, Dr. A. ZIEMIANKOWSKI and all people of the technical staff of the Miecznikov University in Odessa, State Astrakhan Preserve, Gr. Antipa Museum in Bucharest, Zoological Institute of the Polish Academy of Sciences in Warsaw. I am also much indebted to all persons who supplied me with valuable material concerning the actual distribution, numbers and biology of *A. ralloides* in the individual parts of its range. These are Cand. Biol. Sci. T. B. ARDAMACKAYA, Dr. L. BIGOT, Dr. S. DONČEV, Dr. L. HOFFMANN, Cand. Biol. Sci. R. G. JORDANIA, Doc. A. KEVE, Prof. A. B. KISTIakovskiy. Cand. Biol. Sci. N. W. KOKSHAYSKY, Prof. R. KRONEISL-RUCNER, Dr. H. KUMERLOEVE, Doc. M. E. KUTUBIDZE, Cand. Biol. Sci. A. E. LUGOVY, Prof. N. S. OLEYNIKOV, Dr. A. PAPADOPOL, Doc. V. S. PETROV Cand. Biol. Sci. N. N. SKOKOVA, Dr. I. STERBETZ, Dr. A. ŠTOLLMANN, Cand. Biol. Sci. E. E. SYROETSHKOVSKY, Prof. M. A. VOINSTVENSKIY. It is also my pleasant duty to

express my gratitude to Prof. Dr. S. FELIKSIAK who supervised the preparing of the zoogeographical (second) part of this work.

LITERATURE SURVEY

The Squacco Heron belongs to the relatively not numerous group of species which neither in the XIX century nor later inspired a greater interest among ornithologists. This lack of interest may be explained by a scarcity of the species and simultaneously by the technical difficulties in gathering suitable material. Moreover it was always overshadowed by other more spectacular species which arose wider interest (e. g. *Egretta alba* (L.) and *Egretta garzetta* (L.) due to the fashionable interest in their feathers at the end of the past century and intensive extermination of the species connected therewith). Thus the "non-faunistic" literature concerning *A. ralloides* is rather poor and the individual observations on its biology are dispersed in a number of general works and contributions concealed under misleading titles or in papers devoted to other species.

In the survey below I omit almost all faunistic notes and I consider only those which contribute to the knowledge of the biology or to the protection of the species.

One of the first references on the heronries near Bologna, Italy, containing some hints on *A. ralloides* is ALDROVANDI's work of 1599–1603 (BRISSON, 1760; MOLTONI, 1936; ALTINI, 1943). ALDROVANDI knew the Squacco Heron and gave specific information concerning this species.

During the Enlightenment *A. ralloides* was not very well known to zoologists. It is interesting that LINNAEUS does not mention it in any of the editions of his "Systema Naturae" including that of 1758. It was not till 1760 that BRISSON in his "Ornithologie ou méthode contenant la division des oiseaux en ordres etc." gave a few synonyms of French names and a rather detailed description.

The first taxonomic description sensu stricto with a binomial Latin name *Ardea ralloides* was done by SCOPOLI in 1769. The second description under the name *Ardea comata* was done by PALLAS in 1773. Until the first decade of the XX century it was the most frequently used synonym of the species, name. The present name *Ardeola ralloides* was used by BOIE in 1822 thereby separating a new genus *Ardeola*. All descriptions and synonyms quite numerous after 1769 today have only a historical significance. SHARPE (1898) in his list of synonyms gives fairly full list of references relating to the description and distribution in the XVIII and XIX centuries.

Observations of PALLAS (1811) are among the earliest and most accurate ones. This author draws attention to the distribution in separate biotopes during the breeding period pointing out that this species avoids small brooks and during the post-breeding period gathers in flocks. In 1847 BALDAMUS (1851, 1852) gave a series of interesting observations on heronries near the town of Titel made by him during his journey in former Austria-Hungary.

He describes the antagonism between various species forming a colony and as regards the Squacco Heron observes that it is the least shy species of all.

The first really systematic treatise based on comparative anatomy is the study of REICHENOW (1877), wherein the Squacco Heron although still included in the genus *Ardea* is already allotted to the subgenus *Ardeola* similarly to the *Ardeola ibis* allotted to the subgenus *Bubulcus*. Also REICHENOW (1900—01) as one of the first drew attention to the fact, that the biology of Squacco Heron is connected with the aquatic plants especially with the family of *Nymphaeaceae*. RADDE (1885) gave in his work "Ornis Caucasicus" some remarkable details concerning the gregariousness and ethology. TACZANOWSKI (1882) although he never treated this species with special attention, observed on the basis of museum specimens that this species could not be allotted to any of the three genera of the European herons irrespectively to many common characters with each of them.

ALLÉON (1886), who on the basis of his own observations made strange conclusions, considered that this species was characterised by a rather aggressive and quarrelsome behaviour. Quite different was the opinion of NORDMANN (1890) who described *A. ralloides* as a very phlegmatic species. He also gave observations of feeding on the shores of salty lakes. NOBLE (1902) mentions many details about breeding and nesting observed in the heronries in southern Spain. Still more notes concerning the behaviour, colonial life, phenology of the breeding period and numbers in Lenkoran are given by SATUNIN (1907a, b). But he also makes some mistakes in considering this species as sedentary and wintering therein (SATUNIN, 1912). MENZBIER (1904—09) commenting the taxonomic position of *A. ralloides* expressed the opinion that it connects the genera *Ardea* and *Nycticorax*. REISER (1905) critically determines the knowledge of the distribution of the species in Greece pointing out that even such prominent ornithologists as TEMMINCK, BREHM, THIENEMANN, NAUMANN, etc. had erroneously stated the breeding grounds. REISER gives many details concerning migrations. Special attention deserve the very accurate observations of BREHM (1911a, b) concerning the manner of feeding, day activity, mimicry and certain symbiotic ties with semi-wild pigs. Common feeding of pigs and Squacco Herons was observed also by DOMBROWSKI (1912), who in the years 1896—1909 accumulated rich phenological material concerning the migrations in the lower Danube. SUSHKIN (1914) quotes a few interesting details from Trans-Caucasia on the gregariousness in the post-breeding period, on the day activity and moulting.

A separate chapter in the investigations on the biology and especially phenology of the species are the studies carried out by SCHENK in the former Austria-Hungary. Already in his first paper SCHENK (1896) gave an exhaustive list of breeding places. In many following papers (SCHENK 1899, 1901, 1905, 1906a, 1906b, etc. — see bibliography) he gathers copious material concerning the phenology of migrations. In this work he is followed by GRESCHIK (1910),

LAMBRECHT (1910, 1912, 1913) and VEZÉNYI (1902, 1903, 1905). In his further papers SCHENK (1909, 1910, 1912, 1913) gives the results of first Squacco Heron ringing and shortly (SCHENK, 1916) offers for the first time a summary of ringing results observing that the material is still too small to explain sufficiently the migration routes and the winter quarters of this species. In a larger paper on the Obedska Bara heronries he analysed the influence of human activities on the dynamics of quantities of herons (SCHENK, 1908a). He also suggested definite steps for their protection based on scientific principles. These suggestions appear more and more in his further papers (SCHENK, 1908b, 1918, etc.).

The period of World War I brought nothing of interest. Later on the notes of MORGUE (1920) on Squacco Heron observed on the backs of cattle in Tunisia and the data of TICEHURST, BUXTON and CHEESEMAN (1922) on spring plumage during migration in Mesopotamia are worth mentioning. KOENIG (1928) writes about feeding on floating plants on the upper Nile and gives some details on ethology and changes of plumage.

The first larger taxonomic study devoted especially to the genus *Ardeola* is the paper by SALOMONSEN (1929). This author comparing the breeding, winter and juvenile plumage of the species belonging to the genus *Ardeola* and comparing their geographical distribution places them into one "super-species" *A. ralloides* (SCOPOLI) reducing the former species to the subspecies level. He also cancelled the genus *Bubulcus* and transferred it to the genus *Ardeola*. His paper although based on scanty museum material and showing some shortcomings regarding the comparative ecology, contains many valuable ideas and facts giving a new approach to the problem of the evolution of the genus *Ardeola*. An anonymous author in a polemic review note (P. J., 1930) although principally agreed with SALOMONSEN'S views yet considered the revision concept as too courageous and not sufficiently supported by facts. In later literature the SALOMONSEN'S system was partially accepted. Many authors found the inclusion of *Bubulcus ibis* (L.) into the genus *Ardeola* purposeful. However, SALOMONSEN (1933) in a later paper describing on the ground of three specimens a new subspecies *Ardeola speciosa continentalis* from Siam, found himself in an awkward situation. Being consistent with his previous attitude he considered the newly described subspecies as *Ardeola ralloides continentalis*. In this way he created considerable disproportions in the taxonomic values of subspecies which in his opinion belonged to *A. ralloides*. Disregarding the aforementioned inconsequence the author presents a rather convincing hypothesis of the speciation of akin species occupying partially the sympatric ranges (e. g. *A. ralloides* and *A. idae*, and *A. speciosa* and *A. bacchus*).

Observations on the coexistence of *A. ralloides* and *A. idae* in Madagascar were made by DELACOUR (1932) who stated that in this area they biologically pass by one another.

A fairly large series of papers appeared in the 1930s containing new data on the biology of Squacco Heron. GALET (1931) observed late, probably repeated

broods in Camargue. The second summary of the ringing results in Europe based on 17 recoveries was given by SCHÜZ and WEIGOLD (1931).

Important contributions to the knowledge of *A. ralloides* from Italy are to be found in a series of valuable papers by MOLTOMI. He started with a note on breeding grounds in Piemont (MOLTOMI, 1927). In the next study (ARRIGONI, MOLTOMI, 1930) devoted to the biology of birds of a heronry situated in the vicinity of Greggio the authors supply detailed observations on the biology of the breeding period together with the analysis of the contents of a dozen or so stomachs of Squacco Heron. These data were completed in the next paper (MOLTOMI, 1933). A detailed survey of all Italian heronries with their description, history and number of birds was given in the first part of his next paper (MOLTOMI, 1936). The second part of this study contained precise data on the biology of individual species inhabiting the heronries. As regards *A. ralloides* MOLTOMI gives phenological data, describes nests and their distribution, quotes oological material, studies the postembryonal development of nestlings and illustrates it, for the first time in ornithological literature, with colour pictures. Apart from this, in the chapter devoted to *A. ralloides* the author quotes the biometric data and ample ethological, ecological and other observations. For the first time he lists a larger material of the stomach analyses (approximately 50 samples). As a matter of fact the part of this paper concerning the Squacco Heron, although not deprived of apparent subjectivities, makes a tourning point in the studies on the biology of this species. The first part of the paper was read by MOLTOMI at the VIII International Ornithological Congress in Oxford (1938).

Studies of a high standard were carried out by ROMASHEVA in the Astrakhan Preserve. In her first paper (ROMASHEVA, 1938) she worked out a standard method of quantitative studies in heronries. She also gave the quantities of *Ardeidae* in the years 1934–35, detailed descriptions of the types of colonies and an analysis of their specific composition. ROMASHEVA also introduced for the first time the coefficients of encountering and of scattering. Her work contains many details concerning *A. ralloides* and especially its biocenotic relationship with other species in heronries. The latter problem was developed and widely analysed in her next paper (ROMASHEVA, 1940). A wide range of problems of biocenotic relations analysed therein is based on very precise and versatile field observations, connected with a series of experiments. Although the data concerning the biology of Squacco Heron form a small part of the whole material they bring new information, e. g. the rhythm of daily activity. Unfortunately the final conclusions given by the authoress are in many cases too subjective.

An excellent study of the ecto- and endoparasites of *Ardeidae* living in the Astrakhan Preserve is the paper by DUBININS (1940) which enormously enlarges the data previously compiled by NIETHAMMER (1938) on the parasites of Squacco Heron. The DUBININS included in their paper the full phenological data and

a series of new facts on the biology of this heron. VASVÁRI, in the inter-war period, belongs to the most prominent students of the ecology of *Ardeidae*. In a series of papers dealing with the food of *Ardeidae* in Hungary, VASVÁRI (1930, 1938, 1939) does not limit himself to the analysis of food samples but on the basis of it, he tries to grasp the biocenotic relationships between the species and the environment. He also comments the morpho-anatomical adaptations. In an ample study devoted to nourishment relationships of *N. nycticorax* and *A. ralloides*, VASVÁRI (1939) critically summarizes the data of earlier authors and on the basis of 108 food samples of the Squacco Heron gives a manifold analysis of individual groups of food components. After MOLTOMI (1936) this was only the second larger study dealing with the biology of *A. ralloides*.

The II World War interrupted this fine cycle of studies. Some minor notes were published during the War by ALTINI (1943) on the breeding grounds near Bologna and the results of ringing, and by VASVÁRI (1942) from the Banat region containing phenological data from the breeding period. RIDDELL (1944) comparing some aspects of the biology of *A. ibis* and *A. ralloides* discussed the problem of gregariousness, criptic colouration and quantities of both species in southern Spain. However, having fragmentary material only he could not draw any definite conclusions.

The post-war period brings an exuberant development of studies on the *Ardeidae*. YEATES (1946) describes in a very popular form the biology of *Ardeidae* from the Rhône and Guadalquivir deltas. In the next paper (YEATES, 1948) he describes the changes of heronries in the Rhône delta. Although the biology of the Squacco Heron in both papers takes only a marginal place, it is enriched by many details. The paper by MOLTOMI (1948) may be considered as a continuation of his studies of the 1930s. Here, the author gives a list of stomach contents of Italian *Ardeidae* including some samples of the Squacco Heron.

A summary of information concerning the biology and distribution of *A. ralloides* is found in two faunistic papers from the USSR written by TUGARINOV (1947) and DEMENTEV et all. (1951). Irrespectively of the rather rich material collected by them, both these authors underline that in the ecology of the Squacco Heron there still remains much to be done. In the TUGARINOV's paper worth noting is the systematisation and completion of information concerning the plumage change during the annual cycle. SPANGENBERG, as an eminent student of *Ardeidae* criticizes the previous knowledge of biology of them and collects ample phenological data.

The 1950s are characterised in eastern Europe by an especially exuberant development of studies on *Ardeidae* and in general on fish-eating animals mainly from the utilitarian point of view. These studies sometimes lacked a scientific approach and a priori anti-preservation tendencies were often imposed. A nasty book by PACHULSKIY (1951) initiated an unpopular series among nature lovers. In the history of ornithology this was the first example of garbled data picked out from literature and exaggerated by the author. This

paper was an unpleasant mixture of fictitious facts and "studied" objects and their biology. For instance the author constantly confuses the Squacco Heron with the Purple Heron. Although polemics wits such a pseudoscientific study has no sense whatsoever, it is worth noting that the author, basing his reasoning on quantitative data prepared by himself, incited to barbarous extermination of the so called ichthyophages (e. g. by burning out reed and scrub where cormorants and herons are nesting, shooting off pelicans and questioning the protection of egrets, etc.).

NAZARENKO concerned himself with the biology and problems of fish-eating by herons nesting in the heronries of the Dniester delta. In the first paper (NAZARENKO, 1953) dealing with *A. ralloides*, he describes its feeding grounds and analyses 8 food samples concluding that this species is not harmful for the fish husbandry. In the next papers (NAZARENKO, 1957a, b; NAZARENKO, POPOVA, 1959) the author confirms his previous opinion and states that the Squacco Heron is without doubt economically useful. Additionally these studies contain new and interesting data concerning the numbers, rhythm of daily activity and distribution of *Ardeidae* in the Dniester feeding grounds.

The studies of OLEYNIKOV on *Ardeidae* of there tention reservoirs of Manytch were carried out in a narrow utilitarian aspect and not in concord with the ideas of the modern bird protection. In his first work (OLEYNIKOV, 1953) he recommends methods of extermination of fish eating birds similar to those proposed earlier by PACHULSKI (1951). The paper although based on a great number of food samples is characterised by one-side approach and does not take into account the role of *Ardeidae* in the biocenosis of water reservoirs. The Squacco Heron is studied by OLEYNIKOV only incidentally (analysis of 11 food samples). In the next paper (OLEYNIKOV, DANIOVA, 1958) the economic and anti-protection aspects are accented still stronger. To the series of papers which "scientifically" assist the battle against the fish-eating birds also belongs the book by SMOGORZHEVSKIY (1959). The author classifies *A. ralloides* as harmful to the fish husbandry, his reasoning being based on the analysis of 12 stomachs. Also, according to him, this species is a feeding competitor of fish.

To the same period of time belong papers of high value which objectively treat the subject of studies although they were imposed by economical grounds. The excellent paper by SYROETSHKOVSKIY (1955) on the geographical distribution of fish-eating birds in the northern part of Caspian Sea can be considered as the best of them. This study based on manifold and very detailed material gives a full picture of the distribution and numbers of the Squacco Heron. With great knowledge the author analyses the influence of biocenotic and abiotic factors on the dynamics of numbers and distribution of heronries, giving a basis for scientific prognosis of sizes of individual populations. Also LEUS (1959) adds not only new details concerning the feeding biology of the Squacco Heron but he also correctly solves the problem methodically. New data from Lenkoran on feeding in rice fields are given by IVANOV (1952).

CATUNEANU in his excellent paper (1958) describes the shameful extermination of *Ardeidae* in the Danube delta, initiated in 1949 and continued till 1955. The author describes the problem of protection of heronries including *A. ralloides* sketching in a historical aspect its quantities and distribution in the Danube delta during the last two centuries. The problem of fish-eating of *A. ralloides* is also mentioned by PAPADOPOL (1955, 1956) who concluded that its harmfulness for the fish husbandry is minimal. He also gives observations concerning the feeding of this species in the litoral of salt lakes.

Also in western Europe the studies on *Ardeidae* developed considerably in the 1950s. The annual reports on the state of a great herony in Coto Doñana at the mouth of Guadalquivir contain numerical estimates of the Spanish population of *A. ralloides* (BERNIS, VALVERDE, 1952, 1954; VALVERDE, 1956). VALVERDE (1953) gives for the first time a detailed description of Squacco Heron nestlings. In an ecological sketch of Coto Doñana VALVERDE (1958) analyses the habitats of *Ardeidae*, characterises the breeding biotope and feeding of *A. ralloides* and discovers many new details in the feeding biology of this species. In his article dealing with the protection of fauna in Spain VALVERDE (1959) directs his interest especially to the Squacco Heron, correctly determining the situation and conditions that are indispensable for the protection of the small population of this species in the western part of the Palearctic. In his fundamental treatise on the Little Egret in France he gives (VALVERDE, 1955, 1956) valuable material concerning the biology, distribution, and numbers of *A. ralloides*. This work is characterised by unusual universality and a modern approach to the subject. The value of the work is enlarged by a confrontation of the French data with Italian (Piemont) and Spanish (Coto Doñana) material. The work is a tourning point in the studies on *Ardeidae* in Western Europe.

In the French literature a special attention attract the notes by BOUTINOT (1955, 1957) on some details of biology of *A. ralloides* from Dombes, where this species has began nesting since not long ago, and an ample sketch of the ecology of La Camargue by HOFFMANN (1958, 1959) analogical to the VALVERDE's monograph (1958) from the mouth of Guadalquivir. HOFFMANN, basing his description on an ecological transsection of the biotope of the Rhône delta, discusses in detail all types of breeding and feeding biotopes of herons. Although *A. ralloides* in Camargue is not numerous the author rather precisely analyses its milieu and quantities.

FRUGIS (1955) describes the difficult situation of some heronries in the postwar period. He examines the more important factors which influence the decreasing of the Italian population of *Ardeidae*. As regards *A. ralloides* the description of the effects of storms and hails on the status of this species in a herony near Greggio is worth noting. A confrontation of the present state of a large part of the Italian heronries with the data of MOLTINI (1936) from the 1930s is made by WARCKE (1960). The number of *A. ralloides* diminished

considerably in this period of time. The author states that basing only on observations one cannot explain the phenomenon itself.

The note by GÉROUDET (1958) brings much new information on the late-spring and summer nomadic movements in Switzerland. This phenomenon is not new for Western Europe, but it is the least explored aspect of the ecology of this species. According to GÉROUDET, *A. ralloides* was observed in Switzerland only in one year 25 times in 18 localities.

Also from Hungary the 1950's bring essential contributions to the knowledge of the biology of *A. ralloides*. Observations of NAGY (1950) were made in the breeding grounds on the Theiss river near Hortobágy, and those of STERBETZ (1950) in the Sasér Preserve. STERBETZ (1957) analyses historically the influence of man on *Ardeidae* in Hungary observing the heronry in Sasér for a couple of years and adds new or little known details to the knowledge of the biology of *A. ralloides* (STERBETZ, 1954, 1957 — see References). Two paramount monographs are the result of his studies, they will be discussed later on. Also from the Sasér Preserve come the data of FESTETICS (1957, 1959). He analyses the influence of cold and rain on the breeding cycle of *Ardeidae*.

The last monograph by VASVÁRI (1954) is a synthesis of long studies on the feeding biology of *Ardeidae*. The author divides the Hungarian *Ardeidae* into two ecologically different groups. *A. ralloides* is classified together with *Botaurus stellaris*, *Ixobrychus minutus*, *Nycticorax nycticorax* and *Ardea purpurea*. VASVÁRI demonstrates the role played by each species in maintaining the biocentric balance in the biotope. Referring to the economic significance of *Ardeidae* the author underlines its small general influence.

WARGA (1954) supplies material to the problems of quantity dynamics of Kisbalaton herons for the last half century and the results of ringing. The distribution of *A. ralloides* in Hungary is dealt with by SZIJJ (1954). According to him the number of this species in Hungary is very low.

JÓZEFÍK (1954) supplies data on the ecology of the normal and secondary breeding cycle of *A. ralloides* in the Dniester delta. The paper contains besides the phenological data also the quantitative indices of reproductive potential and death rate of nestlings. In the next sketch of the ecology of *Ardeidae* kept in a popular form JÓZEFÍK (1957) analyses the biotope of the species, drafts a sketch on the biology and ethology of the breeding period. He also supplies data on the breeding conservatism and, in a chapter devoted to the biocenotic relationships in the feeding grounds and especially in the breeding colonies, he explains the role of *A. ralloides* as a commensal and mutuant in relation to the remaining *Ardeidae*.

Since SALOMONSEN's revision in 1929 the taxonomy of the genus *Ardeola* was not discussed in a broader sense. Only as late as in 1956 BOCK returns to this problem in a study devoted to *Ardeidae*. He based his studies principally on museum material but supports his conclusions with ample ecological

and zoogeographical data. According to him the genus *Ardeola* comprises seven species of which *A. rufiventris* is most distant from typical *A. ralloides* and, in the author's opinion, probably links the genus *Ardeola* with the genus *Butorides* (BLYTH). *Ardeola (Bubulcus) ibis* remains in the genus *Ardeola*.

On the instance of *A. ralloides* HOSKING and FERGUSON-LEES (1959) examine the interesting but poorly known phenomenon of changes in the colour of legs and bill in the first phase of the breeding period. Independently they compare some points of the biology of *A. ralloides* in the Coto Doñana region with other species and state for example that the Squacco Heron is more specialised in the choice of a nesting place. Many important and new facts on the biology and ethology of this species are gathered in the work of BANNERMAN and LODGE (1957). Among others they state that also the North African population winters southwards to the Sahara whereas *A. idae* is an independent species. The study of MEINERTZHAGEN (1954) brings many details concerning the biology and ethology of migration across the Arabian peninsula.

After 1950 there appears a series of papers and notes enlarging our knowledge on *A. ralloides* in Africa. BANNERMAN (1953) gives a sketch of the biology of a local breeding population and Palearctic migrants in the tropical zone in the Niger basin. This information was enlarged by new details in the already mentioned paper by BANNERMAN and LODGE (1957). BONT (1957) from 1954 for three consecutive years trapped and ringed Squacco Herons wintering on the Kipopo river in the Congo and adds valuable material showing an attachment of birds to the places once occupied as the winter-quarters. In the next note on the water birds BONT (1960) supports the ringing data with detailed observations of wintering Squacco Herons. A precise sketch of the biology of *A. ralloides* in the Congolese winter-quarters is given by CURRY-LINDAHL (1960). This author simultaneously with *A. ralloides* observed *A. idae* and compares some moments of behaviour of the two so closely related species. DRAGESCO (1960, 1961) writes on feeding grounds, mode of feeding and behaviour of Squacco Heron in equatorial Africa. The first larger study from lower Senegal dealing with mixed heronries and rich in valuable details concerning the biology of Squacco Heron, is the paper by the MORELS (1961). This study presents precisely the biology of the breeding period, biocenotic relationships, breeding biotopes and feeding grounds, phenology, etc. of the local African population of the species in question. This paper acquires a greater importance through the fact that it brings comparative material for confrontation with the data concerning with the Palearctic population. Irrespectively the authors compare their own material with DEKEYSER'S (1955) observations from Mali. MACKWORTH-PRAED and GRANT (1957) gather the phenological data on the breeding period of *A. ralloides* from almost all of the African continent, whereas RUWET (1962) examining the influence of the building of retention reservoirs on the Lufira river in the Congo on the water birds, states that *A. ralloides* belongs to the group of species which is most frequently found in such reser-

voirs in winter. Interesting ethological observations on *A. ralloides* and *A. idae* in the Comoro Islands were made by BENSON (1960).

The first biophysical study on the morpho-functional properties of the wing of Squacco Heron and other *Ardeidae* was made by KOKSHAISKIY (1959 b). Examining the mechanism of changing the primaries during the moult period and connected with this the wing load in flight, the author states that the primaries of *A. ralloides* change centrifugally. In contradistinction to large heron species where this process runs polycentrally and has no effect on the flying properties of the wing, *A. ralloides* changes its primaries probably already in the winter-quarters. The pattern of the moult has therefore an adaptive character and cannot be treated as a taxonomic character. The mechanism of flight of *A. ralloides* and other species is analysed by KOKSHAISKIY (1959 a) in close connection with the mode of acquiring, and more precisely of spying the food. Using a movie camera KOKSHAISKIY (1961) closely examines the mechanics of flight of *Ardeidae* and the morpho-functional properties of their catching apparatus. He also confronts the data pertaining to these problems with the ecology of individual species. For the first time he gives the indices referring to the bearing properties of the Squacco Heron's wing.

From further perfecting of the systematics of genus *Ardeola* the paper by SCHEER (1960) must be mentioned. He describes a new subspecies *Ardeola grayii phillippii* from the Maldivian Islands underlining thereby once more the unreality of SALOMONSEN'S conception.

A summary of information concerning the distribution of *A. ralloides* in the Middle East enriched by the data on phenology of the breeding period and migration is found in a paper by KUMERLOEVE (1960).

To other notes enriching our knowledge of the Squacco Heron worth noting are the information on the albinotic specimens of *A. ralloides* observed by GANIUSHKIN (1958) in the Astrakhan Preserve, and the data of POPOVIĆ (1960) on the population dynamics and the species composition in the heronries of Carska Bara in Yugoslavia. An interesting fact of occupying a new breeding place in Spain is given by the Club "Alcyon" (1961, 1963). BERNIS (1961) analysing the number and status of *Ardeidae* in southern Spain describes the situation of *A. ralloides* in the Coto Doñana heronry. In view of the tendency to progress in last years of such species as *A. ibis* and *Ardea cinerea*, the Squacco Heron though not yet firmly stabilised there forms a steady component of this heronry. MOUNTFORT and FERGUSON-LESS (1961) in an ample work treating with birds of Coto Doñana describe i. a. the feeding of *A. ralloides* during an exceptional drought in 1957. They describe the division of feeding grounds by individual species of herons during that disaster and add new material concerning the number, phenology and biology of *A. ralloides*. The history of this famous heronry is added.

Although the papers on the migration are not related here the note by RAINES (1962) deserves an exception. The author offers a full picture

of the phenology of the passage of Squacco Heron across the nort-eastern part of Greece and gives information on the condition of plumage of these birds.

The year 1960 brings some papers of general zoogeographical character where the knowledge of *A. ralloides* was treated more broadly. And so for example VOINSTVENSKIY (1960) states that it inhabits Europe since the paleogen or early neogen periods and nowadays owing to man's expansion its range decreases. VOOUS (1960) is of a similar opinion as regards the decreasing range though the decline in all points may not be explained in this way (e. g. the vanish near Rotterdam). VOOUS points out that the relationships, biology and even distribution of the Asiatic species of the genus *Ardeola* are insufficiently known. The author commits an evident error stating that *A. ralloides* is active at night spending day hidden in reeds.

After the war the first and most comprehensive study on numbers distribution and breeding biotopes of *A. ralloides* in the Kizyl-Agach reserve in Lenkoran (the least examined point of the range) is given by OGANESOV (1960). He also describes the factors influencing the quantities of *Ardeidae* and especially the effect of lowering the level of the Caspian Sea. The latter problem is dealt with especially by LUGOVOV (1959) who, according to air reconnaissance, states that owing to sinking of the sea level, intensive accumulations processes and increase of the Volga delta the heronries in the Astrakhan reserve (once numerous) vanished, whereas in the avandelta zone outside the Reserve new heronries developed. In his next paper LUGOVOV (1961) analyses this problem in detail and gives a historical outline of quantitative changes of *A. ralloides*. A general summary on the Squacco Heron in the Volga delta is to be found in LUGOVOV's general work describing the delta's fauna (1963).

DOBROKHOTOV (1961) mentions the difficulties met with during the studies on *A. ralloides*. This author, taking the advantage of a suitable moment of repeated nesting of a great micropopulation of this species in the part of the Astrakhan reserve in 1955, carried out manifold studies on the ecology of the breeding period. This study acquires an even greater importance if one takes under consideration that the number of *A. ralloides* in the Volga delta is relatively small. Besides an ample material concerning the description of heronries and distribution of nests, the author supplies accurate material on postembryonal development of nestlings, examines the cycle of day activity of adult birds, considers the causes of nestlings' mortality, and devotes much time to the feeding biology analysing 170 food samples.

In the same time the Sasér reserve in Hungary was also a centre of intensive studies on the ecology of *Ardeidae* and especially of *A. ralloides*. STERBETZ (1961) in a monograph of the Hungarian population of *Egretta garzetta* brings also interesting material on the biology, breeding, and biocenotic relations of *A. ralloides* in Sasér. In his next paper devoted exclusively to *A. ralloides*

ides STERBETZ (1962) gives a general summary of our knowledge of this species in Europe, analyses historically its distribution in Hungary and draws attention to the influence of climatic and synanthropic factors. The study of the ecology of *A. ralloides* in Sasér contains an analysis of the population dynamics in the last years. The author examines the fluctuations of the Sasér micro-population but finds no scientific justification of them. STERBETZ draws a special attention to the problem of post-breeding nomadic grounds which consists a separate and little known point. The biology of the breeding period forms in STERBETZ's work a central point. An ample oological and nidological material, detailed observations on ethology, cycle of day activity, development of nestlings, food analyses of individuals feeding in the proper biotope and also on rice fields, the explanation of various general biocenotic problems — this in short is the range of problems studies by the author. The studies of STERBETZ take the central position in the modern literature devoted to *A. ralloides* supplying complete and manifold data for further comparative studies covering a greater area of the Squacco Heron range. With the STERBETZ's paper I close this rather rough review of literature devoted mainly to the biology and taxonomy of the Squacco Heron.

Summing up, the scope of our knowledge of *A. ralloides* remains below the average knowledge of such species as *Nycticorax nycticorax*, *Egretta garzetta* or *Ardea cinerea*. Though the data dispersed in literature and shown here in a highly abridged form may make a general impression that the material is very ample there remain lot of so called classical problems that are unsolved, superficially known or not examined at all. I may mention here such questions as the pre-breeding period with all its problems, the spring nomadic movements, the problem of flock and population structure, the mechanism of genetic exchange. The question of so called nesting conservatism in the breeding period, the sexual selection found no description as yet. The oology is little known, the duration of the incubation period is disputive, the day activity rhythm with nestlings is little known, the final stages of the breeding period are not observed, nothing is known of disintegration of families and the forming of flocks. Many important gaps are found in the knowledge of the biology of the post-breeding period, the regularities of the early autumn dispersion are not known. The problem of migration is known superficially and requires more detailed studies. The ethology is little known and is characterised by many subjective opinions. The process of post-embryonal development requires wider and more accurate examination. The moult and the change of plumage in various parts of the year cycle and the age are also little known. Completely unknown is the temperature rhythmic together with a complicate complex of related problems. The studies on the population dynamics in many-year periods have been only commenced. The reproductivity and mortality of individual populations is also almost unknown.

THE FIELD STUDIES

The main part of the field studies connected with the breeding season was carried out in the Dniester delta between the following localities: Mayaki, Bielayevka, Jasski, Troickoye, Tudorowo and Palanka, i. e. in an area of over 350 square kilometers, enclosed between the proper Dniester bed and its arm Turuntschuk. The studies on the biology of the post-breeding period outside the Dniester delta were carried out also in Kisbalaton, Hungary, in the lower Danube area on the Greaca lake, in the marshes of Comana near Bucharest, in the Danube delta at Tulcea, Maliuc and Mila 23, and finally in the eastern part of the Volga delta in the Obshorovskaya part of the Astrakhan reserve.

During the breeding season observations were of a stationary character in the immediate vicinity of heronries whereas in the spring, late summer and autumn I carried out observations during excursions which extended from a couple of days to two weeks long. In the Dniester delta I used a middle size huntsman boat which during the first two years was my laboratory and living base. Later on, when additional equipment grew, I built stable bases on poles in the vicinity of heronries chosen for detailed studies. On the Danube and Volga I used principally the fishing boats and cutters.

The timetable of my field studies was as follows:

Dniester delta:

12—13 VI 1952. — Reconnaissance of the heronries in the Kwashino lake area. 22 VI — 14 VII 1952. — Observations in the heronries, analysis of the specific composition of heronries, terms of hatching, observations on the biology and ethology of nestlings, examination of floristic components of the biotope, frequency and distribution of *A. ralloides* in the feeding grounds.

10—13 V 1953. — General reconnaissance of the heronries, marking of nests, examination of feeding grounds. 21 V — 15 VII 1953. — Stationary observations in the heronries of lake Kwashino and lake Tudorovo, studies on the breeding period biology, biocenotic relationships, rhythm of day activity, microclimate of the heronries brushwood, collecting material referring to food composition, ringing, etc. 1 — 11 VIII 1953. — studies on the feeding biology and distribution of feeding grounds, post-breeding nomadic movements, gregariousness (observations were carried out in most lakes, flood waters and river arms in the delta). 14 — 16 IX 1953. — Observations on nomadic grounds and departure.

26 V—16 VII 1954. — Observations in heronries on lakes Tudorovo, Zhukovo and Kwashino, studies on the development dynamics of heronries, specific and quantitative composition, topographic survey of heronries, microclimate, breeding biology, temperature rhythms, collecting of biometric material, oological material, food samples, experimental research, observations on the initial phase of post-breeding nomadism. 18 — 27 VIII 1954. — Studies on the distribution of birds in the feeding and nomadic grounds. 19 — 23 IX 1954. — Observations on the passage movements.

5 — 8 V 1955. — Observations on the arrival, pre-breeding period, general reconnaissance of heronries. 17 — 26 V and 8 — 13 VI 1955. — Studies on the breeding period in lake Kwashino and Palanka heronries. 30 VI — 24 VII 1955. — Observations in heronries of Palanka, lake Kwashino and lake Tudorovo. Studies on the biology of the breeding period, biocenotic relationships, microclimate, collecting of biometric material, food samples and other documentation.

Kisbalaton:

22 — 24 VIII 1957. — Observations on distribution of birds in the feeding grounds and the day activity.

Volga delta (Obshorovskaya part of the Astrakhan reserve):

31 VIII — 12 IX 1959. — Observations on distribution of birds in the feeding grounds, day activity, flock structure, examination of some heronries.

Comana swamps (near Bucharest):

21 VIII 1962. Observations on the distribution of birds in the feeding grounds.

Danube delta:

26 VIII — 8 IX 1962. — Studies on the day activity, feeding biology, distribution in the feeding grounds, gregariousness, ethology and passage movements.

Greaca lake (lower Danube):

12 IX 1962. — Observations on the distribution of birds in the feeding grounds.

Summing up, only for field studies 236 days were devoted (excluding time spent for journeys and technical matters). In this period of time over 2900 kms of swamps, lakes and rivers in deltas were penetrated making over 100 trips and passages.

Laboratory work was carried out in the Vertebrate Zoology Laboratory of the Mietshnikov University in Odessa, in the Ornithological Laboratory of the Zoological Institute of the Polish Academy of Sciences in Warsaw. Occasionally I have carried out additional observations on the behaviour of *A. ralloides* in the zoological gardens in Budapest, Bucharest, Prague, Kiev, Odessa and Warsaw. Also I reared experimentally the Squacco Heron on my own.

METHODOLOGICAL REMARKS

While working out a general outline of biology and evolution of *A. ralloides* I had ample data of my own but I supported them in many cases with material taken from literature. The field studies were mainly of autecological character as regards the cognition of interdependence between an individual or a group of individuals and the concretely acting factors of the milieu. I also collected material concerning the zoogeographical, population and biocenotic problems analysed under the aspect of recognising the laws governing the growth and existence of species. Gathering material during the field studies and drawing it from literature I endeavoured to classify it into dependent series being guided by a general conception of knowledge of a species in its dynamics. Approaching generalisations and synthesis I was often compelled to solve some problems deductively being in this respect cautious and moderate.

The historical material has been selected so as to achieve statistical comparison of individual parameters and as an illustration of some features and peculiarities of the palearctic part of the species; it should also be treated as representative in a broader sense.

Having a general tendency to integrate the results I tried to analyse the elements of variability rather cautiously keeping in mind all the dangers connected with an uncritical and mechanical classification of often seemingly homogenous material, especially originating from the literature published before the first World War.

Many problems of zoogeography, ecology and especially concerning the population and flock structure, genetical exchange, propagation and morality could be grasped only after a detailed study of material derived from the whole area investigated. The same applies to the knowledge of the laws of population dynamics, the values of individual indices, adaptive possibilities of species, etc.

An extrapolation of the biological situation of a species both in the past as well as a prognosis for the future could be based only and exclusively on generalised results based on the whole material. In some cases when completing lacking links I was compelled to make use of interpolation methods as regards time and space but always observing the necessary caution.

Handling material of various grades of accuracy I could use it mainly to reveal only the general regularities and trends manifested within the species under examination. The possibility of solving the different problems was always estimated from a perspective of attaining a high grade of representativeness of material and a maximal possibility of error elimination. I gave special attention to the category of errors that revealed a tendency to systematic cumulation. Wherever possible, the historical material was classed in such groups which could ensure a considerable grade of self-levelling of errors. The problem of accuracy and trustworthiness with which the values of individual parameters or their function are given is extremely complicated. This problem that is common in the minds of scientists from other fields of science who also base their investigations on a greater number of historical data, has not found up to date a radical solution and such a solution cannot be hoped for. Only the discernment in a given situation and an estimate of concrete cases entitles the acceptance of appropriate data as authoritative in some grade.

In my work I maintain the concept of measurability of species' characters as well as its milieu in time and space. Hence most of the examined phenomena is in the form of indices, standards, diagrams and equations of their functions. The concept of ecological measurability (similarly as in the past that of morphological, physiological and genetical) finding more and more adherents, results from a necessity to form a more precise apparatus of research methods. It should eliminate the arbitrariness of interpretation and especially limit the method of "intuitionistic deduction" which has a rich tradition in zoology. Therefore, I base myself on methods of quantitative examination of relations of features and phenomena, which give much more chances of finding out and documenting new interpretations and mechanisms conditioning them. The best proof of the trustworthiness of the results obtained is, in my opinion, the multilevel logic

of their sequence, an empirical verification even in the conditions of an experiment, and the conformity with other conclusions documented with the use of other assumptions and methods.

The methodological solutions of the individual parts of this series of papers may, in some cases, evoke objections and incite discussions. This is unavoidable, because in many situations having no appropriate or approximative patterns (e. g. in studies on the distribution structure) I found myself "on a pathless track". It is obvious, that the first trials in each field cannot be perfect, they hide many dangerous "traps" and run a double risk of committing errors.

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Accepted for publication: 1 VI 1968.

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STRESZCZENIE

Niniejsza praca iniejuje zakrojony na szerszą skalę cykl publikacji poświęconych badaniom nad biologią i ewolucją czapli modronosej *Ardeola ralloides* (Scop.). Ogromna większość wykorzystanego materiału pochodzi z półarktycznej części zasięgu. Są to dane wyselekcjonowane z piśmiennictwa ornitologicznego, głównie z ostatnich dwóch stuleci, otrzymane drogą ankietową z różnych ośrodków naukowych Europy oraz materiały zebrane przez autora

w latach 1952–1962 w deltach Dunaju, Dniestru, Wołgi oraz na innych zbiornikach wodnych południowo-wschodnich części Europy. Materiały wyłonione z piśmiennictwa, a dotyczące etiopskiej części zasięgu, stanowią niewielką stosunkowo część zebranej dokumentacji.

Po nakreśleniu zwięzlej charakterystyki ekologicznej, zoogeograficznej i systematycznej *A. ralloides*, autor ogólnie omawia założenia rozpoczętego cyklu. Koncepcja cyklu zakłada możliwe pełne zarysowanie ekologii *A. ralloides* w pełnym cyklu rocznym, analizę struktury rozmieszczenia w areale lęgowym, odtworzenie losów tego gatunku w ciągu XIX i XX w. oraz nakreślenie jego ewolucji. Autor kieruje się też myślą zbudowania na przykładzie *A. ralloides* konkretnego modelu gatunku biologicznego — modelu, który będzie dostatecznie reprezentatywny dla szerokiej grupy lądowych wędrownych socjalnych gatunków ptaków strefy umiarkowanej. Poszczególne części cyklu autor zamierza ujmować tak, aby problemy ogólnobiologiczne stanowiły w nich odrębną zamkniętą całość (aspekt ogólnobiologiczny i ewolucyjny). Całość cyklu ma dostarczyć w zasięgu dysponowanych środków maksimum informacji o jednym z mniej zbadanych gatunków, jakim jest czapla modronosa (aspekt ornitologiczny). Wpływ cywilizacji i procesy synantropizacji stanowiły w badaniach szczególnie uwypuklany moment, jednym bowiem z ważniejszych zadań cyklu jest stworzenie metodologicznych podstaw realizacji ochrony *A. ralloides* i gatunków pokrewnych.

Badania terenowe prowadzone przez autora nosiły przeważnie charakter autekologiczny. Zgromadzono też materiały dotyczące zagadnień populacyjnych, biocenotycznych. Materiały historyczne zostały wyselekcjonowane z piśmiennictwa w płaszczyźnie statystycznej porównywalności poszczególnych parametrów. Elementy zmienności, przy ogólnej tendencji do scalania wyników, były analizowane bardzo ostrożnie. Ekstrapolowanie sytuacji biologicznej gatunku w przeszłość, a także prognozowanie jej na przyszłość jest dopuszczane przez autora jedynie w oparciu o uogólnione przesłanki wynikające z całości materiału. Interpolacje, w odniesieniu zarówno do czasu, jak i przestrzeni były stosowane przez autora w sporadycznych przypadkach i z zachowaniem nadzwyczajnej ostrożności. Zróżnicowana dokładność materiału historycznego pozwalała na wyzyskanie go do wyjawiania jedynie ogólnych prawidłowości charakteryzujących badany gatunek. Możliwość rozwiązywania poszczególnych kwestii oceniana była zawsze z perspektywy uzyskania dużego stopnia reprezentatywności materiału i możliwości maksymalnego wyeliminowania błędów. Autor zwracał szczególną uwagę na kategorię błędów przejawiających tendencje do systematycznej kumulacji. W związku z tym, gdzie było to możliwe, materiał historyczny był szeregowany w takie ugrupowanie, które mogły gwarantować znaczny stopień samoniwelacji błędów. Autor utrzymuje koncepcję wymieralności cech gatunku i jego środowiska. Stąd większość rozpatrywanych zjawisk jest ujmowana w postaci wskaźników, mierników, wykresów oraz równań ich funkcji.

W przeglądzie piśmiennictwa, dającym pogląd na historię badań nad *A. ralloides* autor omawia tylko te prace, które wnoszą jakieś novum do poznania biologii, ewolucji i ochrony tego gatunku. Przegląd rozpoczyna się od wzmianek o dziełach ALDROVANDIEGO (1959—1603), BRISSONA (1760), SCOPOLIEGO (1769), PALLASA (1773). Następnie omawiane są obserwacje nad biologią i etologią poczynione przez PALLASA (1811), BALDAMUSA (1851, 1852), RADDEGO (1885), ALLÉONA (1886), NORDMANNA (1890). Na większą uwagę zasługuje studium REICHENOWA (1877) poświęcone m. in. też taksonomii *A. ralloides*.

Początek XX w. przynosi dość obfitły materiał dotyczący biologii czapli modronosej (REICHENOW, 1900—1901; NOBLE, 1902; REISER, 1905; SATUNIN, 1907a, b, 1912; BREHM, 1911a, b; DOMBROWSKI, 1912; SUSHKIN, 1914). Autor charakteryzuje i podkreśla wybitne osiągnięcia w badaniach nad *A. ralloides* znakomitego badacza czaplowatych, jakim był SCHENK (patrz spis piśmiennictwa). SCHENK m. in. po raz pierwszy podsumowuje wyniki obrączkowania *A. ralloides* oraz wysuwa oparte na naukowych przesłankach postulaty ochrony tego gatunku.

W okresie międzywojennym badania przebiegają wielotorowo i koncentrują się w kilku ośrodkach. Do najważniejszych należą: studium SALOMONSENA (1929) dotyczące rewizji systematyki rodzaju *Ardeola*. Wśród różnych doniesień wspomnieć należy o materiałach zawartych w pracach TICEHUSTA, BUXTONA i CHEESMANA (1922), KOENIGA (1928), GALETA (1931), SCHÜZA i WEINGOLDA (1931) oraz DELACOURA (1932).

Osobny rozdział stanowią znakomite prace MOLTONIEGO (patrz spis piśmiennictwa), ROMASHEVEJ (1938, 1940) oraz VASVÁRIEGO (1930, 1938, 1939) tworzące przełom w badaniach nad autekologią *A. ralloides*.

Z okresu II wojny światowej na uwagę zasługują doniesienia VASVÁRIEGO (1942), ALTINIEGO (1943) oraz RIDDELLA (1944).

Okres powojenny cechuje bujny rozwój różnorodnych badań nad czaplą modronosą. Tak więc YEATES (1946, 1948) podaje nowe szczegóły o biologii z delt Rodanu i Guadalquiviru, ukazuje się praca MOLTONIEGO (1948) będąca kontynuacją badań z okresu międzywojennego. Usystematyzowane wiadomości o biologii z obszaru ZSRR podane zostały w pracach TUGARINOWA (1947) oraz DEMENTEVA, i in. (1951).

W latach pięćdziesiątych rozwijają się w Europie Wschodniej badania nad czaplowatymi jako ichtiofagami. Brak obiektywizmu oraz w złym gatunku utylitaryzm uderza w wielu pracach poświęconych analizom pokarmu. Wręcz skandaliczną pod tym względem jest np. publikacja PACHULSKIEGO (1951), w której autor ten w oparciu o tendencyjnie spreparowane zestawienia statystyczne nawołuje do barbarzyńskiego wyniszczania czaplowatych. Akecję totalnego niszczenia czaplowatych w ramach likwidowania ichtiofagów w Rumunii opisuje CATUNEANU (1958), naświetlając równocześnie historycznie problem ich ochrony. Na szczęście rozwinięta, zwłaszcza w ZSRR i Rumunii, pod presją organów administracyjnych akcja masowego tępienia czaplowatych z jednej

strony potępiana przez opinię publiczną, z drugiej zaś powstrzymywana przez wnikliwe badania nad składem pokarmu czaplowatych w połowie lat pięćdziesiątych, ustaje. Wyróżnić tu należy prace zawierające wyniki analiz pokarmowych *A. ralloides* dokonane przez takich autorów, jak: NAZARENKO (1953, 1957 a, b), VASVÁRI (1954), SYROETSHKOVSKIY (1955), PAPADOPOL (1955, 1956), LEUS (1959), NAZARENKO, POPOVA (1959). Niezależnie od eksponowania zagadnień ichtiofagii pojawiają się doniesienia dotyczące też innych zagadnień biologii *A. ralloides* (IVANOV, 1952; JÓZEFIK, 1954, 1957; SYROETSHKOVSKIY, 1955; NAZARENKO, 1957 a, b; GANIUSHKIN, 1958).

W Europie Środkowej, a zwłaszcza na Węgrzech, dość intensywnie rozwijają się badania prowadzone przez NAGY (1950), STERBETZA (patrz spis piśmiennictwa), FESTETICSA (1957, 1959). Z innych autorów wymienić należy WARGE (1954), który przytacza materiały do poznania dynamiki liczebności *A. ralloides* z Kisbalatonu, SZIJJ'A (1954) — analiza rozmieszczenia na Węgrzech itd.

W Europie Zachodniej pojawiają się liczne publikacje wzbogacające wiedzę o *A. ralloides*. Z ujścia Guadalquiviru (Coto Doñana) pochodzą doniesienia BERNISA, VALVERDE'Á (1952, 1954). VALVERDE (1953) podaje pierwszy szczegółowy opis piskląt czapli modronosej. W szkicu ekologicznym Coto Doñana VALVERDE (1958) daje doskonały obraz środowiska tego gatunku oraz wzbogaca wiedzę o biologii żerowania. Wiele uwagi poświęca też ochronie *A. ralloides* (VALVERDE, 1959). Z Coto Doñana pochodzą też materiały o biologii i zmianach ubarwienia dzioba i nóg przytaczane przez HOSKINGA i FERGUSON-LEESA (1959). W fundamentalnej pracy o *Egretta garzetta* z obszaru Francji VALVERDE (1955, 1956) dostarcza bardzo wartościowych materiałów również o *A. ralloides*. Z piśmiennictwa francuskiego zwracając uwagę doniesienia BOUTINOTA (1955, 1957) spod Dombes, szkic ekologiczny delty Rodanu (Camargue) HOFFMANNA (1958, 1959) zawierające cenne dane o środowisku i biologii *A. ralloides*. FRUGIS (1955) rozpatruje czynniki wpływające na zmniejszanie się liczebności *A. ralloides* we Włoszech. Dane o koczowiskach późnowiosennych i letnich ze Szwajcarii przytacza GÉROUDET (1958). Wiele nowych faktów o biologii *A. ralloides*, w tym również charakterystycznych dla afrykańskiej populacji zestawili w swym dziele BANNERMAN i LODGE (1957). Obfituje w nie również dzieło MEINERTZHAGENA (1954).

Po roku 1950 pojawia się wiele prac wzbogacających wiedzę o *A. ralloides* z obszaru Afryki. Wymienić należy prace DEKEYSERA (1955) MACKWORTH-PRAED i GRANTA (1957), BONTA (1957, 1960), BENSONA (1960), CURRY-LINDAHLA (1960), DRAGESCO (1960–1961), MOREL M. Y. i MOREL G. (1961), RUWETA (1962).

Od czasu rewizji systematyki rodzaju *Ardeola* dokonanej przez SALOMON-SENA (1929) kwestia ta szerzej nie była poruszana. Dopiero BOCK (1956) w studiu o systematyce *Ardeidae* w oparciu o materiały muzealne, dane zoogeograficzne, etologię itd. rysuje nowy układ tej systematyki. Wspomnieć tu należy też o pracy SCHEERA (1960), który opisuje nowy podgatunek *A. grayii phil-*

lipsi. Pierwsze badania biofizyczne z zakresu morfofunkcjonalnych właściwości skrzydła i aparatu chwytnego *A. ralloides* były przeprowadzone przez KOKSHAISKIEGO (1959 a, b).

Lata sześćdziesiąte przynoszą niebywały dotąd rozwit badania nad czaplą modronosą. Zestawienia zoogeograficznej charakterystyki omawianego gatunku znajdują się w dziełach VOINSTVENSKIEGO (1960) i VOOUSA (1960). Ze wschodnich regionów palearktycznej części arealu pochodzą dwie prace poświęcone wyłącznie *A. ralloides*: KUMERLOEVE (1960) zestawia materiały o rozmieszczeniu i fenologii w Azji Mniejszej, DOBROCHOTOV (1961) opisuje powtórne gnieźdzenie się w Rezerwacie Astrachańskim, dostarczając nader obfitego materiału autekologicznego. W innych publikacjach godne uwagi są materiały przytaczane przez LUGOVOJA (1961, 1963) i OGANESOVA (1960). Z Węgier pochodzą dwie obszerne publikacje STERBETZA (1961, 1962). Pierwsza, poświęcona *Egretta garzetta*, zawiera równolegle bogaty materiał o biologii okręgu lęgowego *A. ralloides*. Druga praca dotyczy wyłącznie czapli modronosej. STERBETZ (1962) ogólnie podsumowuje w niej zasób wiedzy o omawianym gatunku z obszaru Europy, analizuje historycznie rozmieszczenie na Węgrzech, nakreśla szkic autekologii z rezerwatu Sasér. Wśród dotychczasowych publikacji o *A. ralloides* praca STERBETZA bezspornie zajmuje centralne miejsce. Z innych jeszcze prac z Europy Środkowej wymienić należy materiały przytaczane przez POPOVIĆ (1960) i RAINESA (1962). Na zachodzie Europy w ostatnich latach ukazały się prace BERNISA (1961), MOUNTFORTA i FERGUSON-LEESA (1961) oraz doniesienia podawane przez Klub „Aleyon” (1961, 1963) — zawierają one dane o populacji hiszpańskiej *A. ralloides*. Nowych materiałów o populacji włoskiej dostarcza WARCKE (1960).

Przegląd piśmiennictwa doprowadzony jest do roku 1963. W podsumowaniu autor stwierdza, że dotychczasowy zasób wiedzy o *A. ralloides* kształtuje się niżej przeciętnej średnio zbadanych gatunków ornitofauny środkowoeuropejskiej. W dalszej części autor zestawia problemy wyjaśnione powierzchownie, bądź zupełnie nie zbadane.

W kolejnym rozdziale podany jest chronologicznie przebieg badań terenowych przeprowadzonych przez autora. W sumie na badania terenowe autor poświęcił 236 dni, prowadząc w koloniach lęgowych prace stacjonarne, a niezależnie penetrując na łodziach i kutrach obszary delt i jezior. W sumie spenetrano ponad 2900 km w linii ciągłej środowisk wodno-błotnych w różnych punktach Europy Środkowej i Wschodniej.

Następna publikacja z zapoczątkowanego tu cyklu poświęcona będzie zmianom sekularnym rozmieszczenia i liczebności *A. ralloides* w palearktycznej części zasięgu lęgowego.

РЕЗЮМЕ

Настоящей статьей автор начинает публикацию запланированного в более широком масштабе цикла работ, посвященных исследованиям по биологии и эволюции желтой цапли, *Ardeola ralloides* (SCOP.). Значительная часть использованного тут материала касается палеарктической части ареала. Это данные, выбранные из орнитологической литературы за последние два столетия, материалы полученные из различных европейских научных центров и учреждений путем анкетного опроса и собранные лично автором в период 1952-1962 гг. во время полевых исследований в дельтах Дуная, Днестра, Волги и на некоторых других водоемах юго-восточной Европы. Литературные материалы касающиеся эфиопской части ареала составляют на общем фоне незначительную часть собранных автором документальных материалов.

После краткой экологической, зоогеографической и таксономической характеристики, автор представляет в общих чертах основную концепцию цикла, заключающуюся в возможно полном начертании экологии желтой цапли в полном годичном цикле, анализе пространственного распределения вида внутри гнездового ареала, реконструкции истории вида на протяжении XIX и XX столетий, исследованиях по эволюции. Автор руководствуется также замыслом построения на примере *A. ralloides* модели биологического вида, в достаточной степени пригодной для обширной группы перелетных колониально гнездящихся видов птиц умеренного пояса Палеарктики. Соответственные части цикла будут так построены, чтобы общебиологические проблемы в каждом из них составляли единое целое (общебиологический и эволюционный аспект цикла), в то время, как задачей полного цикла будет изложение максимума информации об одном из весьма слабо изученных до сих пор видов Старого света, каковым является желтая цапля (орнитологический аспект). Влиянию антропогенного фактора и процессам синантропизации уделялось по ходу работы особое внимание, ибо одной из более существенных задач цикла является подготовка методологических основ для реализации охраны *A. ralloides* и близких к ней видов.

Полевые исследования производились автором с аутэкологическим уклоном. Независимо от этого собирались материалы, касающиеся популяционных и биоценотических вопросов. Исторические данные выбирались с мыслью статистического сравнения соответственных параметров. При стремлении к обобщающим выводам материалы касающиеся изменчивости отдельных элементов анализировались с необходимой осторожностью. Экстраполяция биологической ситуации вида в прошлом, а также прогнозы на будущее допускались автором единственno на основании предпосылок обобщающих весь материал. Также интерполяция относительно пространства, как и времени, применялась в единичных случаях с соблюдением большой осторожности. Различная степень точности исторического материала позволяла воспользоваться им лишь для выявления общих закономерностей. Возможность решения отдельных вопросов оценивалась всегда с учетом степени достоверности и с перспективы максимального устранения ошибок. Особое внимание обращалось

на ошибки, проявляющие тенденцию к систематическому накоплению — поэтому, где это было возможно, исторический материал распределялся в группировки, которые могли гарантировать самонивелирование ошибок. Автор придерживается концепции измеримости как видовых признаков, так и его естественной среды. Поэтому большинство рассматриваемых явлений описывается тут с применением различных коэффициентов, статистических показателей, кривых, а также уравнений их функции.

В обзоре литературы, отображающим историю исследований, автор рассматривает только те работы, которые вносят новое в познание биологии, эволюции и охраны исследуемого вида. Обзор начинается с сочинений Альдрованди (ALDROVANDI, 1599-1603), Бриссона (BRISSON, 1760), Скополи (SCOPOLI, 1769) и Палласа (PALLAS, 1773), затем речь идет о наблюдениях по биологии и этологии, сделанных Палласом (PALLAS, 1811), Бальдамусом (BALDAMUS, 1851, 1852), Радде (RADDE, 1885), Аллеоном (ALLEON, 1886) и Нордманном (NORDMANN, 1890). На внимание заслуживает труд Рейхенова (REICHENOW, 1877), посвященный между прочим таксономии *A. ralloides*.

В начале XX столетия появляются богатые материалы касающиеся биологии (REICHENOW, 1900-1901; NOBLE, 1902; REISER, 1905; SATUNIN, 1907a, б, 1912; BREHM, 1911a, б; DOMBROWSKI, 1912; Сушкин, 1914). В дальнейшем автор характеризует знаменитые работы венгерского исследователя цаплевых, каким был Шенк (SCHENK — см. список литературы). Шенк впервые подвел итоги кольцевания *A. ralloides* и выдвинул основывающиеся на научных предпосылках требования охраны этого вида.

В межвоенном периоде исследования идут по различным направлениям и концентрируются в нескольких научных центрах. Из более существенных публикаций следует упомянуть работу Саломонсена (SALOMONSEN, 1929), рассматривающую систематику рода *Ardeola*. Материалы по биологии содержаться теперь во многих публикациях (TICEHURST, BUXTON, CHEESMAN, 1922; KOENIG, 1928; GALET, 1931; SCHÜZ WEIGOLD, 1931 и т. д.).

Особый раздел составляют обстоятельные работы Мольтони (MOLTONI — см. список литературы), Ромашевой (1938, 1940), а также Васвари (VASVÁRI, 1930, 1938) являющиеся поворотом в исследованиях по аутэкологии желтой цапли.

С периода второй мировой войны следует упомянуть о заметках Васвари (VASVÁRI, 1942), Альтини (ALTINI, 1943) и Ридделя (RIDDEL, 1944).

В послевоенные годы отмечается бурный расцвет разного типа работ. И так Ятес (YEATES, 1946, 1948) приводит новые материалы из дельты Роны и Гвадалквири, появляется новая статья Мольтони (MOLTONI, 1948), которая является продолжением исследований из межвоенного периода. Упорядоченные данные по биологии из СССР были собраны в работах Тугаринова (1947), Спангенберга и др. (1951).

В 50-х годах в Восточной Европе появляются работы по ихтиофагии цаплевых. Многие из них характеризуются субъективной трактовкой вопроса и утилитаризмом. Крайне тенденциозной, не имеющей в орнитологической литературе precedента, была псевдонаучная книжка Пахульского (1951). Кампанию всеобщего

уничтожения цаплевых в Румынии описывает Катуньяну (CATUNEANU, 1958). Приводит он одновременно историю их охраны. К счастью, начатая, особенно в СССР и Румынии, административными властями борьба с ихтиофагами была сурово осуждена общественным мнением. Прекращению кампании способствовали обстоятельные работы по анализу питания цаплевых таких авторов, как: НАЗАРЕНКО (1953, 1957 а, в), ВАСВАРИ (VASVÁRI, 1954), СЫРОЕЧКОВСКИЙ (1955), ПАПАДОПОЛЬ (PAPADOPOL, 1955, 1956), Леус (1959), НАЗАРЕНКО, Попова (1959). Независимо от этого появляются работы по другим вопросам биологии *A. ralloides* (Иванов, 1952; JÓZEFÍK, 1954, 1957; СЫРОЕЧКОВСКИЙ, 1955; НАЗАРЕНКО, 1957 а, б; Ганюшкин, 1958).

В Центральной Европе в Венгрии велись работы несколькими авторами (NAGY, 1950; STERBERTZ — см. список литературы; FESTETICS, 1957, 1959). Особенно существенные тут следующие статьи: WARGA (1954) — по динамике численности *A. ralloides* на Кишбалатоне и SZIJJ (1954) — численность и распределение в Венгрии.

В Западной Европе указываются многочисленные публикации. Из них особенно ценные работы из устья Гвадалквики (Кото Даньяна): BERNIS, VALVERDE (1952, 1954), VALVERDE (1953). Также Вальвердом (VALVERDE, 1953) было впервые подано подробное описание птенцов желтой цапли. В экологическом очерке автор этот (VALVERDE, 1958) приводит не только анализ гнездовых биотопов, но и дает новые данные по биологии питания. Много внимания уделяет вопросам охраны *A. ralloides* (VALVERDE, 1959). Из Кото Доныяна происходят иные материалы по биологии и изменениям окраски клюва и ног (HOSKING, FERGUSON-LÉES, 1959). В основательном произведении, касающимся малой белой цапли во Франции Вальверде (VALVERDE, 1955, 1956) изложил также весьма ценные данные о желтой цапле. Из французских работ обращают на себя внимание статьи Бутинота (BOUTINOT, 1955, 1957) — колонии в Домб, и Гоффманна, (HOFFMANN, 1958, 1959) — экологический очерк гнездовых биотопов в дельте Роны (Камарг). Фруджис (FRUGIS, 1955) рассматривает факторы ограничивающие численность *A. ralloides* в Италии. Интересные данные о поздневесенних и летних кочевках в Швейцарии приводит Жерудет (GÉROUDET, 1958), а Беннерман и Лодж (BANNERMAN, LODGE, 1957), а также Мейнерцхаген (MEINERTZHAGEN, 1954) описывают характерные для африканской популяции факты биологии. Особенно много работ и сводок об *A. ralloides* в Африке появляется после 1950 года (DEKEYSER, 1955; MACKWORTH-PRAED, GRANT, 1957; BONT, 1957, 1960; BENSON, 1960; CURRY-LINDAHL, 1960; DRAGESCO, 1960, 1961; MOREL M. J., MOREL G., 1961; RUWET, 1962).

Со времен ревизии систематики, произведенной Саломонсеном (SALOMONSEN, 1929) этим вопросом никто шире не занимался. Только Бок (BOCK, 1956) в обстоятельной работе, касающейся систематики сем. *Ardeidae* основываясь кроме музеального материала на зоогеографических и этологических данных вновь анализирует систематику рода *Ardeola*. Также Шер (SCHEER, 1960) описывая новый подвид *A. grayii phillipsi* затрагивает таксономические вопросы.

Впервые объектом биофизических исследований вид послужил в работах Кошайского (1959а, б) — морфо-функциональные особенности крыла и ловного аппарата.

В 60-тых годах наблюдается настоящий расцвет исследований по желтой цапле. Зоogeографическую характеристику вида дают Воинственский (1960) и Вуус (Voous, 1960). Восточных частей ареала касаются работы: Кумерлеве (KUMERLOEVE, 1960) — материалы по распространению и фенологии в Малой Азии, Доброхотова (1961) — описание повторного гнездования в Астраханском заповеднике. Из других работ следует упомянуть о новых данных, приводимых Луговым (1961, 1963) и Оганесовым (1960). В Венгрии появляются две обширные публикации Штербец (STERBETZ, 1961, 1962). В первой, посвященной малой белой цапли, параллельно были поданы богатые материалы по биологии гнездового периода *A. ralloides*, во второй, являющейся монографией о желтой цапле в Венгрии, Штербец подводит итоги всего, что известно о ней в Европе, анализирует историческое распространение в Венгрии, дает очерк аутэкологии из заповедника Сасер. Среди появившихся до сих пор публикаций, упомянутая работа занимает центральное положение. Из других работ из Центральной Европы следует отметить публикации Попович (Popović, 1960), Райнеса (RAINES, 1962) и нескольких других из Западной Европы (BERNIS, 1961; MOUNTFORT, FERGUSON-LEES, 1961; Club „Alcyon”, 1961, 1963), главным образом касающиеся испанской популяции. Очень существенных данных из Италии доставляет Варнке (WARNCKE, 1960). Обзор литературы заканчивается на 1963 году.

Подводя итоги, автор подчеркивает, что уровень знаний об *A. ralloides* удерживается ниже средне изученных центрально-европейских видов птиц. Сопоставляет он также вопросы выясненные поверхностью, или же совсем не затронутые орнитологами.

В последующей главе автором хронологически сопоставлен ход полевых работ. В сумме продолжались они 236 дней, главным образом на гнездовых колониях (стационарные исследования). Независимо, во время экскурсий на лодках и катерах по дельтам и озерам велись наблюдения по различным проблемам биологии. Таким образом, автором просмотрено свыше 2900 км по прямой линии различных болотных и водных биотопов в различных районах Центральной и Восточной Европы.

Следующей из начатого тут цикла будет работа, посвященная вековым изменениям распространения и численности *A. ralloides* в палеарктической части гнездового ареала.

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