

Mieczysław JÓZEFIK

Caspian Tern, *Hydroprogne caspia* PALL. in Poland — the biology of migration period

Rybitwa wielkodzioba, *Hydroprogne caspia* PALL. w Polsce — biologia okresu wędrówek

Чеграва, *Hydroprogne caspia* PALL. в Польше — биология миграционного периода

[with 29 diagrams, 12 tables, and 1 map in the text]

Introduction
Material and methods
Character of occurrence in Poland
Frequency in the annual cycle
Rhythm of the daily activity
Social structure, group formation, survival
Factors affecting the migration routes
Conclusions
References

INTRODUCTION

Basic assumptions

The primary aim of the present paper is to analyse the observations recorded within the territory of Poland and concerned with migrations and nomadic movements of the Caspian Tern, *Hydroprogne caspia* (PALL.). The author has included, beside his own material, collected in such a way that specified parametres were born in mind, also historical materials covering the XIXth century as well. Thus the author will discuss here not only problems connected

with the modification of migration routes followed by this species, but he will also deal with numerous problems concerned with the biology of migration period, activity in its daily cycle, social structure, and factors affecting the choice of migration routes. The last of these problems, much wider than the others as it goes beyond the field of the biology of migrations effected by one species, will initiate the series treating of the space orientation displayed by species migrating along water routes.

State of the studies in Poland

The interest in the Caspian Tern has increased in the last decade not only in Poland but also in Europe. We are constantly reminded about that by the increasing number of publications on the subject. *H. caspia* has occupied for the last two decades in the Polish ornithofauna the position of a transmigrant — thus it is high time to investigate this species more carefully. For the first time this species was more closely analyzed by DOBROWOLSKI (in litt.). And it was he who drew up a detailed list of all the recorded observations carried out either in the XIXth or in the first half of the XXth century together with their historical and zoogeographical analysis. So I shall skip here the description of the earlier literature which was exhaustively related by DOBROWOLSKI (in litt.).

The first reports published after the war (BIELEWICZ, 1948, 1949; URBAŃSKI, 1956; WOLK, 1958; DOBROWOLSKI, 1959 a, b; JURCZYK, 1959; ZAJĄC, 1960) indicated the increasing occurrence of the Caspian Tern in Poland, and particularly on the coasts of the Baltic. At the beginning of the sixties this species was already frequently recorded as a transeontinental migrant in the depth of the country which was pointed out by SWIRSKI (1959, 1964), JÓZEFIK and SWIRSKI (1961), LUNIAK (1963, 1964). In the next years there were even more recordings and reports presenting them as observed in the coastal belt (BIEŃ, DOBROWOLSKI, SKOCZYŁAS, 1961; DYRCZ, 1963; BUSSE and JABŁOŃSKI, 1964; ZAJĄC, 1964) as well as inside the country (CZARNECKI, 1962, 1963; DOBROWOLSKI, 1964; LEWANDOWSKI, 1964; LUNIAK, KALBARCZYK, PAWŁOWSKI, 1964; DYRCZ, TOMIAŁOJĆ, 1964; KOZŁOWSKI, 1967; TOMIAŁOJĆ, 1967).

Faunistic materials are continually supplemented with observations on the biology. There have been already published some papers treating the subject more generally. Even DOMANIEWSKI (1921) and DUNAJEWSKI (1938) were still struck by the exceptional rarity of this species on the Vistula. TISCHLER's data (1941) indicated that *H. caspia* started occurring more frequently in the Mazurian Lakes as late as after 1930. The role of the Vistula as a migrating route for the Caspian Tern was pointed out by JURCZYK (1959), SWIRSKI (1959, 1964) and LUNIAK (1963, 1964), while DOBROWOLSKI (in litt.) suggested that the Vistula and the Bug river might constitute one of the migration by-routes for the Baltic population.

JURCZYK concluded (1959) that the autumn flight along the Vistula comprises, as a matter of fact, two waves: the first, not so well attended, falls on July and the first half of August, while the second wave starts in the second half of August and lasts till the beginning of October. Other interesting observations were recorded by URBAŃSKI (1956) in the Western Pomerania, and DOBROWOLSKI (1964) who considered the role of the Caspian Tern in the biocenosis of the Vistula ornithofauna. However the bulk of the materials collected

in the last decade in Poland has not yet been published or used for the purposes of a work more general in character. In the present publication the author has attempted to sum up the material of observations particularly from the depths of the land, parallelly with the processing of the material collected according to a special programme and concerned with the biology of autumn migrations.

The author wishes to express his gratitude for placing at his disposal materials used subsequently in his statistical analysis to Dr A. K. DOBROWOLSKI, Dr M. LUNIAK, J. B. SZCZEPSKI, A. JURCZYK, Dr B. JABŁOŃSKI, Dr L. TOMIAŁOJÓ, Z. SWIRSKI M. Sc., Cz. NITECKI M. Sc., Dr P. BUSSE, Dr R. ZAJĄC, Dr M. GROMADZKI, Dr S. STRAWIŃSKI, J. GOTZMAN M. Sc., Dr Z. PIELOWSKI, Dr B. SZULC-OLECHOWA, N. ŚWITAJ, W. SIWEK, and W. WĄSOWICZ. Besides I should like to express my grateful thanks to Dr M. LUNIAK, J. LINKOWSKI, J. TRUSZKOWSKI M. Sc., J. DESSELBERGER, and K. DUBIŃSKI for their assistance with the field realization of the series.

MATERIAL AND METHODS

Material characterized

The paper is based on the 423 recordings of the Caspian Tern in Poland from the years 1800–1966. Out of this number, 28.4% of the recordings constitute the material gathered by the author in the years 1960–1966 on the middle and lower San, and at the mouth of this river and in the middle reaches of the Vistula in particular. Published data collected from the literature make up only 23.9%, while the unpublished data supplied to me by fellow-ornithologists make up as much as 47.7%.

As a recording of the Caspian Tern I consider a single observation of one individual or a flock, disregarding the size of it. Repeated observations recorded in the course of one day which are known, or are suspected with considerable probability, to concern one and the same individual, are obviously qualified as one recording. Materials found in the literature and including statements more general in character (e.g. regularly observed, recorded every year, recorded very often, etc.) have not been considered for the purposes of the present analysis.

Field methods

Observations were recorded while sailing down the San and the Vistula. Stationary observations were carried out only at the mouth of the San (August–September 1961, April 1963) — in all, 546 hours of observing. They consisted in the unceasing control of the San section at the mouth and the length of the Vistula in this region from dawn (4⁰⁰) to the moment when complete darkness falls (20³⁰). Each observation included the following data: 1) number of birds, 2) character of the grouping (family, compact flock, loose flock, dispersed, single individuals, character of contacts and voice signalling), 3) altitude of the flight, 4) plotting the line of the flight on a map of the area which yielded such data as: direction and character of the flight (directions N, S, the San, the Vistula, straight-line flight, circuitous flight-penetrating), 5) time of the observation, 6) local atmospheric conditions (air temperature, direction of wind, its speed on the Beaufort Scale, degree of overcasting according to a 10° scale).

CHARACTER OF OCCURRENCE IN POLAND

Dynamics of frequency

More intensive frequency of *H. caspia* in the last decade in Poland is a new phenomenon and it is closely connected with the following factors: a) expansiveness of the species in the direction of the north-eastern regions of the Baltic, b) general numerical increase of the Baltic population, c) change of migration routes from maritime to transcontinental. These problems will be dealt with in greater detail in another publication concerned with modifications of migration routes followed by *H. caspia* in Europe. There the author will closely analyse the problem of a possible correlation between an increase in the number of observers and the number of recordings, and the numerical increase of the population in their breeding-sites.

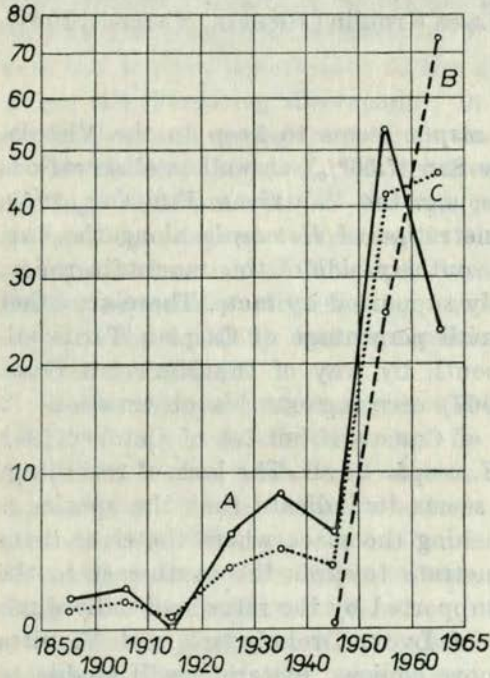
The occurrence of *H. caspia* in Poland in its faunistic aspect gains momentum only after 1930. In view of the 423 recordings considered for the purposes of the present paper (which leaves aside a number of unpublished observations carried out in the coastal region) only 0.71% were collected before 1900, and 5.43% by 1930 (diagram 1). 8.04% of the recordings were added in the next 20 years, and the frequency sharply increased only in the years 1950–1960 — the Caspian Tern becomes a regularly observed transmigrant in the coastal region, along the Vistula and some of its right-side tributaries in the upper reaches (e.g. the San). As many as 41.6% of the recordings fall on the decade mentioned. A further increase in the frequency occurred in the years 1961–1966 — 44.91% of the total number of recordings (!). The frequency dynamics of *H. caspia* for the last two centuries is presented in diagrams 1 and 2.

Frequency in the northern and southern regions of the country

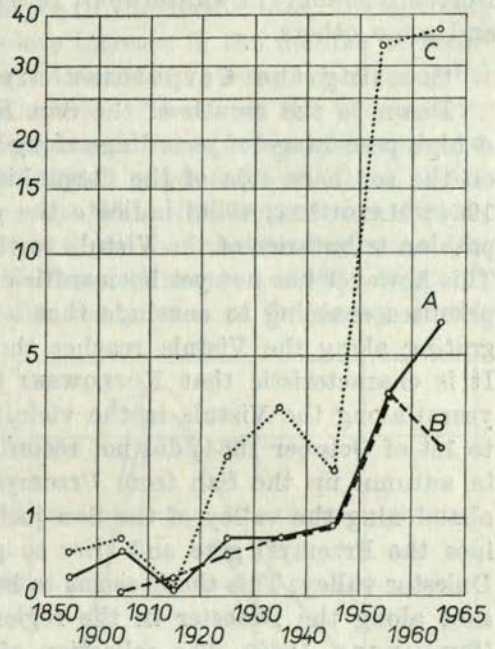
Diagram 1 presents the percentage distribution of recordings in the northern and southern parts of Poland — a conventional frontier between them runs along the 52°30' line of northern latitude. And it becomes striking that the Baltic population has consisted of transcontinental migrants only in the last two decades. There can be certain doubts whether the increase in the frequency of *H. caspia* is only apparent, correlated, for example, with an increase in the number of observers in Poland. As I have mentioned earlier the problem will be considered in greater detail in another publication, and for the present I shall have to use only data indicating an absolute increase in the Baltic population, thus in a way dispersing the fears presented (AUMEEES, 1961; BANCKE, BERGMAN et al., 1960; CURRY—LINDAHL, 1960; KUMARI, 1958; MAYAUD, 1956; NIKLUS, 1959; ROOTSMJAE, 1959).

It can not be denied, however, that the intensity of observations affects in a clear-cut way the course of the frequency curves. This is obviously supported by the two falls in the curves (diagram 1) recorded for the periods of the first and second World War.

42.3% of the observations were recorded in the southern regions of the country. And when we consider that of the 33.3% of the observations from the northern part of the country, the majority of them were recorded in the coastal region, then this considerable southern percentage indicates a significant rise in importance of transcontinental routes.



Graph 1. Distribution of *H. caspia* recordings in Poland in the last 100 years. The vertical axis — number of recordings in per cent in relation to their total number in each category; the horizontal axis — years; A — northern part of Poland; B — southern part of Poland; C — general distribution of recordings for Poland ($n = 423$).



Graph 2. Distribution of *H. caspia* recordings in Poland in different seasons. The vertical axis — per cent of recordings in relation to their total number; the horizontal axis — years; A — recordings in the following months: March, April, and May; B — recordings in June and July; C — recordings in August, September, and October ($n = 423$).

Role of the Vistula and inland bodies of water

48.7% of the observations within the area of Poland were recorded along the Vistula. It seems that the river gained the importance of a large migration route, which can be undoubtedly connected with the growth of Finnish and Estonian colonies of the Caspian Tern (AUMEES, 1961; KUMARI, 1958; NIKLUS, 1959). We can quote for the sake of comparison that the other inland bodies of water collected only 18.0% of the recordings. Particularly significant seems

the fact that the species along the Oder is usually neglected by the observers, although at some places along this river *H. caspia* was not unfrequently observed. For example, on Lake Kunickie it was recorded 21 times in the years 1960–1965 (according to L. TOMIAŁOJÓ'S data).

It is characteristic that *H. caspia* reaches inland lakes. Besides lakes near Legnica, it was also recorded on Lake Gopło (CZARNECKI, 1962), Lake Northern Mamry (LEWANDOWSKI, 1964), Lake Kruklin (JÓZEFIK, SWIRSKI, 1961), and some others.

Crossing the Carpathian arc

Down to the mouth of the San *H. caspia* seems to keep to the Vistula. A high percentage of recordings along the San (7.56%), as well as observations on the southern side of the Carpathians, e.g. the Váh river (FERIANC, 1950, 1964; MATOUŠEK, 1958) indicate the penetration of *H. caspia* along the Carpathian tributaries of the Vistula to the southern side of this mountain range. This however has not yet been sufficiently supported by facts. There are other premises enabling to conclude that a small percentage of Caspian Terns migrating along the Vistula reaches the south by way of the Moravian Gate. It is characteristic that KOZŁOWSKI (1967) carrying out his observations (2 years) along the Vistula in the vicinity of Cracow (from 1st of October 1962 to 1st of October 1964) did not record *H. caspia* at all. The lack of recordings in autumn up the San from Przemyśl seems to indicate that the species is abandoning the valley of the San just behind the place where the river turns into the Przemyśl gate and tries to penetrate towards the south-east to the Dniester valley. This thesis seems to be supported by the returns of individuals shot along the Dniester in the regions of Lvov, Drohobytch and Vinnitsa (SHEVAREVA, 1962). The collection of more copious materials will enable to analyse this interesting subject, so important for inland migrations of *H. caspia*, more deeply.

Role of maritime routes

A relatively high percentage of recordings in the coastal region (33.3%) indicates two facts significant for the biology of the Baltic population: a) separate groups of individuals, before setting out on their proper transcontinental migration in the post-breeding period, remain for a longish period of time in the vicinity of the seashore in the so called post-breeding sites (cf. page 12), b) the coastline of the Baltic, together with inland water routes, is still quite a significant migration route.

FREQUENCY IN THE ANNUAL CYCLE

Frequency of recordings in separate seasons

Diagram 2 presents the frequency of *H. caspia* recordings in separate seasons. These are the salient points: a) obscure differences in the frequency of spring and autumn recordings in the period to 1920, b) the same frequency

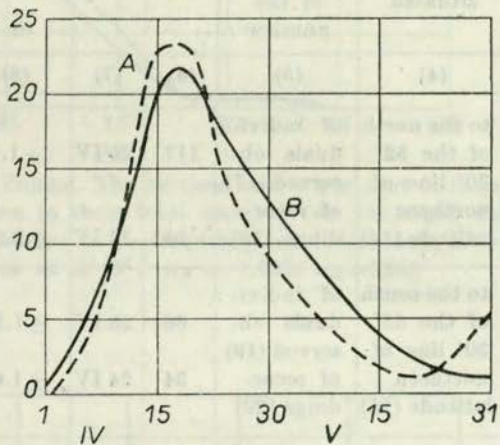
of spring and summer recordings in the phase of a gradual general increase in the population numbers and a gradual preponderance of autumn recordings (till 1960), c) a relative decrease in the number of summer recordings characteristic for the last decade against the background of a considerable general increase in autumn and spring recordings. The situation presented in diagram 2, even without considering additional facts and materials, can be taken as reflecting the ecological situation of *H. caspia* in the Baltic sites. Disregarding here the obvious significance of the absolute increase in the number of recordings, the increasing discrepancy, in separate decades, between the number of autumn and spring recordings underlines the growth of the productivity of the Baltic population. The relative decrease in the number of summer recordings lends authority to the suggestion that a larger number of individuals are getting adapted to nesting in the north. Thus the improvement in the ecological situation of *H. caspia* in the northern and eastern regions of the Baltic, repeatedly stressed by various authors (BERGMAN, 1953; MAYAUD, 1956; NIKLUS, 1959), has repercussions for the picture of frequency of this species in Poland.

Beside this basic reason, we should mention here essential changes in migration routes from maritime to transeontinental (at least to a certain extent). This problem will be discussed in another publication dealing with the Caspian Tern.

Table 1 presents characteristic statistical data of the phenology, while diagrams 3-6 give the frequency distribution (frequency of recordings and frequency of individuals) of *H. caspia* in the course of spring and autumn migrations in Poland.

Spring migrations

Spring migrations are swift and resolute. The average date, in case of both frequency of individuals and frequency of recordings, falls on 25th of April. Differences between northern and southern parts of Poland, and those between the all-Polish average values and northern and southern ones, are statistically insignificant. Judging by the values of standard deviations (Tab. 1), the Caspian Tern flies faster over the southern regions than over the northern ones. Most certainly longer breaks in the flow of transmigrants are caused by spring storms over the Baltic, and also by a tendency displayed by the northern



Graph 3. Spring migration of *H. caspia* in Poland. The vertical axis — per cent of recordings and frequency of individuals in relation to their total number; the horizontal axis — months; A — frequency of individuals, B — number of recordings ($n_A = 183$, $n_B = 58$).

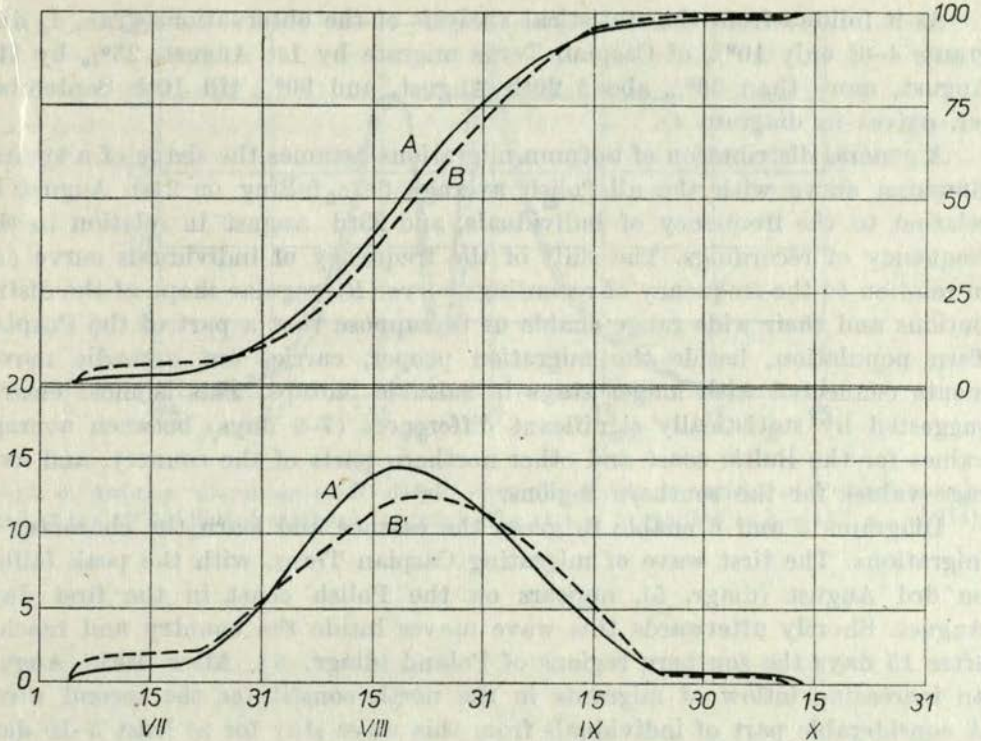
part of Caspian Terns to summer at the Polish coasts. This is clearly indicated by the distribution of the frequency of recordings (diagr. 3) — while in the second half of May the number of recordings, as opposed to the frequency of individuals, decreases continually. Hence the obvious conclusion — summering individuals join in larger flocks. The curves of the diagram mentioned indicate that in the culminating part of the migration the birds fly in flocks. Starting from the last ten days of April, and particularly in the first ten days of May, Caspian Terns display weaker tendencies to flying in flocks which can be explained by the fact that some of them pair off (cf. page 27).

Table 1. Characteristic of spring and autumn migrations of Caspian Tern, *H. caspia* (PALL.) in Poland.

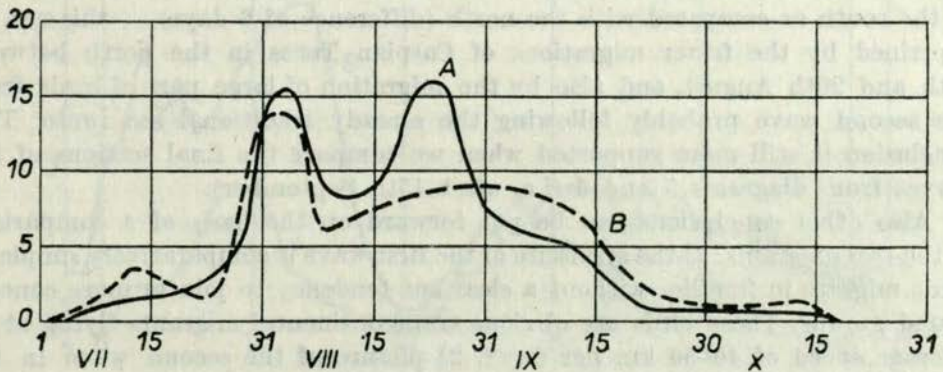
Migration (1)		spring (2)				autumn (3)			
Part of country situated	Calculated on the basis of the number	n	\bar{x}	S_x	σ_x	n	\bar{x}	S_x	σ_x
				(in days)				(in days)	
(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)
to the north of the 52° 30' line of northern latitude (14)	of individuals observed (17)	117	25 IV	±1.33	14.4	604	17 VIII	±0.66	17.4
	of recordings (18)	24	26 IV	±2.96	14.5	122	19 VIII	±1.60	19.5
to the south of the 52° 30' line of northern latitude (15)	of individuals observed (19)	66	25 IV	±1.20	9.8	488	26 VIII	±0.57	12.6
	of recordings (20)	34	24 IV	±1.69	9.9	214	26 VIII	±0.86	12.7
entire area of the country (16)	of individuals observed (21)	183	25 IV	±0.89	12.0	1092	21 VIII	±0.46	15.9
	of recordings (22)	58	25 IV	±1.59	12.1	336	23 VIII	±0.85	16.3

Autumn migrations

Significant statistical differences were recorded between average migration data over the north and south of the country, as well as between the average all-Polish value and the average values for the south and north of Poland (for the frequency of individuals I have taken 0.99 as the level of confidence, while for the frequency of recordings — 0.95) (Tab. 1).



Graph 4. Autumn migration of *H. caspia* in Poland. The vertical axis — per cent of recordings and frequency of individuals in relation to their total number (on the right the cumulative aspect); the vertical axis — months; A' — frequency of individuals; B' — number of recordings (A, B are ogives of A' B'; $n_A = 1,092$, $n_B = 336$).



Graph 5. Autumn migration of *H. caspia* over the northern regions of Poland (northward of the $52^{\circ}30'$ line of latitude). The vertical axis — per cent of recordings and frequency of individuals in relation to their total number; the horizontal axis — months; A — frequency of individuals; B — number of recordings ($n_A = 488$, $n_B = 122$).

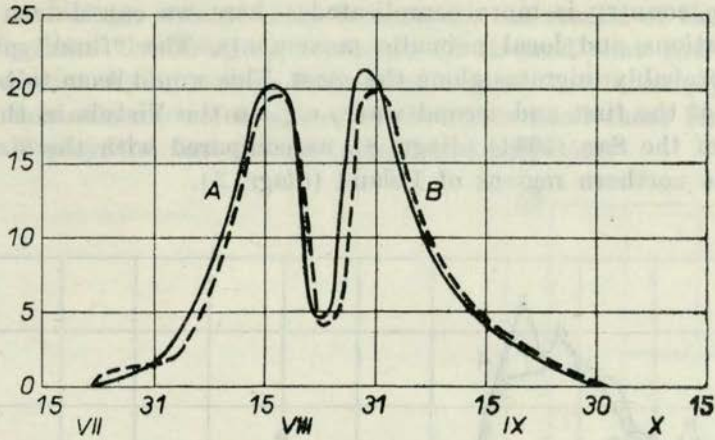
As it follows from the statistical analysis of the observations (Tab. 1, diagrams 4-6) only 10% of Caspian Terns migrate by 1st August, 25% by 7th August, more than 50% about 20th August, and 90% till 10th September (cf. ogives in diagram 4).

A general distribution of autumn migrations assumes the shape of a typical Gaussian curve with the all-Polish average date falling on 21st August in relation to the frequency of individuals, and 23rd August in relation to the frequency of recordings. The shift of the frequency of individuals curve (*A*) in relation to the frequency of recordings curve (*B*), regular shape of the distributions and their wide range enable us to suppose that a part of the Caspian Tern population, beside the migration proper, carries out nomadic movements connected with longer stays in suitable biotops. This is most clearly suggested by statistically significant differences (7-9 days) between average values for the Baltic coast and other northern parts of the country, and average values for the southern regions.

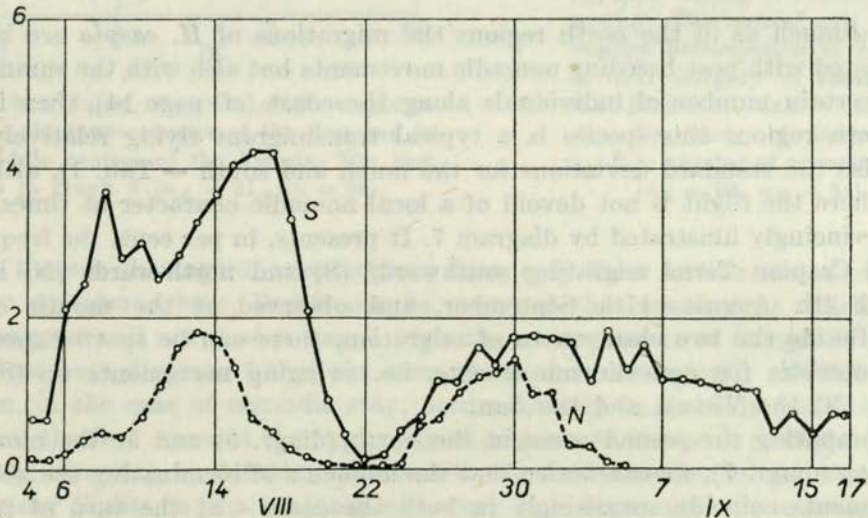
Diagrams 5 and 6 enable to grasp the essence and learn the character of migrations. The first wave of migrating Caspian Terns, with the peak falling on 3rd August (diagr. 5), appears on the Polish coast in the first days August. Shortly afterwards this wave moves inside the country and reaches after 15 days the southern regions of Poland (diagr. 6). After 10th August an increasing inflow of migrants in the north constitutes the second wave. A considerable part of individuals from this wave stay for at least 5-10 days on the Polish coast, and in the period 15-20th August they join in larger flocks. After 25th August the frequency of individuals decreases sharply, but the frequency of recordings stays on the same high level, and it is lowered only after 15th September. This indicates the intensity of migration in the north, after 25th August, displayed by the second wave lasting nearly a month. As there is only an insignificant shift of the phase of the second wave in the south as compared with the north (difference of 6 days) — this can be explained by the faster migrations of Caspian Terns in the north between 10th and 20th August, and also by the migration of large part of birds from the second wave probably following the already traditional sea route. This conclusion is still more supported when we compare the final sections of the curves from diagrams 5 and 6 (i.e. after 15th September).

Also other conclusions can be put forward on the basis of a comparison of the two diagrams: 1) the structure of the first wave is comparatively simple — birds migrate in families without a clear-cut tendency to join in more concentrated groups. These birds are obvious transcontinental migrants flying at an average speed of 40-50 km per day*, 2) picture of the second wave in the

* This speed can be calculated by dividing the difference between the peak of the 1st wave in the north and south (15 days) by the distance, e.g. between the mouth of the Vistula and the mouth of the San (662 km), whence the bulk of our data are derived.

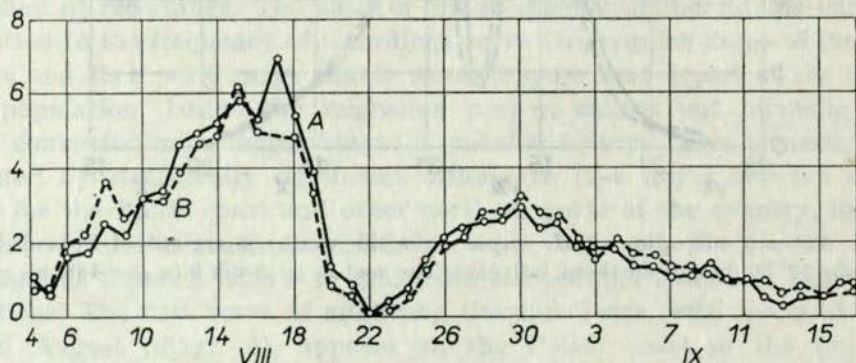


Graph 6. Autumn migration of *H. caspia* over the southern regions of Poland (southward of the $52^{\circ}30'$ line of northern latitude). The rest as in graph 5 ($n_A = 488$, $n_B = 214$).



Graph 7. Flight direction of *H. caspia* during autumn migration in 1961 in the region of the mouth of the San. The vertical axis — per cent of individuals in relation to their total number; the horizontal axis — months; *S* — individuals flying southward; *N* — those flying northward ($n = 203$).

north of the country is more complicated — here we can detect tendencies to concentrations and local nomadic movements. The “final” part of this wave most probably migrates along the coast. This would seem to be indicated by the size of the first and second wave, e.g. on the Vistula in the region of the mouth of the San (1961) (diagr. 8), as compared with the size of these waves in the northern regions of Poland (diagr. 5).

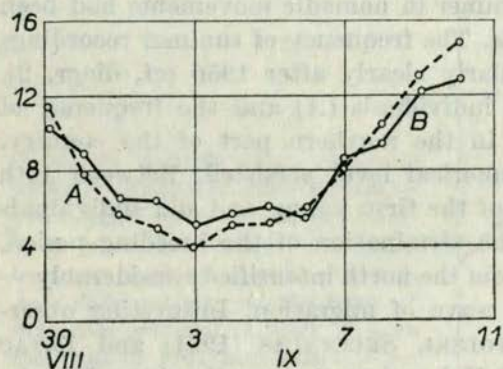


Graph 8. Autumn migration of *H. caspia* in 1961 in the region of the mouth of the San. The vertical axis — per cent of recordings and frequency of individuals in relation to their total number; the horizontal axis — months; A — frequency of individuals, B — frequency of recordings ($n_A = 207$, $n_B = 97$).

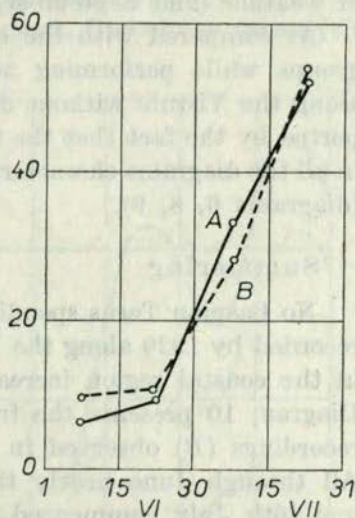
Inasmuch as in the north regions the migrations of *H. caspia* are largely connected with post-breeding nomadic movements but also with the summering of a certain number of individuals along the coast (cf. page 14), then in the southern regions this species is a typical transmigrant flying relatively fast (cf. also the standard deviations for the north and south — Tab. 1), although even here the flight is not devoid of a local nomadic character at times. This is convincingly illustrated by diagram 7. It presents, in per cent, the frequency of all Caspian Terns migrating southwards (S) and northwards (N) in the period 4th August — 17th September, and observed at the mouth of the San. Beside the two clear waves of migration, there can be spotted moments characteristic for nomadic movements, i.e. swinging movements up (S) and down (N) the Vistula and the San.

Comparing the second wave in the north (diagr. 5) and at the mouth of the San (diagr. 7), we can notice that the moments of terminating the nomadic movements coincide surprisingly in both the cases — at the turn of August and September. Although the way of presenting the intensity of nomadic movements illustrated in diagram 7 is undoubtedly more accurate than in the case of diagram 5, where the intensity of nomadic movements can be indirectly deduced from the ratio of the frequency of individuals to the fre-

quency of recordings, it is possible to compare the results of the analysis of the two diagrams. Summing-up, it should be stressed that the part of the Baltic population flying across Poland in August, beside simply migrating, carries out nomadic movements, but on the other hand those birds flying in September display the features of typical transmigrants.



Graph 9. Autumn migration of *H. caspia* in 1960 in the lower courses of the San and in the middle courses of the Vistula. The rest as in graph 8 ($n_A = 91$, $n_B = 39$).



Graph 10. Frequency of *H. caspia* in June and July over the northern regions of Poland (summering). The vertical axis — percentage participation in relation to each category of recordings; the horizontal axis — months; A — frequency of individuals, B — number of recordings ($n_A = 98$, $n_B = 34$).

As there is shortage of more copious data, only those for the season of 1961 can be considered here. But it can be expected that conclusions which they may suggest will not deviate much from the average state of things. It seems to follow from diagram 7 that the occupation of an ecologically suitable river section, in the case of nomadic stay, occurs already in an early phase of the flight of the first wave at the beginning of August. As the peak of flight in the northern direction is shifted in relation to the initial section of the curve representing flights in the southern direction, it is reasonable to suppose that *H. caspia* carries out nomadic movements in the lower and middle courses of the Vistula, but also up the San from its mouth. In the first wave of migration the balance of flights showed the preponderance of direction S, but it was more equal for the initial part of the second wave. This supplies evidence for

another conclusion that the micropopulation forming the second wave of migration and appearing on the Vistula in the last ten days of August can stop altogether in its southern drive performing only local movements connected with searching for food, sometimes even for quite a long time. In 1961 the resolute flight southward followed the coming of a cold spell and deterioration of weather (2nd September).

As compared with the coastal region where *H. caspia* can join in larger groups while performing nomadic movements, they disperse rather evenly along the Vistula without displaying a tendency to form groups. This is supported by the fact that the frequency of individuals and of recordings coincide in all the diagrams characterizing migrations in the southern part of the country (diagrams 6, 8, 9).

Summering

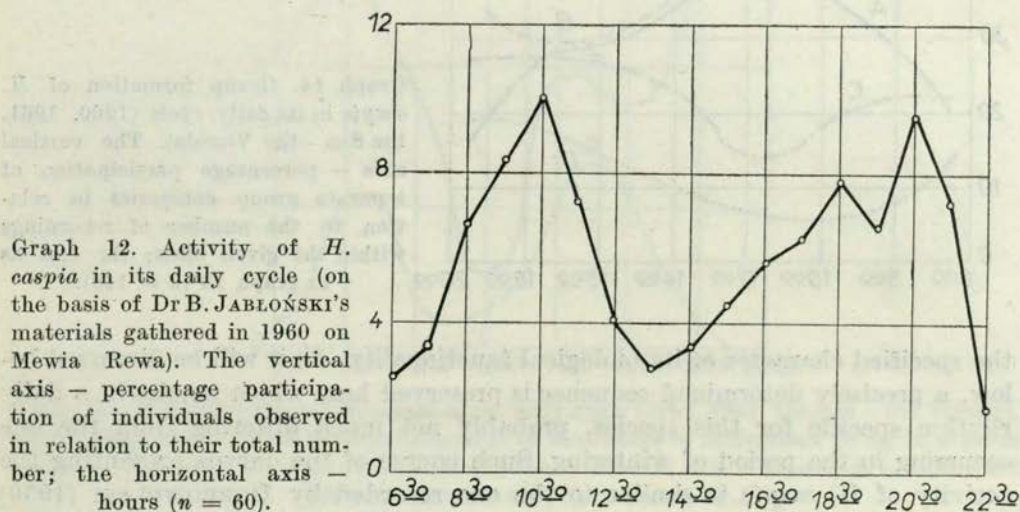
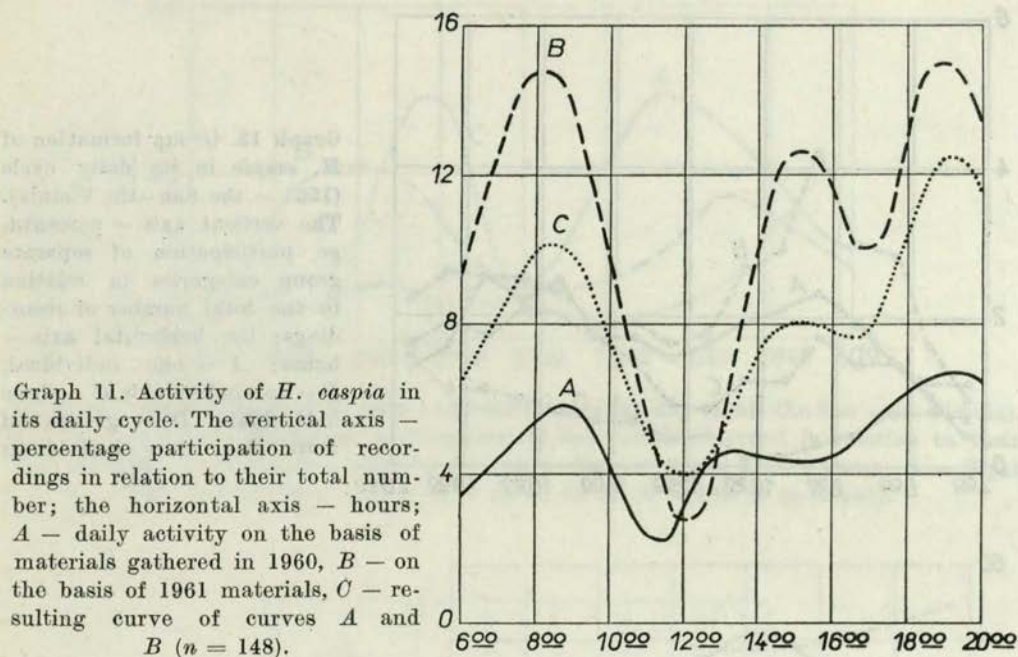
No Caspian Terns spending their summer in nomadic movements had been recorded by 1920 along the Polish coasts. The frequency of summer recordings in the coastal region increased particularly clearly after 1950 (cf. diagr. 2). Diagram 10 presents the frequency of individuals (*A*) and the frequency of recordings (*B*) observed in June–July in the northern part of the country. All through June nearly the same numerical level persisted. Between 10th and 20th July commenced the inflow of the first young and old individuals which were the first to appear after the termination of the breeding period. In the last ten days of July the inflow from the north intensified considerably — this was the initial phase of the first wave of migration. Interesting observations were carried out by DOBROWOLSKI, SKOCZYLAŚ (1961) and ZAJĄC (1964) in the region of the peninsula of Hel and at the mouth of the Vistula. They recorded in June and July separate pairs of adult individuals displaying certain features of breeding behaviour. However they could not record any positive attempts of nesting.

RHYTHM OF THE DAILY ACTIVITY

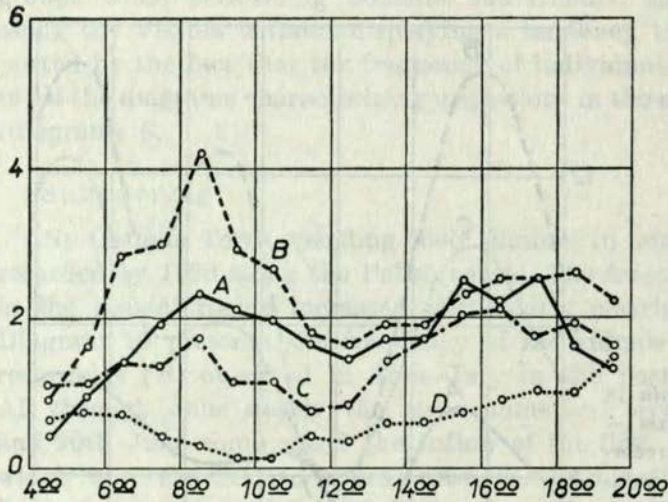
General picture of activity

Diagrams 11 and 12 present the course of daily activity (recordings of birds in flight) along the lower course of the San and the middle course of the Vistula in the period from 30th August to 10th September 1960 (curve *A* — diagr. 11), at the mouth the San — from 4th August to 17th September (curve *B* — diagr. 11), and on Mewia Rewa in the Bay of Puck from 30th July to 6th August — materials supplied by Dr B. JABŁOŃSKI (diagr. 12). A similar course of the curves indicates the regular character of the phenomenon. Thus from dawn to 8⁰⁰ the activity is gradually intensified and reaches its morning peak inside the countryside between 8⁰⁰ and 9⁰⁰, while

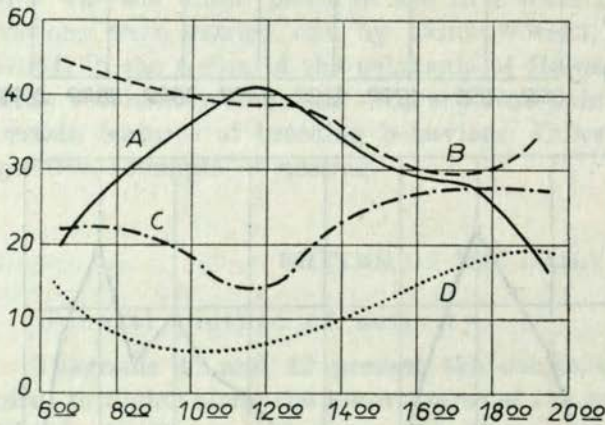
along the coast between 9⁰⁰ and 10⁰⁰. The mid-day break lasts from 11⁰⁰ to 13⁰⁰ in the south, and from 12⁰⁰ to 14⁰⁰ in the north. The afternoon peak fell on 15⁰⁰ inside the countryside, and on 18⁰⁰ on the coast — thus the difference between the countryside and the coast became more marked in the second half of the day. Both in the countryside (17⁰⁰) and on the coast (19⁰⁰) the afternoon decrease in activity preceded the pre-evening intensification which occurred at about 19⁰⁰ in the south and at about 20⁰⁰ on the coast. One of the reasons for



this discrepancy in the timing of activity recorded along the coast and at the mouth of the San was the fact that observations on Mewia Rewa were carried out in the vicinity of the sea-places where Caspian Terns rested and roosted. Thus these peaks reflect the activity connected with joining in groups before roosting or leaving the places of rest. And so in the course of 24-hours the Caspian Tern has both during nomadic movements and while performing migrations proper three peaks of locomotoric activity closely connected with



Graph 13. Group formation of *H. caspia* in its daily cycle (1961 - the San - the Vistula). The vertical axis - percentage participation of separate group categories in relation to the total number of recordings; the horizontal axis - hours; A - one individual, B - two individuals, C - three individuals, D - groups of more than four individuals ($n = 114$).

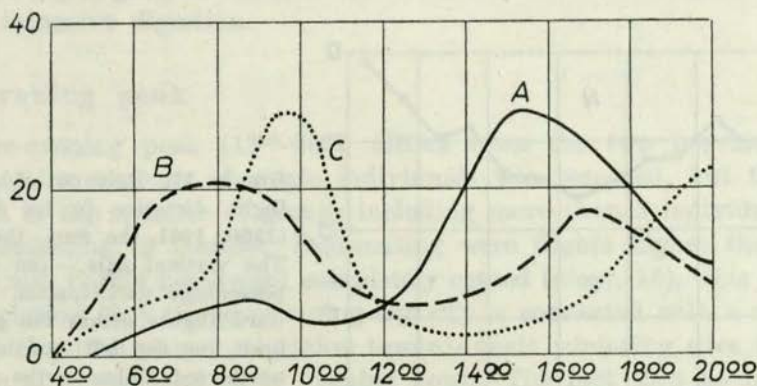


Graph 14. Group formation of *H. caspia* in its daily cycle (1960, 1961, the San - the Vistula). The vertical axis - percentage participation of separate group categories in relation to the number of recordings within the given class; the rest as in graph 13 ($n = 148$).

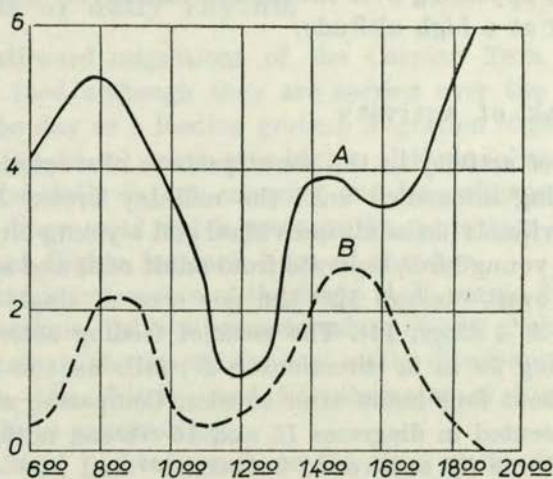
the specified character of its biological functionality. As it will be discussed below, a precisely determined sequence is preserved here which results in a daily rhythm specific for this species, probably not much differing from the one occurring in the period of wintering. Such course of the curves presenting the activity of *H. caspia* is similar to the one recorded by DOBROWOLSKI (1950)

when observing some other water-fowl species along the Vistula near Wyszogród in August 1952 and 1955, and by LUNIAK (1963) who observed *Larus ridibundus* in the middle courses of this river.

On the basis of an analysis of different elements of behaviour, changing in the course of daily cycle, such as a) connections within the flock and the family (diagrams 13, 14), b) altitude of flight (diagram 15), and c) its direction (diagrams 16

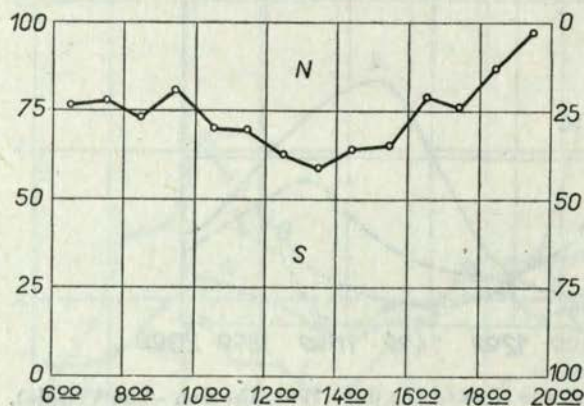


Graph 15. Flight-altitude of *H. caspia* and the time of the day (1961, the San - the Vistula). The vertical axis - percentage participation of individuals recorded in relation to their total number within separate altitude categories; the horizontal axis - hours; A - flight at the altitude of 20 m; B - up to 50 m; C - 150 m ($n = 101$).



Graph 16. Flight direction of *H. caspia* in its daily cycle (1960, 1961, the San - the Vistula). The vertical axis - percentage participation of recordings of individuals flying in a given direction in relation to their total number; the horizontal axis - hours; A - southward flight, B - northward flight ($n = 148$).

and 17) I shall endeavour to reconstruct the biological essence of the rhythm of activity. Three factors are here prominent: feeding, rest, and migrations proper. The rest can be considered on the basis of the decrease in the locomotoric activity (diagrams 11, 12), but we can conclude about feeding and migrations only when analysing jointly the elements of behaviour mentioned above. The most valuable, for the purposes of determining the type of activity, is the characteristic of such parameters of flight as its altitude, direction and line



Graph 17. Balance of *H. caspia* flight direction in its daily cycle (1960, 1961, the San - the Vistula). The vertical axis - (on the right) percentage participation of southward flights within the given time limit, (on the left) participation of northward flights in the given time limit; the horizontal axis - hours ($n = 148$).

(straight flight, circuitous flight-penetrating). Birds searching for food use only low-altitude, penetrating flight and then directions S-N are almost equivalent. Individuals appearing over the area as exclusively transigrants usually fly straight ahead at a high altitude.

Morning peak of activity

Morning peak of activity in the countryside is characterized by dispersion over the river being intensified until the mid-day break. Mostly they form groups of two individuals (an adult individual and a young bird accompanying). After finding food young birds separate from adult ones and search the feeding-ground on their own - before 12:00 the per cent of single birds reaches its maximum (curve A - diagr. 14). The peak of feeding activity (low penetrating flight, swinging 50 m in directions S-N) falls on the hour between 8:00 and 9:00, that is about four hours after sunrise. Comparing altitude and directions of flight presented in diagrams 15 and 16 we can notice that a considerable per cent of birds fly southward between 9:00 and 11:00 - and they fly at the altitude of more than 50 m. As in the morning Caspian Terns fly higher than in the afternoon (diagr. 15), and there are more southward flights, then most probably also before 9:00 some part of Caspian Terns migrate southward.

Afternoon peak

The afternoon peak of activity (14⁰⁰-16⁰⁰) is connected exclusively with searching for food. In this period completely low flights predominate (altitude up to 20 m) penetrating and food-searching (diagr. 15), while the difference between S and N flights is then smallest. A considerable part of birds are still dispersed although there is a tendency to join in flocks (diagr. 14). At about 16⁰⁰ the activity slightly subsides which is connected with resting after feeding and more intensive digestion.

Pre-evening peak

The pre-evening peak (18⁰⁰-20⁰⁰) differs from the two previous peaks. A much smaller number of single individuals was recorded, but there was an increase in the number of groups including more than 3 individuals, that is flocks consisting of families. Dominating were flights higher than 50 m (diagr. 15) and flights northward completely ceased (diagr. 16). This may suggest a conclusion that the pre-evening activity is connected with a migrating flight, and that the proper migration towards their wintering sites is carried out in late afternoon and early evening hours. The fact that no northward flights were observed after 18⁰⁰ seems to suggest that those birds which carry out nomadic movements, i.e. still remaining within the area occupied, take their rest. Whether this picture reflects the real state of things can be decided by observations carried out in the late afternoon from a fast motor-launch.

The functions of daily rhythm

The proper southward migrations of the Caspian Tern do not coincide with searching for food although they are carried over the water area used in some hours of the day as a feeding ground. Migration flights, as opposed to searching for food (10-30 m) occur at a higher altitude (about 80-100 m) and are carried out twice daily in late morning and late afternoon hours. This is best illustrated by diagram 17 which presents the percentage balance of northward and southward flights for each hour of the day.

Separate characteristic features of the flight in *H. caspia* daily cycle depend on its biological functions. Table 2 presents values of test χ^2 showing the dependence of flight altitude on the time of the day, on the directions of flight (S or N), directions the San - the Vistula, and the character of flight (straight-line flight, circuitous flight-penetrating).

Thus the altitude of flight depends on the time of the day (differences in the character of activity peaks), and also on direction N-S (swinging flights while searching for food). Co-dependence of the line and altitude of flight in the light of the connections presented is obvious and does not require any commentaries. On the other hand, the dependence of the altitude of flight on

Table 2. Co-dependence of flight altitude and other elements connected with *H. caspia* daily activity (the San, the Vistula — 1961).

Dependence on	χ^2	<i>df</i>	<i>P</i>
(1)	(2)	(3)	(4)
time of the day (5)	18.32	6	0.01
directions S-N (6)	10.89	3	0.01
directions the San—the Vistula (7)	7.26	3	0.07
line of flight (8)	9.03	3	0.02

the preference of the two possible southward routes, either along the San or the Vistula at the mouth of the San is much less clear. I shall discuss this problem more closely in the penultimate chapter.

The structure of *H. caspia* families and flocks in the daytime changes according to the function of food-searching, migrations proper, and most of all depends on the security arrangements for each of the individuals. From the early morning until the midday break the dispersion of individuals gradually increases. In the second half of the day the opposite tendency can be observed, i.e. efforts to join in larger groups. To dispel any possible doubts the author, when analysing systems of grouping, discusses only flocks observed in flight. Groups of individuals resting on the ground are not analysed here and most probably there are some considerable differences between the two cases.

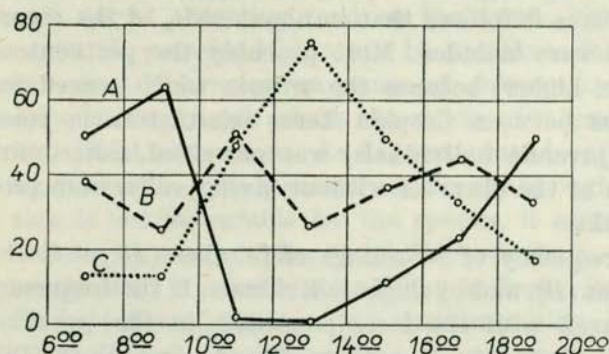
Each of the activity peaks in the daytime has a different qualitative character. The morning peak is the result of two types of activity: searching for food and flight. However there is no ground to suppose that these two functions, as I have pointed out earlier, are carried out simultaneously by the same individuals. On the contrary, a comparison of curves *C* (diagr. 15) and *B* (diagr. 16) leads us to believe that after 9⁰⁰, with the intensification of high-altitude flights, there are fewer northward flights (cf. also Tab. 2). The afternoon peak compares exclusively food-searching, while the pre-evening peak is the result of migration activity or, but this has not been supported sufficiently by observations, it may be caused but the flight of some Caspian Terns straight to their pre-determined roosting places (similarly as with *Larus ridibundus* L. in the same period).

SOCIAL STRUCTURE, GROUP FORMATION, SURVIVAL

Average size of flocks

The Caspian Tern belongs to a small group of species in which connections between parents and their issue last long after the termination of the breeding period, and that includes the period of nomadic movements, autumn migrations, and quite probably they are continued in their winter ranges. This does not

mean that this species does not display other social connections or that they are less pronounced. The structure of flocks not only in the annual cycle, but also, as I have discussed it earlier (cf. page 20), in its daily cycle, is very plastic and can suffer quite significant changes.



Graph 18. Social character of *H. caspia* group formation in its daily cycle during autumn migration (1961, the San - the Vistula). The vertical axis - percentage participation of separate categories of groups within the given time limit; the horizontal axis - hours; A - families, B - flocks, C - separate individuals.

Table 3 presents the average group-size of Caspian Terns recorded in Poland. The difference between the northern and southern parts of the country is quite striking and it indicates that the species flies over the southern regions in spring divided into pairs or at least in the course of pairing off, while the autumn migration is carried out in groups of 2-3 individuals (cf. diagr. 18).

Table 3. Average flock-size of *H. caspia* in the period of migrations in Poland.

Average flock-size (2)	in the course of spring migrations (April, May) (3)	in the course of autumn migrations (August, Sept., Oct.) (4)
Territory of Poland (1)		
north of latitude 52° 30' N (5)	4.87	4.95
south of latitude 52° 30' N (6)	1.94	2.28
entire area of the country (7)	3.16	3.25

Family connections

As it follows from the materials collected at the mouth of the San, 32.6% of all the recordings were of adult birds and young ones starting a family. The following combinations can be discerned: 1 ad. + 1 juv. (30% of all the families recorded), 1 ad. + 2 juv. (32%), 1 ad. + 3 juv. (6%), 2 ad. + 1 juv. (19%), 2 ad. + 2 juv. (6%). Thus it follows that in about 25% of the recordings both males and females were included. Most probably the per cent of birds flying in families is even higher, because the criteria which served for determining family connections between Caspian Terns (characteristic voice signalling between adult and juvenile individuals) was one-sided. Some part of families flying in the region of the observer without giving voice were probably recorded as normal flocks.

Diagram 18 presents the frequency of recordings of families (A), of flocks displaying no family connections (B), and of single individuals. If the frequency of family recordings is compared with the facts presented in the previous chapter (diagr. 11, curve B — diagr. 13; C — diagr. 15; A, B — diagr. 16), then the following conclusion can be drawn: *H. caspia* keeps up family connections almost exclusively in the course of migrations proper southward. In order to supply materials supporting this thesis the author calculated statistically characteristic features of family flights, flights of normal flocks, and of single individuals (Tab. 4).

Table 4. Altitude and directions of *H. caspia* flights in relation to its social structure (in metres, the San — the Vistula, 1961).

Characteristic features (2) Character of groups (1)	\bar{x}	σ_x	S_x	Per cent of individuals flying:	
				southward (6)	northward (7)
families (8)	90.0	33	± 8.5	87.5	12.5
flocks (9)	54.4	41	± 10.2	66.7	33.3
single individuals (10)	44.7	36	± 9.3	63.6	36.4

Thus families, as opposed to flocks and single individuals, use high—altitude flights—differences between the average altitude of family flights and average values of other statistical categories are significant. The same, however, was not recorded for differences of average flight altitudes of flocks and single individuals. Also the per cent of families flying southward differs from the state recorded for other categories.

Social factors affecting the survival

In the light of the facts presented we have to accept a conclusion differing from the positions defended up till now and concerned with the biological essence of family protection in Caspian Terns in the post-breeding period which consists in feeding up young individuals which have not yet acquired the difficult art of obtaining food on their own. The conclusion following from the materials presented here can be put thus: family connections are kept up in the most dangerous moments of autumn migrations, i.e. when flying over unpenetrated areas where the safety of migrants depends exclusively on their individual experience. As I have proved earlier (cf. page...) migration and food-searching are separated in time; although it might seem that such a division is not favourable for the species, it secures in a strange area the degree of security much higher than, for example, in the case of gulls. Because, differently than in other species flying in flocks, juveniles of which join in separate flocks before departure and their mortality in the first year of life exceeds 70%, juvenile Caspian Terns, according to data of ringing, perish less frequently in the first year — the return of rings amounted to only 36% (SHEVA-REVA, 1962).

By proving that the basic idea of keeping up family connections during migrations consists in the protection extended to juvenile birds by the experience of adults, I do not want to underestimate the role of feeding up particularly in late afternoon hours. However in normal conditions it is of secondary importance. Probably only in adverse hydro-meteorological conditions this can affect the survival of juveniles.

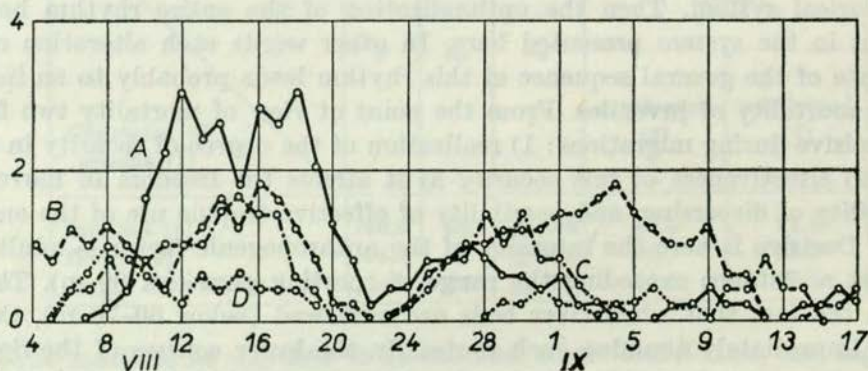
When comparing diagrams 15 and 18, also other suggestions can be put forward which will help to integrate separate sequences of the daily rhythm in a logical system. Then the optimalization of the entire rhythm becomes evident in the system presented here. In other words each alteration or disturbance of the general sequence of this rhythm leads probably to an increase in the mortality of juveniles. From the point of view of mortality two factors are decisive during migrations: 1) realization of the degree of security in a new area, 2) effectiveness of this security as it affects the freedom of movement, possibility of dispersing, and possibility of effective trophic use of the environment. Decisive is here the intensity of the anthropogenic factor — adult birds keep at a distance exceeding the range of sporting guns (ca. 80 m). This explains the fact that when river beds are narrowed (below 60–70 m), Caspian Terns immediately abandon such routes. In the lower courses of the San this phenomenon was observed in the last ten days of August 1961 when the decrease in the number of Caspian Terns recorded coincided with the lowering of the level of water and with the narrowing of the river bed (cf. also diagr. 24).

The entire daily rhythm against the background of family relations can be presented thus: Caspian Terns joining in families during the peak in late

afternoon hours fly southward at high altitudes. Immediately after sunset they make for roosting places (sand-waves, islands). They roost in families. Night and early morning enable to recognize the degree of security in the given area. Then they start morning food-searching and fly southward in the second phase of the morning peak (cf. diagr. 15). In the final phase this gradually becomes the penetrating of a new area, then the birds disperse and start their midday rest. During the break they still try to reconnoitre the area. The afternoon peak of activity is connected exclusively with food-searching. This can be presented in the form of a table:

rest	food-searching, flight	rest	food-searching, flight
reconnaissance		reconnaissance	
night	morning	afternoon	evening
grouped in families		dispersion	joining in families

Each food-searching in the scheme above is preceded by a long reconnaissance to ascertain the degree of security. Each flight connected with migration is preceded by feeding and followed by rest combined with another round of reconnoitring. Sometimes the late afternoon migration becomes a night flight. Caspian Terns flying before midnight or even in the small hours were frequently observed by the author in September 1961. In all such cases adult individuals were flying together with juveniles (characteristic voice signalling). The scheme given here constitutes a sort of rhythm characteristic for migrations. In the cases when Caspian Terns stay for a few days in one area (stationary nomadic



Graph 19. Group formation of *H. caspia* during autumn migration (1961, the San - the Vistula). The vertical axis - percentage participation of separate group categories in relation to the total number of recordings; the horizontal axis - months; group formation: A - single individuals, B - groups of two individuals, C - of three individuals, D - of 4-5 individuals ($n = 83$).

sites) the general plan of activity remains the same (3 peaks of activity), only instead of the migration phase the period of food-searching is accordingly longer. It follows from the comparison of diagrams 7 and 19 that in both the migration waves characteristic nomadic movements resulted in an increase in the recordings of single individuals. Thus it is possible to conclude that family connections are weakened during a nomadic stay — young birds in a well reconnoitred area can be dispersed and at the same time feel secure. This also seems to throw light on the situation in their winter ranges — there probably family connections disappear completely.

Flocks, aggregations

Caspian Terns do not join in flocks as clearly and as permanently as smaller Tern species. As is follows from Table 3, the average flock-size in the north of the country (mainly in the coastal region) both in spring and in the post-breeding period considerably exceeds the one recorded for the southern territories. This can be explained, in the case of spring migrations, by a) proximity of breeding-sites and probably an initial joining in larger groups becoming later their breeding colonies, b) unfavourable atmospheric conditions in the Baltic region in this period hampering their migrations, which results in the formation of larger communities in places where food is abundant.

In the case of post-breeding nomadic movements northern flocks are only insignificantly larger than in spring (Tab. 3). Probably such aggregations are also formed in places suitable for resting and food-searching. The largest flocks recorded in Poland consisted of about 30 individuals — e.g. on 12th of September 1956, Pastwa Sobieszewska (region of Gdańsk) (according to data recorded by J. B. SZCZEPSKI), or on 2nd August 1961 at Mikoszewo (region of Nowy Dwór Gdański) — 33 individuals (ZAJĄC, 1964). It is difficult to decide whether these groups had characteristic features of flocks. According to SWIRSKI's observations (1964, oral information) the largest communities inside the country are formed by individuals resting on river islands — e.g. observations on 12th September 1956 near the locality of Piekło (888 km of the Vistula) (region of Sztum) and concerned with 17 Caspian Terns staying on an island. More observations of a similar kind were carried out in Poland, but still the material is not sufficiently large to lend itself to any far-reaching analysis.

Diagram 18 indicates that in the hours of the midday break birds observed in flight are maximally dispersed (the observer was stationary). At the same time another observer moving in space (boat, motor-launch, ship — as in the case of examples mentioned above) recorded that resting Terns stayed in more or less loose groups, quite often including other species (mainly *Larus ridibundus* L., *Sterna hirundo* L., *Vanellus vanellus* L.).

The gregarious character of small groups was kept up during the food-searching activity (diagr. 18). Birds were clearly in touch with each other and reacted

in an organized way to external stimuli. As opposed to larger aggregations integrating factors are here clearly displayed. I have discerned 4 degrees of involvement in the course of autumn migrations at the mouth of the San (Tab. 5): I — connections between individuals developed to a highest degree, they fly closely together, their movements are completely co-ordinated. So closely integrated can be only families and even so in a small number of cases. II — connections between individuals well developed (particularly voice signalling), the group flies quite dispersed but all changes of direction, altitude, etc., are undertaken simultaneously by all the individuals. 41.8% of individuals were recorded in such groups. III — connections between individuals are not close, they are often broken and disappear completely; if they are kept up then only with the help of voice signalling, or very rarely they can be in touch visually. A very high degree of dispersion so that very often they lose sight of each other. Co-ordination of their movements is only the resultant. 33.6% of individuals were recorded in such groups. IV — almost complete distintegration during flight but for some sporadic attempts to get in touch with other individuals (voice). During the midday break they display a tendency to form aggregations with other species.

Table 5. Integration of *H. caspia* in flocks in the course of autumn migrations (mouth of the San — 1961; in per cent of number of individuals, $n = 101$).

Degree of integration (2) Character of the group (1)	I (3)	II (4)	III (5)	IV (6)	Total (7)
families (8)	4.9	31.7	3.0	—	39.6
flocks (9)	—	10.1	30.6	—	40.7
single individuals, aggregations (10)	—	—	—	19.7	19.7
Total (11)	4.9	41.8	33.6	19.7	100.0

As it follows from Table 5 family connections are strongest. Flocks, which here probably included also some per cent of groups with family connections (cf. page 22), constitute an almost basic form of group formation. The most controversial, as far as the degree of integration and qualification according to the criteria accepted are concerned, seem to be groups at rest (cf. page 25). Taking into account the lack of co-ordination, considerable spacial dispersion,

variable numbers (constant inflow and outflow of single individuals and small groups) I have treated them as aggregations. The integrating factors are the topographical features (favourable position, inaccessibility, visibility, etc.) of a given river island. Still the role of aggregation is significant with a view to securing safety of separate individuals. As I have mentioned earlier (cf. page 25) the final clearing up of the matter requires more copious and accurate materials.

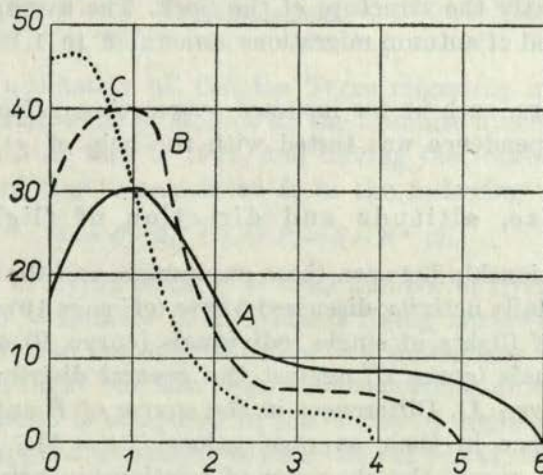
Diagrams 18 and 19 indicate that there is not much stability of groups forming families or flocks in *H. caspia* daily cycle, and also in August and September. The highest degree of integration occurs in face of danger (morning and early evening flights over strange areas, roosting), and the opposite — well penetrated areas enable the highest degree of dispersion.

Pairing off

Spring trans migrants in the southern parts of the country probably fly already paired off (cf. Tab. 3). Other explanations of the average result (amounting to 1.97 individuals) seem less probable. In the coastal region (cf. page 14) separate pairs displaying certain features of the breeding behaviour were also recorded in summer.

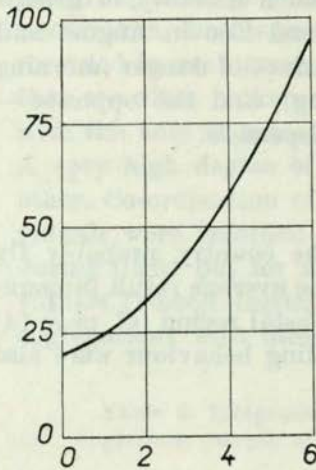
Meteorological factors and flock-size

As I have proved earlier (page 20) the variability of the degree of integration and group-size (families or flocks) in the migration period is a result



Graph 20. Dependence of *H. caspia* flock-size on wind force (1961, the San-the Vistula). The vertical axis — percentage participation of recordings of a given flock category in relation to the total number of recordings in this category; the horizontal axis — wind force on the Beaufort Scale; A — distribution of recordings of single individuals, B — of flocks of two individuals, C — of three individuals ($n = 69$).

of functional necessity. Deciding here is the pressure of food competition within the species and dangers from the environment. The significant factor in our consideration is the plastic structure of the flock and its correspondence with the combination of the factors mentioned, changing regularly in the daily and seasonal rhythm. All the disturbances of the flock structure, particularly in the regularity of changes, are probably harmful. Of these disturbing factors the effect of wind should be considered first. Diagrams 20 and 21 present



the dependence of the flock-size on wind force (on the Beaufort Scale). As it follows from diagram 20, above 4° on the Beaufort Scale no groups of more than 2 individuals were recorded, and in the case of quite strong winds (6°) only single birds were observed. Diagram 21 expresses the same in a more distinctly graphic way. Generally the correlation bet-

Graph 21. Effect of wind force on the dispersion of *H. caspia* (1961, the San-the Vistula). The vertical axis — percentage participation of single individuals in relation to the number of recordings of the other group categories within the given class of wind force; the horizontal axis — wind force on the Beaufort Scale ($n = 69$).

ween the wind force and the flock-size is not very high ($r = 0.71$). Taking into account that strong winds are rare in the time of flights already winds of 4° affect significantly the structure of the flock. The average wind force prevailing in the period of autumn migrations amounted to 1.19° on the Beaufort Scale.

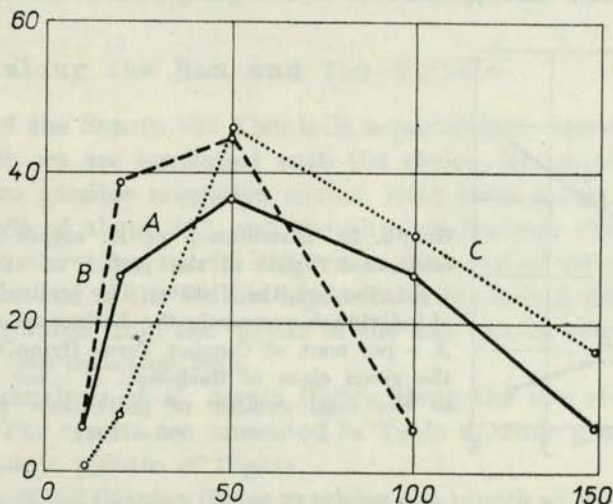
No other factors, such as for instance overcasting, affect significantly the flock-size. The dependence was tested with the help of χ^2 .

The flock-size, altitude and direction of flight

There is a relationship between these parameters and the flock-size reflected in the rhythm of daily activity discussed above (cf. page 19). Graph 22 presents the distribution of flights of single individuals (curve *B*) and flocks of more than two individuals (curve *C*) against the general distribution of *H. caspia* flight altitude (curve *A*). Differences in the course of *B* and *C*, as well as the significant difference in their average values ($\bar{x}_B = 44.7$ m; $\bar{x}_C = 78.5$ m; $\bar{x}_C - \bar{x}_B = 33.8$ m), reveal the character of relationship between the flock-size and flight altitude, and it is a close one ($r = 0.97$).

The relationship between the flock-size and flight directions S-N (graph 23) is of the same character. As it is known, Caspian Terns encountered along the river-bed migrate only partially, i.e. move southward, while the rest of

their activity is confined to carrying out swinging flights S-N searching food and performing other functions. Beside the analysis presented above (cf. page 22) and explaining the connection between the flock-size and the movement southward, it seems that a more searching presentation is still required.



Graph 22. Interrelationship between *H. caspia* flight-altitude and flock-size (1961, the San-the Vistula). The vertical axis — percentage participation of recordings in the given flock category in relation to the total number of recordings in this category; the horizontal axis — flight-altitude in metres; A — general flight distribution of all the flocks recorded, B — distribution of flight-altitude of single individuals, C — flight-altitude of flocks of 3-4 individuals.

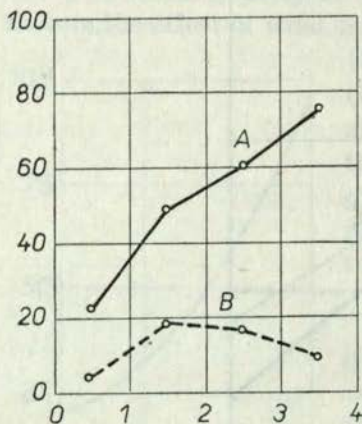
Assuming that ultimately all Caspian Terns migrating in autumn will fly southward, in the conditions of studies on the absolute numerical state carried out at the mouth of the San in 1961, and having the total number of southward and northward flights calculated from the following formulas:

$$P = C - 2N \quad (1) \quad \text{or} \quad P = S - N^* \quad (2),$$

where P = number of flying birds, C = total number of flying or resting individuals observed, N = number of individuals flying northward, S = of those flying southward; we can not only calculate in a simple way the total numbers of the population in flight but also learn the proportions of separate groupings of which the population is composed in the course of migrations. For this formula (1) should be applied separately to each class of size of the groups recorded. Naturally there will be no possibility in such a case to consider the dynamics of group variations, but this would not distort the general picture.

* It will be possible to calculate P in the case of observations connected with birds exclusively in flight.

Such an analysis revealed that Caspian Terns recorded as flying alone only in a small per cent (3.6%) migrate lonely southerward. The highest per cent was recorded for groups of 2 individuals (18.0% of all the Caspian Terns observed over the entire season) and groups of 3 individuals (16.2% of the total) (cf. also curve B — graph 23). The investigation of numerical relations



Graph. 23. Distribution of *H. caspia* flock-size during southward flights in the period of autumn migrations (1961, the San—the Vistula). The vertical axis — per cent of individuals recorded; the horizontal axis — flock-size; A — per cent of Caspian Terns flying southward within the given class of flock-size, B — per cent in relation to the total number of individuals flying southward ($n = 167$).

between individuals flying southward and those carrying out swinging flights S-N within separate classes (curve A — graph 23)-shows that all flocks of 4 birds in 75% of the recordings were in the course of the proper southward migration. This per cent decreases together with the flock-size, and in the case of single individuals as many as 78.6% are birds whose flight was not directly concerned with moving southward.

FACTORS AFFECTING THE CHOICE OF MIGRATION ROUTES

General significance of the problem

The basic reason for locating the field studies of *H. caspia* migrations (as well as other species) at the mouth of the San was the need for materials yielding information on circumstances, causes and factors affecting the choice by the birds of one of the two possible routes of further migration. This question, not analysed satisfactorily so far, of selecting a specified route by species migrating along the course of rivers or along the coastline has recently acquired significance (even for generally theoretical purposes) as it can throw some light on certain mechanisms connected with space-consciousness of migrants.

The preference of one of the two possible routes by *H. caspia* is connected with far-reaching consequences revealed in the course of their further migration — individuals migrating along the course of the Vistula have to over-

come the Carpathian arc in its western part (cf. page 6) and most probably continue their migration across the Hungarian Plain in the direction of the Italian Peninsula; while the birds choosing the valley of the San reach the valley of the Dniester before Przemyska Gate, and thence along the coast of the Black Sea to the eastern parts of the Mediranean Sea.

Migration along the San and the Vistula

The mouth of the San to the Vistula is a particularly convenient point of observation when we are concerned with the choice, by waterfowl migrants, of one of the two possible migration routes. Both these rivers flow into each other at the angle of about 40° , and the physical features and vegetation of the banks do not show any special differences. The bed of the San is only $1/3$ narrower than the bed of the Vistula higher from the mouth (Map 1). The bed of the Vistula upwards from the mouth of the San has its course in direction SSW, while the San direction SSE.

A numerical analysis of *H. caspia* flights along the two rivers was based on formula (1). The results are presented in Table 6, while graph 24 gives an idea of the dynamic picture of flights.

In all, 49.5% of all Caspian Terns reaching the mouth of the San, continue their migration along that river — i.e. nearly half of the total. As it follows from Table 6, 44.3% of all the Caspian Terns recorded along the Vistula were either searching for food or carrying out nomadic movements, while this per cent was lower along the San — 11.6% . Thus the San has gained the importance of a "transit" route. Up the mouth of the San, the Vistula has probably the same significance. It is important that, higher from the mouth of the Dunajec river, only a small part of migrating Caspian Terns were recorded which was reflected in the work of KOZŁOWSKI (1967). The per cent of birds migrating along the middle courses of the Vistula (80.4%) does not differ much from the one for the entire width of the San (88.4%). In the sections adjoining the banks along the Vistula to the mouth of the San only 40.0% (left-hand side section) and 47.4% (right-hand side section) of all the Caspian Terns recorded there, were migrating birds; all the remaining individuals were carrying out nomadic movements.

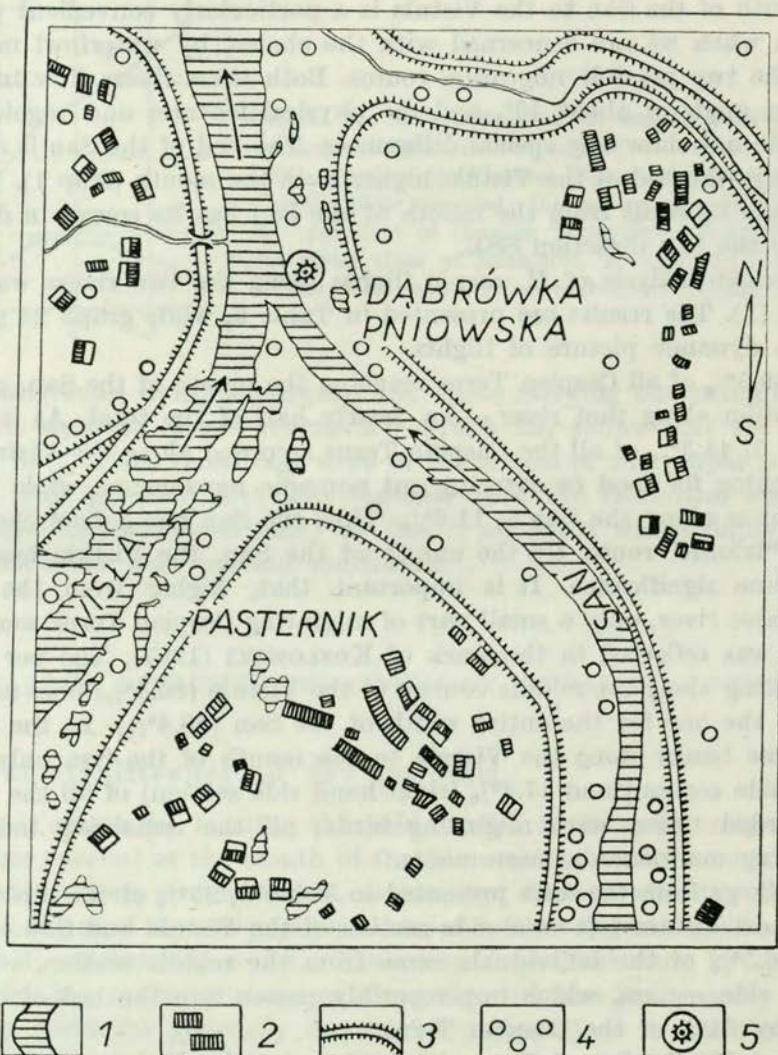
As it follows from the data presented in Table 6, 25% of the birds turned from the most distant left-hand side section of the Vistula and flew on along the San, 46.3% of the individuals came from the middle section, while the right-hand side section, which imperceptibly passes into the bed of the San, was used by 64% of the Caspian Terns.

The time distribution of *H. caspia* frequency along the two rivers in the region of the mouth (graph 24) is quite significant. It supports the conclusion following from the data presented in Table 6 that the San is used (at least in the section at the mouth) as a transit route, while the Vistula beside this

basic role also serves as a feeding ground and as a stationary nomadic site. This conclusion is the more obvious when we compare graph 24 with graphs 7 and 19 which present peaks of nomadic movements of the 1st and 2nd wave.

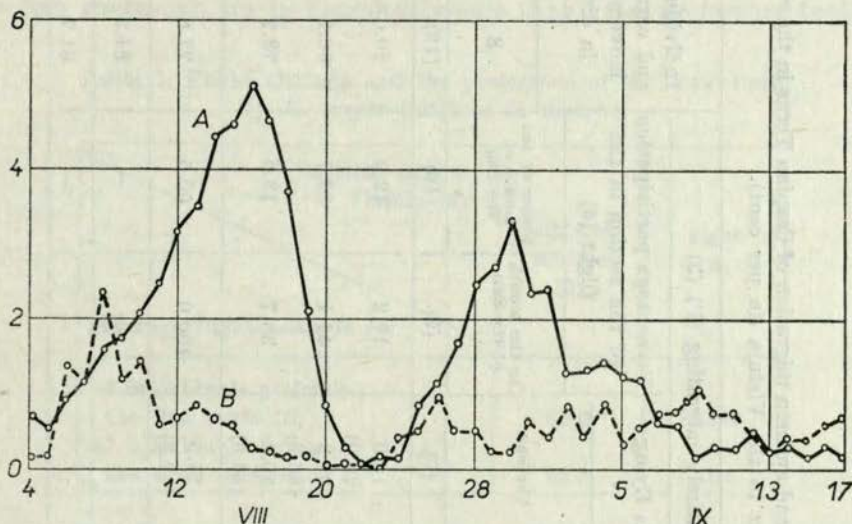
Criteria explaining the choice

The problem of choice will be here discussed in the following order: a) criterium of choice, b) numerical characteristic of the phenomenon, c) external and internal factors limiting the chances of choice.



Map 1. Situational plan of the region around the mouth of the San to the Vistula. 1 — water bodies, 2 — built-up areas, 3 — anti-flood dykes, 4 — tree-covered areas, 5 — observational point while observing *H. caspia* migrations.

The determination and the description of the choice of one of the two possible migration routes by Caspian Terns presents serious difficulties. It does not seem probable that all the birds flying along the right-hand side section of the Vistula, which passes into the bed of the San, could actively choose this particular river. On the other hand the active choice of the San by birds flying along the middle and left-hand side section is beyond doubt. But we are not in a strong position to decide whether the birds flying along the sections mentioned and keeping to the Vistula higher from the mouth of the San actively eliminated the San and chose the Vistula. There are however a few



Graph 24. Preference of the San route or the Vistula route at the junction of these rivers by *H. caspia* (autumn migration of 1961). The vertical axis — per cent of individuals in relation to their total number recorded in flight; the horizontal axis — months; A — individuals preferring the Vistula, B — those preferring the San ($n = 189$).

facts which seem to contradict this thesis. First, the population migrating along the Vistula maintains direction SSE which is shown by the lack of migrating Caspian Terns in the region of Cracow (KOZŁOWSKI, 1967). At the same time I can mention that no right-hand side tributaries of the Vistula lower from the mouth of the San can be treated as a branch of the main migrating route. Thus the observations of Dr B. JABŁOŃSKI proved that the Bug river is not a migrating route of *H. caspia*. He carried out regular observations on flights of *H. caspia* in the years 1966-1967 in the region of Brok district of Ostrów Mazowiecka in the period August-September, and he could not record Caspian Terns there at all. As I have mentioned earlier (cf. page 31) 49.5% of the population migrating along the Vistula choose the San. Thus only the remaining part of the population could use the higher right-hand side tributaries (the Wisłoka, the Dunajec, the Raba). Second, as it follows

Table 6. Analysis of post-breeding nomadic movements and autumn migration of Caspian Terns in the region of the mouth of the San river to the Vistula (in per cent).

River	Section of the river	Individuals entirely migrating (P) (3)					Individuals migrating and carrying nomadic movements – flights in direction (11)		Individuals carrying out entirely nomadic movements
		Per cent of individuals flying along (4)			Percentage participation of the section in the flight (8)		S	N	
		the Vistula lower from the mouth of the San)	the Vistula (higher from the mouth of the San)	the San	to the mouth of the San	higher of the mouth of the San			
		(5)	(6)	(7)	(9)	(10)	(12)	(13)	
the Vistula	left-hand (15)	40.0 (100.0)	30.0 (75.0)	10.0 (25.0)	17.2	12.9	70.0	30.0	60.0
	middle (16)	80.4 (100.0)	43.1 (53.7)	37.3 (46.3)	44.1	23.7	90.2	9.8	19.6
	right-hand (17)	47.4 (100.0)	17.1 (36.0)	30.3 (64.0)	38.7	13.9	73.7	26.3	52.6
	average (18)	55.7 (100.0)	28.1 (50.5)	27.6 (49.5)	100.0	50.5	77.8	22.2	44.3
the San		88.4			—	—	94.2	5.8	11.6
Total (19)		63.4			—	—	81.7	18.3	36.6

from the data presented in Table 7, the average flight-altitude of individuals flying on along the Vistula in the middle section and in the left-hand side one is lower than those preferring the San route. As the preference of the San can only be the result of satisfactory space orientation, improving with altitude, so that birds flying lower have less possibility to estimate properly the situation and undertake the best decision — the best according to the choice of route in agreement with the general direction of migration. Thus we cannot treat the further flight along the Vistula as the preference of this river. The arguments cited support the thesis that only in the case of the preference of the San route can we be completely sure that a real preference took place.

Table 7. Flight altitude and the preference of the San route by *H. caspia* (altitude in metres).

Sections of the Vistula (2) Average flight altitude (1)	left and middle (3)	right (4)
of individuals preferring the San route (5)	65.0	35.2
of individuals flying on along the same section (6)	53.3	51.6

As it was mentioned above, also in the case of Caspian Terns from the right-hand side section turning to the San route, it is impossible to decide whether there occurred an active preference in a number of cases. Hence, when we accept as undeniable facts of preference those which meet the criteria discussed above, they will make up 24.7% of the total number of Caspian Terns migrating along the Vistula, although, as it will be seen from the other part of this chapter (cf. page 39), more than half of Caspian Terns there had good conditions for deciding the right choice. Thus the criteria showing the real preference of one of the two possible migration routes, although limited, are unequivocal. It must be stressed here that we are concerned with the type of preference connected with making a specified decision at the moment of reaching the mouth by a given individual or flock, which becomes obvious by a change in the direction of flight. The character of motivation leading to this decision — instinct or individual experience — is not so significant of itself. Thus we can not take into account the mechanisms revealed prior to reaching the mouth, and securing in difficult atmospheric conditions the right choice of route, as well as the right choice of route on the basis of the trial method.

Factors affecting the preference

Let us consider now which factors and to what extent affect the choice of the San route. On the basis of the percentage distribution of penetration from separate sectors of the Vistula to the San, which increases from left to right, presented in Table 6, it is possible to draw the first conclusion concerning the choice of the further route. Decisive here is the distance from the right-hand side of the Vistula. This dependence of the San route preference on the distance of flight from the bank mentioned was checked with test χ^2 — the effect of this distance is quite significant (at $df = 2$, $\chi^2 = 8.01$, $P = 0.018$).

Which factors decide in turn the choice of the section of the Vistula? As it was stated above this affects the further route of migration (cf. page 30). An analysis of Table 6 shows that individuals flying along the middle section display an unequivocal preference. This is connected with securing the sufficient margin of safety for migrants in a non-roconnoitred area. It is characteristic that beside the middle section also their right-hand side section acquires significance in flights to the mouth of the San (cf. items (9) and (10) in Table 6). Higher from the mouth both the right- and left-hand side sections are of equal significance. Thus we might suppose that Caspian Terns looking for the route in SSE direction want to be on the safe side by keeping to the right-hand side bank so that they can instantly choose the route consistent with the general direction of migration when the possibility arises. Besides the preference of the right-hand side bank may be caused by specified atmospheric conditions as it is shown by the data presented below.

Table 8. Flights of *H. caspia* along the specified section of the Vistula and the choice of the San route depending on the degree of overcasting and wind force ($n = 78$).

River and section (1)	Atmospheric conditions (2)			Wind force (on the Beaufort Scale) (4)				
	Overcasting			0	1	2	3-6	7-12
	0°	1-8°	9-10°					
left-hand side section (5)	22	28	16	29	32	42	27	—
middle section (6)	61	38	33	51	32	0	0	—
right-hand side section (7)	17	34	51	20	36	58	73	—
the San (total) (8)	14	31	41	37	32	43	0	—
the Vistula (total) (9)	86	69	59	63	68	57	100	—

Table 8 presents the percentage distribution of the frequency of individuals in separate sections of the Vistula, and generally along the Vistula and the San, flying in various conditions of overcasting and different wind force.

An increasing degree of overcasting evidently affects the higher relative and absolute altitude of flights along the right-hand side section and along the San. The difference in the frequency of the right-hand side section between conditions of cloudless and overcast sky amounts to 34⁰/₀, and for the San respectively — 27⁰/₀.

Table 9. Dependence of *H. caspia* flight direction on the degree of overcasting (in per cent; $n = 73$).

Degree of overcasting (2)	Flight in direction (1)		
	0°	1-8°	9-10°
S	66	74	85
N	34	26	15

This increasing overcasting can have the following effect: a) Deterioration of visibility (fog, light rain) leading to lower flight-altitude (graph 26). Low flight-altitude limits the space orientation of birds, however not to a degree which would render the flight impossible. On the contrary — the data in Table 9 indicate that the more the sky is overcast, the more intensive are southward flights (cf. also Table 12). It seems possible that in more difficult conditions birds turn instinctively to the right-hand side section. b) A more overcast sky and NW winds are positively correlated (Atlantic low pressure areas). It follows from the data presented in Table 10 that, disregarding completely calm spells, the highest frequency was recorded when NW winds prevailed (21⁰/₀). Previously I have pointed out that Caspian Terns are very susceptible to wind force (cf. graphs 20, 21). In the case of NW winds birds are “pushed” to the right-hand side section by the wind; in NW winds 2-4° on the Beaufort Scale Caspian Terns often flew just above the surface of the water, however slightly shifted to the right. Thus when the sky is overcast on a windy day there is little chance of an active choice of the further route.

Table 10. Frequency of *H. caspia* during autumn migration in calm weather and for winds from different directions (in per cent; $n = 149$).

Conditions of flight (1)	Flight in calm weather (2)	Flight in winds from: (4)							
		N	NE	E	SE	S	SW	W	NW
Frequency in per cent (2)	40	6	0	10	3	11	5	4	21

The effect of wind itself should also be noted. As it follows from Table 8 an increase in wind force is followed by a relative increase in the frequency recorded for the right-hand side section. This increase is quite considerable — between 0° and 6° on the Beaufort Scale it amounts to 53%. The data presented in Table 11 explain why this can occur.

Table 11. Frequency of *H. caspia* as it depends on wind force and direction (in per cent; on the Beaufort Scale).

Wind direction (1)	Wind force (2)			
	2-3°	4°	5°	6°
NW (3)	42.4	30.3	6.1	3.0
Other directions (4)	15.1	—	3.1	—
Total (5)	57.5	30.3	9.2	3.0

This is evidently the result of the dominance of stronger winds from NW. However this does not lead to a proportional increase in the per cent of individuals penetrating the valley of the San. Up to 2° on the Beaufort Scale there is a small increase in the per cent of individuals preferring the San, but starting from 3° the preference of the San falls down to zero (Table 8). The reason for that is as follows: Caspian Terns in strong winds avoid, as a rule, flights in the direction of the wind (flights with the wind), and as the San at the mouth flows in direction NW, all birds turning to fly along the San would have to fly with the wind.

Summing up the following can be pointed out: 1) deterioration of weather conditions is accompanied by an increase in the frequency in the right-hand side section. This increase is mainly the result of the following two situations: a) deterioration conditions for orientation require from the birds to come closer together at the right-hand side bank in order not to miss a suitable branch of the route they have been following so far, being in line with the general direction of their migration, b) an increase in the frequency in the right-hand side section may be caused by the "mechanical" pushing of the birds by the prevailing north-western winds. 2) An increasing degree of overcasting can limit, by the deterioration of the visibility, the possibility of preference only in a small degree, and migrants can overcome this difficulty relatively easily, while on the other hand the increasing wind force, in view of its being parallel to the San leading to the necessity of flying with the wind, there is not much chance of active preference, and the migrants are forced to fly on along the

Vistula deviating to the south-west. 3) When weather conditions deteriorate the element of chance plays more important part in the choice of the further migration route.

Real chances of preference

As we already know the effect of atmospheric conditions on preference, let us consider now the part of Caspian Terns migrating in the region of the mouth in relatively favourable weather, i.e. when they do not have to overcome strong winds or fly in fog or rain. Such conditions are considered in columns (3) and (5) in Table 12.

Table 12. Weather conditions of *H. caspia* autumn migrations in the region of the mouth of the San ($n = 149$).

Weather characteristics	clouds (2-10°) wind (2-6°)	clouds (2-10°) no wind (0-1°)	no clouds (0-1°) wind (2-6°)	no clouds (0-1°) no wind (0-1°)
	(2)	(3)	(4)	(5)
Per cent of individuals migrating in a given type of weather (6)	26.4	52.7	1.1	19.8

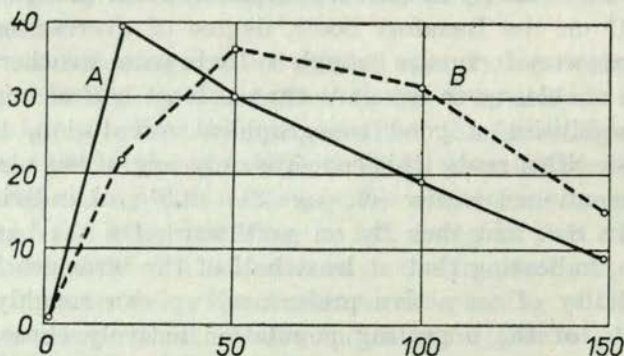
Thus 27.5% of Caspian Terns (columns (2) and (4)) migrate in decidedly bad weather conditions which not only require more effort on the part of migrants but also compel them to fly along the route not always confirmed by their instinct or individual experience. On the other hand, as it follows from Table 12 giving a rough estimate, more than 50% of Caspian Terns migrating along the Vistula fly in almost completely calm though cloudy weather (wind force 0-1° on the Beaufort Scale, degree of overcastening 2-10°), while only 20% of birds were fortunate enough to fly in calm weather with no clouds in the sky. This enables us to conclude that at least half of migrating Caspian Terns have possibilities of good topographical orientation, that is chances of preferring a specified route (this concerns only migrations observed in 1961).

As I have mentioned earlier (cf. page 31) 49.5% of individuals turn into the valley of the San and then fly on southward. On the basis of the facts discussed above, indicating that at least half of the birds reaching the mouth have the possibility of an active preference, we can roughly estimate that on average, 25% of the migrating population actively chose the San route (the other 25% could penetrate the valley of this river on the basis of the "security" mentioned above (cf. page 37), or alternatively on the basis of an "error"). Comparing this estimate with the data presented in Table 6 (columns (9) and (10)) and assuming that all the individuals from the middle and left-hand side sections of the Vistula chose actively the San (cf. page 35), while

those from the right-hand side section reached this river "mechanically", results coinciding with each other can be obtained: 24.7% of the population turned into the valley of the San from the middle and left-hand side sections of the Vistula. Thus about 25% of the population also chose actively the route of migrations along the Vistula, or those from the right-hand side section preferred the San. In the first case the motives of such a choice contrasting with the general tendency become obvious when we take into account the fact that at the end of August a number of sand waves and shallow patches appeared near the mouth as a result of the drop in water level, and the river became considerably narrower.

Flight-altitude and the choice of route

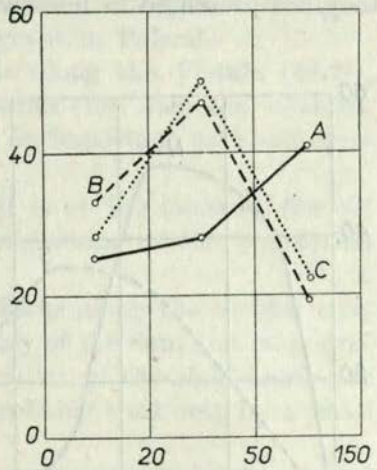
Previously I have shown (cf. page 20, Table 2) that the effect of flight-altitude on the preference of the San route is not very significant (at $df = 3$, $\chi^2 = 7.26$, $P = 0.07$). An analysis of the average flight-altitude (Table 7) reveals closer aspects of this dependence — the lower the flight-altitude in the right-hand side section, the greater the chance of migrating along the San and the smaller the chance of preferring the Vistula. The reverse situation exists in the middle and right-hand side sections: the lower the flight-altitude, the more probability of continuing the migration along the Vistula and less probability of reaching the valley of the San. As the problem in question is the definition of factors affecting the choice of migration route, let us consider now the altitude of flight according to the conclusion following from the data presented in Table 7. Thus when we calculate χ^2 excluding the right-hand side section of the Vistula (i.e. the one from which Caspian Terns reach the San on the basis of "error"), the effect of flight-altitude in the middle and left-hand side sections on the choice of the San route will turn out to be quite



Graph 25. Flight-altitude and the preference of the San route or the Vistula route (1961, the San — the Vistula). The vertical axis — per cent of recordings in relation to their total number recorded for the given route; the horizontal axis — flight-altitude in metres; A — flight-altitude of individuals flying along the Vistula higher from the mouth of the San; B — flight-altitude of Caspian Terns which preferred the San route.

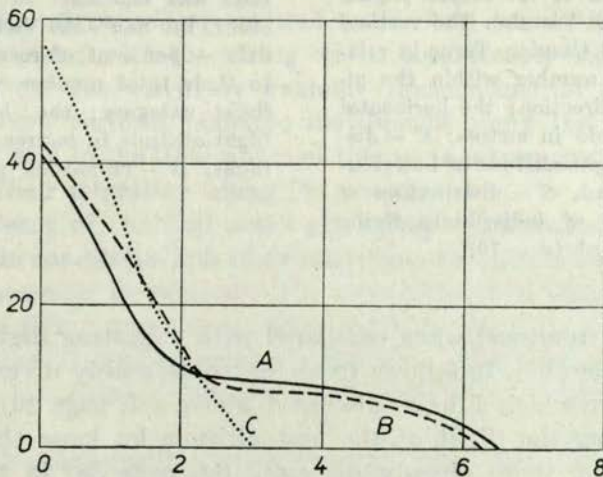
significant (at $df = 1$, $\chi^2 = 4.03$, $P = 0.04$). The distribution of the flight-altitude of Caspian Terns preferring the San and those flying on along the Vistula (graph 25) is also characteristic.

A high flight-altitude, besides giving security to migrants (essential is here the range of the sporting gun), can also enable the best orientation faci-



Graph 26. Effect of overcasting on the flight-altitude of *H. caspia* (1961, the San - the Vistula). The vertical axis - per cent of recordings in the given state of overcasting; the horizontal axis - flight-altitude in metres; A - distribution of flight-altitude in cloudless weather (overcasting 0), B - when degree of overcasting is 1-8°, C - when the sky is completely overcast (degree of overcasting 10°).

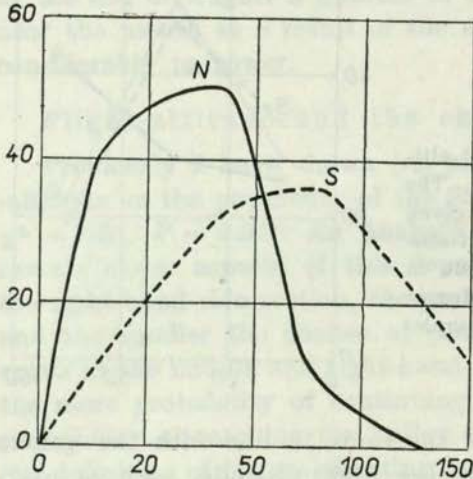
tating at the right moment the choice of the route in line with the general direction of migration. Besides factors limiting flight-altitude, such as overcasting (graph 26) and wind (graph 27), an important part is played by fac-



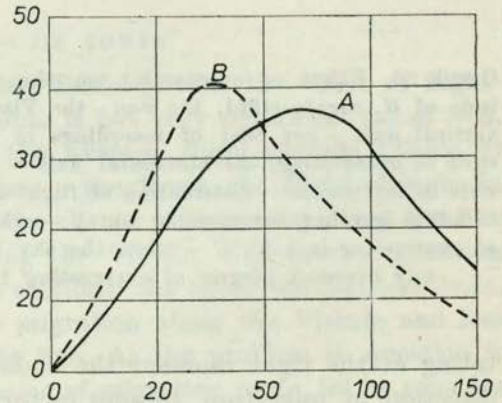
Graph 27. Effect of wind force on *H. caspia* flight-altitude (1961, the San - the Vistula). The vertical axis - per cent of recordings in relation to their number recorded within the given altitude category; the horizontal axis - wind force on the Beaufort Scale; A - distribution of frequency of recordings in the case of Caspian Terns flying at the altitude of 20 m, B - flying at the altitude of 21-50 m, C - at the altitude of 51-150 m.

tors connected with the biology and flock structure of the species (cf. Tables 2 and 4, graphs 15, 22, 25, 28, 29). From the point of view of the biological functionality the importance of sustaining a high flight-altitude in the course of migration becomes evident in the light of the facts cited.

Differences in the altitude of flights when searching for food (in graph 28 they are presented as northward flights, while in graph 29 they are described



Graph 28. Interrelationship between altitude and direction of *H. caspia* flights (1961, the San - the Vistula). The vertical axis - per cent of Caspian Terns in relation to their total number within the given category of direction; the horizontal axis - flight-altitude in metres; *N* - distribution of the flight-altitude of individuals flying northward, *S* - distribution of the flight-altitude of individuals flying southward ($n = 70$).



Graph 29. Interrelationship between altitude and character of *H. caspia* flights (1961, the San - the Vistula). The vertical axis - per cent of recordings in relation to their total number within the given flight category; the horizontal axis - flight-altitude in metres; *A* - straight-line flight, *B* - circuitous penetrating flight.

as penetrating, circuitous) when compared with migrating flights are clear-cut and quite considerable. It follows from the considerably diversified character of their function which I have discussed above (cf. page 20). Hence all the factors hampering the flight at the best altitude let loose the compensating mechanisms - e.g. those already discussed (cf. page 38) in the case of bad visibility and strong wind, that is the fact of keeping to the right-hand side bank. Most probably there are also other mechanisms which enable, in unfavourable conditions, to eliminate the role of accident and make possible the preference according to the instinct in the critical moments of migration (e.g. forking of the route), or according to individual experience.

CONCLUSIONS

1. As a result of the expansion of the Caspian Tern over the north-eastern regions of the Baltic and a general numerical increase of the Baltic population, the species has become more popular in Poland after 1930, while a sudden increase in its frequency has been recorded since 1950 in the period of migrations — *H. caspia* has become a regular transmigrant in Poland.

2. The main migration route in Poland leads along the Vistula (48.7% of the recordings) and its right-hand side tributaries (the San, the Wisloka, the Dunajec). The Bug and the Oder do not play an important part as migration routes.

3. Although the role of transcontinental flights is on the increase, the old maritime route still retains its importance in migrations of the population investigated.

4. The Carpathian arc is skirted by Caspian Terns along the eastern side, they reach the valley of the Dniester from the valley of the San, and most probably it is crossed in its middle part along the valley of the right-hand side tributaries of the Vistula. The Moravian Gate is probably used only by a small per cent of Caspian Terns.

5. Numerical proportions of recordings in separate seasons in the annual cycle give an idea of the general ecological situation, the productivity of the population in their breeding sites in particular.

6. The spring migration across the southern regions of Poland is swifter and brisker than across the northern regions.

7. The autumn migrations are carried out in two waves. The rate of this migration as compared with the spring one is considerably retarded. Caspian Terns flying in the 1st wave are evident transeontinental migrants. Birds from the 2nd wave perform nomadic movements along the Polish coast in the initial phase, and in the final phase of this wave a large per cent of Caspian Terns continue their migration along the sea coast.

8. Caspian Terns of the 2nd wave migrating transeontinental along rivers can in certain conditions halt their migration for quite a long time carrying out only local nomadic movements. The population migrating across Poland in August beside flying southward carries post-breeding nomadic movements, while in September *H. caspia* appears only as a transmigrant.

9. *H. caspia* has started summering at the Polish coast without nesting only since 1950.

10. Statistical characteristic features of the phenology of migration (average dates, standard deviations, etc.) can be treated as significant, relatively permanent features of the population investigated.

11. Migrations of Caspian Terns along the river courses can be carried out as long as the width of the river is sufficient (it can not be narrower than 60-70 m). Decisive here is the security factor dependent on the possibility of space con-

trol, and the radius can not be shorter than the distance of flight of adult individuals characteristic for the species investigated.

12. Once the river gets narrower than this critical width, it is no longer used by the species. Until a new river is encountered (or alternatively a coastline) which will lead the birds, the general, characteristic for the species, direction is maintained. They search for food then on accidentally encountered water bodies (ponds, lakes) or stop temporarily there.

13. In the daily cycle of *H. caspia* migrations three peaks of locomotoric activity can be observed as closely connected with the specific character of its biological function.

14. The morning peak of activity is a result of the overlapping of two types of activity: searching for food and migration proper. Both these types, however, are temporally and functionally separate.

15. The afternoon peak is connected exclusively with searching for food.

16. The pre-evening peak can be described as purely migrational activity.

17. Separate elements of activity form an optimal sequence in the daily cycle which can secure a high degree of survival in an unknown area. The general scheme looks as follows: each searching for food is preceded by a prolonged reconnaissance (penetration) and when their hunger is satisfied it is followed by a rest combined with the next round of reconnaissance.

18. When they carry out their nomadic movements, the general picture of activity remains the same — instead of the phase of migrational flight the period of food-searching is respectively longer.

19. The migrational flight is performed at a higher altitude than food-searching. In the daily cycle it is carried out twice: in the late morning hours and before the evening. Nocturnal migrations of Caspian Terns are not very rare.

20. Flight-altitude depends on its functional character. Straight-line flight, migrational, is performed at a high altitude; food-searching, circuitous flight is carried out at a middle and low altitude.

21. The majority of Caspian Terns are paired off already in the course of spring migrations. The autumn migration is performed in groups of 2-4 individuals.

22. Flock connections in *H. caspia* are less permanent and evident than in other Tern species.

23. The average flock-size during spring migrations, as well as during the autumn migrations in the northern regions of Poland, is higher than in the south. This is connected with: a) initial gathering of birds prior to forming breeding colonies, b) formation of larger aggregations in places favourable for food-searching and resting.

24. The highest degree of flock integration is observed in the moments of danger (migrations proper, roosting). Maximum dispersion is allowed in reconnoitred areas.

25. Irregularities in the rhythm of flock-structure changes in their daily cycle are particularly inconvenient for the species in the period of migration. Of the factors causing these irregularities the effect of strong winds is the foremost one. Other meteorological factors do not show any significant effect.

26. A close positive correlation can be recorded between the flock-size and flight-altitude and its southward course (in the case of autumn migrations). This indicates that Caspian Terns carry out their migrations only in groups.

27. Flock-structure and family connections in the day-time undergo definite changes. They depend closely on the function of food-searching, migrations proper and, first of all, on the fact of securing a high degree of safety for each of the individuals.

28. Family connections between parents and young Caspian Terns are kept up in the entire period of migration and seem to be maintained also after reaching the winter sites. In the daily cycle they are revealed only during the migration proper.

29. The biological idea of maintaining family connections in the post-breeding periods consists in the use of adult experience by young individuals when flying over unreconnoitred areas. Owing to that the mortality of Caspian Terns in their first year of life is small, and for instance twice lower than in the case of larger species which form flocks differing in age. Thus the role of feeding up juveniles is in the case of the species investigated less important.

30. During nomadic movements family connections are loosened, and the dispersion of young individuals increases.

31. In the daily cycle dispersion increases from the morning hours until the afternoon break. In the second half of the day the opposite tendency comes to the front, i.e. integration tendencies.

32. Migrational navigation of Caspian Terns depends to a considerable extent on the use of the so called lines with fixed direction, such as rivers and coastlines. In critical points, at the river mouths and forks, the choice of the proper route decides the future course of migration and the fate of the migrants. Each act of choice beside being the result of individual motivation, depends also on the environmental factors at the time of the migration.

33. The autumn migration at the mouth of the San discussed above, showed that half of the Caspian Terns there had good conditions for space orientation, and thus had possibilities for choosing the right route. About one fourth of the population actively preferred the San.

34. Factors hampering the possibility of preference prepare the ground for compensating mechanisms enabling the passive choice of the right route at critical points (flight along the right-hand side of the Vistula and choice of the San route).

35. Strong NW winds (stronger than 2-3° on the Beaufort Scale) prevailing in the period of migrations are the most important factor lowering the chances

of an active preference. In some situations they can make the preference of the right route quite impossible.

36. In the light of the material analysed it seems not very probable for even older birds with considerable experience to follow the same route every year. The course of the migration, beside depending on individual motivation, is the result of external factors being in force at the time.

REFERENCES

- AUMÉES L. 1961. Novye dannye o gnezdovanii krački-čegravy na ostrovach proliva Muchuviajn. Orn. Kogum., Tartu, 2.
- BANCKE P., BERGMAN G. et al. 1960. Nordens fugle i farver. 4, Skandinavisk Bogforlag.
- BERGMAN G. 1953. Verhalten und Biologie der Raubseeschwalbe (*Hydroprogne tschegrava*). Acta Zool. fenn., Helsingfors, 77.
- BIELEWICZ M. 1948. Egzotyczny gość. Łowiec pol., Warszawa, 11.
- BIELEWICZ M. 1949. Rzadki gość. Wszechświat, Kraków, 1 (1784).
- BIEŃ Z., DOBROWOLSKI K. A., SKOCZYŁAS R. 1961. Przyczynek do znajomości awifauny Półwyspu Helskiego. Przegl. zool., Wrocław, 5, 2.
- BUSSE P., JABŁOŃSKI B. 1964. Letnie obserwacje ptaków na Mewiej Rewie (Zatoka Pucka). Materiały do awifauny Polski. II. Acta orn., Warszawa, 8, 7.
- CURRY—LINDAHL K. 1960. Våra Fåglar i Norden. 2, Stockholm.
- CZARNECKI Z. 1962. Ptaki jeziora Gopło. Acta orn., Warszawa, 6, 11.
- CZARNECKI Z. 1963. Stan badań nad ornitofauną Wielkopolski. Bad. fizjogr. Pol. Zach., Poznań, 12.
- DOBROWOLSKI K. A. 1959a. Badania rytmu dziennego pewnych gatunków ptaków wodnych. Ekol. pol. ser. A, Warszawa, 7, 2.
- DOBROWOLSKI K. A. 1959b. Pierwsze obserwacje ekologiczne awifauny Półwyspu Helskiego i Zatoki Puckiej. Ekol. pol., Warszawa, ser. B, 5, 1.
- DOBROWOLSKI K. A. 1964. Studies on ecological adaptations of birds of the Vistula River. Ekol. pol., Warszawa, ser. A, 12, 33.
- DOBROWOLSKI K. A. (in press). Występowanie rybitwy wielkodziobej, *Hydroprogne caspia* (PALL.) w Polsce w ostatnich 150 latach. Acta orn., Warszawa.
- DOMANIEWSKI J. 1921. Fauna ornitologiczna dorzecza Wisły. Warszawa.
- DUNAJEWSKI A. 1938. Fauna słodkowodna Polski. Ptaki. 3. Warszawa.
- DYRCZ A. 1963. *Hydroprogne caspia* (PALL.). Materiały do awifauny Polski. Acta orn., Warszawa, 7, 9.
- DYRCZ A., TOMIAŁOJĆ L. 1967. Obserwacje ornitologiczne nad dolnym Bugiem. Materiały do awifauny Polski IV. Acta orn., Warszawa, 10, 2.
- FERIANC O. 1950. Tah čegravy veľkozobej (*Hydroprogne t. tschegrava* LEP.) cez Slovensko. Sylvia, Praha, 11/12, 3.
- FERIANC O. 1964. Stavovce Slovenska II. Vtáky I. Bratislava.
- FALTER A. 1940. Raubseeschwalbe bei Swinemünde. Orn. Monatsb., Berlin, 48, 6.
- HORNBERGER F. 1943. Ueber Ereignisse in der Vogelwelt. Vogelzug, Berlin, 14, 4.
- IBARTH A. 1923. Raubseeschwalben an der Danziger Bucht. Orn. Monatsb., Berlin, 31, 2.
- JÓZEFIK M., SWIRSKI Z. 1961. Rzadkie gatunki *Laro-Limicolae* jeziora Kruklin (Pojezierze Mazurskie). Acta orn., Warszawa, 6, 7.
- JURCZYK A. 1959. Ogólna charakterystyka awifauny środkowej Wisły i przegląd sześciu wybranych gatunków (tezy). Zjazd. Anat. Zool. pol., Kraków.

- KOZŁOWSKI J. M. 1967. Ptaki wodne na Wiśle pod Krakowem w latach 1962–1965. Materiały do awifauny Polski IV. Acta orn., Warszawa, **10**, 2.
- KUMARI E. 1958. Visible migration in the East Baltic area. Ibis, London, **100**, 4.
- LEWANDOWSKI A. A. 1964. Ptaki jeziora Mamry Północne (pow. Węgorzewo). Acta orn., Warszawa, **3**, 5.
- LUNIAK M. 1963. Badania nad dynamiką, liczebnością i kierunkami lotów niektórych gatunków *Laridae* na Wiśle pod Warszawą. Acta orn., Warszawa, **7**, 4.
- LUNIAK M. 1964. Ptaki spotykane na Wiśle między Krakowem a ujściem Sanu w końcu kwietnia 1963 roku. Materiały do awifauny Polski II. Acta orn., Warszawa, **3**, 7.
- LUNIAK M., KALBARCZYK W., PAWŁOWSKI W. 1964. Ptaki Warszawy, Acta orn., Warszawa, **3**, 6.
- LÜTTSCHWAGER H. 1926. Ornithologische Beobachtungen im Danziger Gebiet. Orn. Monatsb., Berlin, **34**, 2.
- MATOUŠEK B. 1958. Výskyt niektorých vzácných druhov vtákov na Slovensku. Prir. Sbor. Slov. Muz., Bratislava, **4**, 33.
- MAYAUD N. 1956. Etude sur la migration et les zones d'hivernage des Sternes Caspiennes, *Hydroprogne caspia* (PALLAS) d'Eurasie. Alauda, Paris, **24**, 3.
- NIKŁUS M. Ju. 1959. Gnezdowanie i perelet krački-čegravy v Estonskoj SSR. Tr. 3-j Pribalt. Orn. Konf., Vilnius.
- PRESTON F. 1966. The mathematical representation of migration. Ecology, Brooklyn, Lancaster, Durham, **47**, 3.
- ROBIEN P. 1936. Brutstudien an pommerschen Vögeln. Orn. Monatsb., Berlin, **44**, 5.
- ROOTSMJAE L. G. 1959. Osenniaja migracija vodianych i pribrežnych ptic na severo-zapadnom poberez'e Čudskogo ozera v 1954–1956 gg. Tr. 3-j Pribalt. Orn. Konf., Vilnius.
- SCHÜZ E. 1941. Raubseeschwalben (*Hydroprogne tschegrava*) als Fernwanderer. Vogelzug, Berlin, **12**, 1.
- SHEVAREVA T. P. 1962. Novye dannye o vstrečach okolecovannyh čegrav (*Hydroprogne tschegrava* LEPECHIN). Migracii životnych, Moskva, **3**.
- SOKOŁOWSKI J. 1958. Ptaki Ziemi Polskich. vol. 2, Warszawa.
- SWIRSKI Z. 1959. O niektórych morskich gatunkach ptaków przenikających doliną Wisły w głąb lądu (tezy). Zjazd Anat. Zool. pol., Kraków.
- SWIRSKI Z. 1964. O niektórych morskich gatunkach ptaków przenikających doliną Wisły w głąb lądu. Notatki orn., Warszawa, **5**, 2–4.
- TACZANOWSKI W. 1882. Ptaki krajowe. vol. 2, Kraków.
- TACZANOWSKI W. 1888. Spis ptaków Królestwa Polskiego. Pam. Fizyogr. Warszawa, **8**.
- TISCHLER F. 1941. Die Vögel Ostpreussens. **2**, Königsberg — Berlin.
- TOMIAŁOJC L. 1967. *Hydroprogne caspia* (PALL.). Materiały do awifauny Polski IV. Acta orn., Warszawa, **10**, 2.
- URBAŃSKI J. 1956. Rybitwa wielkodzioba na Pomorzu Zachodnim. Chrońmy Przyr. ojez., Kraków, **12**, 5.
- WOLK K. 1958. Badania ornitologiczne na wyspie Wolin ze szczególnym uwzględnieniem terenu projektowanego Parku Narodowego. Przyr. Polski Zach., Poznań, **1**, (3).
- ZAJĄC R. 1960. Obserwacje ornitologiczne z Jeziora Resko Przymorskie. Przyr. Polski Zach., Poznań, **4**, 1–4.
- ZAJĄC R. 1964. O niektórych rzadszych gatunkach awifauny ujścia Wisły pod Gdańskiem. Część I. Acta orn., Warszawa, **3**, 8.

Accepted for publication 10 XII 1969

Author's address: Instytut Zoologiczny PAN,
Warszawa, ul. Wilcza 64.

STRESZCZENIE

Praca oparta jest na analizie 423 spotkań rybitwy wielkodziobej, *Hydroprogne caspia* (PALL.) z obszaru Polski pochodzących z lat 1800–1966. Z tej liczby 28,4% spotkań, to materiał zebrany przez autora w latach 1960–1966 w środkowym i dolnym biegu Sanu oraz środkowym Wisły. Udział publikowanych danych wyłonionych z piśmiennictwa stanowi 23,9%, materiał udostępniony autorowi przez kolegów—ornitologów do wykorzystania statystycznego obejmuje 47,7% ogółu danych. Podstawowym założeniem pracy jest opracowanie ważniejszych zagadnień biologii i charakteru wędrówek omawianego gatunku w Polsce w aspekcie zmian: a) sekularnych, jakie populacja bałtycka przeżywała w ostatnich dwóch stuleciach, b) w aspekcie zmian obyczajów związanych z wędrówką transkontynentalną. Prócz tego szerzej rozważany jest nowy problem — wpływ czynników zewnętrznych na preferowanie określonego szlaku i przestrzenny przebieg wędrówki.

W zwięzłym zarysie badań w okresie po II wojnie światowej autor uwytknęła istotne, poznane dotychczas momenty biologii rybitwy wielkodziobej (pełny szkic historii badań oraz analiza zoogeograficzna występowania podane zostaną w opracowaniu DOBROWOLSKIEGO (w druku). W podrozdziale poświęconym metodyce autor podkreśla, iż do zagadnień biologii zbierano materiał według specjalnego zaprogramowania (każda obserwacja zawierała dane dotyczące 14 różnych parametrów). W tym celu w okresie sierpień–wrzesień 1961 oraz w kwietniu 1963 przy ujściu Sanu do Wisły (mapa 1) prowadzono „non stop” w godzinach 4⁰⁰–20³⁰ obserwacje nad przelotami notując wspomniane dane na specjalnych kartach (w sumie 546 godzin obserwacji).

W rozdziale poświęconym charakterowi występowania w Polsce autor zaznacza, że w aspekcie faunistycznym występowanie to zaczęło zyskiwać na znaczeniu po 1930 roku (do 1930 roku zanotowano jedynie 5,43% ogółu spotkań). Do 1950 roku przybywa 8,04% dalszych spotkań. Dopiero w latach 1950–1960 następuje gwałtowny wzrost frekwencji — *H. caspia* staje się regularnym w Polsce transmigrantem. Zjawisko to pozostaje w ścisłym związku z ogólną ekspansywnością populacji bałtyckiej w kierunku północno-wschodnich regionów Bałtyku oraz ogólnym jej wzrostem ilościowym. Dynamikę frekwencji w Polsce ilustrują wykresy 1, 2. Głównym szlakiem wędrówki w Polsce jest Wisła (48,7% spotkań krajowych) oraz jej prawobrzeżne dopływy (San, Wisłoka, Dunajec). Bug oraz Odra nie odgrywają istotnej roli jako szlaki wędrówkowe. Autor zauważa, że jakkolwiek rola przelotów transkontynentalnych stale wzrasta, stary szlak morski odgrywa nadal istotną w wędrówkach rolę. Łuk Karpat omijany jest przez rybitwę wielkodziobą od strony wschodniej — przenikanie z doliny Sanu do doliny Dniestru oraz pokonywany prawdopodobnie w części zachodniej dolinami dopływów Wisły. Bramą Morawską przelatuje prawdopodobnie znikomy tylko odsetek rybitw.

W rozdziale poświęconym frekwencji w cyklu rocznym autor stwierdza, że proporcje ilościowe spotkań w poszczególnych sezonach w cyklu rocznym dają pogląd na ogólną sytuację ekologiczną, szczególnie zaś na produktywność populacji na łęgowskich. Przelot wiosenny jest szybki i zdecydowany (średnia ogólnokrajowa — 25 kwietnia), na południu Polski przebiega szybciej, niż w regionach północnych (wykr. 3). Wędrówka jesienna odbywa się w dwóch falach. Tempo tej wędrówki w porównaniu z przelotem wiosennym jest znacznie bardziej wolne (wykr. 4). Rybitwy lecące w pierwszej fali są zdecydowanie migrantami transkontynentalnymi. Ptaki z drugiej fali w początkowej fazie zatrzymują się u wybrzeży polskich na koczowiska; w końcowej fazie tej fali znaczny odsetek wędruje wzdłuż wybrzeży morskich. Wędrujące transkontynentalnie wzdłuż rzek rybitwy drugiej fali mogą w określonych warunkach na dłuższy nawet czas całkowicie wstrzymać przelot wykazując jedynie lokalne ruchy żerowiskowe. O ile przez cały sierpień przelatująca przez Polskę część populacji na równi z wędrówką odbywa koczowiska polegowe, o tyle we wrześniu *H. caspia* występuje w Polsce wyłącznie w roli migranta. Różnice, jakie zachodzą w przelocie jesiennym przez północne i południowe części kraju uwidocznione są na wykresach 5, 6. Na północy kraju przeloty *H. caspia* w szerokiej mierze łączą się z koczowiskami polegowymi oraz spędzaniem lata. W południowych regionach badany gatunek występuje głównie jako transmigrant, chociaż tzw. stacjonowanie koczowiskowe w dogodnych biotopach nie należy do rzadkości (wykr. 7). Spędzanie bez gnieźdzenia się miesiące letnich — wykr. 10 rybitw u wybrzeży polskich notowane jest dość wyraźnie dopiero po 1950 roku. Statystyczną charakterystykę fenologii przelotów (średnie daty, odchylenia standardowe itd. — tab. 1) można uważać za istotne, względnie stałe cechy badanej populacji.

W kolejnym rozdziale analizowana jest rytmika aktywności dobowej. Autor wyróżnia 3 szczyty aktywności lokomotorycznej wiążącej się ściśle z określonym charakterem jej biologicznej funkcjonalności (wykresy: 11, 12). Poranny szczyt (8⁰⁰–9⁰⁰) utworzony jest w wyniku nakładania się dwóch typów aktywności: żerowania oraz właściwego lotu wędrówkowego. Obydwa te typy są jednak czasowo i funkcjonalnie odrębne. Południowa diapauza trwa od 11⁰⁰ do 13⁰⁰ (południe kraju) oraz do 14⁰⁰ na wybrzeżu. Szczyt popołudniowy (14⁰⁰–16⁰⁰) wiąże się wyłącznie z żerowaniem, podczas gdy na szczyt przedwieczorny (18⁰⁰–20⁰⁰) składa się aktywność prawie wyłącznie wędrówkowa. Autor podkreśla, iż funkcjonalny charakter aktywności poszczególnych szczytów mógł być ustalony jedynie na podstawie analizy zmieniających się w cyklu dobowym elementów behawioru (wykresy: 13–17). Szczególnie przydatne jest tu badanie (test χ^2) współzależności wysokości lotu oraz innych jego parametrów (kierunkowość N–S, liniowość — tab. 2). Autor udowadnia, że poszczególne elementy aktywności tworzą w cyklu dobowym ściśle określoną sekwencję, zapewniającą optymalnie w nieznanym terenie wysoką przeżywalność. W ogólnym schemacie przedstawia się ona następująco: każde żerowanie poprzedzane

jest długim rozpoznawaniem bezpieczeństwa żerowiska (penetracja), każdy przelot wędrowski następuje po zaspokojeniu głodu i zakańcza się odpoczynkiem sprężniętym z kolejnym rozpoznawaniem nowego żerowiska. Przelot wędrowski przebiega na kilkakrotnie wyższym pułapie lotu niż żerowanie. W cyklu dobowym podejmowany jest z reguły dwukrotnie: w późnych godzinach porannych oraz przedwieczornych. Wędrowki nocne nie należą do rzadkości. Wysokość lotu uzależniona jest od jego funkcjonalnego charakteru — lot prostoliniowy (wędrowski) przebiega na wysokim pułapie, podczas gdy penetrujący, krzywoliniowy (żerowiskowy) odbywa się na średniej i małej wysokości. Odnośnie cyklu dobowego podczas stacjonowania koczowiskowego autor zauważa, iż ogólny schemat aktywności nie ulega zmianie — zamiast fazy przelotu odpowiednio przedłuża się czas żerowania.

W rozdziale dotyczącym struktury stadnej, powiązań rodzinnych i przeżywalności w okresie wędrowek autor stwierdza, że prawdopodobnie większość rybitw podczas przelotu wiosennego rozbita jest już na pary. Przelot jesienny odbywa się w grupach 2–4 osobniki (tab. 3). Przeciętna wielkość stada podczas przelotu wiosennego, jak również jesiennego w północnych regionach Polski jest większa, niż na południu. Wiąże się to z: a) wstępnym zrzeszaniem się ptaków przed utworzeniem kolonii lęgowych, b) z tworzeniem w dogodnych pod względem żerowiskowym oraz wypoczynkowym miejscach na wybrzeżu większych agregacji. Powiązania stadne u *H. caspia* są mniej trwałe oraz mniej wyraziste, niż wśród mniejszych gatunków rybitw. Między wielkością stada a wysokością lotu oraz ukierunkowaniem na południe (w przypadku wędrowki jesiennej) zachodzi dość ścisła zależność (wykresy: 22, 23). Świadczy to, iż rybitwy właściwej wędrowki dokonują jedynie w grupach. Struktura stadna i powiązania rodzinne w ciągu dnia podlegają określonym zmianom. Ścisłe podporządkowane są one funkcji żerowania, właściwego przelotu wędrowskiego a przede wszystkim zapewnieniu każdemu z osobników maksymalnego bezpieczeństwa. Szczególną uwagę zwraca autor na zagadnienia utrzymywania przez badany gatunek koneksji rodzinnych podczas wędrowek. Są one podtrzymywane przez cały okres wędrowski i trwają najprawdopodobniej do przylotu na zimowiska. W cyklu dobowym przejawiają się wyłącznie podczas właściwego przelotu wędrowskiego (wykr. 18). Sens biologiczny utrzymywania więzi rodzinnych przez czas dłuższy po okresie lęgowym polega na korzystaniu przez osobniki młodociane z doświadczenia osobniczego ptaków dorosłych podczas przebywania w terenie niespenetrowanym. Dzięki temu śmiertelność w pierwszym roku życia rybitw wielkodziobych jest nieznaczna (26%) i np. o połowę niższa, niż u gatunków większych, lecz tworzących odrębne pod względem wieku stada. Rola dokarmiania młodych ma więc znaczenie drugorzędne. Podczas stacjonowania koczowiskowego więzi rodzinne słabną, zwiększa się natomiast dyspersja osobników młodocianych (wykr. 19). Rozpatrując związki przyczynowe między strukturą stadną a przeżywalnością, autor udowadnia, iż maksymalny stopień zintegrowania stadnego obserwuje się w mo-

mentach największego zagrożenia (właściwy przelot wędrownkowy, przebywanie na noclegowiskach). W terenie spenetrowanym dochodzi do największej dyspersji. Decydującymi dla przeżywalności są dwa momenty: a) rozpoznawanie w nowym terenie marginesu bezpieczeństwa (zasadniczą rolę odgrywa tu doświadczenie osobnicze ptaków rodzicielskich), b) efektywność tego bezpieczeństwa rzutująca na możliwość dyspersji i maksymalnego wykorzystania środowiska pod względem troficznym (zasadniczą rolę odgrywa tu nasilenie czynnika antropogenicznego). Zachowanie odpowiedniej struktury socjalnej w cyklu dobowym pozwala migrantom względnie szybko i sprawnie spenetrować nowy teren a w konsekwencji wykorzystać go troficznie. Zakłócenia rytmu zmian struktury stadnej w cyklu dobowym są więc dla gatunku w okresie wędrowek szczególnie niekorzystne. Z czynników zakłócających na plan pierwszy wysuwa się wpływ silniejszych wiatrów (wykresy: 20, 21). Inne czynniki meteorologiczne nie wykazują istotnego wpływu. Ogólnie, w cyklu dobowym obserwuje się narastającą od wczesnych godzin porannych aż do diapauzy południowej dyspersję. W drugiej połowie dnia występuje tendencja przeciwna tj. dążność do integracji. Autor wyróżnia 4 stopnie zintegrowania stadnego wśród *H. caspia* (tab. 5). Najsilniej powiązane są ze sobą ugrupowania rodzinne; najslabiej — typowe agregacje tworzące się w miejscach wypoczynkowych.

Przedostatni rozdział poświęcony jest zagadnieniom wpływu czynników środowiskowych na przestrzenny przebieg wędrownki. Na podstawie analizy zebranego według specjalnego zaprogramowania materiału z rejonu ujścia Sanu oraz ogólnych danych z obszaru całej Polski autor dochodzi do przekonania, że: a) nawigacja wędrownkowa rybitwy wielkodziobej w znacznej mierze opiera się na wykorzystywaniu tzw. linii ukierunkowujących, jakimi są wybrzeża morskie oraz rzeki. W punktach krytycznych przy ujściach rzecznych (rozwidlanie się szlaku) wybór właściwej drogi rzutuje zasadniczo na dalszy przebieg wędrownki oraz losy migrantów. Każdorazowy akt wyboru określonej trasy uzależniony jest, poza motywacją wewnętrzną, od aktualnie oddziaływujących czynników środowiskowych; b) wędrownki badanego gatunku wzdłuż linii rzek mogą odbywać się jedynie do momentu, gdy szerokość rzeki jest jeszcze względnie dostateczna (lustro wody nie węższe, niż 60–70 m). Decydującą rolę odgrywa tu czynnik bezpieczeństwa uwarunkowany możliwością kontroli przestrzeni o promieniu prawdopodobnie nie mniejszym, niż charakterystyczny dla badanego gatunku dystans ucieczki osobników dorosłych; c) z chwilą zwężenia się rzeki poniżej tej krytycznej szerokości, rybitwy porzucają ją. Do chwili odnalezienia nowej rzeki (względnie wybrzeża), stanowiącej nową linię ukierunkowującą, zachowują podczas przelotu ogólny charakterystyczny dla gatunku kierunek. Żerują wówczas, względnie stacjonują, na większych zbiornikach napotykanym przygodnie. Za bardzo istotny moment rzutujący na całokształt wędrownki uważa autor problem preferowania przez migrantów określonego szlaku. W związku z tym koncentruje się on na: a) ustaleniu kryteriów wykrywalności preferencji, b) charakterystyce ilościowej zjawiska oraz

c) przebadaniu czynników limitujących szanse preferowania. Za bezsporne fakty preferencji trasy „San” przyjmuje autor obieranie koryta tej rzeki przez osobniki lecące środkowym oraz lewym sektorem Wisły (24,7% ogółu przelatującej populacji) (tab. 3). Na ilościowy aspekt zjawiska rzutuje wysokość lotu (tab. 7, wyk. 25), od której uzależniony jest stopień orientacji przestrzennej a zatem szansa preferowania właściwej trasy. Do czynników najbardziej obniżających szanse aktywnego preferowania określonego szlaku należą dominujące (w przypadku przelotu jesiennego) silniejsze wiatry NW (powyżej 2–3° Beauforta) (tabele: 8–11; wykresy: 26–27). W niektórych sytuacjach mogą one zupełnie uniemożliwić preferowanie właściwej trasy. Sądząc z przykładu wędrówki jesiennej w rejonie ujścia Sanu (wykr. 24), z górą połowa rybitw miała dobre warunki atmosferyczne dla orientacji przestrzennej, a więc nie była pozbawiona możliwości obrania szlaku zgodnego z motywacją wewnętrzną (tab. 12). Czynniki zakłócające możliwość preferencji wyzwalają działanie mechanizmów kompensacyjnych pozwalających w punktach krytycznych na bierne obieranie właściwej drogi (lot prawym sektorem Wisły). W dalszej części rozdziału autor szczegółowo analizuje zależność szans preferencji od wysokości lotu (wykresy: 25–29), dochodzi do wniosku, iż czynniki kształtujące tę wysokość faktycznie wspomniane szanse limitują. W końcowej konkluzji autor podkreśla, iż w świetle przeanalizowanych materiałów wydaje się mało prawdopodobne, by nawet ptaki starsze, posiadające znaczne doświadczenie osobnicze, mogły co roku odbywać wędrówkę ściśle tą samą trasą. Przestrzenny przebieg wędrówki, prócz ogólnie ukierunkowującej motywacji wewnętrznej, kształtowany jest przez oddziaływanie w każdym momencie konkretnych czynników zewnętrznych.

Objaśnienia do wykresów, mapy i tabel:

Wykres 1. Rozkład spotkań *H. caspia* w Polsce w ostatnich 100 latach. Oś pionowa — liczba spotkań w procentach w stosunku do ogólnej ich liczby w każdej kategorii; oś pozioma — lata; A — północna część Polski; B — południowa część Polski; C — ogólny dla Polski rozkład spotkań ($n = 423$).

Wykres 2. Rozkład spotkań *H. caspia* w Polsce w poszczególnych porach roku. Oś pionowa — odsetek spotkań w stosunku do ogólnej ich liczby; oś pozioma — lata; A — spotkania w miesiącach: marcu, kwietniu i maju; B — spotkania w czerwcu oraz lipcu; C — spotkania w sierpniu, wrześniu oraz październiku ($n = 423$).

Wykres 3. Przelot wiosenny *H. caspia* w Polsce. Oś pionowa — odsetek spotkań oraz frekwencja osobników w stosunku do ich ogólnej liczby; oś pozioma — miesiące; A — frekwencja osobników; B — liczba spotkań ($n_A = 183$, $n_B = 58$).

Wykres 4. Przelot jesienny *H. caspia* w Polsce. Oś pionowa — odsetek spotkań oraz frekwencja osobników w stosunku do ogólnej ich liczby (z prawej — w ujęciu kumulatywnym); oś pozioma — miesiące; A' — frekwencja osobników; B' — liczba spotkań (A, B są ogiwanymi krzywych A', B') ($n_A = 1092$, $n_B = 336$).

Wykres 5. Przelot jesienny *H. caspia* w północnych regionach Polski (na północ od 52° 30' szer. półn.). Oś pionowa — odsetek spotkań oraz frekwencja osobników w stosunku

do ich ogólnej liczby; oś pozioma — miesiące; A — frekwencja osobników; B — liczba spotkań ($n_A = 604$, $n_B = 122$).

Wykres 6. Przelot jesienny *H. caspia* w północnych regionach Polski (na południe od $52^\circ 30'$ szer. półn.). Oznaczenia jak na wykresie 5 ($n_A = 488$, $n_B = 214$).

Wykres 7. Kierunkowość lotu *H. caspia* podczas wędrówek jesiennych w 1961 roku w rejonie ujścia Sanu. Oś pionowa — odsetek osobników w stosunku do ogólnej ich liczby; oś pozioma — miesiące; S — osobniki lecące w kierunku południowym; N — w kierunku północnym ($n = 203$).

Wykres 8. Przelot jesienny *H. caspia* w 1961 roku w rejonie ujścia Sanu. Oś pionowa — odsetek spotkań oraz frekwencja osobników w stosunku do ogólnej ich liczby; oś pozioma — miesiące; A — frekwencja osobników; B — częstość spotkań ($n_A = 207$, $n_B = 97$).

Wykres 9. Przelot jesienny *H. caspia* w 1960 roku w dolnym biegu Sanu oraz w środkowym biegu Wisły. Oznaczenia jak na wykresie 8 ($n_A = 91$, $n_B = 39$).

Wykres 10. Spotykalność *H. caspia* w czerwcu i lipcu w północnych regionach Polski. Oś pionowa — udział procentowy w stosunku do każdej kategorii spotkań; oś pozioma — miesiące; A — frekwencja osobników; B — liczba spotkań ($n_A = 98$, $n_B = 34$).

Wykres 11. Aktywność *H. caspia* w cyklu dobowym. Oś pionowa — udział procentowy spotkań w stosunku do ogólnej ich liczby; oś pozioma — godziny; A — aktywność dobową na podstawie materiałów zebranych w 1960 roku; B — na podstawie materiałów z 1961 roku; C — wypadkowa krzywych A , B ($n = 148$).

Wykres 12. Aktywność *H. caspia* w cyklu dobowym (na podstawie materiałów dra B. JABŁOŃSKIEGO zebranych w 1960 roku na Mewiej Rewie). Oś pionowa — udział procentowy obserwowanych osobników w stosunku do ich liczby ogólnej; oś pozioma — godziny ($n = 60$).

Wykres 13. Grupowość *H. caspia* w cyklu dobowym (1961, San-Wisła). Oś pionowa — udział procentowy poszczególnych kategorii grupowych w stosunku do ogólnej liczby spotkań; oś pozioma — godziny; kategorie grup: A — 1 osobnik, B — 2 osobniki, C — 3 osobniki, D — grupy powyżej 3 osobników ($n = 114$).

Wykres 14. Grupowość *H. caspia* w cyklu dobowym (1960–1961, San-Wisła). Oś pionowa — udział procentowy poszczególnych kategorii grupowych w stosunku do liczby spotkań na obrębie danego przedziału klasowego; pozostałe oznaczenia jak na wykresie 13 ($n = 148$).

Wykres 15. Wysokość lotu *H. caspia* a pora dnia (1961, San-Wisła). Oś pionowa — udział procentowy spotkanych osobników w stosunku do ich liczby ogólnej w obrębie poszczególnych kategorii wysokości; oś pozioma — godziny; A — lot na wysokości do 20 m; B — do 50 m; C — do 150 m ($n = 101$).

Wykres 16. Kierunkowość lotu *H. caspia* w cyklu dobowym (1960, 1961, San-Wisła). Oś pionowa — udział procentowy spotkań osobników lecących w danym kierunku w stosunku do ich liczby ogólnej; oś pozioma — godziny; A — lot w kierunku S , B — w kierunku N ($n = 148$).

Wykres 17. Bilans kierunkowości lotu *H. caspia* w cyklu dobowym (1960, 1961, San-Wisła). Oś pionowa — (z prawej) udział procentowy lotów w kierunku S w obrębie danego przedziału czasowego, (z lewej) udział lotów N w danym przedziale czasowym; oś pozioma — godziny ($n = 148$).

Wykres 18. Charakter socjalny ugrupowań *H. caspia* w cyklu dobowym podczas przelotu jesiennego (1961, San-Wisła). Oś pionowa — udział procentowy poszczególnych kategorii ugrupowań w obrębie danego przedziału czasowego; oś pozioma — godziny, A — rodziny, B — stada, C — pojedyncze osobniki.

Wykres 19. Grupowość *H. caspia* podczas przelotu jesiennego (1961, San-Wisła). Oś pionowa — udział procentowy poszczególnych kategorii ugrupowań w stosunku do ogólnej liczby spotkań; oś pozioma — miesiące; ugrupowania: A — pojedyncze osobniki, B — składające się z 2 osobników, C — z 3, D — z 4–5 osobników ($n = 83$).

Wykres 20. Zależność wielkości stada *H. caspia* od siły wiatru (1961, San-Wisła). Oś pionowa — udział procentowy spotkań danej kategorii stada w stosunku do ogólnej liczby spotkań tej kategorii; oś pozioma — siła wiatru w stopniach skali Beauforta; *A* — rozkład spotkań pojedynczych osobników, *B* — stad utworzonych z 2 osobników, *C* — z 3 ($n = 69$).

Wykres 21. Wpływ siły wiatru na rozproszenie *H. caspia* (1961, San-Wisła). Oś pionowa — udział procentowy pojedynczo spotykanych osobników w stosunku do spotkań pozostałych kategorii ugrupowań w obrębie danej klasy siły wiatru; oś pozioma — siła wiatru w stopniach skali Beauforta ($n = 69$).

Wykres 22. Współzależność wysokości lotu *H. caspia* i wielkości stad (1961, San-Wisła). Oś pionowa — udział procentowy spotkań danej kategorii stada w stosunku do ogólnej liczby spotkań tej kategorii; oś pozioma — wysokość lotu w m; *A* — ogólny rozkład lotu wszystkich notowanych stad; *B* — rozkład wysokości lotu pojedynczo spotykanych osobników; *C* — wysokość lotu stad liczących 3-4 osobniki.

Wykres 23. Rozkład wielkości stad *H. caspia* podczas przelotu na południe w okresie wędrówek jesiennych (1961, San-Wisła). Oś pionowa — odsetek obserwowanych osobników; oś pozioma — wielkość stada; *A* — odsetek rybitw lecących na południe w obrębie danej klasy wielkości stada; *B* — odsetek w stosunku do ogólnej liczby osobników lecących na południe ($n = 167$).

Wykres 24. Obieranie przez *H. caspia* trasy „San” względnie „Wisła” przy zlewaniu się tych rzek (przelot jesienny w 1961 r.). Oś pionowa — odsetek osobników w stosunku do ogólnej ich liczby notowanej podczas przelotu; oś pozioma — miesiące; *A* — osobniki obierające Wisłę; *B* — obierające San ($n = 189$).

Wykres 25. Wysokość lotu a preferencja trasy „San” względnie „Wisła” (1961, San-Wisła). Oś pionowa — odsetek spotkań w stosunku do ogólnej ich liczby notowanej dla danej trasy; oś pozioma — wysokość lotu w m; *A* — wysokość lotu osobników powyżej ujścia Sanu nadal lecących Wisłę; *B* — wysokość lotu rybitw, które wybrały trasę „San”.

Wykres 26. Wpływ zachmurzenia na wysokość lotu *H. caspia* (1961, San-Wisła). Oś pionowa — odsetek spotkań rybitw obserwowanych przy danym stanie zachmurzenia; oś pozioma — wysokość lotu w m; *A* — rozkład wysokości lotu przy bezchmurnej pogodzie (zachmurzenie 0); *B* — przy stanie zachmurzenia 1-8°; *C* — przy całkowitym zachmurzeniu (stopień zachmurzenia 10°).

Wykres 27. Wpływ siły wiatru na wysokość lotu *H. caspia* (1961, San-Wisła). Oś pionowa — odsetek spotkań rybitw w stosunku do liczby notowanej w obrębie danej kategorii wysokości; oś pozioma — siła wiatru w stopniach skali Beauforta; *A* — rozkład częstotliwości spotkań rybitw lecących na wysokości do 20 m; *B* — lecących na wysokości 21-50 m; *C* — na wysokości 51-150 m.

Wykres 28. Współzależność wysokości i kierunkowości lotu *H. caspia* (1961, San-Wisła). Oś pionowa — odsetek rybitw w stosunku do ich ogólnej liczby w obrębie danej kategorii kierunkowości; oś pozioma — wysokość lotu w m; *N* — rozkład wysokości lotu osobników lecących w kierunku *N*; *S* — rozkład wysokości lotu osobników lecących w kierunku *S* ($n = 70$).

Wykres 29. Współzależność wysokości i charakteru lotu *H. caspia* (1961, San-Wisła). Oś pionowa — odsetek osobników w stosunku do ich ogólnej liczby w obrębie danej kategorii lotu; oś pozioma — wysokość lotu w m; *A* — lot prosty; *B* — lot krzywoliniowy penetracyjny.

Mapa 1. Plan sytuacyjny rejonu ujścia Sanu do Wisły. 1 — zbiorniki wodne, 2 — zabudowania, 3 — wały przeciwpowodziowe, 4 — zadrzewienia, 5 — punkt obserwacyjny podczas badań nad wędrówkami *H. caspia*.

Tabela 1. Charakterystyka przelotu wiosennego i jesiennego *H. caspia* w Polsce. (1) — przelot, (2) — wiosenny, (3) — jesienny, (4) — obszar kraju leżący; (5) — obliczono na podstawie liczby; (6), (10) — liczba obserwowanych osobników względnie liczba spotkań, (7), (11) — średnia, (8), (12) — błąd standardowy (w dniach), (9), (13) — odchylenie stan-

dardowe (w dniach), (14) — na północ od 52°20' szer. półn., (15) — na południe od 52°30' szer. półn., (16) — cały obszar kraju, (17), (19), (21) — obliczono, według liczby obserwowanych osobników, (18), (20), (22) — obliczono według liczby spotkań.

Tabela 2. Współzależność wysokości lotu oraz innych elementów związanych z aktywnością dobową *H. caspia* (1961, San-Wisła). (1) — zależność od: (2) — χ^2 , (3) — df (liczba stopni swobody), (4) — P (prawdopodobieństwo), (5) — zależność od pory dnia, (6) — od kierunkowości S-N, (7) — od kierunkowości San-Wisła, (8) — liniowość lotu (prosty, krzywoliniowy penetracyjny).

Tabela 3. Przeciętna wielkość ugrupowań stadnych *H. caspia* w okresie przelotów w Polsce. (1) — terytorium Polski leżące, (2) — przeciętna wielkość ugrupowania, (3) — podczas przelotu wiosennego, (4) — podczas przelotu jesiennego, (5) — na północ od 52°30' szer. półn., (6) — na południe od 52°30' szer. półn., (7) — cały obszar Polski.

Tabela 4. Wysokość i kierunkowość lotu *H. caspia* w zależności od struktury socjalnej ugrupowania (wysokość w m), (1961, San-Wisła). (1) — charakter ugrupowania, (2) — charakterystyka, (3) — średnia, (4) — odchylenie standardowe, (5) — błąd standardowy (6) — odsetek osobników lecających w kierunku S, (7) — lecających w kierunku N, (8) — rodziny, (9) — stada, (10) — pojedyncze osobniki.

Tabela 5. Integracja stadna *H. caspia* podczas przelotu jesiennego (w ujęciu procentowym według liczby osobników; 1961, San-Wisła). (1) — charakter ugrupowania, (2) — stopień zintegrowania, (3) — (6) — gradacja zintegrowania, (7) — razem, (8) — rodziny, (9) — stada, (10) — pojedyncze osobniki.

Tabela 6. Analiza przebiegu koczowisk połgowych oraz przelotu jesiennego *H. caspia* w rejonie ujścia Sanu (w ujęciu procentowym). (1) — rzeka, (2) — sektor rzeki, (3) — osobniki wyłącznie wędrowne, (4) — odsetek osobników lecających, (5) — Wisła poniżej ujścia Sanu, (6) — w dalszym ciągu Wisła powyżej ujścia, (7) — dalej tylko Sanem, (8) — udział sektora w przelocie, (9) — do ujścia Sanu, (10) — powyżej ujścia Sanu, (11) — osobniki wędrowne i koczujące łącznie — loty w kierunku, (12) — na południe, (13) — na północ, (14) — odsetek osobników koczujących, (15) — sektor lewy, (16) — środkowy, (17) — prawy, (18), (19) — ogólnie.

Tabela 7. Wysokość lotu a preferowanie przez *H. caspia* trasy „San” (wysokość w m). (1) — przeciętna wysokość lotu, (2) — sektory Wisły, (3) — lewy i środkowy, (4) — prawy, (5) — wysokość lotu osobników obierających trasę „San”, (6) — osobników lecających dalej tym samym sektorem Wisły.

Tabela 8. Przelot *H. caspia* określonym sektorem Wisły oraz preferowanie trasy „San” w zależności od stopnia zachmurzenia i siły wiatru (w ujęciu procentowym). (1) — rzeka i sektor, (2) — czynniki atmosferyczne, (3) — zachmurzenie (według 10-stopniowej skali), (4) — siła wiatru (według skali Beauforta), (5) — sektor lewy, (6) — środkowy, (7) — prawy, (8) — San (ogólnie), (9) — Wisła (ogólnie).

Tabela 9. Zależność kierunkowości lotów *H. caspia* od stopnia zachmurzenia (w ujęciu procentowym). (1) — lot w kierunkach, (2) — stopień zachmurzenia (według 10-stopniowej skali).

Tabela 10. Frekwencja *H. caspia* podczas przelotu jesiennego w warunkach bezwietrznej pogody oraz przy różnych kierunkach wiatru (w ujęciu procentowym). (1) — warunki przelotu, (2) — frekwencja w ujęciu procentowym, (3) — lot przy bezwietrznej pogodzie, (4) — lot przy wietrze z kierunków.

Tabela 11. Frekwencja *H. caspia* w zależności od siły i kierunku wiatru (w ujęciu procentowym; według skali Beauforta). (1) — kierunek wiatru, (2) — siła wiatru, (3) — kierunek NW, (4) — inne kierunki, (5) — ogółem.

Tabela 12. Warunki pogodowe przelotu jesiennego *H. caspia* w rejonie ujścia Sanu. (1) — charakter pogody, (2) — pochmurna (2-10°), wietrzna (2-6°), (3) — pochmurna (2-10°), bezwietrzna (0-1°), (4) — bezchmurna (0-1°), bezwietrzna (0-1°), (6) — odsetek osobników wędrujących przy danym typie pogody.

РЕЗЮМЕ

Работа основывается на материале состоящим из 423 встреч чегравы, *Hydroprogne caspia* (PALL.) в Польше в течение 1800—1966 гг. Из этого числа 28,4% встреч составляют материалы собранные лично автором в период 1960—1966 гг. в среднем и нижнем течении реки Сан и в среднем течении Вислы. Опубликованные, выбранные из орнитологической литературы данные составляют 23,9%, материалы предоставленные автору польскими орнитологами для статистического использования охватывают 47,7%. Основной целью работы является разработка более существенных вопросов биологии миграционного периода в следующих аспектах: а) вековых изменений, которым подвергалась балтийская популяция чеграв в течение двух последних столетий, б) изменении обычаев в связи с переходом на трансконтинентальную миграцию. Кроме того, более широко будет анализирован новый вопрос — влияние внешних факторов на преференцию определенного пути и пространственный ход перелета.

В кратком пересмотре работ опубликованных в послевоенный период автор обращает внимание лишь на более существенные моменты биологии (полный пересмотр исследований по чеграве а также зоогеографический анализ встреч чегравы в Польше будет подан в работе Добровольского (в печати)). В подразделе касающимся методики автором подчеркивается, что материалы относительно биологии собирались по специальной программе (в каждом наблюдении учитывалось 14 различных параметров). С этой целью при устье Сана в Вислу в течение августа—октября 1961 г. и в апреле 1963 г. велись непрерывно в течение дня (4^{00} — 20^{00}) наблюдения над перелетом (в сумме 546 часов наблюдений).

Во второй главе, посвященной характеру пребывания в пределах Польши, автором отмечается, что с фаунистической точки зрения появление чегравы стало приобретать значение после 1930 года (до 1930 года отмечено единственно 5,4% встреч). До 1950 года количество встреч возрастает до 8,04%, и в период 1950—1960 наступает внезапное увеличение встречаемости — чеграва становится регулярно перелетающим через Польшу видом. Остается это в тесной связи с общей экспансивностью балтийской популяции в северо-восточных районах Балтики и общим количественным ее возрастанием. Динамика встречаемости чегравы в Польше представлена на графиках 1, 2. Основным миграционным путем в Польше является Висла (48,7% встреч в пределах страны) и ее правобережные притоки (Сан, Вислока, Дунаец). Реки Буг и Одра не имеют существенного значения, как миграционные пути. Автором отмечается, что, хотя значение трансконтинентальных перелетов все возрастает, старый морской путь по-прежнему играют известную роль в перелетах. Горную цепь Карпат огибает чеграва с восточной стороны — из долины Сана проникает в долину Днестра, а также долинами притоков Вислы, как следует предполагать, перелетает эти горы в западной их части. Через Моравские Ворота перелетает, вероятно, незначительный процент исследуемого вида.

В подразделе касающемся встречаемости в годичном цикле численные соотношения в соответственных временах года, как подчеркивает автор, отображают

общую ситуацию, в частности величину репродукции на гнездовках. Весенний перелет проходит быстро и компактно (в среднем для Польши — 25 апрель), на юге Польши перелет проходит более быстро, чем в северных районах (график 3). Осенний перелет пробегает в двух волнах. Скорость миграции по сравнению с весенним перелетом является более замедленной (график 4). Чегравы перелетающие в первой волне ведут себя решительно как трансконтинентальные мигранты, участвующие во второй волне в первоначальной стадии задерживаются у польских побережий Балтики, где проводят кочевки, в последней фазе этой волны значительная часть птиц летит вдоль морских побережий. Мигрирующие вдоль рек чегравы из второй перелетной волны могут задерживаться в определенных условиях даже на более продолжительное время производя единственно местные кочевки. Поскольку пролетающие в течение августа чегравы наравне с сугубо миграционным перелетом производят типичные для послегнездового периода кочевки, постольку в сентябре этот вид появляется в Польше исключительно в качестве мигранта. Различия наблюдаемые между осенним перелетом в северных и южных районах страны показаны на графиках 5, 6. На севере перелет в большой степени совмещается с послегнездовыми кочевками и летованием, на юге чеграва встречается главным образом в качестве трансмигранта, хотя стационарные кочевки в благоприятном биотопе не считаются редкостью. Летование без признаков гнездования в течение летних месяцев на польском побережье отмечается более определенно после 1950 года. Статистическую характеристику фенологии миграционного периода (средняя величина, среднее квадратическое отклонение и т. д. — таб. 1) можно считать за существенные относительно постоянные свойства исследуемой популяции.

В последующей главе анализируется ритмика суточной активности. Автором выделяются 3 пика локомоторной активности непосредственно связанной с определенным характером ее биологической функциональности (графики 11, 12). Утренний пик (8⁰⁰—9⁰⁰) состоит из суммирующегося эффекта двух типов активности: кормежек и собственно миграционного перелета, однако оба типа, как во времени, так и функционально пробегают независимо друг от друга. Полуденное снижение активности на юге длится с 11⁰⁰ по 13⁰⁰, а на побережье до 14⁰⁰ часов. Послеобеденный пик активности (14⁰⁰—16⁰⁰) охватывает исключительно кормежки, в то время как предвечерний пик (18⁰⁰—20⁰⁰) состоит из перелетов почти исключительно миграционного характера. Автором подчеркивается, что функциональный характер активности соответствующих пиков мог быть обнаружен единственно на основании анализа изменяющихся в суточном цикле элементов поведения (графики 13—17). Особенно полезным оказалось тут применение теста χ^2 для исследования взаимозависимости высоты полета и других его параметров (направленность S—N, прямолинейность — таб. 2). Автор доказывает, что отдельные элементы суточной активности в суточном цикле составляют определенную секвенцию обеспечивающую на неразведанной территории высокую степень переживаемости. В общем представляется она следующим образом: каждой кормежке предшествует длительное разведывание степени безопасности территории кормежек, каждый сугубо миграционный перелет следует после утоления голода и заканчивается отдыхом совпа-

дающим с одновременным распознаванием степени безопасности мест новой кормежки. Миграционный перелет пробегает на высоте в несколько раз больше, чем полеты связанные с разыскиванием пищи. В течение дня, как правило, птицы принимают его дважды: в поздние утренние часы и предвечернее время. Не считаются редкостью ночные перелеты. Высота перелета зависит от его функционального характера — перелет прямолинейный (миграционный) проходит на высоком потолке, в то время как полет связанный с разыскиванием пищи неупорядоченный по направленности наблюдается на средней и низкой высоте. Относительно суточного цикла в период стационарных кочевков, автором отмечается, что общая схема активности не изменяется — вместо фазы миграционного перелета соответственно продлевается время кормежек.

В главе посвященной структуре стада, семейных взаимоотношений и переживаемости в период миграции автором констатируется, что, по всей вероятности, большинство особей во время весеннего перелета уже образовала пары. Осенью чегравы летят в стадах по 2—4 особи (таб. 3). В среднем величина стай как во время весеннего перелета, так и осенью больше на севере Польши, чем на юге. Объясняется это: а) предварительным соединением птиц перед моментом образования гнездовых колонии, б) скоплением в более крупные агрегации на местах благоприятствующих кормежкам а также на местах отдыха. Стайные связи у чегравы менее устойчивые и не так выраженные, как у более мелких видов крачек. Между величиной стада а высотой полета и его направленностью к югу (в случае осенней миграции) наблюдается тесная взаимосвязь (графики 22, 23), что является доказательством совершения чегравой миграционных перелетов единственно в стаях. Стадные и семейственные соотношения в течение дня подвергаются определенным изменениям. Они тесным образом зависят от совершения кормежек, собственно миграционного перелета и прежде всего от обеспечения каждой особи в максимальной степени безопасности. Автором обращается особое внимание на проблему семейственных соотношений в течение миграционного периода. Непосредственные связи между взрослыми и ювенальными птицами поддерживаются в течение всего миграционного периода и продолжают, по всей вероятности, вплоть до прилета на зимовки. В суточном цикле проявляются они исключительно во время собственно миграционного перелета (график 18). Биологический смысл поддержания в течение более продолжительного времени семейных связей состоит в использовании молодыми особями опыта взрослых на неразведанных еще территориях, благодаря чему смертность чеграв на первом году жизни является незначительной (26%), и например в два раза ниже, чем среди более крупных видов, но образующих отдельные по возрасту стада. Значение подкармливания молодых является таким образом второстепенным. Во время стационарных кочевков семейные связи ослабевают, возрастает пространственная дисперсия молодых особей (график 19). Рассматривая причинные связи между структурой стада и выживаемостью, автором доказывается, что максимальная степень интеграции стада наблюдается в момент наиболее для птиц опасный т. е. во время собственно миграционного передвижения и ночевков. В пределах территории хорошо разведанных наблюдается дисперсию птиц в максимальной степени.

Решающими для переживаемости являются два момента: а) рекогносцировка на новой территории степени безопасности (решительную роль играет тут индивидуальный опыт взрослых особей — родительских птиц), б) эффективность этой безопасности отражающаяся на возможности дисперсии и максимального использовании биотопов в трофическом отношении (основное значение имеет тут степень влияния антропогенных факторов). Удерживание соответственной стадной структуры в цикле суточной активности позволяет мигрантам относительно быстро и беспрепятственно совершать перелет и одновременно проводить кормежки на не достаточно разведанной территории. Всякие нарушения цикла изменений стадной структуры в течение дня оказываются для вида весьма неблагоприятными. Из факторов нарушающих стадную структуру на первое место следует отнести влияние более сильных ветров (графики 20, 21). Другие метеорологические факторы не оказывают существенного влияния. В общем, в суточном цикле констатируется увеличивающаяся с ранних утренних часов дисперсию, которую во второй половине дня замещает противоположная тенденция т. е. стремление к интеграции. Автором выделяются 4 степени стадной интеграции (таб. 5). Наиболее сильно связаны между собой семейные группировки; наиболее слабо — типичные агрегации возникающие на местах отдыха.

Предпоследнюю главу посвящает автор проблеме влияния внешних факторов на пространственный ход миграции. На основании анализа собранного по специальной программе материала при устье Сана а также общих данных из всей Польши автор приходит к мнению, что: а) навигационные способности исследуемого вида основываются в значительной степени на использовании так называемых направляющих линий таких, как морские побережья и реки. В критических пунктах, какими являются слияние двух рек (расхождение перелетных путей), преференция правильного пути решительным образом влияет на дальнейший ход перелета и судьбу мигрантов. Каждый из случаев преференции определенного пути, кроме внутренней мотивировки, зависит всецело от воздействующих в данный момент внешних факторов; б) миграции чегравы пробегают вдоль речных русел единственно до момента, когда их ширина еще достаточна для обеспечения необходимой для птиц безопасности (ширина водяного зеркала не меньше, чем 60—70 м). Решающим является тут фактор безопасности обуславливающий возможность контроля пространства радиусом не меньше, чем характеристическая для чегравы дистанция побега взрослых особей; в) с моментом снижения ширины реки ниже этой критической ширины чегравы покидают реку. До момента находки новой реки (или-же морского побережья) являющейся новой направляющей путь перелета линией, мигранты летят удерживая в общем характерное для вида общее направление. Совершают они тогда кормежки и проводят кочевки на встречаемых попутно более крупных водоемах. Наиболее существенным моментом определяющим общий ход миграции считает автор каждый из случаев преферирования мигрантами определенного пути, в связи с чем сосредотачивается он на таких проблемах, как: а) определение критериев обнаруживаемости случаев преференции, б) количественная характеристика явления, в) исследование факторов ограничивающих возможность пререрирования. В каче-

стве неоспоримых факторов предпочтения перелетного пути „Сан” принимаются автором случаи поворачивания чеграв в русло Сана, которые до сих пор летели центральным и левым сектором Вислы (24,7% перелетающей популяции) (таб. 3). На количественный аспект предпочтения влияет высота лета (таб. 7, граф. 25), от которой зависит пространственная ориентировка птиц а затем и возможность предпочтения соответственного правильного пути. К факторам наиболее снижающим возможность совершения птицами активного выбора определенного пути следует причислить господствующие (в случае осеннего перелета), более сильные ветры норд-вест из северо-запада (сильнее 2—3° по Бофорту) (таблицы: 8—11; графики: 26—27). При некоторых обстоятельствах могут они полностью сделать невозможным выбор данного пути. Судя по анализируемому автором примеру осенних перелетов чеграв в районе устья реки Сан (граф. 24), свыше половина мигрантов имела благоприятные метеорологические условия для пространственной ориентировки, а затем имела полную возможность предпочтения дальнейшего пути согласно внутренней мотивировке (таб. 12). Факторы нарушающие возможность предпочтения способствуют компенсационным механизмам, которые позволяют птицам в критических моментах совершить пассивный выбор правильного пути (например лет правым сектором Вислы). В последующей части работы автором подробно анализируется зависимость шансов совершения предпочтения от высоты полета (графики: 25—29). Автор приходит к выводу, что факторы влияющие на высоту полета фактически определяют возможности предпочтения. В заключении автором подчеркивается, что на основании проанализированного тут материала, вряд ли возможным будет считать, что даже взрослые старые птицы, обладающие в значительной степени накопленным индивидуальным опытом смогут ежегодно совершать миграцию по одному и тому же пути. На пространственный ход перелета, кроме внутренней общенаправляющей мотивировки, складывается влияние воздействующих на птиц в каждом моменте внешних факторов.

Объяснения к графикам, картам и таблицам:

График 1. Распределение встречаемости чегравы в Польше в течение последних 100 лет. По вертикали — процент встреч по отношению к общему их числу в пределах каждой категории; по горизонтали — годы; *A* — северная часть Польши; *B* — южная часть; *C* — общее для Польши распределение встреч ($n = 423$).

График 2. Встречаемость чегравы в Польше в соответственные времена года. По вертикали — процент встреч по отношению к общему их числу; по горизонтали — годы; *A* — встречи в месяцах: марте, апреле, мае; *B* — встречи в июне и июле; *C* — встречи в августе, сентябре, октябре ($n = 423$).

График 3. Весенний перелет чегравы в Польше. По вертикали — процент встреч а также встречаемость особей по отношению к общему их числу; по горизонтали — месяцы; *A* — встречаемость особей; *B* — встречаемость стад ($n_A = 183$, $n_B = 58$).

График 4. Осенний перелет чегравы в Польше. По вертикали — процент встреч стад и особей по отношению к общему их числу (с правой стороны — в кумулятивном аспекте); по горизонтали — месяцы; *A'* — встречаемость особей; *B'* — встречаемость стад (*A*, *B* — кумулятивные огивы кривых *A'*, *B'*) ($n_A = 1092$, $n_B = 336$).

График 5. Осенний перелет чегравы в северных районах Польши (севернее 52°30' сев. шир.). По вертикали — процент встреч стад и особей по отношению к общему их числу; по горизонтали — месяцы; *A* — встречаемость особей; *B* — встречаемость стад ($n_A = 604$, $n_B = 122$).

График 6. Осенний перелет чегравы в южных районах Польши (южнее 52°30' сев. шир.). Обозначения — как на граф. 5) ($n_A = 488$, $n_B = 214$).

График 7. Направленность перелета чегравы при устье Сана во время осенней миграции в 1961 году. По вертикали — процент особей по отношению к общему их числу; по горизонтали — месяцы; *S* — особи летящие к югу; *N* — к северу ($n = 203$).

График 8. Осенний перелет чегравы при устье Сана в 1961 году. По вертикали — процент встреч стад и особей по отношению к общему их числу; по горизонтали — месяцы; *A* — встречаемость особей, *B* — встречаемость стад ($n_A = 207$, $n_B = 97$).

График 9. Осенний перелет чегравы в нижнем течении Сана и среднем течении Вислы в 1960 году. Обозначения — как на графике 8 ($n_A = 91$, $n_B = 39$).

График 10. Встречаемость чегравы в июне и июле в северных районах Польши. По вертикали — процент по отношению к каждой категории встреч; по горизонтали — месяцы; *A* — встречаемость особей; *B* — встречаемость стад ($n_A = 98$, $n_B = 34$).

График 11. Суточная активность чегравы. По вертикали — процент встреч по отношению к общему их числу; по горизонтали — время суток; *A* — суточная активность по материалам собранным в 1960 году; *B* — по материалам с 1961 года; *C* — кривая результирующая *A*, *B* ($n = 148$).

График 12. Суточная активность чегравы (на основании материалов доктора Б. Яблонского собранных в 1960 году на Мевей Реве под Гданьском). По вертикали — процент встреченных особей по отношению к общему их числу; по горизонтали — время суток ($n = 60$).

График 13. Стадность чегравы в суточном цикле (1961 г., Сан—Висла). По вертикали — процентные соотношения соответственных категории группировок по отношению к общему числу встреч; по горизонтали — время суток; категории группировок: *A* — 1 особь, *B* — 2 особи, *C* — 3 особи, *D* — группы свыше 3-х особей ($n = 114$).

График 14. Стадность чегравы в суточном цикле (1960—1961, Сан—Висла). По вертикали — процентные соотношения соответственных категории группировок по отношению к общему числу встреч в пределах данного класса; остальные обозначения — как на графике 13 ($n = 148$).

График 15. Высота полета чегравы и время дня (1961, Сан—Висла). По вертикали — процент встреч особей по отношению к общему их числу в пределах соответственной категории высоты лета; по горизонтали — время суток; *A* — полет на высоте до 20 м; *B* — до 50 м; *C* — до 150 м ($n = 101$).

График 16. Направленность полета чегравы в суточном цикле (1960, 1961, Сан—Висла). По горизонтали процентное соотношение особей совершающих полет по данному направлению по отношению к общему числу встреч; по горизонтали время суток; *A* — лет по направлению к югу, *B* — лет по направлению к северу ($n = 148$).

График 17. Баланс направленности полета чегравы в суточном цикле (1960, 1961, Сан—Висла). По вертикали — (с правой стороны) процентное соотношение летов к югу в пределах данного класса по времени, (с левой стороны) соотношение летов к северу в пределах данного класса по времени; по горизонтали — время суток ($n = 148$).

График 18. Социальный характер группировок чегравы в суточном цикле во время осеннего перелета (1961, Сан—Висла). По вертикали — процентные соотношения соответственных категории группировок в пределах данного класса по времени; по горизонтали — время суток; *A* — семьи, *B* — стада; *C* — отдельные особи.

График 19. Стадный характер группировок чегравы во время осеннего перелета (1961, Сан—Висла). По вертикали процентное соотношение соответственных категории группировок по отношению к общему числу встреч; по горизонтали — месяцы; группировки: *A* — отдельные единичные особи, *B* — группы состоящие из 2-х особей, *C* — из 3-х, *D* — из 4—5 особей ($n = 83$).

График 20. Зависимость величины стада чеграв от силы ветра (1961, Сан—Висла). По вертикали — процентное соотношение встреч данной категории стада по отношению к общему числу

встреч в этой категории; по горизонтали — сила ветра по шкале Бофорта; *A* — встречи отдельных единичных особей, *B* — стад состоящих из 2-х особей, *C* — из 3-х особей ($n = 69$).

График 21. Влияние силы ветра на дисперсию чегравы (1961, Сан—Висла). По вертикали — процент единично встречаемых особей по отношению к численности встреч остальных категории группировок в пределах данного класса по силе ветра; по горизонтали — сила ветра по баллам шкалы Бофорта ($n = 69$).

График 22. Взаимозависимость между высотой полета чегравы и величиной стада (1961, Сан—Висла). По вертикали — процент встреч данной величины стада по отношению к общему числу встреч в данной категории; по горизонтали — высота полета в м; *A* — общее распределение высоты полета всех отмеченных стад; *B* — распределение высоты полета единично встречаемых особей; *C* — стад насчитывающих 3—4 особи.

График 23. Распределение величины стада чегравы во время перелета на юг (птицы летящие к северу тут не принимались во внимание — осенний перелет, 1961 г., Сан—Висла). По вертикали — процент отмеченных особей; по горизонтали — величина стада; *A* — процент чеграв в пределах данного класса по величине стада; *B* — процент по отношению к общему числу птиц летящих к югу ($n = 167$).

График 24. Преферирование чегравой пути „Сан” или „Висла” при соединении обеих рек (осенний перелет в 1961 г.). По вертикали — процент особей по отношению к общему их числу во время перелета; по горизонтали — месяцы; *A* — особи преферирующие Вислу; *B* — особи преферирующие Сан ($n = 189$).

График 25. Высота полета а преференция пути „Сан” или „Висла” (1961). По вертикали — процент встреч стад по отношению к общему их числу для данного пути; по горизонтали — высота лета в м; *A* — высота полета особей летящих выше устья Сана в дальнейшем Вислой; *B* — высота полета чеграв, которые преферировали русло Сана.

График 26. Влияние облачности на высоту полета чегравы (1961, Сан—Висла). По вертикали — процент встреч особей наблюдаемых при данном состоянии облачности; по горизонтали — высота полета в м; *A* — распределение высоты полета при безоблачной погоде (облачность 0); *B* — при облачности 1—8°; *C* — при полной облачности (10°).

График 27. Влияние силы ветра на высоту полета чегравы (1961, Сан—Висла). По вертикали — процент встреч по отношению к их числу в пределах данной категории высоты; по горизонтали — сила ветра по баллам Бофорта; *A* — распределение встреч чеграв летящих на высоте до 20 м; *B* — на высоте 21—50 м; *C* — 51—150 м.

График 28. Взаимозависимость высоты и направленности полета чегравы (1961, Сан—Висла). По вертикали — процент особей по отношению к общему их числу в данной категории по направленности; по горизонтали — высота лета в м; *N* — распределение высоты лета особей летящих к северу; *S* — распределение высоты лета особей летящих к югу ($n = 70$).

График 29. Взаимозависимость высоты полета и его функциональной характеристики (1961, Сан—Висла). По вертикали — процент особей по отношению к общему их числу в пределах данной категории лета; по горизонтали — высота полета в м; *A* — лет прямолинейный; *B* — лет извилистый (разведование и поиски корма).

Карта 1. План расположения топографических пунктов в районе устья Сана в Вислу. 1 — водоемы, 2 — жилые постройки, 3 — дамба предохраняющая от паводков, 4 — лесопосадки, 5 — наблюдательный пункт по перелетам чегравы.

Таблица 1. Характеристика весеннего и осеннего перелета чегравы в Польше. (1) — перелет (2) — весенний, (3) — осенний, (4) — территория страны расположена, (5) — вычислено на основании, (6), (10) — численность отмеченных особей или встречаемости стад, (7), (11) — в среднем, (8), (12) — средняя ошибка (в днях), (9), (13) — среднее квадратическое отклонение (в днях), (14) — к северу от 52°30' сев. шир., (15) — к югу от 52°30', сев. шир., (16) — территория всей страны, (17), (19), (21) — вычислено на основании числа отмеченных особей, (18) (20), (22) — вычислено на основании числа встреченных стад.

Таблица 2. Взаимозависимость высоты полета и параметров суточной активности чегравы (1961, Сан—Висла). (1) — в зависимости от, (2) — χ^2 , (3) — df (число степеней свободы) (4) — P (сте-

пень вероятности), (5) — в зависимости от времени дня, (6) — в зависимости от направленности север — юг, (7) — в зависимости от направленности Сан—Висла, (8) — линейность полета (прямолинейный, извилистый, поисково-разведочный).

Таблица 3. Средняя величина стадных группировок чегравы в Польше в период перелетов. (1) — территория Польши расположенная, (2) — величина группировки в среднем, (3) — в период весеннего перелета, (4) — в период осеннего перелета, (5) — к северу от 52°30', сев. шир., (6) — к югу от 52°30' сев. шир., (7) — территория всей Польши.

Таблица 4. Высота и направленность полета чегравы в зависимости от социальной структуры группировки (высота в м, 1961, Сан—Висла). (1) — характер группировки, (2) — характеристика, (3) — средняя величина, (4) — среднее квадратическое отклонение, (5) — средняя ошибка, (6) — процент особей летящих к югу, (7) — летящих к северу, (8) — семьи, (9) — стада, (10) — отдельные единичные особи.

Таблица 5. Стадная интеграция чегравы во время осеннего перелета (выражено в процентах по отношению к общей численности особей; 1961, Сан—Висла). (1) — характер группировки, (2) — степень интеграции, (3)—(6) — градация степени интеграции, (7) итого, (8) — семьи, (9) — стада, (10) — отдельные единичные особи.

Таблица 6. Анализ хода послегнездовых кочевков и осеннего перелета чегравы в районе устья Сана (в процентах). (1) — река, (2) — сектор реки, (3) — особи исключительно перелетающие, (4) — процент особей пролетающих, (5) — вдоль Вислы ниже устья Сана, (6) — в дальнейшем вдоль Вислы выше устья, (7) — в дальнейшем только вдоль Сана, (8) — участие сектора в перелете, (9) — по устью Сана, (10) — выше устья Сана, (11) — особи совершающие кочевки и перелеты рассматриваемые в общем — полет по направлению, (12) — к югу, (13) — к северу, (14) — процент особей совершающих кочевки, (15) — левый сектор, (16) — центральный сектор, (17) — правый сектор, (18), (19) — в общем.

Таблица 7. Высота полета и преферирование чегравой пути „Сан” (высота в м). (1) — высота полета в среднем, (2) — секторы Вислы, (3) — левый и центральный, (4) — правый, (5) — высота полета особей преферирующих путь „Сан”, (6) — особей в дальнейшем летящих этим же самым сектором Вислы.

Таблица 8. Перелет чегравы вдоль определенных секторов Вислы и преферирование пути „Сан” в зависимости от облачности и силы ветра (подано в процентных соотношениях). (1) — река и сектор, (2) — метеорологические факторы, (3) — облачность (по 10-бальной шкале), (4) — сила ветра (по Бофорту), (5) — левый сектор, (6) — центральный сектор, (7) — правый сектор, (8) — Сан (в общем), (9) — Висла (в общем).

Таблица 9. Зависимость направленности полета чегравы от облачности (подано в процентных соотношениях). (1) — полет по направлению, (2) — облачность (по 10-бальной шкале).

Таблица 10. Встречаемость чегравы в период осеннего перелета при безветренной погоде и при ветре из различных направлений (подано в процентных соотношениях). (1) — условия перелета, (2) — встречаемость в процентных соотношениях, (3) — перелет при безветренной погоде, (4) — перелет при ветре из направлений.

Таблица 11. Встречаемость чегравы в зависимости от силы ветра и его направления (в процентных соотношениях; по шкале Бофорта). (1) — направление ветра, (2) — сила ветра, (3) — северо-западное направление, (4) — другие направления, (5) — в общем.

Таблица 12. Метеорологические условия осеннего перелета чегравы в районе устья Сана. (1) — характер погоды, (2) — пасмурная (2—10°), (4) — безоблачная (0—1°), безветренная (0—1°), (6) — процент особей совершающих перелет в условиях данного типа погоды.

Redaktor pracy — mgr. Z Swirski

Państwowe Wydawnictwo Naukowe — Warszawa 1969
Nakład 1180+90 egz. Ark. wyd. 5; druk. 4. Papier druk. sat. kl. III 80 g B1. Cena zł. 18.
Nr zam. 47/69 — Wrocławska Drukarnia Naukowa