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Food requirement and effect of Starling, *Sturnus vulgaris* L., on agriculture in Żuławy Wiślane

[With 8 tables and 1 figure in the text]

Abstract: This paper summarises the results of four year investigations on the density, productivity, habitat selection, food composition and migration of the starlings in the Żuławy Wiślane and gives some conclusions on the role of this species in the agriculture of investigated area. Food requirement was estimated by calculating the daily energy budget (increased during the migration period by the energy requirement of preparation) with the coefficient of food assimilation taken in to consideration. During the growing season starlings take 5363450 Kcal/km^2; about 7 % of these is taken by breeding population and 73% by migrant birds during spring and autumn migrations. Starlings can do damage on crop fields locally only but in general they have not significant impact on agriculture (they consume not more than 2% of the amount of seedgrain sown in 1 ha). Their feeding on insects contributes to the reduction of the abundance of the pest populations.

INTRODUCTION

The objective of this study was an attempt to define the food requirement of the starling population of the Żuławy Wiślane and its effect on the agriculture of the area. At the same time this paper summarises the results of the investigations carried out on the starling in the Vistula Żuławy from 1971–1975 within a PAS project called "Significance of birds in agrocoenoses".

Within the above-mentioned project investigations on the starling in Poland were carried out at several sites, but wide-ranging and intensive investigations were carried out only in Wielkopolska and Żuławy. Both subprograms were to study the same problems and to provide an estimate of the significance of starlings in two, in many respects completely different, regions. Due to difficulties of methodology the program of investigation in Wielkopolska was limited to a broadly interpreted breeding period completely ignoring birds on passage (Bogucki 1977) which, as it will be shown in this paper, may be, and most frequently are, of crucial importance for an estimate of the role of a given bird species in nature and of its economic effect.

The author of this paper may be accused of over-simplification and accepting arbitrary assumptions but, at the present stage of knowledge, this is necessary for obtaining a general picture of the phenomena studied. Moreover the author believes that the need for such studies is so great that it is impossible to wait until the collection of detailed data is complete and ideal study methods have been worked out. This, of course, does not mean that these should be neglected. Such an opinion accords with those appearing in world literature in recent years (Dobrowolski 1973; Wiens, Dyer 1975; Wiens, Nussbaum 1975; Wiens, Scott 1975 et al.).

The starling was chosen as the subject of the investigations for the following reasons. Firstly, it is one of the most numerous birds in Europe (Bogucki 1977). It is also one of the bird species occurring most commonly in agrocoenoses and throughout the year, it collects in that habitat most of the food it eats (Gromadzki 1969).

Secondly, the starling is a species expanding its range and population density in Europe (Berthold 1968). This expansion may be due both to natural factors such as the climate (Kalela 1949, 1950) and man-made ones such as changes in the systems of agriculture or urbanization (Lehtoranta 1952; Oelke 1967); the problem of the practical protection of this species due to this expansion (Havlin et al. 1965) is certainly overestimated by some research workers (Bogucki 1977; Gromadzki 1978). Population parameters such as migration and productivity (Berthold 1968) and the feeding habits (Delvingt 1961) undergo changes as a result of the influence of external factors.

Thirdly, the starling is an omnivorous species whose diet includes a considerable percentage of insects, among which are many agricultural pests (Gro-

MADZKI 1969; BOGUCKI 1974; GROMADZKA, GROMADZKI 1978). This is the reason why in many countries the starling is considered an undoubtedly useful bird. However, the starling causes considerable losses in fruit-farming, especially in areas of intensive migration and its wintering grounds (MAHJOUB manuscript; TAHON 1973). This is why many countries have taken measures in order to reduce the extent of losses. The methods used vary greatly, from a complete destruction of starlings to driving them away from areas most at risk (MAHJOUB manuscript; TAHON 1973). Apart from this, the necessity for an intensification of investigation on this species has been postulated by other authors (KEIL 1972; TAHON 1973).

There are two reasons why the Żuławy Wiślane have been chosen as an area for investigation of the effect of starlings on agriculture. Firstly, they are an area where this species is very numerous throughout the main part of the growing season (GROMADZKI in press a); secondly, Żuławy are an area of highly developed, intensive agriculture. Since farmers kept reporting losses caused by starlings it became very important to check the correctness of their opinions.

STUDY AREA, METHODS, MATERIAL

The Żuławy Wiślane are an alluvial delta plateau of the Vistula. They lie between longitudes 18°35′ E and 19°28′ E and latitudes 54°00′ N and 54°21′ N. The highest point is 11 m above sea-level and 28% of the area is below sea-level; the soils are muds, peat soils and peat muds. The whole area is covered by a network of numerous rivers, old river-beds, drainage canals and ditches.

The climate of Żuławy is varied and greatly influenced by the sea. Spring is late and could, autumn long and warm. Considerable variation in the weather, both from day to day and year to year, is characteristic of the area. Air humidity is high, strong and cold north and north-westerly winds are very frequent. The average annual precipitation is 550 mm.

About 50 % of the area of Żuławy is ploughland and about 20% is covered by meadows and pastures. A detailed geological-biological survey of Żuławy and a description of the economy there have been presented in collective studies edited by MONIAK (1974) and AUGUSTOWSKI (1976).

Data collected in Żuławy from 1971–1974 have been used in the present study. Detailed descriptions of the methods of collecting and describing the material as well as a discussion on these methods have been given in previous papers (GROMADZKI 1978, in press a, b; GROMADZKA, GROMADZKI 1978). The amount of material collected has also been given there. Some general information on the methods of collecting data in the field is given in the next chapter of this study which is a summary of the invstigations carried out in Żuławy.

REVIEW OF THE RESULTS OF INVESTIGATIONS CARRIED OUT IN THE ŻUŁAWY WIŚLANE

On the basis of recoveries of starlings ringed in Poland an analysis of the phenology of starling migrations in Poland has been made and wintering grounds and migration routes of particular populations have been established (Gromadzki, Kania 1976). On the basis of migration habits starling populations in Poland have been divided into three subpopulations: north-Polish, mid-Polish and south-Polish; this division differs slightly from the one suggested earlier by Rydzewski (1960a, 1960b) – into two populations separated by a clinal transtitional belt. Particular populations live in different regions of Poland and winter in different areas. Unlike the other two, the north-Polish population migrates not only in spring and autumn but also in summer and in the latter migration mainly young birds are involved. Starlings living in Żuławy belong to the north-Polish population.

The productivity of starlings was studied in experimental colonies of nest boxes (Gromadzki in press b). The north-Polish population had only one brood a year; as in other areas, the start of egg-laying is highly synchronised. The period of egg-laying can be divided into two distinct subperiods: during the first called the basic period over 80 % of eggs are laid in a given year; these are all first clutches. The second subperiod called the supplementary period is more prolonged in time and clutches laid then are delayed clutches or repeat clutches following the loss of the first ones – only 4.5 % of all eggs laid in a given year fall into the latter category.

Many young females breed in their first full summer. The proportion of these depended on the length of time a colony had existed; it was 66 % in the first year and about 30 % of all breeding females in consecutive years. That proportion increased when older females were reduced by predators. Young females began egg-laying later than older ones and they laid fewer eggs.

The size of a clutch decreased as the breeding season progressed; on average it was 4.5 eggs in the basic period. On average, 4.3 eggs hatched and 3.4–3.8 young birds fledged per clutch. Breeding success (number of young birds leaving the nest in relation to the number of eggs laid) was from 70 % to 80 %; the mean percentage of delayed and repeated clutches in the total production of young was 6.5 %.

In the area studied, more than a half (53 %) of starling nests had been built in buildings: 42 % of all nests were recorded in tree holes and only 5 % in nest boxes (Gromadzki 1978).

The density of breeding pairs and the spatial distribution of nests were studied in a census plot of 35 km^2 (Gromadzki 1978). That density wa 12 pairs/km^2 and the distribution of the nests was of concentric characte

The composition of the food of starling pulli was studied by collectin material by the collar method (Gromadzka, Gromadzki 1978). It was found that nestlings were fed with animal food only, and that *Lepidoptera* larvae and *Coleoptera* and *Diptera* imagines constituted the main part of that food. Larvae of *Chareas graminis* and *Hadena* sp., the cockchafer *Cantharis fusca* and imagines of *Bibio* species were most frequent in those groups. No relationship between food composition and the age of pulli was recorded.

The change in population density throughout the growing period and the degree of utilization of different habitats in Żuławy as feeding grounds have been worked out on the basis of data collected on long routes where the author rode on a motor-bicycle or drove a car (Gromadzki in press a). The lowest density was in the breeding season, the highest during the passage months. Grassland was the main feeding habitat of starlings. Starlings fed on no potential crop but corn; they could only damage sprouting corn.

A preliminary estimate of the significance of the starling in Żuławy has been limited to the breeding season (Gromadzki 1976). It has been estimated that a starling population, experimentally densified to 21 pairs/km^2, took 428.459 Kcal/km^2 from 15 April to 20 June.

BIOLOGICAL CYCLE OF A STARLING POPULATION IN THE ŻUŁAWY WIŚLANE

The biological cycle of a starling population in Żuławy was divided into six distinct periods (Fig. 1):

1) spring migration – began about mid-March and lasted till mid-April; during that period the local breeding population arrived and populations living in Baltic countries, in the north-western part of Russia and in north Byelorussia passed through (Gromadzki, Kania 1976; Gromadzki in press a).
2) breeding period – egg-laying began about 23 April, delayed and repeated egg-laying lasted till the first days of June. The main period of feeding the young was from 10 to 30 May, fledging occurred at the end of May and at the beginning of June (Gromadzka, Gromadzki 1978; Gromadzki in press b).
3) post-breeding nomadic life – occurred in the early part of June and passed smoothly to the next period – summer migration.
4) summer migration – started in the latter part of June and lasted till mid-July or even mid-August. During this time local young starlings flew towards the west and young starlings from the east appeared in Żuławy (Gromadzki, Kania 1976; Gromadzki in press a, Gromadzki mat. unpubl.).
5) moulting period – began at the end of June and finished in mid-September (Gromadzki in press a).
6) autumn migration – began in September; throughout that period great numbers of starlings from the east migrated over Żuławy (Gromadzki, Kania 1976; Gromadzki in press a). The autumn migration was completed in the last days of October and after that only a few starlings remained in Żuławy.

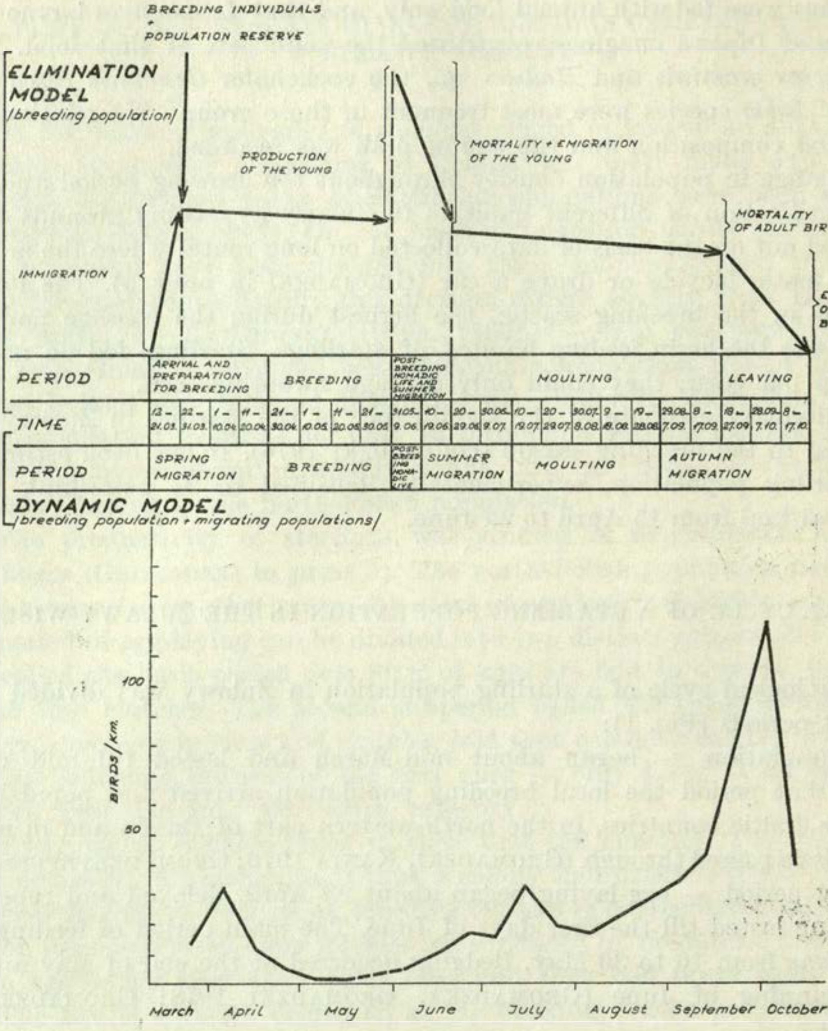

Figure 1. Change in population density of the Starling in the Żuławy Wiślane presented on the basis of the elimination and dynamic models.

FOOD REQUIREMENT OF A STARLING POPULATION

An estimate of the energy flow in a population is one of the basic data necessary for understanding its role in the functioning of an ecosystem (PETRUSEWICZ, MACFADYEN 1970). In cases when the energy consumption by a population from the unit area in unit time and the sources of this energy are the basic required values, the estimate of the full energy flow may be reduced to an estimate of energy requirement and next food requirement of a population. The basis for calculating that value is information on the number of birds in particular sex and age classes, numerical changes in consecutive life periods of a population and data on the food requirement of an individual (of a given age and sex) at consecutive stages of its life. However, obtaining detailed estimates of the above-mentioned parameters is very difficult or, in some cases, even impossible. In such cases it is necessary to use a simplified model which, in spite of its numerous inaccuracies, makes a general estimate of the studied phenomena possible.

Estimation of population density

Density changes in a population of birds living in a given area may be considered on the elimination model (e.g. WIENS, DYER 1975; WIENS, NUSSBAUM 1975; WIENS, SCOTT 1975) or the dynamic model (e.g. HOLMES, STURGES 1973; WEST, DE WOLFE 1974; WEINER, GŁOWACIŃSKI 1975). Figure 1 presents both model sworked out for a starling population living in Żuławy. The elimination model examines changes in the number of individuals based on data on the initial population state and such parameters as productivity, mortality, immigration and emigration in particular age and sex classes. The initial population comprises breeding adults and the population reserve, consisting of a usually unknown percentage of sexually mature individuals which for some reason do not start breeding (von HAARTMANN 1971) and of sexually immature birds. The size of the latter group is unknown; it contains some females and probably all males in their first full summer (BERTHOLD 1964). It is probable that some immature birds do not return to their breeding grounds, but remain in wintering grounds or transit areas till the following breeding period (GROMADZKI, KANIA 1976).

Estimation of the productivity of the starling is fairly simple, but the other parameters are difficult to calculate. However, when the elimination model is used it is most difficult to overlap the models worked out for all populations which stay in the studied area in different seasons (Fig. 1). For migrant species this is next to impossible.

The dynamic model is based on estimates of abundance carried out at definite time intervals. It records numerical changes without allowing for distinguishing between changes caused by mortality and emigration and by production and immigration and therefore estimates of these parameters are not essential for using it. This is the only model which makes a complete estimate of changing density of migrant birds in a given area possible.

During the breeding season mean density of a starling population in Żuławy was, on the average 12.54 pairs/km^2, i.e. 25 birds/km^2 (for the confidence level of 0.01 it was 13-36 birds/km^2) (GROMADZKI in press a).

The change in population density of starlings throughout the growing season is presented as changes in the number of birds recorded in 1 km of the route (Fig. 1), (GROMADZKI in press a). Assuming that the detectability of starlings is

Table 1. Density of starlings in consecutive ten-day periods of the growing season

Ten-day periods (1)	1.04 – 10.04	11.04 – 20.04	21.04 – 30.04	1.05 – 10.05	11.05 – 20.05	21.05 – 30.05	31.05 – 9.06	10.06 – 19.06	20.06 – 29.06	30.06 – 9.07	10.07 – 19.07
Individuals/km of the route (2)	32.6	11.5	5.3	1.7	2.1	–	4.7	9.3	19.0	16.2	33.9
Density coefficient (3)	15.5	5.5	2.5	0.8	1.0	–	2.2	4.4	9.0	7.7	16.1
Density individuals/ /km^2 (4)	389	138	63	25[1)]	25	25[1)]	55	110	226	193	404
Ten-day periods (1)	20.07 – 29.07	30.07 – 8.08	9.08 – 18.08	19.08 – 28.08	29.08 – 7.09	8.09 – 17.09	18.09 – 27.09	28.09 – 7.10	8.10 – 17.10	18.10 – 27.10	
Individuals/km of the route (2)	22.2	17.7	23.7	29.6	37.7	45.6	86.9	120.1	41.1	66.3	
Density coefficient (3)	10.6	8.4	11.3	14.1	18.0	21.7	41.4	57.2	19.6	31.6	
Density individuals/ /km^2 (4)	266	211	283	354	451	544	1 038	1 435	492	793	

1) It has been assumed that the density equals that in the period from 11.05–20.05.

the same throughout the growing season, the number of birds recorded during the breeding season is taken as "1" and the density coefficients for all other ten-day periods are calculated by relating the numbers of birds recorded in those periods to this (Table 1). The values for densities of birds/km^2 for the whole growing season were obtained by multiplying the density value for the breeding season by the density coefficient of particular ten-day periods (Table 1). To simplify the calculation it has been accepted that the density in a given ten-day period is constant.

Estimation of the food requirement of an individual

Pulli. The food requirement of starling pulli has been estimated by WESTERTERP (1973). On the basis of his data it has been assumed that brood of 4 pulli requires 3140 kcal, during its 20 days in the nest (GROMADZKI in press b); thus the food requirement of pullus during its development is 785 kcal. This value, accepted for further calculations, does not include the influence of clutch – size on the food requirement of pulli (ROYAMA 1966; BRISBIN 1969; MERTENS 1969). However, this is justified in the face of the fact that the mean numbers of eggs hatching (4.25 per nest) and young birds leaving the nest (3.53) (GROMADZKI in press b) are, in Żuławy, very close to 4; besides, there are no data making more precise calculations possible.

The mean food requirement of a brood of starlings in the second and third ten-day periods of May (Table 2) has been calculated on the basis of the extent

Table 2. Food requirement of a starling brood ($\bar{x}$ abundance 3.53 pulli/nest) during the 20 days in the nest (kcal/brood) with regard to pulli that have died during this time

Period (1)		11–20.05	21–30.05	Total (2)
Nestlings living for (3) about	2.5 days	15.81	–	15.81
	7.5 days	40.26	–	40.26
	12.5 days	49.98	19.92	69.90
	17.5 days	5.88	7.31	13.19
	> 20 days	1 037.82	1 729.70	2 767.52
	Total (2)	1 149.75	1 756.93	2 906.68

and time distribution of mortality starling pulli, the mean size of a brood (GROMADZKI in press b) and the cumulant of the daily food requirement of pulli during their development (WESTERTERP 1973).

Adult birds. So far the value of the food requirement of adult starlings has not been experimentally estimated. It has been theoretically estimated by calculating the daily energy budget – DEB (KENDEIGH, DOLNIK, GAVRILOV 1977) (increased during the migration period by the energy requirement of preparation for migration) with the coefficient of food assimilation taken into consideration.

DEB and the estimation of total food requirement

The daily energy budget (DEB) comprises the total existence energy and costs energy demanding activities, including the costs of breeding and moult, but without the energy expense of migration (KENDEIGH, DOLNIK, GAVRILOV 1977). Assuming that the dependence of DEB on the body weight of a bird is the same the dependence of the existence metabolism (KENDEIGH 1969, 1970), KENDEIGH, DOLNIK and GAVRILOV (1977) have presented equations which make it possible to calculate DEB values of a bird of a given body weight (W) at a given ambient temperature. The equations have been given separately for the breeding and moulting period and the other parts of the year.

For *Passeriformes* they are as follows:

the breeding and moulting periods

ambient temp. 30°C $DEB = 1.647\ W^{0.621}$

ambient temp. 0°C $DEB = 5.755\ W^{0.530}$

the remaining part of the year

ambient temp. 30°C $DEB = 1.682\ W^{0.621}$

ambient temp. 0°C $DEB = 4.641\ W^{0.530}$

Temperatures used in the calculations are means of monthly temperatures over many years in Nowy Dwór Gdański (KWIECIEŃ, TARANOWSKA 1974); weights are mean monthly weight of starlings caught in Żuławy (Gromadzki, mat. unpubl.). In the post-breeding period, the mean of the weight of adults plus young birds has been accepted as the mean weight of a starling; this has been based on the assumption that the ratio of adult to young birds is the same in the population studied.

In calculating the total food requirement it has been accepted that the coefficient of food assimilation has a constant value of 0.75. This value is in the centre of the range of values of the coefficient recorded so far in different birds kept on different diets and at different ambient temperatures (WEINER, GŁOWACIŃSKI 1975; KENDEIGH, DOLNIK, GAVRILOV 1977).

The calculated values of DEB and the total food requirement together with the initial values of temperature and body weight have been presented in Table 3.

Estimation of the energy requirements for preparation for migration

Migratory movements of passerine birds are characterized by periods of intensive migration separated by periods of less intensive migration or of no migration. This feature of migration is connected with the energy economy of

Table 3. DEB and the daily food requirement of a starling of the average body weight (W) in particular months

Month (1)	t°C	Body weight (W) (g) (2)	DEB (kcal)	Food requirement (Kcal) (3) [1])
III	0.7	78	46.2	61.6
IV	5.5	78	51.8	69.1
V	11.2	78	45.5	60.7
VI	15.2	69	38.3	51.1
VII	18.0	73	36.8	49.1
VIII	17.0	78	39.0	52.0
IX	12.9	81	38.3	51.1
X	8.6	85	42.5	56.7

[1]) calculated by multiplying DEB by a conversion factor, with 75 % food assimilation taken into account.

birds (Bljumental'et al. 1967) which, during the intervals, replenish their fat deposits for further migration.

While estimating the total food requirement of a population of birds during migration, the food requirement calculated on the basis of DEB must be increased by the daily expense of accumulating storage reserves (fat) for further migration.

Table 4. Estimate of energy requirements of preparation for migration

		Month (1)		
		III-IV	IX	X
Kcal/g/km[1])		0.00223	0.00221	0.00219
Assumed length of one stage of migration (2)		200	200	200
Average body weight (g) (3)		78	81	85
Total energy expense of one stage of migration (4)	Kcal	34.8	35.8	37.2
	g of fat[2])	8.70	8.95	9.31
Expense of building up fat reserves (Kcal)[3])	(5)	52.2	53.7	55.8
Food requirement connected with the building up of fat reserves[4]) (Kcal) necessery for covering one stage of migration	(6)	69.6	71.6	74.5

[1]) Calculated on the basis of the equation log Kcal/g/km = −2.2221 −0.227 log W (Tucker 1971, according to Kendeigh, Dolnik, Gavrilov 1977).

[2]) With the assumption that the catabolism of 1g of fat provides 4.0 Kcal (Kendeigh, Dolnik, Gavrilov 1977).

[3]) The anabolism of 1g of fat requires 6 Kcal (Kendeigh, Dolnik, Gavrilov 1977).

[4]) The coefficient of food assimilation = 75 %.

With the equation given by TUCKER (1971, according to KENDEIGH, DOLNIK, GAVRILOV 1977) it is possible to estimate the expense of a flight of a bird of a particular body weight over a particular distance. Table 4 presents the results of calculations in which the mean starlings body weight in a given month has been used as the weight and where it has been assumed that starlings cover a distance of 200 km at a time and therefore before resuming their migration they must, through intensive feeding, accumulate an amount of fat sufficient for the next stage. The length of time (in days) necessary for accumulating an adequate reserve still remains an unknown value. For the calculations it has been taken to be 2 days during the spring migration and 3 days during the autumn one. Starlings breeding in or migrating through Żuławy fly to British Islands or northern France in autumn — a distance of about 1200 km; in spring, starlings passing through this area may continue NE as for as the region of the Onega Lake, a distance of about 1300 km (GROMADZKI, KANIA 1976). Accepting two-and three-day periods of accumulating fat reserves means that the autumn migration of one bird would last for about 3 weeks and the spring one for about 2 weeks, which is quite possible.

The second value which must be estimated is the number of birds actually preparing for migration. It has been accepted that during the spring passage it is the same as density estimated for particular ten-day periods minus the density of a breeding population. During the autumn migration when practically all starlings leave Żuławy it has been accepted that starling from mid-September, which is the beginning of intensive migration (GROMADZKI, KANIA 1976), all birds are preparing for migration. The energy expense of the summer migration has not been taken into consideration.

Food requirement of the total population

Multiplication of density values by the value of individual food requirement in particular ten-day periods gives the food requirement of the population present in Żuławy in a particular ten-day period (Table 5) expressed in the form kcal/km^2/day. The total amount of energy consumed by a population in a given ten-day period may be calculated by multiplying the numbers given in the Table by 10.

The food requirement of the population is highest during the autumn migration (Table 6), which is to be expected from the high numbers of starlings present at that period. However, most astonishing is the minimal share of the breeding season in the total amount of energy used, since this period is often treated as the basis for an estimate of the role of birds in an ecosystem. A whole breeding population takes, throughout the period it stays in its breeding ground, only about 7 % of the total amount of energy collected by starlings from that area. These data indicate that in future studies on the effect of birds on agriculture or in natural systems it will be necessary to include in the studies the whole

Table 5. Food requirement of a starling population in consecutive ten-day periods of the growing season

Ten-day periods (1)	Daily food requirement (Kcal/indiv.) (2)	Expense of preparation for migration (Kcal/indiv./day) (3)	Expense of the development of pulli (Kcal/nest/day) (4)	Total food requirement of a populati (Kcal/km^2/day) (5)
22.03–31.03	61.6	34.8	—	12626
1.04–10.04	69.1	34.8	—	39547
11.04–20.04	69.1	34.8	—	13468
21.04–30.04	69.1	34.8	—	5675
1.05–10.05	60.7	—	—	1517
11.05–20.05	60.7	—	114.9	2963
21.05–30.05	60.7	—	175.7	3725
31.05–9.60	51.1	—	—	2811
10.06–19.06	51.1	—	—	5621
20.06–29.06	51.1	—	—	11549
30.06–9.07	49.1	—	—	9476
10.07–19.07	49.1	—	—	19836
20.07–29.07	49.1	—	—	13061
30.07–8.08	52.0	—	—	10972
9.08–18.08	52.0	—	—	14716
19.08–28.08	52.0	—	—	18408
29.08–7.09	51.1	—	—	23046
8.09–17.09	51.1	—	—	27798
18.09–27.09	51.1	23.9	—	77850
28.09–7.10	56.7	24.8	—	116952
8.10–17.10	56.7	24.8	—	40098
18.10–27.10	56.7	24.8	—	64630

period when a species stays in a given area with particular regard to the period of migrations and regardless of any methodological and technical difficulties.

FEEDING HABITATS AND AGRICULTURAL SIGNIFICANCE

Studies on the feeding intensity of starlings in different habitats have been carried out in the Żuławy Wiślane (Gromadzki in press a).

Starling feed in all types of land habitats, utilizing them to a different degree in different seasons (Gromadzki 1969, in press a). The degree of utilization of a given habitat is influenced not only by its own attractiveness, but also by the accessibility and attractiveness of other feeding places at that time.

Table 6. Food requirement of a starling population in consecutive periods of the biological cycle

Period (1)	Food requirement throughout the period (2)	
	kcal/km²	%
Spring migration (3)	656 410	12.2
Breeding season (4)	138 800	2.6
Post-breeding nomadic life (5)	84 320	1.6
Summer migration (6)	539 220	10.1
Moult period (7)	671 420	12.5
Autumn migration (8)	3 273 280	61.0
Total (9)	5 363 450	100.0
Breeding population throughout the period it remained in the area (10)	352 810	6.6

Starlings prefer feeding in areas without vegetation or covered with low vegetation, but they also feed in habitats covered with tall vegetation if its density is not too great. Therefore, in Żuławy starlings feed in corn, poppy and caraway walking between rows of plants. Possibly the sight of starlings sitting in a crop makes some farmers think them destructive, but this opinion has been proved true during the investigations (Gromadzki in press a).

The plant food of starlings includes seeds of cultivated plants, mainly corn (Gromadzki 1969), but this fact alone does not prove that starlings are destructive (the situation is similar in the case of other species, e.g. the rook – Gromadzka in press) because grain is often collected in a form in which it cannot be used by man (e.g. corn scattered on a stubble field, on roads, among straw, in manure). For feeding to be proved destructive it must be shown that large amounts of seed-grain or crop are taken before harvesting. However, even then the case is not proven because, as has been shown by Dyer (1975), plants damaged by birds may, as a result of compensation growth, give a greater and more valuable crop than plants on which birds have not fed (the case decribed by Dyer referred to a different bird species, but nevertheless, his paper is a clear warning against a one-sided interpretation of different biological phenomena).

As previously mentioned, starlings have not been recorded pecking out grain from standing plants; pecking grain out of ears of corn put in stacks has been recorded sporadically (Gromadzki in press a) but this is of no economic importance. However, starlings have been recorded feeding in newly-sown and sprouting corn. In the latter case it was found that starlings walking along a row of sprouting corn pulled out the young plants and ate the swollen grains. The feeding intensity of starlings in newly-sown crops and the estimated amount of seed-grain consumed have been presented in Table 7. Since the area of crop cultivation in Żuławy is about 30 % of the whole area (LASKOWSKI 1974), the total consumption of seed-grain from 1 ha from April to October is 3.9 kg. The values presented in Table 7 are undoubtedly overstated since they have been calculated on the assumption that starlings, feeding in newly-sown and sprouting corn eat only grains. In fact they eat invertebrates at the same time. For instance, in the second ten-day period of May, for which the value of grain consumption has been estimated as 0.8 kg/km^2 (Table 7), starlings intensively feed their young and no corn has been recorded in the food of pulli in Żuławy (GROMADZKA, GROMADZKI 1978). However, ignoring the fact that the totals are an over- estimate and accepting the result of calculations as the true extent of the consumption of seed-grain it is still possible to state that this consumption is of no agricultural significance since it constitutes only about 2 % of the amount of seed-grain sown in 1 ha.

It is more difficult to estimate the usefulness of starlings as predators on pest species of invertebrates which occur in crops. The amount of invertebrates removed from a unit of the area of a crop has been estimated for grassland only because it has been possible to assume that in this habitat starlings eat animal food only. In order to simplify the calculations it has been assumed that this food consists entirely of insects. According to the results of the calculations a starling population eats, through its annual cycle, 52 kg of insects from 1 ha of grassland (Table 8).

The above data show that a starling population does not cause any economically significant damages in agriculture in the Żuławy Wiślane, but, thanks to its large consumption of invertebrates among which are many pest insects (GROMADZKI 1969; GROMADZKA, GROMADZKI 1978), it may contribute to the reduction in density of a pest population and therefore to an increase in crops.

DISCUSSION

The accuracy of results of an estimate of the food requirement of a starling population, based on one or other model, depends on two factors. On the one hand, it depends on the correctness of the construction of the model and, on the other, on the kind and accuracy of numerical data which characterize the studied population and its habitat and which are used as initial data for an analysis (WIENS, INNIS 1974). At the present moment, for most animal species there are no basic initial data or they are so inaccurate that constructing more precise and complicated models is impossible (LEVINS 1966, accor-

Table 7. Feeding intensity of starlings feeding in newly sown seed-grain and in sprouting corn and the amount of seed-grain consumed

	Period of spring sowing (1)					Period of aftercrop sowing (2)			Period of autumn sowing (3)				Total (4)
Ten-day periods (5)	1–10.04	11–20.04	21–30.04	1–10.05	11–20.05	20–29.06	30.06–9.07	10–19.07	18–27.09	28.09–7.10	8–17.10	18–27.10	
Percentage of all feeding birds (6)	33	22	3	4	8	1	6	1	11	1	6	8	–
Grain consumption [1] kg/km^2/period (7)	43.4	9.9	0.6	0.2	0.8	0.4	1.9	0.7	28.5	3.9	8.0	17.2	115.2

[1]) calculated with the assumption that the calorific equivalent of 1 g of dry mass = 4,3 and the water contents in wet mass of grain = 30 %.

Table 8. Consumption of insects by a starling population in grassland

Consumption (1)	Period						Total (8)
	Spring migration (2)	Breeding (3)	Post-breeding nomadic life (4)	Summer migration (5)	Moulting (6)	Autumn migration (7)	
Kcal/period/km^2 of the whole area (9)	282 915	75 226	74 729	333 736	320 140	716 655	1 803 401
g of wet mass/period/km^2 of the whole area[1]) (10)	171 463	45 592	45 290	202 262	194 022	434 332	1 092 961
g of wet mass/ha/period[2]) (11)	8 165	2 171	2 157	9 632	9 239	20 682	52 046
g of wet mass/m^2/period (12)	0.82	0.22	0.22	0.96	0.92	2.07	5.20

[1]) calculated with the assumption that the calorific equivalent of 1 g of dry mass of insects = 5.5 (Kale 1965), and the water contents in wet mass of the insects = 70 %.

[2]) area of grassland in the Żulawy Wiślane = about 21 % of the whole area (Laskowski 1974).

ding to WIENS, INNIS 1974). Using the analysis of the sensitivity of a simulation model of the energy flow in a population WIENS and INNIS (1974) have demonstrated that those parameters which have the greatest influence on the accuracy of obtained results are population density and the coefficient of food assimilation. Their analysis has also revealed that parameters connected with breeding have a very small influence on the general result of an analysis. The results presented in this paper are an experimental corroboration of this statement. On the basis of these results it is possible to conclude that, in some situations, even a complete omission of the breeding population in an analysis would not change the general result. This is made clear by bearing in mind that the substantial proportion of energy flow is influenced first by the number of individuals and the length of their stay and not by the intensity of biological processes (e.g. growth) because the basic energetistic need of birds (KENDEIGH, DOLNIK, GAVRILOV 1977) is not to breed, but to maintain a high body temperature.

In the present study an estimate has been made of the impact of starlings on crops in the Żuławy Wiślane and it has been shown that their eating seed-grain is of no economic significance. The above conclusion may be considered true for the whole country because the density of the starling in Żuławy is probably higher than in other parts of Poland. However, damages in orcharding have not been included here because they are a completely different problem.

Hitherto estimates of the effect of starlings on agricultural ecosystems limited in their time range to the breeding season, have led their authors to a conclusion that starlings have no or only a minimal influence on the abundance of insects they feed on. KLUIJVER (1933, 1938) has estimated that starling pulli eat, throughout their development, 0.03 % of an earth-worm population and about 1 % of a population of *Tipula* sp. larvae. DUNNET (1955) has estimated the value of the food of starling pulli to be 1–7 % of a population of *Tipula* sp. larvae. BOGUCKI (1977) has estimated that, in the area of his study, a breeding population of the starling eats about 0.12 % of an earth–worm population and about 1.5 % of a Colorado beetle population.

At the same time these and other authors have recorded instances when starlings destroyed centres of mass occurence of insects, both in forests and in open areas (KLUIJEV 1938; WEINZIERL 1961; BULL 1973) which prevented the vegetation of a given area from being destroyed.

The above facts belong to two opposing groups. One comprises data collected by means of experimental-analytic methods and they seem to indicate that starlings have no influence on the abundance of insects constituting their food. The other group consists of data from frequently accidental observations and they indicate something completely different. A similar divergence of opinion is found in relation to other bird species, both when considering them separately or in complexes inhabiting particular habitats (McLELAN 1958;

Gibb 1960; Tinbergen 1960; Kamm 1973; Wiens 1973; Holmes, Struges 1974; Wiens, Nussbaum 1975; Wiens, Scott 1975; Bengtson et al. 1976).

However, the above-mentioned divergence of facts is an apparent one and it is a result of the methods used in investigating the impact of birds on the abundance of their prey. Examples recorded of the reduction of invertebrate populations by birds illustrate what birds can do in this respect; These possibilities may be realized when two basic conditions are satisfied: a high density of birds in a given place and at a given time and their attention being fixed on a particular kind of prey. It would seem that in nature these conditions occur far more frequently than is reflected in results of investigations. Birds base their food selectivity on a "profitability" principle (Royama 1970), they concentrate in places of mass occurrence of insects (Ejgelis 1961) — the investigation models used do not usually include this phenomenon because of methodological difficulties connected with it. Secondly, due to difficulties connected with an estimate of the abundance of birds during the non-breeding period, most of the analyses have till now concerned the breeding season only. Apart from this, again due to methodological difficulties such estimates have considered only a part of a population, usually without the population reserve and the non-breeding group of immature birds.

Estimates for periods longer than the breeding season which have been carried out by means of elimination models (e.g. the model of Wiens, Innis 1974) have also been based on an estimate of the abundance of birds during the breeding season. Estimates for the whole year carried out by means of dynamic models are usually based on population counts done at long time intervals (e.g. Weiner, Głowaciński 1975) — usually month or two-week intervals. Such intervals are too long for observing changes in bird abundance caused by the waves of migrants passing a given area.

The resources of a given area are not accesible to a population to the same degree throughout the year and therefore only a small percentage of these resources may be utilized under natural conditions (Remmert 1973). An increase in the ecological efficiency may be obtained by supplementing reserves of resources in unfavourable seasons through an import of these resources from other habitats or areas, which is a common practice in stock-breeding. An import of resources may be substituted by a translocation of consumers which is a frequent mechanism in wild nature. Migrations of animals are such a mechanism. Birds, as a group of animals, have brought this mechanism to perfection and it may be expected that advantages resulting from migrations, an increase in the ecological efficiency among others are particularly high in this group of animals. If periods of migrations are still omitted while estimating the significance of birds, only the margins of the studied phenomenon will be investigated. The 6.6 % of the share of the breeding population in the total amount of energy consumed by a given species in a given area throughout the year are a plain proof of this.

CONCLUSIONS

1. The food requirement of a starling population during the whole period of its staying in Żuławy is 5 363 450 $Kcal/km^2$.

2. 2.6 % of the energy taken by starlings from this area is for the breeding season whereas throughout the period a breeding population stays in the area it takes only 6.6 % of the total energy removed by the whole population from this area.

3. 73% of the energy taken by starlings in Żuławy is for the periods of spring and summer migrations.

4. In Żuławy a starling population does not causy any economically significant damages in agriculture and, to a considerable degree, it contributes to the reduction of the abundance of pest populations. Since the density of starlings in Żuławy Wiślane is probably higher than in other parts of Poland, this conclusion may be considered true for the whole country. Damages in orcharding, being an entirely different problem, are not included here.

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STRESZCZENIE

[Zapotrzebowanie pokarmowe oraz rola szpaka, *Sturnus vulgaris* L. w gospodarce rolnej na Żuławach Wiślanych]

Celem pracy jest próba oceny zapotrzebowania pokarmowego populacji szpaka na Żuławach Wiślanych oraz roli jaką gatunek ten odgrywa w gospodarce rolnej tego terenu. Jednocześnie jest ona podsumowaniem wyników badań prowadzonych nad szpakiem na Żuławach w latach 1971–1974, w ramach zespołu problemowego PAN „Rola ptaków w agrocenozach".

Dokładne opisy stosowanych metod zbierania i opracowywania materiału zostały podane w innych publikacjach; w niniejszej ograniczono się do podania informacji ogólnych oraz sposobu dokonania obliczeń, stanowiących zasadniczą część tej pracy.

Cykl biologiczny populacji szpaka na Żuławach podzielono na sześć okresów: wędrówki wiosennej, rozrodu, koczowania polęgowego, wędrówki letniej, pierzenia i wędrówki jesiennej. Zmiany liczebności szpaków w ciągu całego cyklu rozpatrywano stosując tzw. model dynamiczny, oparty na przeprowadzanych w określonych odstępach czasu ocenach stanów liczebności. Model ten, w przeciwieństwie do tzw. modelu eliminacyjnego, którego zastosowanie ograniczone jest praktycznie tylko do populacji lęgowych, pozwala na ocenę dynamiki liczebności wędrownych gatunków ptaków na określonym terenie.

Dynamikę liczebności szpaków przedstawiono w postaci zmian liczby ptaków spotykanych na odcinku 1 km. Zakładając, że wykrywalność szpaków jest taka sama w ciągu całego okresu wegetacyjnego, za "1" przyjęto liczbę ptaków spotkanych w okresie karmienia młodych i odnosząc do niej liczby ptaków obserwowanych w innych okresach, obliczono dla nich współczynniki zagęszczenia.

Współczynniki te, pomnożone przez wielkość zagęszczenia z okresu lęgowego, pozwoliły na ocenę zagęszczenia w ciągu całego okresu wegetacyjnego.

Zapotrzebowanie pokarmowe piskląt oceniono w oparciu o dane experymentalne, natomiast wielkość zapotrzebowania pokarmowego ptaków dorosłych oszacowano drogą obliczenia dziennych budżetów energetycznych (DEB), w okresach wędrówki zwiększonych o przypuszczalny energetyczny koszt przygotowań do wędrówki, z uwzględnieniem współczynnika przyswajalności pokarmu.

Zapotrzebowanie pokarmowe populacji szpaków jest największe w okresie jesiennej wędrówki; łącznie, w okresach wędrówek, szpaki zjadają 73 % ogółu pokarmu pobieranego przez ten gatunek na badanym terenie. Udział okresu lęgowego, jak również populacji lęgowej przez cały okres przebywania jej na badanym obszarze są tu znikome (odpowiednio 2.6 % i 6.6 %). Dane te wskazują, że badania nad rolą ptaków jako konsumentów powinny obejmować cały okres przebywania danego gatunku na badanym terenie i nie mogą być ograniczane do okresu lęgowego jak to często ma miejsce. Niewłaściwe jest także pomijanie populacji przelotnych i koncentrowanie uwagi na populacji lęgowej.

Oceniono ilość ziarna siewnego zjadanego przez szpaki z powierzchni 1 ha upraw zbożowych oraz ilość owadów zjadanych przez te ptaki z powierzchni 1 ha użytków zielonych. W konkluzji stwierdzono, że populacja szpaka na Żuławach nie wyrządza rolnictwu szkód istotnych ekonomicznie, natomiast dzięki zjadaniu dużej ilości bezkręgowców w tym wielu owadów uznanych za szkodniki, może w znacznym stopniu przyczyniać się do poprawienia zdrowotności upraw, a tym samym do zwiększenia plonów.

Objaśnienia do tabel i wykresu:

Tabela 1. Zagęszczenie szpaków w kolejnych dekadach okresu wegetacyjnego. (1) — dekady; (2) — osobników/km trasy; (3) — współczynnik zagęszczenia; (4) — zagęszczenie osobników/km^2; [1]) przyjęto, że zagęszczenie jest równe zagęszczeniu w dekadzie 11.05–20.05.

Tabela 2. Zapotrzebowanie pokarmowe lęgu szpaka ($\bar{x}$ liczebność 3.53 piskląt/gniazdo) w okresie 20 dni przebywania w gnieździe (kcal/lęg) z uwzględnieniem piskląt, które zginęły w czasie rozwoju. (1) — okres; (2) — razem; (3) — pisklęta przeżywające średnio.

Tabela 3. Dzienny budżet energetyczny (DEB) oraz dzienne zapotrzebowanie pokarmowe szpaka o średniej masie ciała (W), w poszczególnych miesiącach roku. (1) — miesiąc; (2) — masa ciała; (3) — zapotrzebowanie pokarmowe; [1]) obliczono przez pomnożenie DEB przez przelicznik uwzględniający 75% przyswajalności pokarmu.

Tabela 4. Ocena energetycznych kosztów przygotowań do wędrówki. (1) — miesiąc; (2) — założona długość etapu wędrówki; (3) — średnia masa ciała; (4) — ogólny koszt energetyczny etapu wędrówki; (5) — koszt wytworzenia rezerw tłuszczowych; (6) — zapotrzebowanie pokarmowe związane z wytworzeniem rezerw tłuszczowych potrzebnych do pokonania etapu wędrówki; [1]) obliczony na podstawie równania log kcal/g/km = −2.2221 −0.227 log W; [2]) przy założeniu, że katabolizm 1 g tłuszczu dostarcza 4.0 kcal; [3]) anabolizm 1 g tłuszczu wymaga 6 kcal; [4]) współczynnik asymilacji pokarmu = 75%.

Tabela 5. Zapotrzebowanie pokarmowe populacji szpaka w kolejnych dekadach okresu wegetacyjnego. (1) — dekady; (2) — dzienne zapotrzebowanie pokarmowe kcal/osobnika; (3) — koszt przygotowania do wędrówki kcal/osobnika/dzień; (4) — koszt rozwoju piskląt kcal/gniazdo/dzień; (5) — sumaryczne zapotrzebowanie pokarmowe populacji kcal/km²/dzień.

Tabela 6. Zapotrzebowanie pokarmowe populacji szpaka w kolejnych okresach cyklu biologicznego. (1) — okres; (2) — zapotrzebowanie pokarmowe w całym okresie; (3) — wędrówka wiosenna; (4) — okres lęgowy; (5) — koczowanie polęgowe; (6) — wędrówka letnia; (7) — okres pierzenia; (8) — wędrówka jesienna; (9) — razem; (10) — populacja lęgowa przez cały okres przebywania na badanym terenie.

Tabela 7. Intensywność żerowania szpaków na zasiewach i wschodach zbóż oraz ilość zjadanego ziarna siewnego. (1) — okres siewów wiosennych; (2) — okres siewu poplonów; (3) — okres siewów jesiennych; (4) — razem; (5) — dekady; (6) — % ogółu żerujących ptaków; (7) — konsumpcja ziarna km²/kg/okres; [1]) obliczono przy założeniu, że ekwiwalent kaloryczny 1 g suchej masy ziarna = 4.3, zaś zawartość wody w świeżej masie ziarna = 30 %.

Tabela 8. Konsumpcja owadów przez populację szpaka na użytkach zielonych. (1) — konsumpcja owadów na użytkach zielonych; (2) — wędrówka wiosenna; (3) — okres lęgowy; (4) — koczowanie polęgowe; (5) — wędrówka letnia; (6) — okres pierzenia; (7) — wędrówka jesienna; (8) — razem; (9) — kcal/okres/km² ogólnej powierzchni; (10) — g świeżej masy/okres/km² ogólnej powierzchni; (11) — g świeżej masy/ha/okres; (12) — g świeżej masy/m²/okres; [1]) obliczono przy założeniu, że ekwiwalent kaloryczny 1 g suchej masy ciała owadów = 5.5, zaś zawartość wody w świeżej masie ciała = 70 %; [2]) areał użytków zielonych na Żuławach Wiślanych = ca 21 % ogółu powierzchni.

Wykres 1. Dynamika liczebności szpaka na Żuławach Wiślanych przedstawiona w oparciu o model eliminacyjny i model dynamiczny.

РЕЗЮМЕ

[Заглавие: Пищевая потребность и роль скворца, *Sturnus vulgaris* L. в сельском хозяйстве на Вислинских Жулавах]

Целью работы является попытка оценки пищевой потребности популяции скворца на Вислинских Жулавах и роли этиго вида, которую он играет в сельском хозяйстве рассматриваемого региона. Одновременно в настоящей работе подводится итог исследований, проводимых по скворцу на Вислинских Жулавах в 1971–1974 годах в рамках проблемной группы ПАН „Роль птиц в агроценозах".

Подробное описание примененных методов сбора и обработки материала было приведено в иных публикациях; в настоящей автор ограничивается только до представления общих информаций и способов, при помощи которых произвел рассчеты, составляющие основную часть работы.

Биологический цикл популяции скворца с Вислинских Жулав был поделен на шесть периодов: весенняя миграция, размножение, послегнездовая кочевка, летняя миграция, линька и осенняя миграция. Изменение численности скворцов на протяжении всего цикла рассматривалось при посредстве так называемой динамической модели, основанной на оценке состояния численности, производимой с определенными промежутками времени. Эта модель, в противоположность так называемой элиминирующей модели, которая может быть применена практически

только к гнездовым популяциям, позволяет оценить динамику численности мигрирующих видов птиц на определенных пространствах.

Динамика численности скворца представлена в виде изменений числа птиц, встречающихся на отрезке 1 км. Исходя из принципа, что обнаружение скворцов не меняется на протяжении всего вегетационного периода, за „1" была принята численность скворцов, встречающихся в период выкармливания птенцов. К этой исходной величине была отнесена численность птиц, наблюдаемых в других периодах, и таким образом высчитаны коэффициенты плотности.

Пищевая потребность птенцов оценивалась на основании экспериментальных данных, у взрослых же птиц пищевая потребность определялась путем исчисления дневного энергетического бюджета (DEB), который в период миграции, видимо, повышается на величину подготовки к миграции, с учетом показателя усвоения корма.

Самая высокая пищевая потребность популяций скворца наблюдается в период осенней миграции; в общем на протяжении периодов миграции скворцы съедают 73% всего потребляемого этим видом на исследуемой территирии корма. Часть, припадающая на гнездовой период, а также на гнездовую популяцию за весь период ее пребывания на исследуемой территории весьма незначительна (соответственно 2.6% и 6.6%). Эти данные указывают на то, что исследования по роли птиц как потребителей должны охватывать весь период пребывания данного вида на исследуемой территории и не могут быть ограничены только до гнездового периода, как это часто бывает. Необходимо также принимать во внимание пролетные популяции, а не концентрироваться только на гнездовой популяции.

Оценивалось количество посевного зерна, съедаемого скворцами с 1 га посевных площадей, и количество насекомых, съедаемых этими птицами с 1 га пастбищных угодий. Результаты свидетельствуют о том, что популяция скворца на Жулавах не приносит сельскому хозяйству существенных экономических убытков. Наоборот, благодаря потреблению значительного количества беспозвоночных, в том числе многочисленных признаных вредными насекомых она может способствовать улучшению состояния сельскохозяйственных угодий, а этим самым повышению их урожайности.

Подписи к таблицам и графику:

Таблица 1. Плотность скворцов в очередных декадах вегетативного периода. (1) — декады; (2) — особей/км маршрута; (3) — коэффициент плотности; (4) — плотность особей/км^2; [1]) принято, что плотность равна плотности в декаде 11.05–20.05.

Таблица 2. Пищевая потребность выводка скворца ($\bar{x}$ численность 3.53 птенца/гнездо) на протяжении 20 дней пребывания в гнезде (ккал/выводок) с учетом птенцов, погибших в период развития. (1) — период; (2) — всего; (3) — птенцы прожившие в среднем.

Таблица 3. Дневной энергетический бюджет (DEB) и дневная пищевая потребность скворца со средним весом тела (W) по отдельным месяцам года. (1) — месяц; (2) — вес тела; (3) — пищевая потребность; [1]) высчитанная путем умножения DEB на условную единицу, учитывающую усвоение пищи в 75%.

Таблица 4. Оценка энергетических потребностей на подготовку к миграции. (1) — месяц;

(2) — предполагаемая продолжительность периода миграции; (3) — средний вес тела; (4) — общая затрата энергии в период миграции; (5) — расход энергии на построение жировых запасов; (6) — пищевая потребность, связанная с построением жировых запасов, необходимых для преодоления этапа миграции; [1]) высчитанный на основании уравнения log ккал/г/км = — 2.2221–0.227 log W; [2]) при принципе, что катаболизм 1 г жира дает 4.0 ккал; [3]) анаболизм 1 г жира требует 6 ккал; [4]) коэффициент ассимиляции пищи = 75%.

Таблица 5. Пищевая потребность популяции скворца по очередным декадам вегетационного периода. (1) — декады; (2) — дневная пищевая потребность в ккал/особь; (3) — расход на подготовку к миграции в ккал/особь/день; (4) — расход на развитие птенцов в ккал/гнездо/день; (5) — суммарная пищевая потребность популяции в ккал/км^2/день.

Таблица 6. Пищевая потребность популяции скворца в очередных периодах биологического цикла. (1) — период; (2) — пищевая потребность за весь период; (3) — весенняя миграция; (4) — гнездовой период; (5) — послегнездовые кочевки; (6) — летняя миграция; (7) — период линьки; (8) — осенняя миграция; (9) — всего; (10) — гнездовая популяция в течение всего периода пребывания на исследуемой территории.

Таблица 7. Интенсивность кормежки скворцов на посевах и всходах злаковых культур и количество поедаемого посевного зерна. (1) — период весенних севов; (2) — период пожнивных севов; (3) — период осенних севов; (4) — всего; (5) — декады; (6) — % всех кормящихся птиц; (7) — потребление зерна в км^2/кг/период; [1]) высчитана, исходя из принципа, что калорийный эквивалент 1 г сухой массы зерна равен 4.3, а содержание воды в свежей массе зерна составляет 30%.

Таблица 8. Потребление популяцией скворца насекомых на пастбищны хугодиях. (1) — потребление насекомых на пастбищах; (2) — весенняя миграция; (3) — гнездовой период; (4) — послегнездовые кочевки; (5) — летняя миграция; (6) — период линьки; (7) — осенняя миграция; (8) — в общем; (9) — ккал/период/км^2 всей площади; (10) — г свежей массы/период/км^2 всей площади; (11) — г свежей массы/га/период; (12) — г свежей массы/м^2/период; [1]) высчитано, исходя из принципа, что калорийный эквивалент 1 г сухой массы тела насекомых равен 5,5, а содержание воды в свежей массе составляет 70%; [2]) площадь пастбищных угодий составляет на Жулавах около 21% общей площади.

График 1. Динамика численности скворца на Вислинских Жулавах, представленная на основании элиминирующей модели и динамической модели.

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