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Diet of nestling Barn Swallows *Hirundo rustica* in rural areas of Poland

Research Article

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Abstract: Analysis of faecal sacs of nestling Barn Swallows *Hirundo rustica* from 52 breeding colonies located within fifteen spatially-separated villages in Poland has revealed that the basic component of the diet was Coleoptera (56.1% of all identified prey items), followed by Hymenoptera (24.1%), Diptera (16.1%) and Hemiptera (3.3%). The average mass of all prey items with known weight amounted to 3.40 mg (95% CL, 3.16–3.63 mg; median=0.49 mg) dry weight. Coleopterans associated with dung and manure jointly made up 23.5% of the number and 24.3% of the total biomass of all representatives of the order. Statistically significant negative relationships between the average weight of prey and number of prey found in 52 analyzed breeding sites suggest a particular need for Barn Swallows to find larger-bodied prey rather than to exploit the local abundance of smaller prey. The high percentage of Coleoptera in the diet of nestling Barn Swallows probably results from extensive or traditional farm management based on rules of organic farming in agricultural areas of central Europe, mainly commonly used organic fertilizers, and suggests the importance of these insects as a more easily accessible and larger-bodied prey in comparison to some small Diptera or Hymenoptera. We believe that a large number of randomly collected faecal samples from tens of breeding sites allow us to precisely describe variation in the diet of the Barn Swallow. Our work has great importance for documenting of the food composition of the Barn Swallow in traditional European countrysides, *i.e.* under environmental and agricultural conditions which, as a result of transformations of the system of farming, ceased to exist in the western and northern part of this continent.

Keywords: *Aerial-feedings birds • Airborne insects • Bird diet • Diet composition • Insect biomass • Prey selection • Farmland*

1. Introduction

Many species of birds associated with agricultural areas of Europe shown steady declines, which is the result of reduced food resources as a consequence of agricultural intensification [1-3]. An example of a bird species closely associated with agricultural activities and humans, and very sensitive to recent changes in agriculture, is the Barn Swallow *Hirundo rustica* [4-6]. This species breeds mainly in buildings where farm animals, mainly cows or pigs, are kept [7-11]. The ongoing intensification of agriculture, especially a decline in the number of small farm holdings, termination of dairy farming and changes in the distribution of cattle, are shown as the main factors reducing breeding sites. This, in turn, has affected the negative trend of Barn Swallow numbers in rural areas of north-western Europe [3,5-15]. Møller [8,9] maintains that the decline of Barn Swallow populations is caused mainly by the reduction of its food resources, large Diptera, associated with cow rearing, mostly horse flies Tabanidae, hover flies Syrphidae and muscid flies Muscidae, which may constitute over 90% of the diet [5].

Although it seems that the diet of Barn Swallows was sufficiently known [reviews in 4,5,16], there are no recent dietary studies on this bird from Europe. Most such studies come from the 1970s and 1980s, mainly from optimal breeding places, *i.e.* large cattle farms [17-21]. However, recent revolutionary changes in agricultural practices and the introduction of the modern tillage system – *sensu* Robinson and Sutherland [1], have altered the food resources of farmland birds [22,23], implying the need for new studies on food composition in the Barn Swallow. In light of recent changes in agricultural activity, it seems that dietary studies in

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central Europe, where agriculture is still characterized by a traditional system of animal rearing, might be helpful in explaining the causes of the negative trend of Barn Swallow numbers in rural areas of this continent. Especially, that a reduction in food availability during the breeding season is suggested to have reduced Barn Swallow breeding success [8,10].

The diet of Barn Swallows can be highly differentiated. In general, Diptera are recognized as the main component of the Barn Swallow diet [reviews in 4,5,16]. However, some authors have revealed that dipterans can represent only a small proportion of the food consumed by Barn Swallow (1.9% in adult individuals in late summer [24]). The diet of Barn Swallows can be strongly dependent on the progression of the breeding season, weather conditions and local food resources [17-21].

Papers focusing on the Barn Swallow diet pertain mainly to food boluses obtained by the ligature method, and are less frequently based on faecal analysis from a small number of breeding colonies (references herein). In earlier studies, analysis of faeces was successfully employed to determine the food composition in hirundines [25-28]. This method yields a reliable picture of diet in the case of insectivorous birds; the differences obtained by the two methods is used to establish the proportions in a diet of different taxonomical groups of insects, e.g. analysis of food samples and faeces obtained from the same chicks, do not exceed 2% [29].

Many papers dealing with the diet of the barn swallow or other hirundines concern prey selection as related to the abundance, biomass and size of available insects. The results show that the average size of prey taken by hirundines is always larger than the average size of prey available in a given habitat [21,28-32]. The same is true for other farmland birds, e.g. red-backed shrike *Lanius collurio* [33], which is suggestive of other problems linked to agriculture intensification and the potential importance, availability and selection of different prey in relation to quality of the traditional agricultural landscapes of central Europe.

The present paper aimed to characterize the diet composition and prey in nestling Barn Swallows from tens of breeding colonies located in fifteen spatially separated villages of Poland. This area may represent the traditional countryside of the central Europe. Many of the breeding sites were characterized by a traditional system of animal rearing, *i.e.* keeping a small number of animals on the farm representing a few species (mainly poultry, cattle and pigs), which often remained in the open around the buildings. The rearing system is extensive in comparision to northern and western Europe. This enabled our study to document the Barn Swallow diet under environmental and agricultural conditions which, as a result of transformations to farming systems, ceased to exist in western Europe in the 1960s. The present paper also discusses the variability and differences in the composition of diet at particular breeding sites and selection of insects by Barn Swallow in relation to their weight, biomass and abundance in different agricultural landscape habitats.

2. Experimental Procedures

Sampling of faeces was conducted during consecutive visits to houses and farm buildings located in fifteen villages of south-west and central Poland (extreme locations: 51°10′57″ N, 16°57′18″ E; 51°21′41″ N, 18°41′01″ E). Faeces were collected at 52 sites (buildings) with occupied Barn Swallow nests present. The collection of faeces was carried out between 30 June and 4 August 2005. The faeces were collected from farmstead buildings used for rearing animals, mainly cattle and pigs, and also from buildings inhabited by people on farms where no livestock had been kept. In one breeding site we only collected faeces once. At individual breeding sites (buildings), the number of nests and farm animals was established through counts and direct interviews with farm owners. In all colonies from which faeces were collected, 291 occupied nests of the Barn Swallow were recorded; range 1-25 pairs (distribution of the number of nests / number of colonies: 1/12, 2/8, 3/4, 4/3, 5/8, 6/6, 8/3, 10/3, 17/2 and 25/3).

Under occupied nests, from a few to a dozen or so faecal sacs were collected. In further analysis, to determine the food items for each individual breeding site, five faecal samples were used. We conducted this assessment for the five faecal sacs simultaneously because of differences in their size and because some of them broke into smaller pieces.

Nestling Barn Swallows, start to defecate outside the nest at the age of ca four days; before this, the faecal sacs were removed by the parents to a greater distance. It cannot be excluded, however, that faeces of adult birds may have been taken for analysis, a possibility suggested by some authors [27,28]. The faeces collected were kept in a freezer at –20ºC. Identification of faecal components was performed under a binocular (×20), after prior defrosting and separation in Petri dishes. The number of prey items representing particular invertebrate species (mainly insects) was established based on the quantity of fragments of chitin parts, chiefly the elytra (for different families and genera of Coleoptera, Homoptera or Heteroptera), wings (in the case of Diptera, Hymenoptera, Odonata), mouthparts (most of the orders) and other preserved organs (e.g. limbs, petiolus, clypeus, mandibule). When determining of number of prey belonging to a particular species, we applied a rule of summation of different chitin parts to the level of one individual, *i.e.* two or more different fragments of chitin parts (e.g. head, mandibles, six legs and other parts in the case of ants) from one dropping was treated as belonging to the same individual of a given species. Special attention was paid to the presence of small prey items, mainly Diptera and Hymenoptera.

The diet composition at particular breeding sites was assessed as the number, proportions and mass of four main insect orders, namely Coleoptera, Diptera, Hymenoptera and Hemiptera, found in the faeces, and have been calculated based on the actual number of representatives of particular orders. The order Heteroptera has been treated jointly with the order Homoptera, the latter scarcely represented in the study material (Heteroptera + Homoptera = Hemiptera; after [30]).

The mass of prey has been expressed as dry mass, *i.e.* mg d.w.; these values were obtained from detailed measurements of insect weights based on analysis of 479 087 individuals of different taxa of insects [34-36] and was used in other studies on diet of insectivorous birds to assess the biomass of prey [33,37,38].

In order to illustrate prey selection by the barn swallow in relation to the general diversity of airborne insects available in the different habitats of the agricultural landscape, we used results from investigations carried out in western Poland from 1975–1979 [34-36]. We realize that these data were collected in the fairly distant past. Because we did not conduct qualitative and quantitative assessment of flying insects in the vicinity of breeding sites of barn swallows, the use of these data could only give a general outline of the composition and biomass of insects in different habitats of agricultural landscape. Studies from 1975–1979 characterize the species composition and biomass of flying insects occurring in eight types of habitat (villages, roads, spring crops, winter crops, perennial crops, meadows, hedgerows and woodland). For insect catching, the method of motor-netting was employed, *i.e.* three catching nets (each 0.5 m in diameter), fixed to a moving motorcycle, which caught insects at three levels of height (0.5, 1.5 and 2.5 m). During sampling journeys the speed of motor bike was ca. 35 km/h. The length of journeys ranged between 200 and 1500 m. In total 1161 journeys were conducted (3 483 for three nets). The catches were performed throughout the vegetation season (from mid-March till the second half of October) on warm days of fine weather between 11 a.m. and 4 p.m. During the study, a total of 479 087 insects, representing 172 families were motor-netted (more details in [34-36]).

2.1 Statistical analysis

Statistical analysis of the collected material was conducted with the help of Statistica (StatSoft, Statistica©, version 7.1., Tulsa, USA, 2006) and Excel software. The probability of $P<0.05$ was assumed as statistically significant.

The differences in average individual mass of insects, representing the four predominating orders (Coleoptera, Diptera, Hemiptera and Hymenoptera) was tested with the use of a Kruskall-Wallis test.

The chi-square (χ^2) test was applied to compare the distribution of the the weight of the four main orders of aerial insects in different farmland habitats and identified in the diet and to assess the differences in the food composition between breeding sites (buildings) located in the area of one village. Percentage data were *arcsine*-transformed ($Y'=\text{arcsine}\,(Y)^{-1}$) prior to analysis [39].

Pearson correlation coefficients were applied to assess the relationships between main indices of diet expressed as number, proportions and mass of four main orders of insects and average mass and number of all prey items found in 52 breeding sites where faecal samples were collected. To normalise the distribution, most variables were *log*-transformed before analysis.

For the sake of large extent of time the collection of faeces encompassed (30 June – 4 August 2005), we divided all samples in two groups; first (30th June – 3rd July; n=43) and second (23rd July and 4th August; n=9). For these two groups we compared the three indices of diet, *i.e.* number, proportion and average mass of four main orders of insects (Coleoptera, Hymenoptera, Diptera and Hemiptera) using a Mann-Whitney test.

3. Results

3.1 General composition of the diet

In total, 3 152 items, representing 98 taxa of invertebrates were identified in the collected faecal sacs of nestling Barn Swallows (Table 1). The basic component was insects, which constituted 98.2% of all identified items. Among insects, the predominant order was Coleoptera, *n*=1741 prey items and total biomass 5082.7 mg d.w. The second order was Hymenoptera (*n*=747; 2043.8 mg d.w.), followed by Diptera (*n*=501; 2276.8 mg d.w.). The proportion of number and biomass among four main orders of insects (Coleoptera, Hymenoptera, Diptera and Hemiptera) was different the largest difference was found in Hemiptera (*n*=103; 1169.3 mg d.w.) (Figure 1).

Order	Family	Genus (species)[1]	Individual mass (mg d.w.)[2]	Total number of individuals (items)	Total mass (mg d.w.)	Number of sites with a given item (%)
		INSECTS				
Coleoptera	Anthicidae	*Notoxus*	1.296	32	41.472	12 (23.1)
		Anthicus (O)	0.477	2	0.954	1 (1.9)
	Carabidae	*Amara* (O)	8.491	37	314.167	23 (44.2)
		Bembidion	1.171	23	26.933	14 (26.9)
		Poecilus	26.125	1	26.125	1 (1.9)
		Pterostichus	54.187	1	54.187	1 (1.9)
	Cerambycidae	*Donacia*	9.666	1	9.666	1 (1.9)
	Chrysomelidae	*Lema* sp.	3.125	11	34.375	9 (17.3)
		Psylliodes	1.813	5	9.065	3 (5.8)
		Chaetocnema	0.861	3	2.583	2 (3.8)
		Lema melanopa	3.396	2	6.792	1 (1.9)
		Phyllotreta	0.506	2	1.012	1 (1.9)
	Coccinellidae	*Coccinellidae*	4.406	1	4.406	1 (1.9)
	Curculionidae	*Ceutorrhynchus*	0.837	33	27.621	16 (30.8)
		Curculio	37.271	21	782.691	3 (5.8)
		Otiorrhynchus	37.271	15	559.065	11 (21.2)
		Apion	0.477	8	3.816	3 (5.8)
		Phyllobius	3.660	7	25.62	5 (9.6)
		Sitona	4.665	6	27.99	3 (5.8)
		Anthonomus	0.837	4	3.348	1 (1.9)
		unident.	2.797	18	50.346	9 (17.3)
	Elateridae	*Agriotes*	9.666	80	773.28	24 (46.2)
		Adrastus	1.962	2	3.924	1 (1.9)
	Histeridae	*Hister purpurescens* (C)	7.016	25	175.4	7 (13.5)
		unident. (C)	3.891	8	31.128	8 (15.4)
	Hydrophilidae	*Cercyon* (C)	1.066	30	31.98	15 (28.8)
		Laccobius nigriceps (C)	1.066	4	4.264	4 (7.7)
		Helophorus (C)	0.330	3	0.99	3 (5.8)
		Sphaeridium (C)	4.170	2	8.34	1 (1.9)
	Lathridiidae	*Cartodere*	0.109	5	0.545	2 (3.8)
	Nitidulidae	*Meligethes*	0.421	937	394.477	44 (84.6)
		Glischrochilus	4.470	33	147.51	17 (32.7)
		Epurea	0.601	7	4.207	5 (9.6)
		Soronia	0.421	3	1.263	3 (5.8)
	Oedemeridae	*Oedemera*	4.515	1	4.515	1 (1.9)
	Phalacridae	*Stilbus*	0.473	4	1.892	4 (7.7)
		Olibrus	0.445	1	0.445	1 (1.9)
	Scarabaeidae	*Aphodius* (C)	6.735	58	390.63	31 (59.6)
		Phyllopertha	17.352	25	433.8	7 (13.5)
		Onthophagus (C)	9.693	22	213.246	6 (11.5)
	Scydmaenidae	*Euthiconus*	0.328	1	0.328	1 (1.9)
	Silphidae	*Silpha*	26.003	13	338.039	13 (25.0)
		Catops	1.066	2	2.132	1 (1.9)

Table 1. Diet composition of nestling Barn Swallows *Hirundo rustica* from 52 different breeding sites in Poland. [1]Coleoptera, associated with dung and manure of large farm animals; coprophagous species (C); predators (P); omnivores (O) (after [41,43,45]). [2]Data on the individual mass of insects after Karg [36].

Order	Family	Genus (species)[1]	Individual mass (mg d.w.)[2]	Total number of individuals (items)	Total mass (mg d.w.)	Number of sites with a given item (%)
	Staphylinidae	*Oxytelus* (C)	0.328	133	43.624	25 (48.1)
		Aleochara (C)	0.158	36	5.688	1 (1.9)
		Philonthus (C)	1.435	25	35.875	14 (26.9)
		Tachyporus (P)	0.492	23	11.316	6 (11.5)
		Heterothops	0.297	9	2.673	1 (1.9)
		Ontholestes (P)	16.120	1	16.12	1 (1.9)
		unident.	1.791	8	14.328	3 (5.8)
	Coleoptera unident.			7		4 (7.7)
Diptera	Anthomyiidae	unident.	1.194	21	25.074	14 (26.9)
	Calliphoridae	unident.	14.142	123	1739.466	49 (94.2)
	Muscidae	unident.	5.817	7	40.719	5 (9.6)
	Scatophagidae	unident.	6.128	2	12.256	1 (1.9)
	Syrphidae	unident.	9.157	2	18.314	2 (3.8)
	Tachinidae	unident.	3.408	4	13.632	4 (7.7)
	other Diptera	*Brachycera*	14.142	30	424.26	1 (1.9)
		Nematocera		5		1 (1.9)
	small Diptera (Sciaridae, Cypselidae, Phoridae)		0.010	ca. 307	3.070	3 (5.8)
Heteroptera	Corixidae	unident.	2.045	1	2.045	1 (1.9)
	Cydnidae	*Thyreocoris*	2.180	1	2.18	1 (1.9)
	Lygaeidae	*Trapezonotus*	2.045	1	2.045	1 (1.9)
		unident.	1.271	8	10.168	4 (7.7)
	Miridae	*Lygus*	2.045	10	20.45	2 (3.8)
		unident.	2.160	3	6.48	3 (5.8)
	Nabidae	*Nabis*	2.008	22	44.176	14 (26.9)
	Pentatomidae	*Aelia*	14.276	33	471.108	11 (21.2)
		Eurygaster	36.258	13	471.354	3 (5.8)
		Dolycoris	11.580	1	11.58	1 (1.9)
		Eurydema	8.158	1	8.158	1 (1.9)
		Pentatoma	32.654	1	32.654	1 (1.9)
		unident.	26.156	3	78.468	1 (1.9)
Homoptera	Cercopidae	*Aphrophora*	6.548	1	6.548	1 (1.9)
	Iassidae	*Empoasca*	0.461	4	1.844	2 (3.8)
Hymenoptera	Apidae	*Apis mellifera*	21.448	31	664.888	9 (17.3)
		Andrena	8.780	10	87.8	7 (13.5)
		Bombus	50.731	2	101.462	1 (1.9)
		unident.	19.819	2	39.638	2 (3.8)
	Bethylidae	unident.	0.351	1	0.351	1 (1.9)
	Braconidae	*Chelonus*	1.091	2	2.182	1 (1.9)
		unident.	0.283	3	0.849	3 (5.8)
	Cephidae	*Cephus*	2.005	4	8.02	1 (1.9)
	Formicidae	*Formica*	1.178	76	89.528	9 (17.3)
		Camponotus	1.178	3	3.534	2 (3.8)
		unident.	0.625	205	128.125	34 (65.4)
	Ichneumonidae	unident.	2.450	351	859.95	51 (98.1)
	Myrmicidae	*Lasius*	0.625	38	23.75	8 (15.4)

continued **Table 1.** Diet composition of nestling Barn Swallows *Hirundo rustica* from 52 different breeding sites in Poland. [1]Coleoptera, associated with dung and manure of large farm animals; coprophagous species (C); predators (P); omnivores (O) (after [41,43,45]). [2]Data on the individual mass of insects after Karg [36].

Order	Family	Genus (species)[1]	Individual mass (mg d.w.)[2]	Total number of individuals (items)	Total mass (mg d.w.)	Number of sites with a given item (%)
		Myrmica	1.178	6	7.068	4 (7.7)
		unident.	1.178	5	5.89	2 (3.8)
	Pteromalidae	unident.	0.222	3	0.666	3 (5.8)
	Torymidae	unident.	0.149	2	0.298	2 (3.8)
	Tenthredinidae	unident.	9.636	2	19.272	2 (3.8)
	Small Hymenoptera		0.500	1	0.500	1 (1.9)
Odonata	Calopterygidae	*Calopteryx*	15.430	3	46.29	3 (5.8)
OTHER ITEMS OF THE DIET						
Mollusca				2		2 (3.8)
Nematoda (parasites of Apis)				4		4 (7.7)
Araneae				1		1 (1.9)
small stones				40		19 (36.5)
fragments of glass				6		6 (11.5)
small seeds				3		3 (5.8)
fragments of vegetative parts of plants				1		1 (1.9)
TOTAL				3 152	10 640.3	

continued **Table 1.** Diet composition of nestling Barn Swallows *Hirundo rustica* from 52 different breeding sites in Poland. [1]Coleoptera, associated with dung and manure of large farm animals; coprophagous species (C); predators (P); omnivores (O) (after [41,43,45]). [2]Data on the individual mass of insects after Karg [36].

A division of the prey items into families demonstrates that the highest biomass was large dipterans, Calliphoridae (16.3%), followed by Ichneumonidae (8.1%). These two groups of prey were detected in faecal samples coming from the largest number of sites. Among Diptera the largest differences between number and biomass was found for small Diptera, which constitute 9.7% by number, and only 0.03% by biomass of all prey items (Table 1).

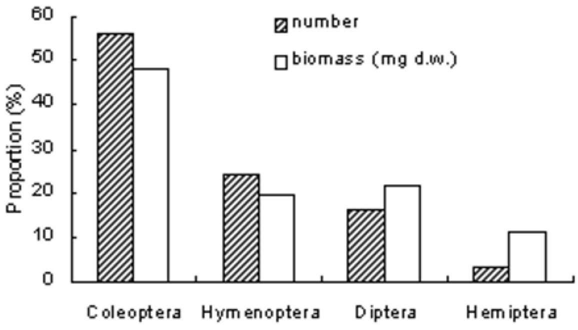

Figure 1. Comparison of the total proportion of the number and biomass of four main orders of insects (Coleoptera, Hymenoptera, Diptera and Hemiptera) found in faecal samples of nestlings of Barn Swallows in Poland.

3.2 Prey characteristic

The individual dry mass of prey for 96 taxa of insects ranged from 0.01 to 54.19 mg (Table 1).

The average mass of all prey items with known weight (n=3 095) amounted to 3.40 (95% CL, 3.16–3.63; median=0.49) mg. The highest values of average mass were characteristic for Hemiptera, 10.42 (8.23–12.61; median=2.16) mg d.w, followed by Diptera, 4.46 (3.90–5.02; median=0.01) mg d.w., Coleoptera, 2.97 (2.67–3.28; median=0.42) mg d.w. and Hymenoptera, 2.62 (2.25–2.99; median=1.18) mg d.w. The average individual mass of insects from the four predominating orders, *i.e.* Coleoptera, Diptera, Hemiptera and Hymenoptera was high significantly different (Kruskall-Wallis test, $H_{3,3088}$=371.8, P<0.0001).

Among Diptera, distribution of body weight showed two separate groups, first with small prey, <0.05 mg d.w. (near 62%) and second, large prey (30%) (Figure 3). In Coleoptera the dominant prey had a body weight between 0.05 and 0.5 mg d.w. In Hemiptera and Hymonoptera larger prey >1 mg d.w. dominated (Figure 3).

Analysis of the 52 breeding sites revealed statistically significant relationships between the average weight of prey and number of prey (Figure 4; Pearson correlation coefficient, r=-0.440, P=0.001). Similar analysis conducted for the main indices of diet for four main orders of insects showed statistically significant positive relationships between number of Hemiptera, proportion of Hemiptera, average mass of Coleoptera and average weight of all prey; between number of Coleoptera, Diptera and Hymenoptera and number of all prey; and negatively relationship between average mass of Diptera and number of all prey (Table 3).

3.3 Comparison of diet between different breeding sites and progress of the season

At 52 breeding sites, the proportion of the four dominant orders of insects were highly diverse (Table 2; Figure 2). On average, at all sites the highest proportion was made up by Coleoptera (Table 2). Next in decreasing order these were Hymenoptera (recorded at 51 sites), Diptera (50 sites) and Hemiptera (28 sites) (Table 2). For nine of the 11 villages where at least two breeding sites were located, significant differences were found in the composition of food consumed by nestling Barn Swallows occupying neighbouring breeding sites (Figure 2).

A comparison between the first (30th June – 3rd July) and second (23rd July and 4th August) period of faeces

Characteristic (variable)	Value				
	average	95% CL	median	min	max
Number of Coleoptera	33.5	18.9-48.1	18	1	357
Number of Diptera	5.8	3.5-8.1	3	0	41
Number of Hemiptera	1.9	1.0-2.8	1	0	15
Number of Hymenoptera	14.4	10.8-18.0	9.5	0	74
Proportion of Coleoptera (%)	52.4	46.7-58.2	51.7	8.3	92.2
Proportion of Diptera (%)	11.7	8.6-14.8	7.6	1.3	52.4
Proportion of Hemiptera (%)	4.6	2.3-6.9	1.5	0.7	40
Proportion of Hymenoptera (%)	31.3	26.3-36.3	29.0	4.9	83.3
Average mass of Coleoptera (mg d.w.)	4.0	3.0-5.0	2.7	0.4	19.1
Average mass of Diptera (mg d.w.)	9.7	8.3-11.0	10.7	1.6	14.1
Average mass of Hemiptera (mg d.w.)	8.9	5.5-12.3	6.1	0.8	36.2
Average mass of Hymenoptera (mg d.w.)	2.9	2.1-3.7	2.1	0.4	14.7
Average mass of all prey (mg d.w.)	4.3	3.4-5.2	3.6	0.7	16.7
Number of all prey	63.5	44.2-82.7	40.0	9	387

Table 2. Quantitative characteristics of the main indices of diet expressed as number, proportion and mass of four main orders of insects found in the faecal sacs of nestling Barn Swallows *Hirundo rustica* for 52 breeding sites located in rural areas of Poland.

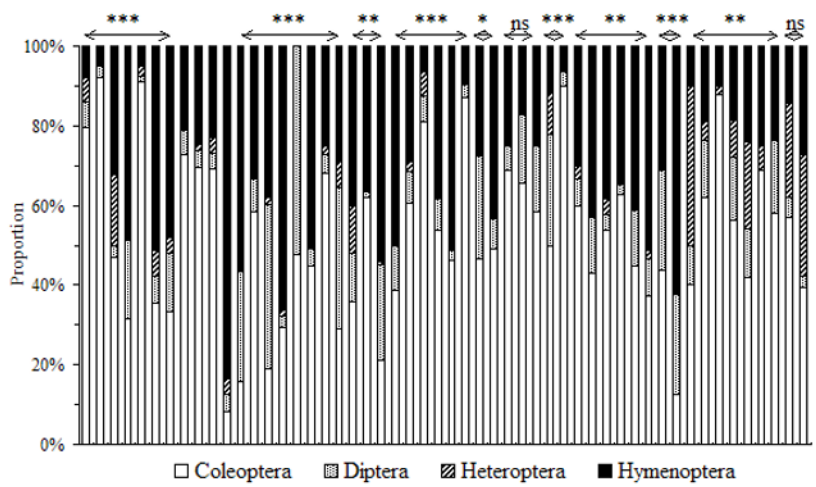

Figure 2. Proportions of the four main orders of insects in the diet of nestling Barn Swallows *Hirundo rustica* in 52 sites located in 15 villages in Poland. Arrows connect the breeding sites (buildings) located within the area of one village; asterisks denote the significance level obtained in the chi-square test calculated for *arcsine*-transformed data: * $P<0.05$, ** $P<0.01$, *** $P<0.001$; ns – not significant ($P>0.05$); d.f. ranged between 3 and 21.

Variable	Average mass of all prey		Number of all prey	
	r	*P*-value	r	*P*-value
Number of Coleoptera	-0.033	0.868	0.636	<0.001
Number of Diptera	-0.331	0.085	0.791	<0.001
Number of Hemiptera	0.493	0.008	-0.056	0.777
Number of Hymenoptera	-0.245	0.209	0.407	0.032
Proportion of Coleoptera (%)	0.035	0.861	0.236	0.226
Proportion of Diptera (%)	-0.124	0.531	0.102	0.606
Proportion of Hemiptera (%)	0.578	0.001	-0.342	0.074
Proportion of Hymenoptera (%)	-0.309	0.110	-0.085	0.667
Average mass of Coleoptera (mg d.w.)	0.502	0.007	0.003	0.989
Average mass of Diptera (mg d.w.)	0.351	0.067	-0.562	0.002
Average mass of Hemiptera (mg d.w.)	0.333	0.083	0.040	0.841
Average mass of Hymenoptera (mg d.w.)	0.283	0.144	-0.002	0.994

Table 3. Pearson correlation coefficients between *log*-transformed main indices of diet expressed as number, proportion and mass of four main orders of insects and average mass and number of all prey items found in 52 faecal samples of nestling Barn Swallows *Hirundo rustica* in rural areas of Poland; percentage data were *arcsine*-transformed; bold indicates statistically significant relationships

collection conducted for 52 breeding sites shows significantly higher values of the average weight of all prey (respectively, average for first and second period: 3.75 mg d.w. *vs* 6.80 mg d.w.; U=91.0, P=0.013) and of the diet parameters connected with Heteroptera, *i.e.* their number (1.40 *vs* 5.22; Mann-Whitney test, U=83.5, P=0.008), proportion (2.32% *vs* 15.4%; U=64.0, P=0.002) and total biomass (7.82 mg d.w. *vs* 86.57 mg d.w.; U=105.5, P=0.033). The first period was characterized also by significantly higher proportion of Hymenoptera (33.8% *vs* 7.3%; Mann-Whitney test, U=90.5, P=0.013).

3.4 Selection of insects in relation to their weight and abundance in different farmland habitats

The distribution of the weight of insects in the air and those in the diet clearly differed. As compared with the distribution of insect weights in the air, in the diet of nestlings larger insects decidedly predominated (Figure 3; chi-square test for *arcsine*-transformed data, χ^2=39.9, df=5, P<0.001). Insects weighing ≤0.50 mg d.w. accounted for almost 86.0% of all insects caught, whereas in the diet this group of prey constituted 50.3% (Figure 3).

In eight farmland habitats of western Poland surveyed in the years 1975–1979, the highest density and biomass of air-borne insects was recorded for Diptera (respectively the total density and biomass, 80% and 74%), and this order of insects predominated in all the habitats under analysis (Figure 5). In particular habitat types the density and biomass of the four predominating insect orders changed to a negligible extent. The distribution of the number of prey and biomass of the four orders of insects in the air and in the diet was sigificantly different (respectively a chi-square test for the number of prey and biomass of the four main insect orders with d.f.=3; χ^2=91.6 and 75.8, P<0.001). In comparison with the distribution by number of insects in the air (cf. data for all farmland habitats, Figure 5A and 5B), a higher proportion (both for number and biomass) of Coleoptera was found in the diet. A particularly wide disproportion was observed in the case of Diptera, whose proportion in the diet was lower than in the air by 79.6% and 78.8% respectively by number and biomass. The biomass of Heteroptera constituted merely 2.7% of the mass of insects in the air and as much as 35.2% of that in the diet (Figure 5B).

4. Discussion

Our results are the first attempt to describe the variation of diet of Barn Swallows in a large number of breeding sites. One result from the present study that differed from previous studies was the relatively small proportion of Diptera (an average of 11.7% for 52 sites) recorded in the food composition of the species. The dominant component of the diet of nestling Barn Swallows was Coleoptera, which jointly constituted 56.1% of all identified prey items. Such a high total proportion of beetles in the diet had not been noted for the Barn Swallow before, which can partly be accounted for by the similar extensive or traditional farm management and practices at studied breeding sites of Barn Swallow based on rules of organic farming. Published papers revealed that the proportion of Coleoptera in the diet of the Barn Swallow was very different, however higher proportion of these insects were found in studies based on faecal analysis (26.07%, [25]) in comparison to the ligature method (1.4%, Thomas 1934–1940 cited in [4]; 3.9%, [17]; 2%-15.6%, average, 4.0% [19]; 3.8%, [9]). These discrepancies might indicate methodological imperfections connected with different digestion processes of chitin parts of different prey groups [33,38,40], which in the case of our study, may point to the higher number of hard elytra, limbs and mandibles of Coleoptera, ants and other Hymenoptera, which are probably more preserved than remains of small diptera. However, in many earlier studies, analysis of faeces was successfully employed to determine the food composition in hirundines [25-28]. According to Poulsen and Aebischer [29], analysis of faeces yields a reliable picture of diet in the case of insectivorous birds. These authors have revealed that the differences in the assessment of the proportion in the diet of main order of insects, *i.e.* Diptera, Hymenoptera, Coleoptera and Hemiptera from colar samples and faeces collected from the same chicks at similar times did not exceed 2% [29]. Hence, it should be emphasized that despite potential biases in detailed quantification of animal prey, our results prevent relative assessment of the diet diversification because a uniform method was employed to analyze all the samples. Moreover, a high proportion of small-bodied Diptera in some faecal samples (see Figure 3) suggests that our results are reliable in relation to actual consumed prey items.

The high proportion of Coleoptera in the diet of nestling Barn Swallows obtained in the present study probably results from food selectivity of this bird species (cf. [20]), and from the actual high densities and biomass of these insects, particularly the species which are linked with the presence of dung and manure of large farm animals, close to the breeding sites investigated (cf. [41-43]) and might suggest a particular need for

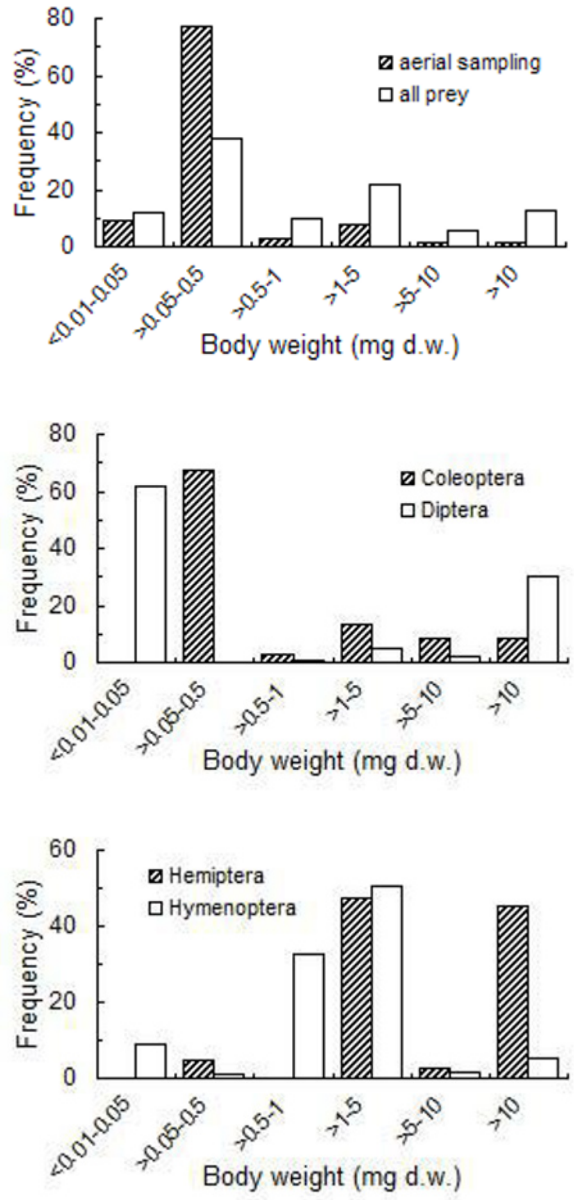

Figure 3. Comparison of the percentage distribution of insect weights (mg d.w.) in aerial samplings and in the diet of nestling Barn Swallows *Hirundo rustica*; the upper chart used data on all species of insects; data on the density and biomass of aerial insects come from earlier research conducted in western Poland [36].

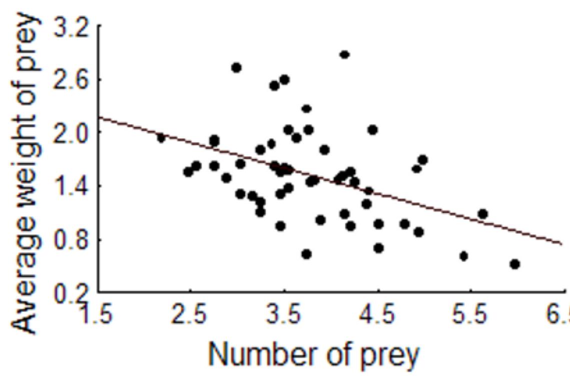

Figure 4. Relationship between *log*-transformed average weight of prey (mg d.w.) and number of prey found in 52 faecal samples of nestling Barn Swallows *Hirundo rustica* in rural areas of Poland; Average weight of prey = 2.6075 – 0.2874 × Number of prey.

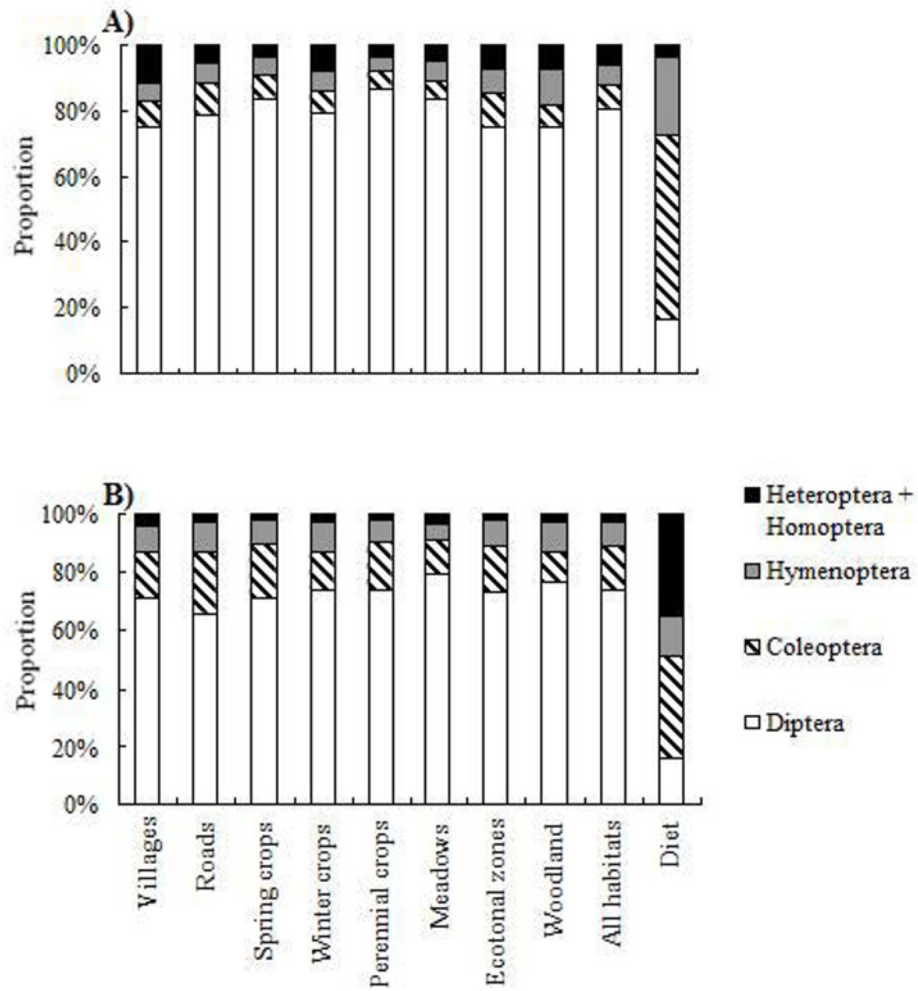

Figure 5. Comparison of the proportion (expressed by number (A) and biomass (B)) of the four main orders of aerial insects found in different farmland habitats and in the diet of nestling Barn Swallows *Hirundo rustica* (calculated on the basis of the total number (n = 3092) and total biomass of main prey; 10 572 mg d.w.) in 52 breeding sites in Poland. Data on the density and biomass of aerial insects came from earlier studies conducted in western Poland in the years 1975–1979 [36]. The distribution of the number of prey items representing the four main orders of insects and their biomass in the air ("All habitat") and in the diet was highly significant (for *arcsine*-transformed data; chi-square test for the number and biomass of prey of the four insect orders, d.f.=3; χ^2=422.5 and 337.5, P<0.001, respectively).

Barn Swallows to find larger-bodied prey rather than exploit a local abundance of smaller prey. Our study also revealed significant negative relationships between the average weight of prey and number of prey found in 52 analyzed breeding sites (Figure 4). This finding mirrors a general relationship between abundance and body size of prey, which resulted from a higher energetic value of larger prey exploitation by aerial-feeding birds [21,28]. Similarly, statistically significant positive relationships between number of Hemiptera, proportion of Hemiptera, average mass of Coleoptera and average weight of all prey; and a negative relationship between average mass of Diptera and number of all prey may indicate an exploitation of larger-bodied prey by feeding Barn Swallows. These results agree with optimal foraging theory in Barn Swallows and other hirundines [21,28-32].

According to Turner [25], the proportion of Coleoptera in the Barn Swallow diet (based on faecal analysis) equals 26.07%, while in the air, beetles always constitute less than 9.4% of all insects. The latest research by Sanchez-Pinero and Avila [43] demonstrates that Coleoptera are the most abundantly represented order of insects when collected in dung-baited traps located on the ground (60% of over 29,000 arthropods), followed by Hymenoptera (34%) and Diptera (5.6% mainly larvae). Dung and manure on pastures and near farm buildings constitute nutrientrich food resources that provide a diverse community, not only of coprophagous species of Coleoptera (list of species in Appendix 1), but also other trophic groups of these insects (*i.e.* omnivores, predators and detrivores) [41,43-45]. In the present study, coleopterans associated with dung and manure jointly made up 23.5% of the number (*n*=409) and 24.3% of the total biomass (1283.7 mg d.w.) of all representatives of the order (see Table 1).

General information indicates that dunghills may serve as the main foraging sites and manure facilities strongly positively influence the number of Barn Swallows during the breeding season [7,46]. The breeding sites from which faeces of Barn Swallows were collected were located mostly within areas of organic small-scale farming, rarely in large cattle farms, however in both these environments manure and slurry was available or commonly used as organic fertilizers. Manure is an important factor enhancing the species richness and biomass of many groups of insects, including Carabidae [47,48]. Jones [42] has demonstrated that in the diet of an insectivorous bat, *Rhinolophus ferrumequinum*, the proportion of coprophagous beetles *Aphodius* increases (up to ca 60% of all food) during the immigration of the bats into farm buildings; and this species is also one of the most frequently found representatives of Coleoptera in our study (Table 1).

The second abundant group of insects noted as a component of the Barn Swallow diet was Hymenoptera (the average for 52 sites was 31.3%). The high proportion of Hymenoptera was mainly due to high representation in the diet of two families, *i.e.* ants Formicidae and Ichneumonidae, which jointly constituted 20.1% of all prey. Both of these families of Hymenoptera are characterized by poor flight, which makes them easy aerial prey. The very high proportion of ants and ichneumonids in the Barn Swallow diet at some of the breeding sites point to the fact that the swallows will, if necessary, exploit a local abundance of small-bodied prey that occur unpredictabely in space and time. According to Głowacki [24], Hymenoptera made up 78% of all insects detected in the stomachs of adult Barn Swallows from central Poland, trapped at sites without animal husbandry.

We realize that comparing the composition of the barn swallow diet with the historical data on the occurrence of aerial insects in the 1970s (Figure 5) is not based on similar methods, or habitats, nevertheless, this gives an overview of insect diversity in different farmland habitats. Ultimately, it is worth mentioning that establishing real prey selection can be a difficult task, not only in our case (because of different sampling years and places), but also from a statistical point of view, sampling effort, weather condition, detectability and digestibility of prey [33,38].

The average mass of prey found in the present research for the Barn Swallow amounts to 3.40 mg d.w. This is lower than the value obtained by Bryant and Turner [20] – 6.01 (± SD=5.64) mg d.w., based on an analysis of food boluses obtained by collaring nestlings. However, in another study, taken using same methods (after [20,27]), the average mass of prey equalled 3.5 mg d.w., a value approximating the results here. The analysis of faeces of adult, egg-laying, birds performed by Turner [25] yielded a lower value, *i.e.* 2.59 (± SD=2.37) mg d.w. The wide discrepancies noted in the average weight of prey are undoubtedly involved with diverse proportions of particular orders of insects in the diet of Barn Swallows.

Finally, it should be emphasized that Coleoptera are probably more accessible and larger-bodied prey in comparison to some small Diptera or Hymenoptera. Similar, significantly higher values of the lower average number of prey and higher proportion of Hymenoptera found in the first period of collection of faeces is probably an effect of higher proportion of the most heavy group of prey, *i.e.* Heteroptera, in this time in comparison to the late summer; the numbers and biomass of heteropterans increase substantially during this time (J. Karg – unpublished data), which agrees with our data on the food composition of the Barn Swallow. Simultaneously, these results may indicate on exploitation by feeding Barn Swallows in different habitats, and available insects, including gregariously swarming small dipterans and hymenopterans (discussed in [19,49]).

The significant differences in the diet of Barn Swallows between neighouring breeding sites revealed by our study (Figure 2) can be interpreted in several ways, mainly as local availability of different taxonomic groups of insects, the progress of breeding season, habitat and crop composition and weather conditions [17-21,49-51), however all these factors could be closely related. Furthermore, we believe that other important factors explaining the food composition are farm animals, mainly cattle, which are suggested to be a main variable associated with the number of breeding populations of foraging Barn Swallows in agricultural areas of north-western Europe [7-11,46-52]. This assumption implies the need for further analyses to determine the environmental factors (*i.e.* habitat composition around the breeding colony, intensity of agriculture or size of farms along with the presence of various species of livestock) explaining the large variation of food composition of Barn Swallows in rapidly changing rural and agricultural areas of Europe.

Finally, we believe that a large number of randomly collected faecal samples from tens of breeding sites allows us to prescisely describe the variation in the diet of the Barn Swallow. Our work has great importance for documenting the food composition of the Barn Swallow in traditional countrysides of Europe *i.e.* under environmental and agricultural conditions which, as a result of transformations of farming systems, ceased to exist in the western and northern part of this continent.

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