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Source: Acta Ornithologica, 39(1) : 45-51

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: <https://doi.org/10.3161/068.039.0110>

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Food of the Willow Warbler *Phylloscopus trochilus* nestlings: differences related to the age of nestlings and sex of feeding parents

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Krupa M. 2004. Food of the Willow Warbler *Phylloscopus trochilus* nestlings: differences related to the age of nestlings and sex of feeding parents. Acta Ornithol. 39: 45–51.

Abstract. The study was conducted in the Lake Karaś reserve (N Poland), where the density of Willow Warblers in osier and birch thickets reached 28.7–33.3 p/10 ha. Collar rings were used to collect the food brought to the nestlings. 487 food samples were collected from 26 nests, comprising 2573 food items. 167 of the samples were from females (652 individual food items), 95 from males (616 food items). The nestlings were fed mainly on Arthropoda (94.6%) and Mollusca (5.4%). The dominant food items were Diptera (29.8%), Homoptera (28.7%), Ephemeroptera (10.5%), Araneida (7.6%) and Trichoptera (6.5%). The composition of the dominant food items and the average mass of food deliveries changed markedly with nestling growth. The types of food brought by each sex also varied significantly. Males brought heavier portions of food consisting of larger numbers of lighter prey. However, the composition of these portions was not as diverse as those brought by females. This may be related to differences between males and females in their respective territories and foraging techniques.

Keywords: Willow Warbler, *Phylloscopus trochilus*, nestling diet, food composition, age-related differences, parental provisioning

Received — Feb. 2004, accepted — April 2004

INTRODUCTION

The composition of food provided to nestlings is not only influenced by the availability of prey in a particular territory and stage of nestling development (Mackowicz 1970, Evans et al. 1997, Brodman & Reyer 1999, Naef-Daenzer et al. 2000), but also by the distribution of prey items in the territories of specific pairs (Rauter et al. 2000, Bańbura et al. 2001). Males and females of many bird species are known to have different feeding territories (Schulze-Hagen et al. 1989, Bańbura et al. 2001, Krupa 2001), where species composition and potential prey availability can differ, resulting in differences in the types of food brought to nestlings by each of the sexes.

The Willow Warbler is a generally monogamous species, with both sexes involved in parental care. Nestlings fledge between 12–14 days after hatching (Schönfeld 1982, Cramp 1992). Polygamy

occurs among some members of the breeding population. Polygamous males exhibit varying degrees of parental behaviour, depending on the status of their mates. Males help feed the nestlings of their first mate, but either provide little or no assistance to their second and third mates. Females can compensate for this low involvement of males in parental care by increasing the intensity of feedings and bringing the nestlings different food items (Neergard & Arvidsson 1995, Bjoernstad & Lifjeld 1996).

The literature contains some information about the food composition of Willow Warbler nestlings; however, it is frequently of a general nature. Quantitative data, based on analyses of food collected by collar method, are available only from Germany (Dornbusch 1981, Emmrich in Schönfeld 1982) and Russia, including the northern Ural Mountains (Ryabitshev et al. 1980), south-eastern Yamal (Danilov et al. 1984) and the environs of

St. Petersburg (Bozhko 1958, Malchevskiy 1959, Prokofieva 1973). Until now, neither the composition of food brought to nestlings at different phases of their lives nor differences in food brought to the nestlings by each parent have been studied. Nystöm (1991) proved that females, which are smaller and have more rounded wings than males, are better adapted to hovering in the air and more effective in catching prey from the undersides of birch and willow leaves. This suggests that the composition of food brought to nestlings by the female and male can differ.

This study was conducted to: 1) determine the composition of food provided to nestlings in northern Poland, 2) determine if there are any differences in the food brought to nestlings on subsequent days of their lives, and 3) compare the composition of food brought by females and males.

MATERIALS AND METHODS

The study was conducted in the Karaś Lake reserve (53°34'N, 19°28'E, N Poland). The study area included two plant communities: willow thicket *Salicetum pentandro-cinereae* and birch thicket from association *Alnion glutinosea* (Markowski et al. 2000). The density of Willow Warblers in these habitats was very high — 28.7–33.3 p/10 ha (Krupa et al. 2000).

The composition of food items brought to nestlings was studied in 2001–2002, from May 26 to July 13. Feedings were collected by collar method (Kluijver 1933, Bogucki 1964) placed on the nestlings at the age of 6 to 11, 1–2 times per day for a period of 50–60 minutes. Food was removed every 15–20 minutes and if the feeding parents were observed from a blind, food was removed after each feeding. Each time the collar ring was removed, the nestling was fed with invertebrates collected from around the nest, which compensated to a certain degree for the time of fast. The prey was weighed while moist to the nearest 1 mg.

Twelve nests were observed from blinds, where one person observed the feeding process and noted the sex of the bird bringing the food. After each feeding, a second person approached the nest and removed the meal. Adult birds were caught in mist-nets at the beginning of the breeding season, ringed, sexed and individually marked with coloured rings.

487 samples of food deliveries were collected from 26 nests, comprising 2573 food items. 167 samples brought by females contained 652 indi-

vidual prey items, while and 95 samples brought by males contained 616 prey items.

The frequency of prey items in the food was calculated as a proportion of the feeding samples, categorised by the appropriate taxon and expressed as a percentage of the number of analysed feeding samples. The mass of the food brought by both sexes was compared using the Mann-Whitney U-test, and the t-test was used to test its differentiation. The composition of food items by specific taxon between males and females and the composition of main food categories brought on successive days to the nestlings were compared using the χ^2 test. The mass of the food delivered was analysed using the Kruskal-Wallis test, and the Dunn test was applied post-hoc (Zar 1996). The Statistica 5.0 software was used for the calculations.

RESULTS

The spectrum of food items provided to Willow Warbler nestlings was relatively broad. Most of the food consisted of invertebrates, with 94.6% ($n = 2573$) Arthropoda, and 3.15% Mollusca. In terms of numbers, Diptera (mainly Chironomidae and Culicidae), Homoptera (Aphidodea and Cicadodea), Ephemeroptera, Araneida and Trichoptera dominated (Table 1). In terms of weight, Diptera (mainly Tabanidae and Chironomidae), Lepidoptera (mainly Noctuidae and Geometidae), Araneida, Trichoptera, Homoptera and Hymenoptera dominated. The taxa already mentioned together with Heteroptera, Coleoptera and Stylommatophora also dominated in terms of the frequency with which they appeared in the feeding samples (Table 1).

A female was observed flying to the nest with a large downy feather, about 8 cm long. She gave it to a begging nestling, which swallowed it as if it were a large portion of food. Feathers were confirmed as food items in 7 nests.

As the nestlings developed, the number of prey items in the food as well as the mass of the food changed significantly (number of prey items: days 6–7 vs 8–9: $\chi^2 = 22.96$, $df = 4$, $p < 0.001$; days 8–9 vs 10–11: $\chi^2 = 118.33$, $df = 4$, $p < 0.001$; mass of the food: days 6–7 vs 8–9: $\chi^2 = 1956.89$, $df = 5$, $p < 0.001$; days 8–9 vs 10–11: $\chi^2 = 572.36$, $df = 5$, $p < 0.001$). The number of Diptera and Araneida decreased as a prey item, while Homoptera increased. As to the mass, Lepidoptera and Trichoptera increased, while Araneida decreased (Fig. 1).

Based on these observations, it was determined that small prey items, that is Homoptera, small

Table 1. The composition of food brought to the nestlings (N = 2573 prey items, 487 feeding samples). Im. — imagoes, Lar. — larvae, % — total of imagoes and larvae.

Taxon	Number			Mass			Frequency of occurrence		
	Im.	Lar.	%	Im.	Lar.	%	Im.	Lar.	%
Basommatophora									
Planorbidae	5	—	(0.2)	69	—	(0.2)	5	—	(1.0)
Stylommatophora									
Vertiginidae	11	—	(0.4)	28	—	(0.1)	8	—	(1.6)
Succineidae	59	—	(2.3)	1242	—	(3.2)	48	—	(9.9)
Zonitidae	1	—	(0.0)	20	—	(0.1)	1	—	(0.2)
Veneroida									
Sphaeriidae	5	—	(0.2)	17	—	(0.0)	3	—	(0.6)
Araneida	195	—	(7.6)	6216	—	(15.9)	165	—	(33.9)
Opilionidea	11	—	(0.4)	526	—	(1.3)	11	—	(2.3)
Odonata									
Agrionidae	10	—	(0.4)	829	—	(2.1)	10	—	(2.1)
Ephemeroptera	271	—	(10.5)	1584	—	(4.1)	102	—	(20.9)
Orthoptera									
Tettigonidae	—	2	(0.1)	—	41	(0.1)	—	2	(0.4)
Homoptera									
Cicadodea	143	93	(5.6)	453	1457	(4.9)	41	67	(21.1)
Aphidodea	596	—	(23.2)	310	—	(0.8)	87	—	(17.9)
Heteroptera									
Pentatomidae	22	1	(0.9)	341	20	(0.9)	10	1	(2.1)
Miridae	6	—	(0.2)	34	—	(0.1)	6	—	(1.2)
others	12	10	(0.9)	59	40	(0.3)	11	7	(3.5)
Coleoptera									
Hydrophilidae	—	3	(0.1)	—	55	(0.1)	—	2	(0.4)
Cyphonidae	29	—	(1.1)	143	—	(0.4)	23	—	(4.7)
others	4	2	(0.2)	17	5	(0.1)	4	2	(1.2)
Neuroptera									
Chrysopidae	11	—	(0.4)	173	—	(0.4)	9	—	(1.8)
Hemerobiidae	1	—	(0.0)	4	—	(0.0)	1	—	(0.2)
Diptera									
Tipulidae	42	—	(1.6)	536	—	(1.4)	30	—	(6.2)
Fungivoridae	16	—	(0.6)	77	—	(0.2)	12	—	(2.5)
Culicidae	169	—	(6.6)	416	—	(1.1)	55	—	(11.3)
Chironomidae	377	—	(14.6)	1968	—	(5.0)	127	—	(26.1)
Rhagionidae	21	—	(0.8)	805	—	(2.1)	20	—	(4.1)
Tabanidae	73	—	(2.8)	4861	—	(12.5)	70	—	(14.4)
Empididae	9	—	(0.3)	21	—	(0.1)	7	—	(1.4)
Syrphidae	9	19	(1.1)	307	428	(1.9)	8	12	(4.1)
Chloropidae	6	—	(0.2)	37	—	(0.1)	6	—	(1.2)
Muscidae	14	—	(0.5)	315	—	(0.8)	13	—	(2.7)
Foridae	4	—	(0.2)	4	—	(0.0)	3	—	(0.6)
others	9	—	(0.3)	44	—	(0.1)	8	—	(1.7)
Hymenoptera									
Tenthredinidae	2	—	(0.1)	24	—	(0.1)	2	—	(0.4)
Formicidae	4	—	(0.2)	39	—	(0.1)	4	—	(0.8)
others	1	44	(1.7)	4	1948	(5.0)	1	40	(8.4)
Trichoptera	166	—	(6.4)	4455	—	(11.4)	84	—	(17.2)
Lepidoptera									
Geometridae	1	61	(2.4)	18	2959	(7.6)	1	39	(8.2)
Noctuidae	7	20	(1.0)	582	2804	(8.7)	7	20	(5.5)
others	17	15	(1.2)	711	1725	(6.2)	14	14	(5.7)
plant fragments	40	—	(1.6)	184	—	(0.5)	40	—	(7.0)
down feathers	13	—	(0.5)	30	—	(0.1)	11	—	(2.1)
Cervidae hair	3	—	(0.1)	5	—	(0.0)	3	—	(0.6)
twine	1	—	(0.0)	14	—	(0.0)	1	—	(0.2)
Total	1804	769	(100)	27386	11618	(100)			

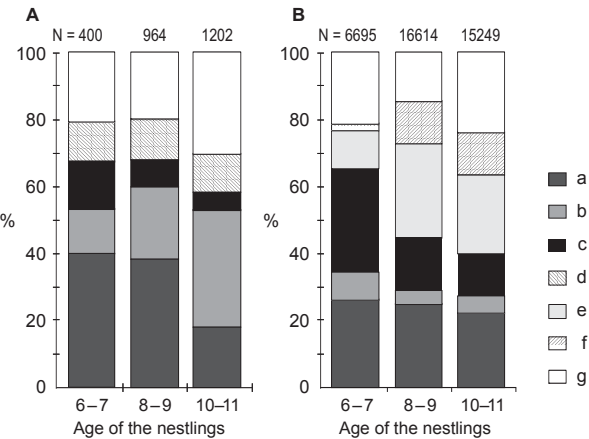


Fig. 1. The composition of food brought to nestlings at 2-day stages of their lives. A – structure expressed in amount, B – structure expressed in mass, a –Diptera, b –Homoptera, c – Araneida, d – Ephemeroptera, e – Lepidoptera, f – Trichoptera, g – others.

Diptera (among them Cuicidae, Chironomidae, Fungivoridae), Araneida, and Ephemeroptera dominated in the food of nestlings during their first days of life. As the nestlings grew, ever-larger prey items were brought, such as Trichoptera, caterpillars, Lepidoptera imagoes and large Diptera (among them Asilidae, Tabanidae, Syrphidae and Rhagionidae).

The number of prey items in one feeding sample ranged from 1 to 106 with a median of 3 (n = 487). The median mass of the prey was 4 mg (n =

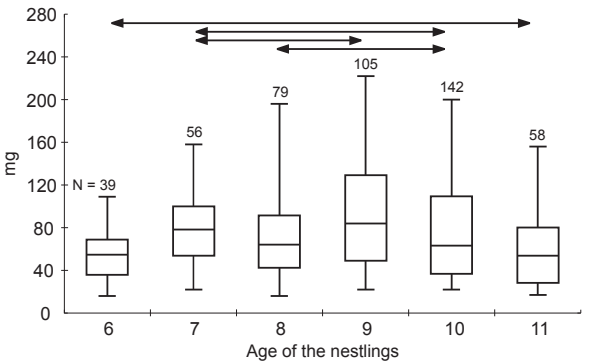


Fig. 2. Mass of the feeding samples brought to nestlings on successive days of their lives. The median (horizontal line), quartiles (rectangle) and percentiles (vertical line) are provided. Arrows indicate the age categories where no significant differences were found (Dunn test, $p > 0.05$).

2573). 69.81% of the prey was within the size class of 0–10 mg, of which 42.07% weighted up to 1 mg. The median weight of the feeding samples was 66 mg (n = 487). Changes in the mass of the feeding portions brought to the nestlings on successive days of their lives was found to be significant (Kruskal-Wallis test, $H = 24.56$, $p < 0.001$). Nestlings in the 6th and 11th day of life received the lightest food portions (Dunn test, $p < 0.01$) (Fig. 2).

Feeding samples with large, easily identified items, such as Lepidoptera, caterpillars, Odonata and Tabanidae comprised from 3.2% (n = 587) to 7.9% (n = 660) of all samples brought to feed the

Table 2. Comparison of the types of food brought to the nestlings by females (F) and males (M). The number of prey items and its proportional representation of the total composition (in parentheses) are presented. $\chi^2 - \chi^2$ test; * – $p < 0.05$, *** – $p < 0.001$, ns – no significant differences ($p > 0.05$).

Taxon	Number				Mass			
	F		M	χ^2	F		M	χ^2
Basommatophora	–	–	2 (0.3)		–	–	17 (0.2)	
Stylommatophora	29 (4.4)		12 (1.9)	6.33 *	596 (6.5)		124 (1.7)	215.27 ***
Araneida	48 (7.4)		29 (4.7)	3.91 *	1345 (14.7)		800 (11.2)	41.7 ***
Opilionidea	4 (0.6)		–		147 (1.6)		–	
Odonata	2 (0.3)		–		158 (1.7)		–	
Ephemeroptera	33 (5.1)		38 (6.2)	0.73 ns	130 (1.4)		151 (2.1)	11.61 ***
Orthoptera	1 (0.2)		1 (0.2)		37 (0.4)		4 (0.1)	
Homoptera	281 (43.1)		301 (48.9)	4.24 *	715 (7.8)		371 (5.2)	43.39 ***
Heteroptera	31 (4.8)		5 (0.8)	17.85 ***	402 (4.4)		44 (0.6)	213.83 ***
Coleoptera	6 (0.9)		6 (1.0)	0.01 ns	65 (0.7)		31 (0.4)	5.15 *
Neuroptera	10 (1.5)		–		167 (1.8)		–	
Diptera	104 (16.0)		130 (21.1)	5.59 *	2336 (25.5)		1990 (27.9)	12.21 ***
Hymenoptera	13 (2.0)		19 (3.1)	1.75 ns	472 (5.1)		676 (9.5)	115.08 ***
Trichoptera	32 (4.9)		39 (6.3)	1.21 ns	749 (8.2)		623 (8.7)	1.67 ns
Lepidoptera	33 (5.1)		25 (4.1)	0.73 ns	1790 (19.5)		2284 (32.0)	334.99 ***
others	25 (4.0)		9 (1.5)		69 (0.7)		21 (0.3)	
Total	652 (100)		616 (100)		9178 (100)		7136 (100)	

nestlings. Prey items with a mass over 50 mg were found in 21.1% ($n = 487$) of the samples. In 48.5% cases, these larger items comprised the only prey in the sample, while in the remaining samples they were found with 1–30 other smaller prey items (average 4.6, $SD = 5.4$, $n = 103$).

Variety in the number of prey items and their mass by sex of the feeding parent was found to be significant (Table 2). Food brought to the nestlings by the female was more various in composition ($H' = 1.12$) than that brought by the male ($H' = 0.92$) (t test, $t = 5.81$, $p < 0.001$). Males brought significantly heavier feeding samples than females (57 and 48 mg respectively) (Mann-Whitney test, $Z = 2.66$, $p < 0.01$). But these feeding samples included a greater amount of lighter-weight prey items (Mann-Whitney test, number of prey items: $Z = 2.53$, $p < 0.05$; mass of the prey: $Z = -2.00$, $p < 0.05$).

There was no significant difference between the median mass of feeding samples brought by females with no help from males ($Me = 52$, $n = 53$) and females assisted by males ($Me = 48$, $n = 114$) in feeding the nestlings (Mann-Whitney test, $Z = 0.78$, $p > 0.05$).

DISCUSSION

Willow Warbler nestlings in the study plot were fed mainly on soft-bodied prey, that is, Diptera, Hemiptera, Araneida and Lepidoptera, a diet similar to that of nestlings in other areas of this species' breeding range (Bozhko 1958, Malchevskiy 1959, Prokofieva 1973, Ryabitsev et al. 1980, Dornbusch 1981, Danilov et al. 1984). However, it was also found (Bozhko 1958, Prokofieva 1973, Ryabitsev et al. 1980, Dornbusch 1981) additional species in the food of nestlings that were not seen in this study, such as Plecoptera, Psocoptera, Mecoptera and Megaloptera as well as the fruit of mountain ash. When Kuusisto (1941) analysed the stomach contents of 12 nestlings, he found stones in three of them, most likely functioning as gastrolites. The Vertiginidae and Sphaeridae found in the nestlings' diet in this study may have functioned similarly. Their shells, 3–4 mm long, are very hard and may have substituted for stones which were absent in the study areas. The shells of *Succinea* sp. snails brought to the nestlings may have also functioned as gastrolites, however these shells are relatively soft. Also Dornbusch (1981) notes a high proportion (5.5%, $n = 254$) of small snails, 2–4 mm in length, in the food of Willow Warbler nestlings.

There were several items found as food in this study that were not reported in other research

such as down feathers, Cervidae hairs and a thin piece of twine. Most of the feathers (12 of 13) were very small and most likely were collected unintentionally with other prey items. Also the twine was probably picked up by accident while food was collected from the ground. However, it may be possible that adults have such a strong feeding instinct while caring for their nestlings that they try to feed them all the types of food collected, limited only by the ability of the nestling to swallow, not by the energy value of the item being eaten.

The available literature also lacks data on the size and mass of prey items brought to Willow Warbler nestlings. Prokofieva (1973) found the largest prey items in nestlings' food to be Tabanidae, as well as some Trichoptera and Lepidoptera, albeit these were rarely part of the menu. Some authors state that small items dominate among the prey (Brown 1963, Averin & Ganya 1970), however, these may be based on subjective assessments. Only Ryabitsev et al. (1980) report that over 90% of the food mass consisted of Hymenoptera (mainly Tenthredinidae larvae), Diptera and Lepidoptera larvae. About 50% ($n = 1.228$) of the prey was up to 5 mm long, and about 75% of the prey weighed up to 19.5 mg, with most in the 2–3.5 mg category. The large number of prey with a mass up to 1 mg reflects the dominance of Homoptera in the food collected in northern Poland. It seems that the Willow Warbler prefers to feed its nestlings on the same size and number of prey in different areas of its breeding range.

It is reasonable to assume that nestlings receive a gradual increase in the mass of food and size of prey as they grow. The size of the nestling and its ability to swallow are factors limiting the size of prey brought by the adults. Portions of food brought to the nest in the first days of a nestling's life are 1.5–2.0 mm long and are often difficult to see in a bird's bill (Schönfeld 1982). An increase in the size of prey is also observed in the Wood Warbler *Phylloscopus sibilatrix* as its nestling grow. In studies conducted by Temrin et al. (1997), food portions were the smallest at day 1–3 of a nestling's life, and the largest at day 10. The simultaneous increase in the size of the food items provided and the daily number of feedings as the nestlings grow suggest that just increasing the number of feedings would not be enough to provide nestlings with the appropriate amount of food and energy. The energy requirements of Willow Warbler nestlings increases over 10 times, from 3.3 kJ at day 1 of life to 39 kJ during its last 6 days in the nest (Tiainen 1983).

In many species, the size and mass of food provided decreases during the nestlings' last few days in the nest (Temrin et al. 1997, Kleinschmidt 2001). This, coupled with a decrease in the number of daily feedings (Mackowicz 1970, Krupa 2001), may indicate that food resources have been exhausted in the feeding territory, especially near the nest. Changes occurring in the number and mass of food provided does not necessarily mean a decrease in food quality. As the nestlings grew in the nests studied, the proportion of Araneida in the food decreased, a prey of low caloric content (7.06 kJ/g of moist mass), but the proportion of Trichoptera significantly increased, a prey of high caloric content (13.44 kJ/g of moist mass).

Based on their observations of feeding Willow Warblers, Brown (1963) and Arvidson (1984) found that the female often foraged near the nest, not collecting more than 1–2 prey items each time. Females foraged for a short time, usually not longer than 10 min. Males, however, often flew far from the nest and collected several or several dozen small prey items. This study confirms that the variability in food brought by females and males is most likely a result of differences in the feeding territories and foraging methods used by each sex. The greater proportion of fast flying prey, such as Odonata, Lepidoptera, Neuroptera or Syrphidae, in the food brought by females could serve as evidence of different foraging techniques used by females and males. These do not appear in the food brought by males.

Differences among the sexes in their use of time, seen, for example, in the more frequent feedings of Willow Warbler females as opposed to males (M. Krupa unpublished data) may result in females having less time for foraging and being less selective in the type of prey collected. On the other hand, males that feed nestlings less frequently have more time to look for food and can be more selective in their choice of larger prey (Bańbura et al. 2001). This may result in a greater variety of prey brought by females and a smaller variety in the food brought by males. In cases where the feeding territories of both sexes overlap, the variety, number and mass of prey items may be identical (Kleinschmidt 2001). Willow Warbler males brought significantly heavier food samples than females in the study area, which may compensate for their lower participation in feeding the nestlings to a certain extent. The provision of heavier or larger prey items to nestlings by males was also observed in the

1987), Willow Tit *Parus montanus* (Rytönen et al. 1996) and Blue Tit *P. caeruleus* (Bańbura et al. 2001). Second females compensated for the lack of assistance from males among Great Reed Warblers *Acrocephalus arundinaceus* by increasing the intensity of feedings to the nestlings and bringing heavier prey. As a result, their nestlings obtained the same amount of food as the nestlings of other females (Sejberg et al. 2000).

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STRESZCZENIE

[Pokarm piskląt piecuszka: różnice wynikające z wieku piskląt i płci ptaków przynoszących pokarm]

Badania prowadzono w rezerwacie Jezioro Karaś (53°34'N, 19°28'E) w latach 2001–2002, w okresie od 26 maja do 13 lipca. Kontrolowano

gniazda położone w dwóch zbiorowiskach roślinnych: łożowisku *Salicetum pentandro-cinereae* i brzezynie mszarnej ze związku *Alnion glutinosae*. Celem pracy było zbadanie składu pokarmu piskląt piecuszka, jego zróżnicowania w kolejnych dniach życia piskląt oraz porównanie pokarmu przynieszonego przez samce i samice.

Pokarm przynoszony pisklątom badano za pomocą pierścieni uciskowych, które zakładano pisklątom w okresie od 6 do 11 dnia życia, 1–2 razy dziennie na okres 50–60 minut. Przy 12 gniazdach ustawiono namioty obserwacyjne, z których kontrolowano przebieg karmienia i oznaczano płeć ptaka, który przyniósł pokarm. Dorosłe ptaki na początku sezonu lęgowego chwymano w sieci typu mist-net, obrączkowano oraz znakowano indywidualnie systemem kolorowych obrączek.

W 26 gniazdach zebrano 487 prób pokarmowych, w których oznaczono 2573 ofiary. W przypadku 262 prób określono płeć ptaka, który je przyniósł do gniazda (samice – 167 prób, 652 ofiary; samce – 95 prób, 616 ofiar). Pokarm piskląt stanowiły Arthropoda (94.6%, w tym Insecta 86.6% i Arachnida 8.0%) oraz Mollusca (5.4%). Spośród rzędów najliczniej reprezentowane były: Diptera (29.8%; w tym rodziny Chironomidae i Culicidae), Homoptera (28.7%), Ephemeroptera (10.5%), Araneida (7.6%) i Trichoptera (6.5%) (Tab. 1). W kolejnych dniach życia piskląt stwierdzono istotne zmiany udziału głównych grup pokarmu (Fig. 1) oraz zróżnicowanie średniej masy prób pokarmowych (Fig. 2). Stwierdzono także istotne zróżnicowanie pokarmu przynieszonego przez obie płcie (Tab. 2). Samce przynosiły cięższe porcje pokarmu, w których znajdowało się więcej lżejszych ofiar. Przynoszony przez nie pokarm był natomiast mniej zróżnicowany niż pokarm przynoszony przez samice. Wskazuje to na zróżnicowanie areałów żerowiskowych i sposobów żerowania obu płci.

PODZIĘKOWANIA

Dziękuję wszystkim osobom, które pomagały mi w pracach terenowych, przede wszystkim dr Robertowi Krupie, mgr Romanowi Kalince, Adamowi Smolarczykowi, Marzenie Lempie i Cezaremu Dziubie. Dr Karolowi Komosińskiemu i mgr Dawidowi Marczakowi dziękuję za pomoc w oznaczaniu zebranych bezkręgowców, a Robertowi Krupie i prof. Maciejowi Luniakowi za uwagi dotyczące wcześniejszej wersji niniejszej pracy.