

FORAGING STRATEGY OF AQUATIC WARBLERS ACROCEPHALUS PALUDICOLA DURING BREEDING SEASON COMPARED TO STRATEGIES OF OTHER BIRDS BREEDING ON SEDGE FEN MIRES

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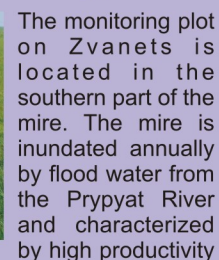


We carried out a comparative investigation into the diet and foraging strategy of Aquatic Warblers and four other bird species similarly supported by sedge fen mires of Belarus. The species we analyzed have different feeding strategies. Aquatic Warblers and Sedge Warblers are least selective in their prey choices (varied prey equally occur in their diet, a list of shared prey is long), forage within the vicinity of the nest, the size of prey is relatively small. The foraging patterns of Meadow Pits and Reed Buntings are quite similar: these species search and fly for food to areas of heavy prey concentration, sometimes far away from the nest. Because of long flights, these birds show high selectivity in prey choice (some prey are more dominant than the others, a list of shared prey is short), sorties for food are long; the mass of food delivered per one foraging visit is much larger than for birds foraging near the nest. Grasshopper Warbler is the most selective in food choice of all: despite a small around-the-nest radius of food collection, their chicks primarily feed on large caterpillars. Differences in feeding behaviour and adaptations to the environment are explained by the breeding system of the species (partial promiscuity or monogamy), flexibility in nest site selection. Given biological peculiarities of this stenotopic species, Aquatic Warblers appear to be most vulnerable of all birds breeding on fen mires. In years when the conditions are unfavourable across the entire mire throughout the breeding season, Aquatic Warblers do not breed, whereas other species move to different habitats for nesting. In this context, to preserve the species, it is necessary to ensure the best nesting conditions during the breeding season and seek to set up a network of fen mires located within a short distance of one another.

The diet of Aquatic Warblers and other birds was studied on three fen mires located in the Belarusian Polesie, which together hold more than 50 percent of the Aquatic Warbler world population. These three mires differ from one another in a number of characteristics. The Dikoe Mire is located on the watershed and corresponds to a transitional type of mire - from the Hyprum-sedge to the sedge-Sphagnum stage with prevailing atmospheric type of feeding. Zvanets is a typical sedge fen mire located in the peripheral part of the Prypyat River floodplain and fed mainly by surface water. The SporoVo Mire is a typical floodplain sedge fen mire. The entire study was conducted on monitoring plots selected in the most typical parts of the mires.



The monitoring plot on Dikoe is located in the part of the mire where the input of nutrients is the poorest among all studied habitats (the species in Belarus (water mineralization is 106.6 mg/l). The vegetation of the monitoring plot is characterized by alternation of a large number of various associations, but the dominant species in the projective coverage are Carex lasiocarpa, Carex limosa, to a lesser extent Carex chordeorhiza, Carex diandra and Carex rostrata, Eriophorum polystachyon, Calamagrostis neglecta. In some places the following species of Carex elata (58.3%) and Carex appropinquata are very abundant; Menyanthes trifoliata the mean coverage of 25% and (36.5%) dominate this monitoring plot. The water Comarum palustre the coverage varies from 2% to 65%. Carex elata is found level in the mire fluctuates in April-May and reaches only in depressions and along the ditches. The mire's surface is practically flat, +55 cm above the soil and in June-July drops to -63 cm. The water table during the nesting period fluctuates greatly from +40 to -30 cm in relation to the soil.



The monitoring plot called «Peschanka» is located in the Yaselskiy River floodplain on the SporoVo Mire. This part is characterized by high productivity (water mineralization is 298-322 mg/l). It should be noted that the productivity value of the site can vary from year to year depending on whether the site was flooded in spring or not. The projective coverage of Caricetum elatae community, which is typical of mires with rich mineral content, is 89.1% of the total area of Peschanka plot. Tussocks are slightly prominent; they are not higher than 20 cm. The water table during the nesting period fluctuates greatly from +40 to -30 cm in relation to the soil.

Table Years of dietary studies in different mires

Species	Study years				
	Sporovo	Zvanets	Dikoe	Servech	
Aquatic Warbler	2000	2001, 2003, 2004	2001	-	-
Sedge Warbler	-	2003, 2004	-	-	-
Meadow Pipit	-	2003	2001	2003	-
Grasshopper Warbler	2003	2005	-	-	-
Reed Bunting	2003	-	2001	2003	-

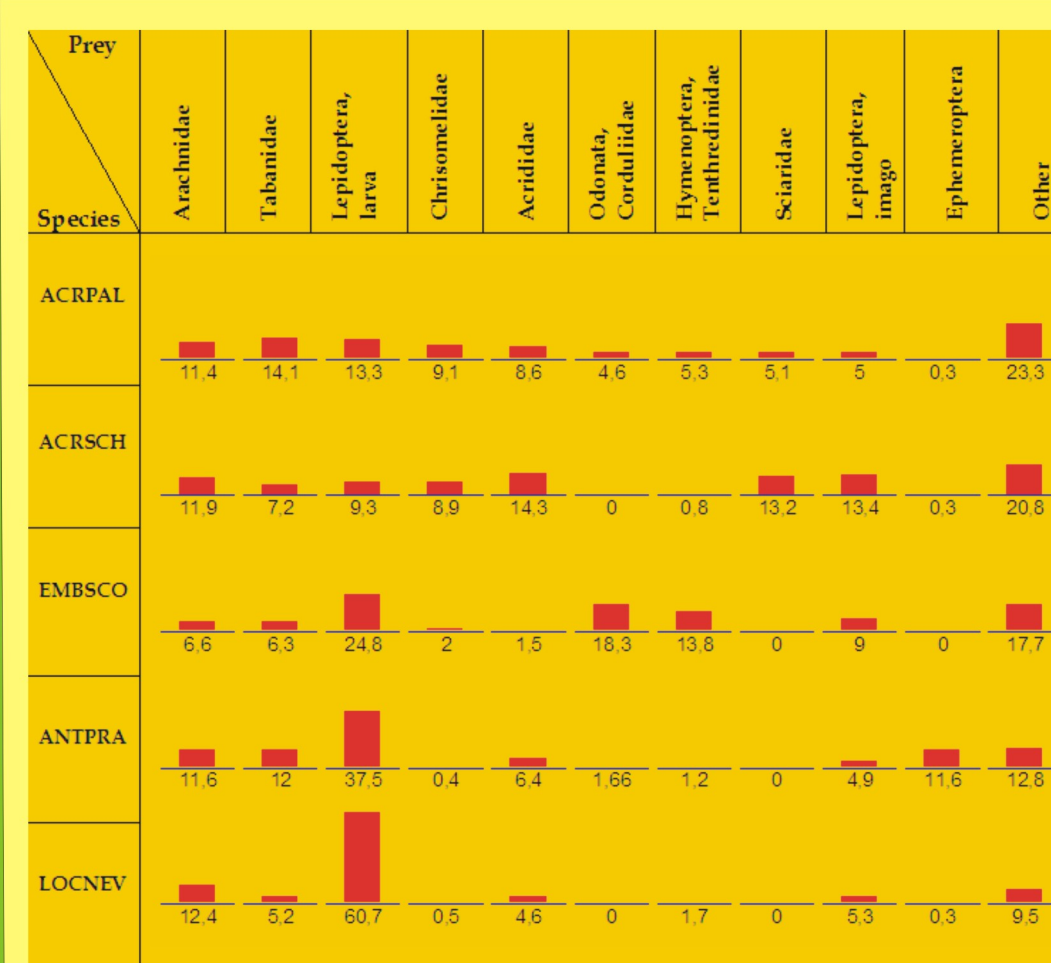
Table Avian dietary study materials

	ACRPAL	ACRSCH	ANTPRA	EMBSCH	LOCNEV
Number of nests	32	17	5	12	2
Number of ligature samples	859	535	131	220	69
Number of prey	3,422	3,003	712	679	208
Prey weight, total	21,271.4	12,055	3,620	8,902	2,195

We carried out dietary studies of fen-mire birds from mid-May until mid-July in 2000-2005 in key habitats of Aquatic Warblers in Belarus

We used the neck-collar method, which makes it possible to accurately identify prey, calculate biomass and size. The ligature around the neck of the nestling is tight enough to hinder the swallowing of food and loose enough to let chicks breathe. Chicks with ligatures were left for 15-20 minutes, then the food was carefully extracted from the throat using a pair of tweezers and placed in a 70%-alcohol test-tube, while the chick was fed similar food using a pair of tweezers. On hot sunny days, the diet was studied from 5AM until 11AM and from 4PM until 9PM. On cloudy days food samples were collected during other hours of the day.

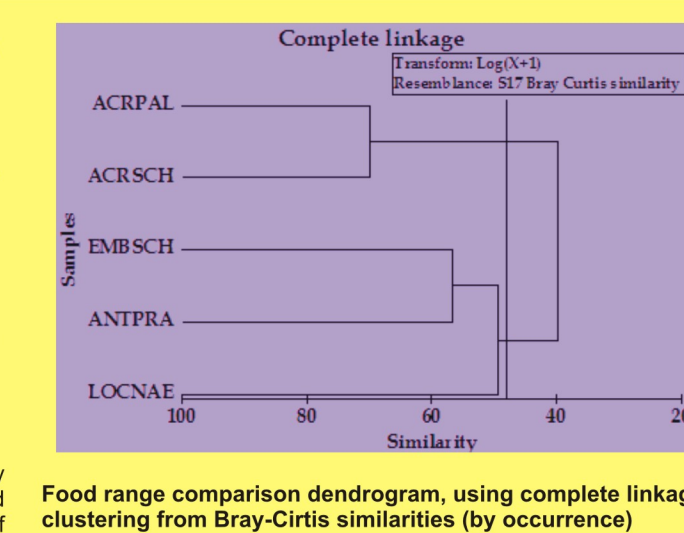
Food samples were collected from chicks aged between four to ten days. Identification of food was generally to the level of family, less often to the level of genus or species. Prey items were determined, measured, and then dried at room temperature to constant weight. All prey items were weighed on a precision balance (0.0001 g). We separately weighed together all the food from one test-tube, i.e. determined the weight of food delivered by a female per one visit. We also calculated the number of prey items brought per one sortie. The procedure to calculate dietary composition of bird species was as follows. The number of different prey items was taken as 100% for calculating the percentage frequency of various prey occurrences in the diet (%OC). In a similar fashion we calculated the percentage ratio of dry mass of different prey individuals in bird diet (%BC). We separately determined flight distances covered by provisioning females on foraging trips. Observers positioned themselves at such a distance from the nest as to not to disturb the female and be able to record approximate distances of each foraging flight. Distances were mainly calculated within the accuracy of 5 meters.



Aquatic Warbler's chick diet consisted of 77 prey items. Sedge Warbler 68, Reed Bunting 50, Meadow Pipit 50, Grasshopper Warbler 30.

In the chick diet of Aquatic Warblers, all families are represented quite evenly, with dominant spiders 11.4%, Chironomidae (Platemeris sp.) 9.1%, Noctuidae (larvae) 13.3%, Tabanidae (Hibomitra sp.) 14.1%. When summed, all dominant prey groups account for 68.9% of the total prey weight; the remaining groups with occurrences under 4% constituted 23.3%. The chick diet of Sedge Warblers also represents fairly even shares of prey families with a slight domination of spiders 11.9%, Acrididae 14.3%, Lepidoptera (larvae) 9.31, Lepidoptera (imago) 13.4, Sciaridae 13.2%. These seven dominant prey groups account for 78.2% of the total prey weight.

Reed Bunting's chick diet is clearly dominated by prey from two families: Odonata (Cordulidae) 18.3% and Lepidoptera (larvae) 24.8%. Prey occurrence of each of the remaining dominant families does not exceed 13.8%. In their entirety, these seven prey groups constitute 86.5% of the total prey weight. Meadow Pits feed their chicks mainly on Lepidoptera (larvae) 37.5%; prey occurrence of each of the remaining dominant families is no greater than 12%. Unlike other species that show a nearly accidental occurrence of the family Ephemeroptera (Baetidae) in their diet, this prey represents 11.0% in Meadow Pipit's diet. As a sum, five prey groups make 78.5% of the total prey weight. The diet of Grasshopper Warblers is totally dominated by Lepidoptera (larvae) 60.7%. Other groups are less prevalent: spiders 12.4%, Acrididae 4.6%, Lepidoptera (imago) 5.3%. When summed, these four prey groups account for 83% of the total prey weight.

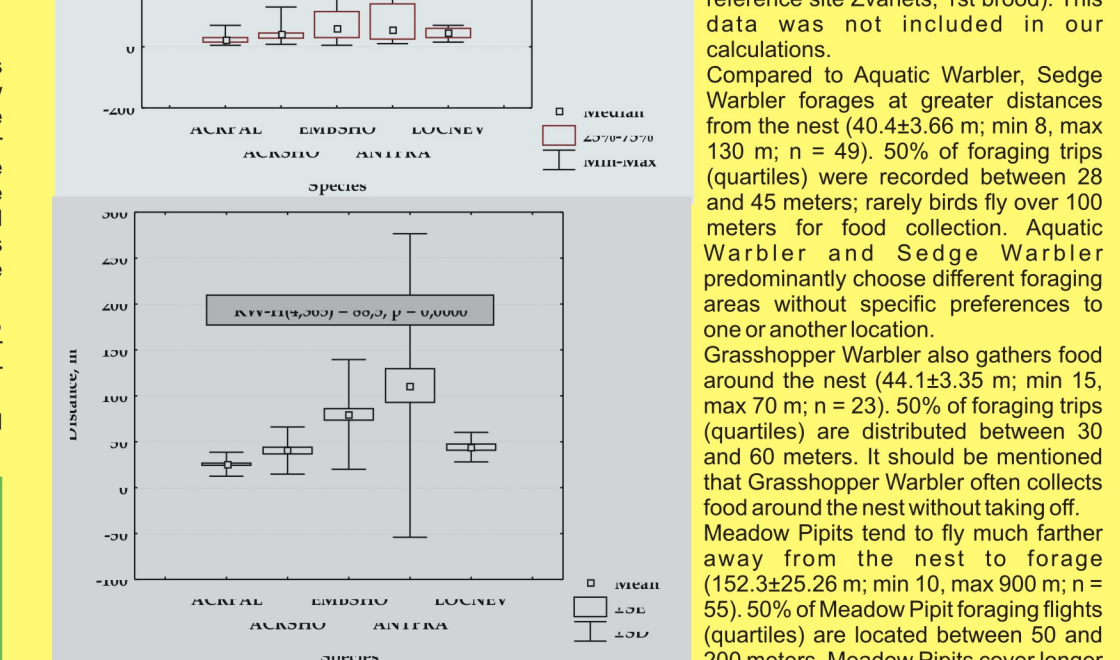


Food range comparison dendrogram, using complete linkage clustering from Bray-Curtis similarities (by occurrence). Two-dimensional ordination of food range of bird species (by occurrence) based on Log(X+1) transform and Bray-Curtis similarities (stress=0.01).

Dietary similarities and dissimilarities (by occurrence) of different birds were analyzed based on the results of complete linkage clustering. The birds were divided into two separate clusters with the similarity level of around 49.4%. 1 Aquatic Warbler and Sedge Warbler, 2 Reed Bunting, Meadow Pipit and Grasshopper Warbler. The results of complete linkage clustering of bird food range by prey biomass also allow for the division into two separate clusters at the similarity level of approximately 54.6%. A MDS analysis also confirms the existence of two clusters.

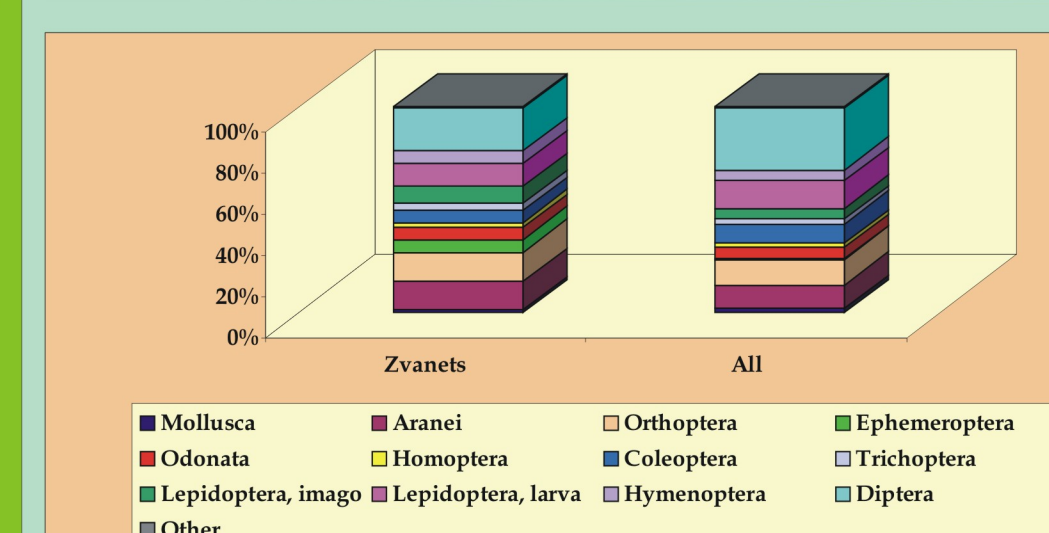


An Aquatic Warbler female flies the shortest distances from the nest to forage (24,540.99 m; min 5, max 70 m; n = 160). 50% of foraging trips (quartiles) are distributed between 15 and 30 meters. There was only one nest, from which a female flew to collect food to a nearby drainage system about 100 meters away during the year marked by an extreme food shortage (2001, reference site Zvanets, 1st brood). This data was not included in our calculations. Compared to Aquatic Warbler, Sedge Warbler forages at greater distances from the nest (40,443.66 m; min 8, max 130 m; n = 49). 50% of foraging trips (quartiles) were recorded between 28 and 45 meters; rarely birds fly over 100 meters for food collection. Aquatic Warbler and Sedge Warbler predominantly choose different foraging areas without specific preferences to one or another location. Grasshopper Warbler also gathers food around the nest without taking off. Meadow Pits tend to fly much farther away from the nest to forage (152,342.26 m; min 10, max 250 m; n = 55). 50% of Meadow Pipit foraging flights (quartiles) are located between 50 and 200 meters. Meadow Pits cover longer distances when they face food shortages near the nest. In 2003, for example, after a spring fire on the Zvanets Mire, Meadow Pits mostly chose mineral islands over 200 meters from the nest as foraging locations. Reed Bunting also collects food at a considerable distance from the nest (90,526.55 m; min 5, max 250 m; n = 55). 50% of Reed Bunting foraging flights (quartiles) are distributed between 50 and 130 meters. In 2001, vegetation burning at the Zvanets site led to scarcity of food causing all Reed Buntings breeding on the mire to fly up to 1,000 meters away to drained fields for foraging. This data was not taken into account in calculating flight distances. It is important to say that on their long trips Reed Buntings and Meadow Pits fly to the same foraging locations, apparently with high food concentration (coastal areas of water reservoirs, mineral islands, etc.).



Comparison of foraging flight distances of different bird species breeding on fen mires

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Main prey groups occurrence in Aquatic Warbler diet on the Zvanets Mire (2001-2005) and all 3 mires together, %

There is the structure of diet of Aquatic Warbler on the Zvanets Mire by results investigation in 2001-2005 at 1st and 2nd brood except for 2002 year. It doesn't differ significantly from the structure of diet of Aquatic Warbler on three fen mires together.



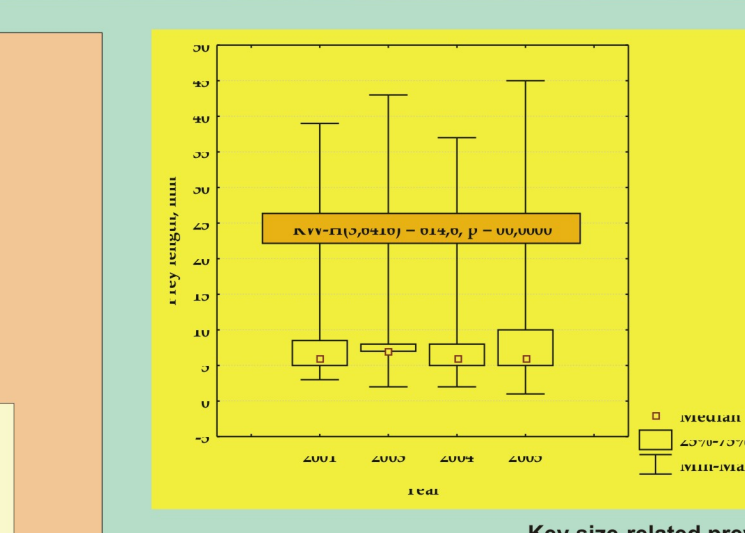
Key prey groups occurrence in Aquatic Warbler diet (Zvanets, 2001-2005), by prey biomass in 1st and 2nd brood

In first brood all key prey groups were represented quite evenly, with small dominant of spiders 11.4%, Chironomidae (Platemeris sp.) 9.1%, Noctuidae (larva) 12.1%, Hymenoptera (Tenthredinidae) 9.2%, Tabanidae (Hibomitra sp.) 13.1%. In second brood in the first place two kinds of forage dominated Orthoptera (Acrididae) 30.1% and Odonata (Lestidae) 29.6%.

Key size-related prey parameters (Mean ± SE) in chick diet of Aquatic Warbler breeding on fen mire Zvanets (2001-2005) in 1st and 2nd brood

	1	2
Number of nests	21	11
Number of ligature samples	841	538
Prey weight	4.64±0.13	7.13±0.30
Prey length	7.57±0.07	9.18±0.13
Food weight	23.78±0.51	27.88±0.95

Key size-related prey parameters (Mean ± SE) in chick diet of Aquatic Warbler breeding on fen mire Zvanets (2001-2005), 1st and 2nd brood

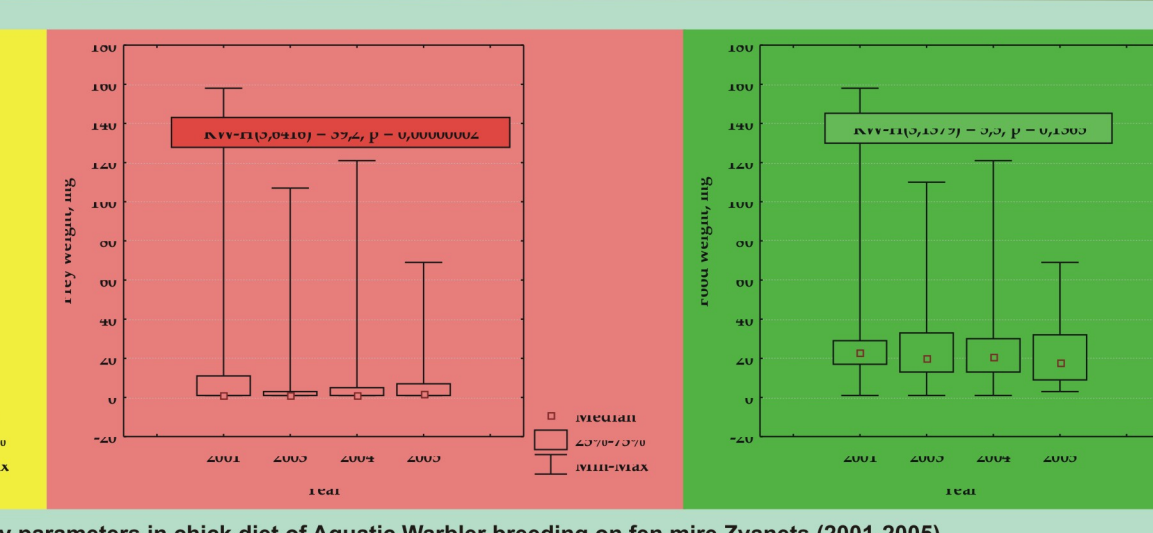


Key size-related prey parameters in chick diet of Aquatic Warbler breeding on fen mire Zvanets (2001-2005)

Key size-related prey parameters (Mean ± SE) in chick diet of Aquatic Warbler breeding on fen mire Zvanets in different years

Year	2001	2003	2004	2005
Number of nests	10	9	11	2
Number of ligature samples	166	670	506	37
Prey weight	8.06±0.62	4.97±0.17	5.38±0.21	8.62±1.41
Prey length	7.66±0.19	8.54±0.09	7.47±0.10	10.02±0.81
Food weight	27.76±1.72	25.58±0.69	24.55±0.73	22.62±2.84

Key size-related prey parameters (Mean ± SE) in chick diet of Aquatic Warbler breeding on fen mire Zvanets in different years



Dynamics of Aquatic Warbler diet composition during breeding season, 1st (upper one) and 2nd (bottom one) brood

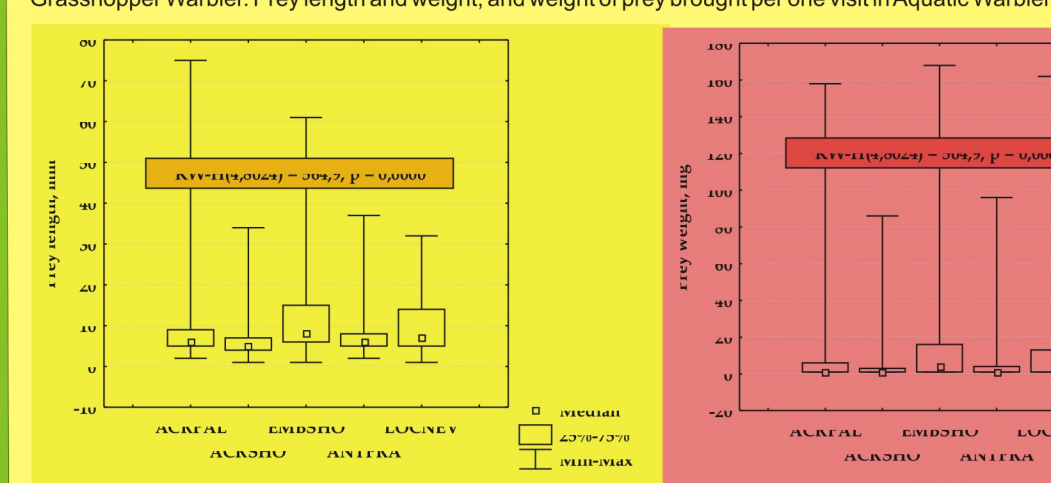
In chick diet of Aquatic Warblers spiders proportion doesn't change considerably 17.9% in 1st brood and 15.9% in 2nd brood. Ratio of all types of Diptera also doesn't change significantly. Orthoptera (Acrididae) increases from 1st to 2nd brood from 7.6% to 23.3% and Odonata takes about 11.3%. Trichoptera (Limnephilidae) and Hymenoptera (Tenthredinidae) proportions are bigger in 1st brood, correspondingly 15.1% and 12.3%. Other types of prey, for example Ephemeroptera (Baetidae), appear during their development cycle. Quantity of Coleoptera was bigger in 1st brood more than in 2nd brood. We think, they are the spare feed, and its part increases in Aquatic Warbler diet composition when change for the worse foraging takes place.

Comparison of prey length, prey weight and food weight showed that if prey length and prey weight differ through years then food weight doesn't differ significantly. It confirms that species strategy consists in catching mass species of prey with minimal selectivity in close range of nest.

Key size-related prey parameters in chick diet of different bird species breeding on fen mires (Mean ± SE)

	ACRPAL	ACRSCH	ANTPRA	EMBSCH	LOCNEV
Prey weight	6.22±0.19	4.01±0.14	5.10±0.38	13.11±0.84	10.55±1.37
Prey length	7.87±0.09	6.25±0.07	7.79±0.18	11.45±0.35	9.92±0.51
Food weight	24.76±0.60	22.53±0.62	27.71±1.63	40.46±2.16	31.81±2.319

Warbler and Meadow Pipit, Reed Bunting and Grasshopper Warbler, while in the remaining cases highly significant differences were recorded (P<<0.001, Tukey HSD tests). We also calculated the total weight of prey brought by a bird to its chicks per one visit. Reed Buntings bring to their young the largest amount of food per one visit, followed, in the descending order, by Grasshopper Warbler, Meadow Pipit, Aquatic Warbler and Sedge Warbler. For this parameter significant differences were recorded between Aquatic Warbler and Reed Bunting, Sedge Warbler and Reed Bunting, Reed Bunting and Meadow Pipit (P<<0.001, Tukey HSD tests), Aquatic Warbler and Grasshopper Warbler (P=0.044, Tukey HSD tests). Differences between Aquatic Warbler and Sedge Warbler as well as Aquatic Warbler and Meadow Pipit were not significant. It is noteworthy that Aquatic Warbler's maximum prey length is greater than that of all the other species, while the maximum weight of prey is nearly the same as of larger Reed Bunting and Grasshopper Warbler. Prey length and weight, and weight of prey brought per one visit in Aquatic Warblers is significantly greater than in similarly-sized Sedge Warblers.



Key size-related prey parameters in chick diet of different bird species breeding on fen mires



Despite sharing the same habitat of open sedge mires, the species we analyzed have different foraging strategies. Since Aquatic Warblers feed their chicks alone, they have to be near the nest during foraging. Given a limited space within the vicinity of the nest and high feeding frequency, females have to use every food resource available to them, which explains low prey selectivity vis-a-vis other birds. On the other hand, to enhance feeding efficiency, females tend to give priority to larger prey items. As a stenotopic species, Aquatic Warblers are forced to breed in the same habitat every year even though feeding conditions may strongly vary from year to year. The species has made adaptations to the broadest variety of food in such conditions. If food resources are compromised as a result of spring fires or long floods, the species switches to backup food items, such as Chironomidae (Platemeris sp.) and Sciaridae, which are rarely found in their diet in good years. On the other hand, as foragers sticking to their nests, Aquatic Warblers are very particular about their nesting grounds, so when the conditions are adverse in some locations (shortage of insects after spring fires, no flood, low water level), they hold the nesting period until better days or move to better grounds where there is more food, sometimes even building heavy nest concentrations there.

Sedge Warbler is the closest kin of Aquatic Warbler by foraging behaviour, however in spatial terms nesting locations of these two overlap only on the Zvanets Mire. On other reference sites (Dikoe, Servech) the species breeds sporadically along the mire periphery, while on the SporoVo Mire it concentrates in mosaic willow carrs, where Aquatic Warbler is not to be found. Sedge Warbler breeds on the Zvanets Mire only in years of insect abundance, reaching and even surpassing Aquatic Warbler by density. The species also collects food near the nest, but the foraging radius is almost twice the size of Aquatic Warbler's. In years of impoverished food resources on fen mires (especially with few Noctuidae, Sciaridae insects), Sedge Warbler moves to other habitats to breed. Apparently, the species cannot effectively collect other small insects. Foraging strategies of Meadow Pipit and Reed Bunting are quite alike. These species locate and fly for food to areas with high prey concentrations, at times taking long flights. Apparently productivity value of such foraging locations offsets any energy losses associated with long flights. Because of long flights, prey weight delivered to the nest by these species in one visit is much greater than that of birds foraging around the nest.

So, the species breeding on sedge fen mires demonstrate different habitat adaptation strategies. Monogamous species with a strictly fixed breeding period have the following set of adaptations:

- ability to breed in different habitats and, when conditions are bad, move from sedge mires to other habitats for nesting without changing the breeding period (Sedge Warbler, Grasshopper Warbler, Meadow Pipit, Reed Bunting);
- ability to carry out long foraging sorties to locations with highly concentrated prey presence when the conditions are unfavourable near their nests (Reed Bunting, Meadow Pipit);
- the length and weight of prey items collected per one visit are relatively large;
- even distribution on nesting grounds due to male territoriality;
- inability to change nesting locations during the breeding season when adverse conditions set in, because other locations are occupied by territorial males;
- breeding period is fixed because males have limited time in which they are willing to mate.

Stenotopic Aquatic Warbler, which forms no permanent breeding pairs and whose females feed chicks themselves, has the following adaptive responses to variable nesting conditions on sedge fen mires:

- the lowest food selectivity driven by foraging in a limited space and the necessity to use all food resources available;
- around-the-nest radius of food collection is marginal, because females feed chicks unassisted;
- male activity throughout the season enables females to change breeding dates from early May to late July timing it to periods with best safety and food conditions;
- lack of permanent pairs gives females the flexibility to move to territories of other males during the breeding season, richer in food, and build nest clusters in the most favourable locations.

Such adaptations of Aquatic Warblers to habitat instabilities have become possible only owing to their specific breeding system - partial promiscuity. The ultimate cause of such breeding system must have been the need of this stenotopic species to adjust to highly unstable fen mire setting. The primary prerequisite of partial promiscuity in Aquatic Warblers was food overabundance on fen mires, where females could fledge chicks themselves. Considering biology, Aquatic Warbler is most vulnerable of all species breeding on fen mires, because if unfavourable conditions develop across the mire throughout the breeding season, the species does not breed that year, whereas other birds move to other habitats. This is because all key habitats of Aquatic Warbler represent spatially isolated mires, so birds cannot move from one set of mires to another. In this context, to preserve the species, it is necessary to ensure the best nesting conditions during the breeding season and seek to set up a network of fen mires located within a short distance of one another.

