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Breeding ecology of Aquatic Warblers *Acrocephalus paludicola* in their key habitats in SW Belarus

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Abstract. The breeding ecology of the Aquatic Warbler was studied on the three largest mires in Belarus in 1998–2004. Numbers of male Aquatic Warblers on these mires range from 6370 to 11500, which is more than 50% of the species world population. In years with favorable nesting conditions breeding success on the three mires varies from 36.3% to 54.1%. In years with significant water level fluctuations and irruptions of shrew populations the breeding success decreases sharply, varying from 2.9% to 27.7%. The main reason for the mortality of eggs and nestlings was predation, probably by small insectivorous mammals. The species is well adapted to the unstable nesting conditions in fen-mires; but in years with serious flooding, high water levels throughout the nesting season, disturbances to the vegetation structure after spring fires or in years with a high density of shrews, breeding success decreases significantly.

Key words: Aquatic Warbler, *Acrocephalus paludicola*, breeding success, predation, shrews, mires, reedbeds, threatened species

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INTRODUCTION

The Aquatic Warbler is a globally threatened species bound to lowland bogs and marshes. The core of the contemporary breeding range of the species is located in the Belarus and Polish “Polessye lowland”. More than 70% of the European Aquatic Warbler population inhabits only four large mire tracts in Poland and Belarus (Aquatic Warbler Conservation Team 1999).

The breeding ecology of Aquatic Warbler has been studied just on one marshland so far — the Biebrza river valley (NE Poland). Moreover, most investigations were carried out just on one monitoring plot in Poland situated in a non-flooded zone and characterized by relative stability in terms of hydrology and vegetation dynamics (Dyrcz & Zdunek 1993a, 1993b, Schulze-Hagen et al. 1999). There are reasons to believe that the breeding data obtained from only one site may not reflect neither all the peculiarities of the breeding ecology of the species nor the full range of its adaptive capacities under different environments.

Additionally, a number of recent studies in Belarus prove that fen bogs — which are the habitats of the species — are quite unstable ecosystems (Kozulin et al. 1998, 1999, Kozulin & Flade 1999, Kalinin & Obodovskiy 2003). As a consequence, density and number of the Aquatic Warbler fluctuate significantly within and between seasons. These fluctuations are influenced by a number of natural and anthropogenic factors, such as vegetation successions, water table oscillations and fires (Kozulin et al. 2004). However, the mechanisms by which these factors influence the state of the Aquatic Warbler population have not been discovered yet.

Therefore, to better understand the contemporary condition and population trends of this globally threatened species, and also to work out clear recommendations for its conservation, it is necessary to study its breeding ecology in different types of marshes. This publication presents results of a study on Aquatic Warbler breeding success in the major European nesting habitats located in SW Belarus which host ca. 50% of the global population of this species.

STUDY AREA

The breeding success of the Aquatic Warbler was studied on three fen marshlands located in the Belarussian Polessye (Fig. 1):
1) Dikoe — located on the watershed and corresponds to a transition type of marshes, from the *Hypnum*-sedge to the sedge-*Sphagnum* stage (Kozulin et al. 1998), mostly rain-dependent. The 100 ha monitoring plot was located in the part of the marshland where the input of nutrients was the poorest among all studied habitats of the Aquatic Warbler in Belarus (water mineralization level — 106 mg/l). The vegetation of the monitoring plot was characterized by alternation of a large number of various plant associations, but the dominant species in the projective coverage are *Carex lasiocarpa*, *C. limosa*, to a lesser extent *C. chordorrhiza*, *C. diandra* and *C. rostrata*, *Eriophorum polystachyon*, *Calamagrostis neglecta*. In some places *Menyanthes trifoliata* (mean coverage of 25%) and *Comarum palustre* (coverage varies from 2% to 65%) were very abundant. *Carex elata* was found only in depression areas and along the ditches. The marshland was practically flat; with tussocks of plants covering no more than 5% of it. During the nesting period the groundwater table usually coincided with the topsoil level, but in certain years, as a result of heavy rains, the mire surface was inundated.
2) Zvanets — a typical sedge fen marshes located in the peripheral part of the Pripyat′ river floodplain and mainly dependent on ground water.

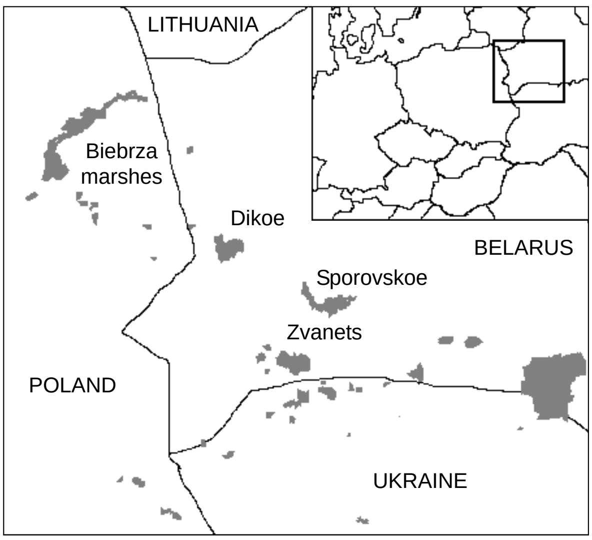

Fig. 1. Location of main habitats of the Aquatic Warbler and study sites.

The 48 ha monitoring plot was located in the southern part of the marshland. The marshland was inundated annually by flood water from Pripyat′ and was characterized by high productivity (water mineralization was 244–347 mg/l). Associations of *Carex elata* (58.3%) and *C. appropinquata* (36.5%) were dominating on this monitoring plot. The whole mire surface was covered with tussocks of 10–30 cm high plants. In the spring, the marshland was flooded 20–50 cm above the soil level. When flood waters recede, the water level gradually drops to the soil level, normally by early-mid March. From June through September or October, the water level continues to drop gradually down to 10–50 cm below the soil level because evaporation is greater than precipitation. In the late autumn, the water level begins rising slowly. During the time of this study there were extremely unstable nesting conditions. In 1999, during the first clutch period water level was higher than the tussocks of plants. Owing to the absence of fires during that year, dry vegetation was well preserved and Aquatic Warblers built nests above the water, in tangles of old vegetation. During the second clutch 1999 water lowered and nests were arranged in accumulations of old vegetation on plant tussocks′ tops or on the soil surface and were well covered by vegetation. Nesting conditions in 2001, 2003 and 2004 were similar. During the first clutch in 2001, after a spring fire, dry vegetation was preserved just on 25% of the area and 30% of nest were arranged on plant tussocks or in the burnt tussock holes without proper concealment. In 2003 and 2004 dry vegetation was practically absent and about 80% of nests were arranged opportunistically (A. Kozulin, L. Vergeichik in prep.). During the second clutch, green vegetation was already well-developed;
3) Sporovskoe bog in Sporovskiy Reserve — typical floodplain sedge fen bog stretching along the Yaselda River for about 35 km. A 24 ha monitoring plot was located in the part of the marshland characterized by the highest productivity (water mineralization was 289–322 mg/l). It should be noted that the productivity value of the site changed from year to year depending on whether the site was flooded in spring or not. Projective coverage of the *Caricetum elatae* community, which was typical of marshes with rich mineral content, was 89.1% of the total area of the monitoring plot. Tussocks of plants were slightly prominent; they were not higher than 20 cm. The water table during the nesting period fluctuated greatly from +40 cm to -30 cm in relation to the soil level and it

fully depended on the water level dynamics in the Yaselda River. Currently water level of both the river and marshland fully depended on the patterns of water resource use at the Selets reservoir and a fish farm constructed in the upstream part of the river. In humid years and in years with excessive precipitation, supplemental discharge of water from the reservoir leads to long inundation of the mire; in dry years most water is used to secure the needs of the fish-farm, which is accompanied by a drastic drop of the water level in the mire.

MATERIAL AND METHODS

Field data

The bulk of the field work took place on the monitoring plots from 15 May to 15 August, in 1998–2004. Breeding investigations within the Dikoe marshland were carried out in 1999 and 2001, at Zvanets — in 1999, 2001, 2003 and 2004, and at Sporovskoe — in 1998 and 2000.

All the nests located on the monitoring plots were identified basing on observations of female behavior. The location of nests and worried females were marked on a map of the area in the field. Nests with chicks were monitored every day, when possible. Nests with eggs were visited less frequently, according to the stage of their incubation. In order to avoid attracting predators the tracks were located 5 m away from the nest, and further, the observer had to approach the nest with long steps without disturbing the vegetation structure.

Identification of predators

The area within a 3 m radius of any failed nest or of a nest with partial losses was carefully examined for signs that could help determine the cause of failure. The following signs were recorded: partial or complete disappearance of the nest contents, intact or destroyed nest, character of bite traces on the eggs and nestlings, a distance of the found dead nestlings from the nest, predators' footsteps, water level in relation to the nest's bottom. All cases of predation were divided into two groups, according to predator species:

1) shrews *Sorex* sp. — when the nest and surrounding vegetation were found undisturbed, though the nest contents had completely or partially disappeared. An additional cue was if there were no traces of attacks by large mammals or birds-of-prey (such as trampled grass around the nest, or deformations in the nest construction). In those cases, thorough examination of the nest surroundings usually revealed eggs or nestlings with bite traces found at a 20–100 cm distance. Also trap experiments near nests after disappearance of one nestling resulted in the almost immediate catching of shrews. Also the aggressive behavior of Aquatic Warbler females protecting their nests from a shrew was observed (Authors' unpubl. data);

2) "other predators" — when the nest was found destroyed, the surrounding grass was stamped flat; feathers, typical feeding tables, etc. were found around the nest. In such cases it was often impossible to identify the predator. However, in most cases we can presume that the following predators were likely to have devastated the nests: the Marsh Harrier *Circus aeruginosus*, White Stork *Ciconia ciconia*, Water Vole *Arvicola terrestris*, Ermine *Mustela vision*, Raccoon Dog *Nyctereutes procyonoides* or an unidentified large terrestrial predator. In most cases nest devastation by those predators is casual and happens usually when the Aquatic Warbler is nesting in unusual conditions.

Abundance of shrews

The catching of shrews was carried out by the modified Barber's peatful trap method. Glasses of 0.5 l in volume and 18 cm high were placed into soil at the distance of 5 m from each other, forming a transect that crossed the monitoring plot. Glasses were 1/3 filled with attraction mixture (beer, vinegar, water and solt). The mean relative abundance of shrews belonging to the genus *Sorex* (Aquatic Warbler nest potential predator) at Dikoe plot was 8.46 ± 4.01 (0–13.3) individuals collected per 100 catch-days (V. E. Sidorovich, unpubl. data). At Zvanets mean relative abundance of shrews was 7.25 ± 2.63 individuals (4.57–10.88) collected per 100 catch-days (M. L. Minets, unpubl. data) and at Sporovskoe — 6.66 ± 4.09 individuals (3.17–11.15) collected per 100 catch-days (M. L. Minets, unpubl. data).

Data analysis

Daily egg and nestling mortality rates were calculated using the Mayfield method (Mayfield 1975); the number of dead/predated eggs (or nestlings) was divided by the egg-days or the nestling-days number (which is the number of eggs or nestlings multiplied by the number of exposure days). The standard deviation of the estimates was calculated using the Hensler method (Hensler 1985). In addition, daily mortality rates due to identified reasons were calculated (Mayfield 1975). The overall breeding success was defined as the proportion of eggs that produce fledglings in successful nests — nests with at least one fledgling. In addition, the following indicators were calculated — a frequency of nests destroyed by predators and the mean number of fledglings per nest.

RESULTS

Breeding of Aquatic Warbler on the Dikoe marshland

Breeding density and clutch size. The average density of singing males per km^2 (1996–2005) was 47.1 ± 3.86 (18–63, n = 10) during the first clutch and 35.1 ± 7.22 (12–65, n = 10) during the second clutch. The density of breeding females was quite low: in 1999 — 22 females/km^2 (18 females during first clutch and 5 — during the second), in 2001 — 11 females/km^2 (all the females bred in first clutch, no one breeding female was detected during the second one). All data presented below refer to the first clutch period, because the nest density during the second clutches was very low.

The mean clutch size was 4.68 ± 0.82 (3–6, n = 28). It varied from 4.59 ± 0.87 in 1999 to 4.82 ± 0.75 in 2001 but those differences were not significant ($t = 0.72$, $df = 26$, $p = 0.48$).

Indicators of breeding success. During the two years, 7 out of 28 nests (25% of all nests found) were completely depredated by shrews, from 5 other nests (17.8%) chicks or eggs disappeared partially, also due to the shrew predation. Other 2 nests (7.1%) failed as a result of the female disappearance.

Out of 131 eggs laid, 20 were lost (15.3%) over the whole observation period. Most of the eggs were lost as a result of embryo mortality (9 eggs, 45% of all eggs lost) and shrews' predation (8 eggs, 40%). Among 111 nestlings, 43 (38.7%) died. The main cause of chick mortality was the shrew predation (36 nestlings, 83.7% of all died chicks).

The embryo mortality calculated as a cumulative share of eggs with dead embryos and unfertilized eggs in the overall number of eggs present just before hatching (Paevsky 1985) was 7.5% and differences between years were not significant ($\chi^2 = 0.87$, $df = 1$, $p = 0.35$, Table 1).

The daily egg mortality rate in 2001 (12.2 ± 3.45%) was considerably higher than in 1999 (3.9 ± 1.28%, $t = 2.24$, $p < 0.05$). Also the daily nestling mortality rate varied between both years of the study (3.45 ± 0.8% vs 12.37 ± 2.36%, $t = 3.6$, $p < 0.01$).

Predation by shrews on Aquatic Warbler nests at the nestling stage turned out to be higher than at the egg stage (5.04% vs 2.5%, $t = 2.03$, $p < 0.05$). Both the mean daily egg and nestling mortality rates caused by predation in 2001 were significantly higher than in 1999 (difference in daily egg predation rates: 0.87 ± 0.61 vs 6.67 ± 2.63, $t = 2.15$, $p < 0.05$; difference in daily nestling predation rates: 2.3 ± 0.66 vs 12.37 ± 2.36, $t = 4.14$, $p < 0.01$).

The overall breeding success calculated by Mayfield method was 18.47 ± 4.26%, but varied significantly between years (36.3 ± 7.62% in 1999 vs 2.89 ± 1.92% in 2001, $t = 4.33$, $p < 0.01$).

Breeding of the Aquatic Warbler on the Zvanets marshland

Breeding density and clutch size. The average density of singing males/km^2 was 81.0 ± 8.17 (35–103, n = 8) during the first clutch and 89.5 ± 10.9 (17–115, n = 8) during the second one. Density of breeding females changed between different years and within particular breeding seasons. In 2001, there was 116 females/km^2 (72 females during the first clutch and 44 during the second one), in 2003 — 66 females/km^2 (34 and 32 females, respectively) and in 2004 — 102 females/km^2 (37 and 65).

The mean clutch size for the complete study period was 4.61 ± 0.77 eggs (3–7, n = 99). It ranged from 4.52 ± 0.78 (in 2004) to 4.73 ± 0.59 (in 1999). On average, the size of the first clutch was larger than of the second one ($t = 4.28$, $df = 97$, $p < 0.001$, Table 1).

Indicators of breeding success. Among 99 nest monitored during the study, 15 (15.2%) failed completely (among them 13 nests were devastated by predators, one failed because of the female's absence and one more because of ectoparasites). Partial losses were observed in 14 (14.1%) nests (in 11 nests the losses were caused by predation, in 1 by flood, in 1 by the sun and in 1 by parasites — see below). Shrews destroyed 75% (7 completely and 11 partially) of all predated nests, other predators — 25% of all predated nests (6 completely destroyed ones).

Out of 456 eggs laid, 60 (13.2%) were lost over the period of study. Egg losses were caused mostly by "other predators" (20 eggs, 33.3% of all eggs lost) and as a result of embryo mortality (28 eggs, 46.7% of all eggs lost); 8 eggs (13.3%)

were predated by shrews and 4 eggs (6.7%) were abandoned by female (due to human disturbance at the early incubation stage). Among 396 nestlings, 60 (15.2%) died. Nestlings were killed mostly by shrews (38 nestlings, 63.3% of all dead chicks); a negligible amount of nestlings died from flood and parasites (poultry red mite *Dermanyssus gallinae*), one nestling died due to overheat in a non-concealed nest.

Embryo mortality calculated as a cumulative share of eggs with dead embryos and unfertilized eggs in the overall number of eggs present just before hatching (Paevsky 1985) was 6.6% (differences between years were not significant, χ^2 = 4.13, df = 7, p = 0.76, Table 1).

The daily egg mortality rate was lowest in 2004 (2.14 ± 0.75%) and highest in 2003 (5.1 ± 0.95%, t = 2.43, p < 0.02). Daily nestling mortality rate in 1999 (5.13 ± 1.33%) was higher than in all other years (vs 2001 — t = 2.24, p < 0.05; vs 2003 — t = 2.3, p < 0.05; vs 2004 — t = 1.96, p = 0.05).

Daily egg predation rate was highest in 1999 (3.87 ± 0.98%) — (vs 2001 — t = 3.9, vs 2004 — t = 3.55, p < 0.01) and in 2003 (2.26 ± 0.65%) — (vs 2001 — t = 3.5, vs 2004 — t = 2.85, p < 0.01). This indicator was related to "other predators" pressure (r = 0.93, p < 0.05), which happened in 1999 and 2003 during the first clutch period (Fig. 2).

Daily nestlings predation rate increased in 1999 — 3.93 ± 1.28% (vs 2003 — t = 2.01, p < 0.05) and 2004 — 2.35 ± 0.52% (vs 2003 — t = 2.12, p < 0.05). It was determined by daily predation rate due to shrews (r = 0.94, p < 0.05). Shrew predation on nestling stage was high in the second clutch period of 1999 and remains quite high during the whole breeding season of 2004 (Fig. 2).

Daily predation rate of shrews was lower at the egg stage than at the nestling stage (0.52% vs 1.52%; t = 3.24, p < 0.01, Table 1). Daily mortality rate due to predation of "other predators" at the egg stage was higher (1.32% vs 0.39%; t = 2.88, p < 0.01) than at the nestling stage.

The overall breeding success of Aquatic Warblers calculated by the Mayfield method was 42.28 ± 3.4%, the lowest in 1999 (27.68 ± 6.68%) and the highest in 2004 (54.07 ± 6.74%, t = 2.78, p < 0.01).

Breeding success during the first clutch was lower than during the second clutch (39.1% vs 55.89% t = 2.25; p < 0.05). Breeding success was determined here mostly by egg mortality rate (r = -0.65) and almost didn't depend on shrews predation.

Table 1. Breeding statistics of Aquatic Warbler in Belarus and Poland (mean ± SD, range). * — data from Dyrcz & Zdunek 1993a, 1993b, Schulze-Hagen et al. 1999.

	Dikoe (2 years)	Zvanets (4 years)	Sporovo (2 years)	Biebrza, Poland (4 years)*
N of nests	28	99	34	157
Mean clutch size	4.68 ± 0.82 (4.59–4.82)	4.61 ± 0.77 (4.52–4.73)	4.88 ± 0.91 (4.62–5.5)	4.81 ± 0.73 (4.69–5.00)
Mean size of the first clutch	4.68 ± 0.82 (4.59–4.82)	4.86 ± 0.69 (4.77–5.06)	5.00 ± 0.95 (4.81–5.6)	5.11 ± 0.60
Mean size of the second clutch		4.24 ± 0.73 (4.26–4.50)	4.69 ± 0.85 (4.25–5.40)	4.37 ± 0.60
Embryo mortality (%)	7.5 (4.54–9.21)	6.6 (1.79–9.78)	2.13 (1.8–2.6)	8.6 (6.2–10.7)
Nests destroyed by predators (%)	25 (11.8–45.4)	13.13 (8.57–33.33)	2.94 (0–10)	11.1 (10–12)
Daily egg mortality rate (%)	6.27 ± 1.36 (3.93–12.22)	4.93 ± 0.50 (2.14–5.09)	13.61 ± 2.48 (3.6–17.8)	
Daily nestling mortality rate (%)	5.87 ± 0.88 (3.45–12.37)	2.39 ± 0.31 (1.85–5.13)	2.58 ± 0.46 (2.06–5.10)	
Daily egg predation rate caused by shrews (%)	2.5 ± 0.87 (0.87–6.67)	0.52 ± 0.18 (0–1.32)	0	
Daily nestling predation rate caused by shrews (%)	5.04 ± 0.82 (2.3–12.37)	1.52 ± 0.24 (0.28–3.29)	0.34 ± 0.17 (0–0.41)	
Nest success (%)	39.41 ± 14.27 (7.91–73.51)	63.5 ± 8.06 (38.13–85.21)	18.06 ± 13.15 (4.38–87.68)	62.7 (60–67)
Breeding success (%)	52.67 (33.96–65.38)	73.68 (57.75–78.63)	66.26 (38.18–80.18)	62
Mean number of fledged chicks/nest	2.46 (1.64–3.00)	3.39 (2.73–3.55)	3.24 (2.10–3.71)	3.2 (1.86–4.56)

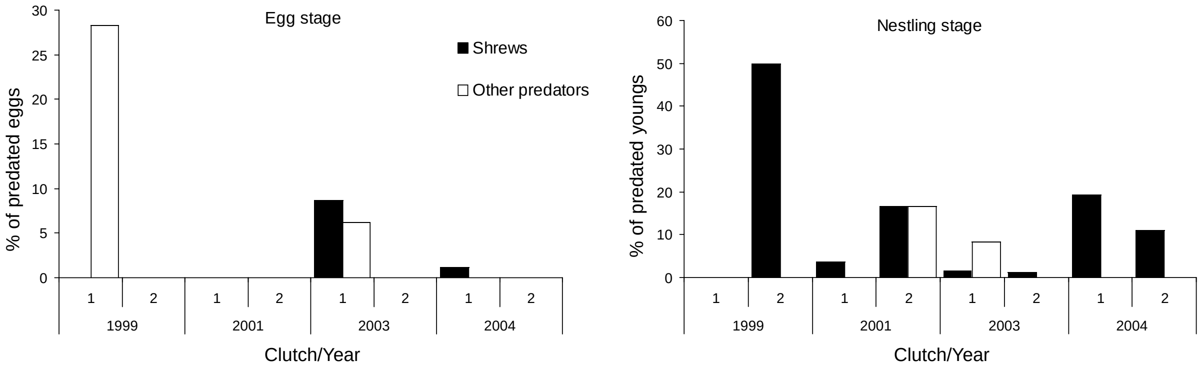

Fig. 2. Predation of shrews and "other predators" on the Zvanets mire.

Breeding of Aquatic Warbler on the Sporovskoe marshland

Breeding density and clutch size. The average density of singing males/km^2 (1996–2005) was 48.4 ± 12.2 (0–135, n = 10) during the first clutch and 33.1 ± 10.4 (0–95, n = 10) during the second one. Density of breeding females changed in different years and within the breeding season. In 2000 there were 87 females/km^2 (58 females during the first clutch and 29 during the second) but in 2005 — 128 females/km^2 (128 and 0).

The mean clutch size was 4.88 ± 0.91 eggs (3–6, n = 34). It varied from 4.63 ± 0.92 in 2000 to 5.5 ± 0.53 in 1998 (t = 2.79, df = 32, $p < 0.01$). Mean size of the first clutch was larger than of the second one, but this difference was not significant (t = 0.95, df = 32, p = 0.35, Table 1).

Indicators of breeding success. Among 34 nests monitored during study, 8 (23.5%) failed completely (seven of them failed due to flood and one due to predation), partial losses were observed in 6 (17.6%) other nests (in 1 nest the losses were caused by starvation, in 2 by flood, in 3 as a result of predation by shrews). Out of 166 eggs laid, 26 (15.66%) were lost. Losses were caused mostly by flood (22 eggs, 84.6%). 4 eggs (15.4%) were lost as a result of embryo mortality. Among 140 nestlings hatched, 30 (21.43%) died. Among them 19 chicks (63.3%) died due to flood, 9 nestlings (30%) were predated and 2 more died of starvation (during prolonged rains).

Embryo mortality calculated as a cumulative share of eggs with dead embryos and unfertilized eggs in the overall number of eggs present just before hatching (Paevsky 1985) was 2.13% (difference between years was not significant, $\chi^2 = 1.69$, df = 1, p = 0.19).

Daily egg mortality rate in this mire was lowest in 2000 (3.57 ± 2.48%) and highest in 1998 (17.78 ± 3.29%, t = 3.45, $p < 0.01$). Over two years of survey no predation was recorded at the egg stage. There were no significant difference between years in the mean daily nestling mortality rate (t = 1.86, $p > 0.05$).

The main causes of nestling mortality were flood and predation. In 1998 during the first clutch no losses were detected at the egg stage and they were minimal at the nestling stage. However, all the nests found in July had been inundated by the rain flood.

In 2000 there were no losses at the egg stage during the first and the second clutches, chicks mortality rate due to predation by shrews was low. However, during the second clutch, as a result of rains, the water level on the mire rose, which led to increase in nestling mortality due to inundation of nests.

The overall breeding success was 10.36 ± 3.94%. This figure varied significantly between years (t = 2.67, $p < 0.01$).

Breeding success during the first clutch, calculated for the two years pulled together, was higher than during the second clutch (55.61% vs 0.07%, t = 4.87, $p < 0.01$). Mortality due to flood was higher during the second clutch both at the egg and nestling stages.

DISCUSSION

The main factor of the nests failure in the Sporovskoe marshland area was wide water level fluctuations during the nesting period. Rain-related floods usually occur in July and can lead either to complete inundation of all the second clutch nests (in the case of abrupt rise of water table) or to increased chick mortality in waterlogged nests (when water table rises gradually). However when nests are not inundated breeding success may be rather high (breeding success during the first clutch was 55.61%).

In the two other marshland areas, Dikoe and Zvanets, the main factor influencing the breeding success was predation. In the Dikoe marshland site the main predators of Aquatic Warbler nests were shrews. Outbreaks of shrew populations in certain years lead to abrupt drops in the breeding success. In the Zvanets marshland, shrew predation had no considerable influence on the Aquatic Warbler breeding success. However, breeding success drop in years with unusual environmental conditions (higher water table, immaturity of green vegetation, absence of previous year vegetation) when birds built their nests in an unusual way (in broken vegetation above water, in burnt tussock holes, just on tussocks, with no disguise above). In dry vegetation and when green vegetation is underdeveloped, nests of Aquatic Warblers are poorly disguised and thus are more vulnerable to predators. Usually in such cases egg mortality rises due to the activity of either "other predators" or shrews. As a rule, nesting conditions are abnormal mostly during the first clutch, whereas before beginning of the second clutch conditions usually normalize (water table restores, green vegetation develops).

Differences between years in predation rate and composition of predators within the Zvanets marshland could be explained by variations in nesting conditions and, hence, in the patterns of nests arrangements (see above), as well as by changes in numbers of predators themselves. No case of shrew predation was recorded during the first clutch 1999 owing to the high water level on the mire, but predation by "other predators" at the egg stage (Marsh Harrier and Water Vole) was increased (Fig. 2). Apart from this, the weight of nestlings in some nests hanging above water tipped their balance, resulting in the nestlings falling out of the nests into the water (13.5% of all chicks during the first clutch 1999). During the second clutch of 1999, the chick mortality due to shrews was the highest during the study period (Fig. 2). Investigations into the shrew distribution on the mire indicated that during the flood period of that year (May–June) shrews were concentrated on islands, and only after water receded (July) they redistributed over the whole area of the mire (M. L. Minets, unpubl. data).

Perhaps, poor nests disguise in 2003 due to burning of dry vegetation and underdeveloped green grass was one of the reasons of increased eggs mortality as a result of either predation by other predators or by shrews (Fig. 2).

Daily egg mortality rate (including embryo mortality) in all the marshlands studied exceeds daily chick mortality rate. However predation by shrews at the nestling stage was much higher than at the egg stage (Table 1). This probably results from the fact that shrews react to sounds, smell and touch while searching for prey (Pattie 1969, Churchfield 1990) and, therefore, they are more skilled to find nestlings than eggs.

Egg and chick mortality caused by shrews in the Dikoe and Zvanets marshes was considerably higher than in the Sporovskoe site (Table 1), which could be explained by a difference in the shrew abundance between these marshlands. Differences in the shrew density on different mires might be connected with differences in hydrological regime. Frequent and prolonged floods in the absence of islands could be the main reason for low abundance of shrews in the Sporovskoe marshes in the years of survey. High abundance of shrews in Dikoe and Zvanets might be explained by the fact that long-lasting floods are very rare here (Dikoe) or by existence of numerous islands (Zvanets) where shrews concentrated during floods (M. L. Minets, unpubl. data).

A proportion of Aquatic Warbler nests destroyed by predators in the Biebrza marshes was higher than in the Sporovskoe bog and lower than in the Dikoe and Zvanets sites (Table 1). For the Biebrza case the list of potential predators of the Aquatic Warbler was quite long (Dyrcz & Zdunek 1993a), but shrews are listed among others as a potential cause of mortality. The Polish researchers noted that despite the presence of a large number of potential predators in the study areas, Aquatic Warbler nest losses due to predation on the monitoring plot were extremely low compared to other ground-nesting small passerine species. Nests of Aquatic Warblers are relatively well secured, because they are well camouflaged from top, and are difficult to access for most predators because of the high standing water level. An important factor which contributes to releasing the predation pressure on the nests is the behavior of the Aquatic Warbler female: it flies up and lands at some distance from the nest, getting to the nest on foot, invisible among sedges (Wawrzyniak & Sohns 1977). The fact that the male does not participate in feeding, and only one bird shows by the nest further lowers the chances of predators to find it. Many birds produce alert cries near the nest with eggs, whereas the Aquatic

Warbler does that only at the advanced stage of nestling period (Dyrcz & Zdunek 1993a). It is worth pointing out that all these factors lose their significance when shrews are key predators (Pattie 1969, Churchfield 1990).

While studying the reaction of Aquatic Warblers to potential predators, some researchers discovered that females were far more aggressive in response to small mammals approaching the nest than to birds-of-prey (Halupka 1993). The fact that small insectivore mammals are the main predators of Aquatic Warbler nests is corroborated by the findings on the behavior of nestlings. Other *Acrocephalus* fledglings conceal as a response to disturbance, while young Aquatic Warblers tend to fly upwards, performing high jumps. Such type of behavior may be interpreted as antipredator strategy against small ground-dwelling mammals (Schulze-Hagen et al. 1999).

This justifies the assumption that predation by small insectivore mammals is a constant factor defining the breeding success of Aquatic Warblers, which, as a result, caused the evolution of adequate anti-predatory adaptations. In years with favorable nesting conditions (water level about the soil surface, abundant green and last year vegetation) and mean shrew abundance, predation by shrews does not lead to serious disturbances in breeding success, which is supported by the absence of correlation of breeding success with the rate of shrews-related chick mortality. In years when birds have to nest in unusual places or in years with shrew population peaks, predation by small insectivore mammals can greatly decrease overall breeding success. Preliminary data suggest that comparable mortality caused by shrews is also observed in other marshland bird species. In 2004, in Zvanets marshland area breeding success of Sedge Warbler *Acrocephalus schoenobaenus* was also studied. In the Aquatic Warbler, daily egg mortality rate due to shrews in 2004 was 0.27%, and, in comparison, in the Sedge Warbler it was 0.96%. Daily nestling-stage predation rate by shrews was 2.35% in the Aquatic Warbler, while this indicator was 0.72% in Sedge Warblers. Nestling mortality in the Reed Bunting *Emberiza shoeniclus*, Meadow Pipit *Anthus pratensis* and Yellow-headed Wagtail *Motacilla citreola* due to shrew predation was also recorded (Authors' unpubl. data).

Breeding success (including partial losses) on all the marshlands was considerably lower than nest success (considering only completely failed nests), which proves that applying the nest success indicator for calculating breeding success is incorrect. The main reason for partial mortality is predation by shrews (Dikoe, Zvanets), but it also happens quite often as a result of individual nestlings falling into water (Zvanets) or dying in wet nests (Sporovskoe) during flood periods.

The Aquatic Warbler breeding success (Mayfield method) on all the marshlands in years with favorable nesting conditions (without floods, availability of dry vegetation for nests disguise, mean shrews abundance) ranged from 36.3% to 54.07%. These indicators are close to breeding success (Mayfield method) of other species nesting on the ground: the Tree Pipit *Anthus trivialis* — 44.9%, Thrush Nightingale *Luscinia luscinia* — 43.0%, Yellowhammer *Emberiza citrinella* — 38.4% (Paevski 1985). However, in years of rain floods, outbreaks in shrew populations, the breeding success decreased and ranged form 2.89% to 27.68%. The mean breeding success for the whole period of this study was 28.88%. Over eight seasons of the study the breeding success was higher than Belarussian mean during five seasons and it was lower during the three other seasons. Mean values of breeding success are comparable with the analogous values for the Biebrza Aquatic Warblers. However, on the Biebrza marshland this indicator was quite stable during a four-year study (Dyrcz & Zdunek 1993a), whereas on Belarussian mires it varied greatly between different years (Table 1). Yet the study on Aquatic Warblers in the Biebrza valley was conducted in a very specific location, characterized by relatively stable environmental condition with no succession towards reedbeds or scrub, resulting from the hydrology of the site (Dyrcz & Zdunek 1993a, 1993b). In contrast, fen mire ecosystems in Belarus are extremely unstable (rain floods, extreme droughts, frequent spring fires, outbreaks in populations of small insectivores). On the Sporovskoe marshland, between 1981 and 2002, the number of years with successful first-clutch breeding of the species amounted to 11 (47.8%), while the number of years with successful second clutch was only 4 (17.3%). In the same period, there were 9 years (39%) when both the first and the second clutches were unsuccessful (Kozulin et al. 2004).

At present, when the areas of the major Aquatic Warbler habitats are protected, the main threat for the species is the reduction of favorable habitats caused by overgrowing of open mires with shrubbery and reeds. However, constant impact of a number of factors listed above can also lead to a decline in the species abundance.

Therefore it is necessary to elaborate management plans in which special attention should be paid to the optimization of water level.

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STRESZCZENIE

[Biologia lęgowa wodniczki w kluczowych dla gatunku siedliskach na Białorusi]

W latach 1998–2004 elementy biologii lęgowej były badane na trzech największych terenach podmokłych północno-zachodniej Białorusi (Fig. 1). Łączna liczebność (szacowana) wodniczki na tych terenach wahała się od 6370–11500 śpiewających samców, co stanowi ponad 50% światowej populacji tego gatunku.

W latach o sprzyjających warunkach dla odbycia lęgu sukces lęgowy (liczony jako prawdopodobieństwo sukcesu liczone od złożenia jaj do wylotu piskląt) wahał się od 36.3 do 54.1%. W latach o silnych fluktuacjach poziomu wody i wysokiej liczebności drobnych gryzoni, głównie ryjówek sukces lęgowy zmniejszał się istotnie i mieścił się w zakresie 2.9–27.7%. Głównym powodem strat w lęgach, tak na etapie jaj jak i piskląt było drapieżnictwo, najprawdopodobniej drobnych ssaków owadożernych (Fig. 2). Wyniki zebrane dla każdego z terenów porównano z danymi zebranymi dla populacji występującej na Bagnach Biebrzańskich (Tab. 1).

Wydaje się, że wodniczki są dobrze dostosowane do zmieniających się warunków środowiskowych terenów podmokłych, ale w latach z silnymi opadami powodującymi podtopienia, całorocznym wysokim poziomem wód, z wiosennymi pożarami oraz przy wysokich zagęszczeniach ryjówek, sukces lęgowy jest istotnie mniejszy.