Changing nesting dates and nest placement as adaptations of Aquatic Warbler *Acrocephalus paludicola* to unstable nesting conditions on fen mires in Belarus

Lyubov Vergeichik & Alexander Kozulin

Between 1998 and 2005, several studies were undertaken into breeding phenology and nest placement of the Aquatic Warbler on the three largest fen mires in Belarus (Dikoe, Sporovo and Zvanets). These sites form the main breeding grounds of the species within its entire range. Nest placement in the first and second clutches (n = 191 nests) in different nesting conditions were as follows: standard placement under old vegetation 54.4%, in tussock hollows and holes 18.8%, under a canopy of only green vegetation 19.8% and in old sedge tangles above water 6.8% of nests. There are usually two periods of egg-laying, but it appears that only part of the females breed in both periods and others produce only one clutch in either period. However, when nesting conditions are unfavourable, females shift the timing of breeding quite freely, and in certain years all females nest within a single short period. Major factors determining the timing of breeding and the way of nest placement of Aquatic Warbler are water level fluctuations and changes in the composition of vegetation due to fires and water levels.

**Key words:** Aquatic Warbler *Acrocephalus paludicola*, breeding phenology, nest placement, habitat management.

1. Introduction

It is critical to know how Aquatic Warbler *Acrocephalus paludicola* can adjust itself to different environmental factors to ensure proper habitat management for this species. Studies on nest placement and timing of breeding of the Aquatic Warbler have been limited to only one mire, the Biebrza in Poland. DYRCZ & ZDUNEK (1993) concluded that the timing of breeding was pretty well defined, and laying eggs during the first and second clutches occurs in the same periods in different years.

A study of Aquatic Warbler breeding ecology on different types of mires in Belarus indicated extremely unstable nesting conditions for the species. In order to survive in such varying conditions the species must be able to shift the timing of breeding as well as nest placement. It is particularly interesting to see how the unique breeding system of the species allows to adapt to unstable habitats and to what extent the development of such a mating system is determined by instability of habitat conditions in fen mires.

2. Study area

In 1998–2005, breeding phenology and nest placement of the Aquatic Warbler were studied on the three largest fen mires in Belarus (Dikoe, Sporovo and Zvanets; Fig. 1) – the main breeding grounds of the species within its entire range. Together, these sites support more than 50% of the world population of the species. The fen mires differ from each other by a number of characteristics. The whole study was conducted on monitoring plots set up in the most typical parts of the mires.

**Fig. 1:** Location of main habitats of Aquatic Warbler and study sites. – Lage der wichtigsten Lebensräume des Seggenrohrsängers und der Untersuchungsgebiete.
socks cover no more than 5% of it. For more than 30 years, the mire has not been used for hay making, and no burning of vegetation has taken place. This, as well as low spring floods, cause the accumulated layer of last-year sedge to hamper the development of new vegetation. Green vegetation develops usually only in depressions of the mire, where the higher water level causes old vegetation to decompose relatively quickly. Most of the Aquatic Warbler nests are located exactly in such depressions.

**Sporovo** mire (Fig. 3) is located in the Yaselda River floodplain and characterised by an extremely unstable water level which also varies within a nesting period. The average density of singing males during the first clutch (Peschanka monitoring plot) was 48.4 ± 12.2/km² (range 0–135/km²; n = 10 years, 1996–2005) and during the second one 33.1 ± 10.4/km² (range 0–95/km²; n = 10). The mire can be divided into two parts. The first part is a narrow, 0.5–2 km wide and extremely water-logged floodplain of the Yaselda River stretching for some 25 km. The largest portion of the floodplain on both banks of the river is a typical sedge fen mire. The relief of the mire is flat, tussocks are slightly prominent, some 15–20 cm high. Kostiuki (40 ha) is located 14 km further downstream. The self-purification capacity of the river contributes to a lower production value of this part of the mire (water mineralisation is 145.4 mg/l). Tussocks are 10 cm high.

**Zvanets** mire (Fig. 4) is located in a landscape depression some 20 km away from the Pripyat River channel. The average density of singing males during the first clutch (Povitie monitoring plot) was 81.0 ± 8.2/km² (range 35–103/km²; n = 8 years, 1998–2005) and during the second one 89.5 ± 10.9/km² (range 17–115/km²; n = 8). Springtime flooding occurs annually, with the water level rising up to 50 cm above ground. From May to September the water drops to 50 cm below the ground level. In late autumn and winter the water table rises back to the ground level. Open fen mires dominate the area. The southern part of the mire – a supplier of flood

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**Fig. 2:** The Caricetum lasiocarpaceae association dominates in the mesotrophic sedge-Hyppnum fen mire Dikoe. – Die Assoziation Caricetum lasiocarpaceae dominiert auf dem mesotrophen Seggen-Braunmoos-Niedermoor Dikoe. Photo: A. KOZULIN.

The size of the monitoring plot in **Dikoe** mire (Fig. 2) is 100 ha. The average density of singing males during the first clutch was 47.1 ± 3.9/km² (range 18–63/km²; n = 10 years, 1996–2005) and during the second clutch 35.1 ± 7.2/km² (range 12–65/km²; n = 10). Nesting conditions at the Dikoe mire are stable. In spring, water level rises not more than 20 cm; in May and the first half of June, the water level is close to the soil surface, and the layer of old vegetation is thick. The surface of the mire is virtually flat; 10–15 cm tussocks cover no more than 5% of it. For more than 30 years, the mire has not been used for hay making, and no burning of vegetation has taken place. This, as well as low spring floods, cause the accumulated layer of last-year sedge to hamper the development of new vegetation. Green vegetation develops usually only in depressions of the mire, where the higher water level causes old vegetation to decompose relatively quickly. Most of the Aquatic Warbler nests are located exactly in such depressions.

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waters – is characterised by higher productivity (mineralization 347.7 mg/l) and dominated by the association *Caricetum elatae*. Here, tussocks can be as high as 30 cm. Povitie monitoring plot (60 ha) is set up in the most typical part of the southern section of the mire. From here northwards, mineralisation decreases reaching its low in the northernmost part of the mire (210 mg/l), accompanied by a substantial increase in the occurrence of the association *Caricetum lasiocarpeae*. Novoselki monitoring plot is set up in the northern part of the mire (32 ha). A smaller range of water table fluctuations here explains shorter tussocks (15–20 cm). Heavy fires destroying all dry vegetation on parts of the mire occur almost every year in late autumn or early spring.

3. Methods

The studies were carried out during eight breeding seasons (1998–2005). The timing of breeding was established for 205 nests; nest placements were described for 191 nests. The monitoring plots were used as study sites. Nest identification was based on the observation of female behaviour. Nests were marked by tags and mapped, and the following key nest parameters were recorded: egg incubation stage according to water testing, age of nestlings according to plumage development and weight, nest placement, distance between the base of the nest and the water, nest masking.

The first-egg date of the clutch was assumed to be 18 days prior to the hatching of nestlings (13 days of the mean incubation period, plus five days of the mean egg-laying period). The hatching date was established on the basis of physical observations, as well as by age of nestlings. In parallel, the following nesting conditions of the species were described during the first and second clutches:

- Water level in cm in relation to the soil surface. In the figures, the water level is indicated in metres above sea level.
- Presence of dry vegetation from last year and the year before last:
  - old vegetation is absent as a result of fires (0%),
  - in the absence of fires the last-year vegetation was preserved entirely (100%).
- Extent of green vegetation development:
  - green vegetation fully developed by late May. This is observed in years with prolonged floods, with the water level in May at the soil surface and above;

3. Methods

Fig. 4: Associations of *Carex elata* (58%) and *Carex appropinquata* (37%) dominate on the Zvanets fen mire. – *Assoziationen von Carex elata* (58%) und *Carex appropinquata* (37%) dominieren im Moor von Zvanets. Photo: A. KOZULIN.

Fig. 5: Breeding conditions of pattern 5 (see methods): water level close to soil surface, 100% of dry vegetation (only last-year vegetation), development of green vegetation is approaching 100% (June 2005, with nest of Short-eared Owl *Asio flammeus*). – *Brutbedingungen der Kategorie 5 (s. Methoden): Wasserstand nahe der Bodenoberfläche, Deckung der trockenen Vegetation vom Vorjahr 100 % und der grünen Vegetation annähernd 100 % (Juni 2005; mit Sumpfohreulen-Nest Asio flammeus).* Photo: A. KOZULIN.
5: The water level is close to the soil surface, the coverage of dry vegetation (only last-year vegetation) and green vegetation is 100% and approaching 100%, respectively (Fig. 5).

4: In the absence of dry vegetation, the water level is close to the soil surface. Green vegetation is still incompletely developed in May and the first half of June.

3: Dry vegetation is absent and the water level is close to the soil surface. Green vegetation is completely developed, which is usually observed in late June and July (Fig. 6).

2: With the water level at the top of tussocks and despite green vegetation completely developed, nesting is possible only if dry vegetation is abundant above the water.

1: Nesting is impossible due to the absence of dry vegetation and a water level at top of tussocks.

0: The water level is above the tussocks, nesting is impossible.

4. Results

4.1. Nest placement patterns

The Aquatic Warbler was found to use different nesting strategies in response to changing nesting conditions. During the study four typical patterns of nest placement were recorded:

“Standard” nests were found in breeding condition 5 and made up 54.4% of the 191 nests examined. They were placed in a small depression of soil or moss, in accumulations of old vegetation on the tops of tussocks or on the soil surface. They were well covered by last-year and green vegetation (Fig. 7).

“Tussock type” nests (nesting condition 4, 18.8%) were placed in burnt hollows or in rodent holes in tussocks and thus remained invisible. They were usually built in May in the absence of old vegetation and when green vegetation developed poorly (Fig. 8).

“Surface type” nests (nesting condition 3, 19.8%) were placed on the soil surface or on the tops of tussocks and were covered only by green vegetation (Fig. 9). They were usually observed in June and July in the absence of last-year vegetation, provided that green vegetation was high enough to cover the nests sufficiently.

“Above water” nests (nesting condition 2, 6.8%) were placed on old sedge tangles and occurred when the water level was above the surface of the tussocks and when old vegetation was abundant (Fig. 10). Cover was available by dry as well as by green vegetation.
Fig. 8: Nest in hollows of burnt tussocks (Zvanets, May 2003). – Nest in Hohlräumen verbrannter Seggenhorste (Zvanets, Mai 2003). Photo: V. YURKO.

Fig. 9: Nest under green vegetation only (Zvanets, June 2004). – Nur von grüner Vegetation überdecktes Nest (Zvanets, Juni 2004). Photo: A. KOZULIN.

Fig. 10: Nest building above water in the tangles of dry vegetation (Zvanets, May 1999). – Über dem Wasser im Gewirr trockener Seggen gebautes Nest (Zvanets, Mai 1999). Photo: A. KOZULIN.
4.2. Timing of the breeding and nest placement at Dikoe

Studies at the Dikoe mire were carried out in 1999 and 2001. Nesting conditions were stable. The layer of old vegetation was thick, green vegetation in different parts of the monitoring plot covered 25–100%. During the study period, the timing of breeding was typical for the species (Fig. 11). Most females started breeding during May (first clutch). Of those females that had bred during the breeding season only 13–15% laid eggs in the second clutch period in late June and early July.

All nests found were constructed according to the “standard” type which is most common for the species (Table 1): the nest base was located in a depression in the moss or a thick layer of dry vegetation on a tussock, or – in the absence of tussocks – on small elevations. All nests were well disguised under dry vegetation.

4.3. Timing of the breeding and nest placement at Zvanets

Studies at the Zvanets mire were carried out during five breeding seasons (1999, 2001, 2003, 2004, 2005). Nesting conditions were extremely unstable and changed not only from year to year, but also within a breeding season (Table 1).

In 1999, from May to the mid June, the water stayed above tussocks (pattern 2). Dry vegetation was abundant due to the absence of fires during the year. For their first clutch Aquatic Warblers built nests above the water in tangles of old vegetation. At the end of June and in July the water level dropped, so breeding conditions were regular during the second clutch (pattern 5). The timing of breeding in 1999 was typical for the species: the first clutch started in May/June (73% of all females which bred during the breeding season) and the second one (27%) in July (Fig. 12A).

Nesting conditions in 2001, 2003 and 2004 were similar (patterns 4 and 3). In 2001, only few plots with dry vegetation remained in the wake of a fire (up to 25% of the area). In 2003 and 2004, there was virtually no dry vegetation after spring fires. In mid-May 2001 and 2004, the water level of Povitie monitoring plot was already below the soil surface (Fig. 12B, 12D). Just after tussocks had dried out, females started to arrange vitally all nests in burnt hollows in tussocks and in holes of the Water Vole Arvicola terrestris, as dry and green vegetation was very scarce and low and could not disguise the nests.

In the second half of May 2003, the water level was still higher than the soil in the Novoselki plot (Fig. 12 C). The Aquatic Warbler could not start building nests in wet tussocks. First nests appeared in May just after tussocks dried out. The second nesting period was observed in June when ground vegetation became fully developed. As a result, nesting started continuously without clearly visible peaks.

In mid June 2001, 2003, 2004, once green vegetation had fully developed (pattern 3), most of the nests were built on the tops of tussocks under a continuous canopy of green vegetation. The timing of breeding in those years did not significantly differ from normal, but the number of females that nested during the second clutch was much higher than in regular years (2001 38%; 2003 55%; 2004 41%).

In 2005, the water level on Povitie plot was above the ground from early May to 10th July. There was no old dry vegetation due to a winter fire. As a result, only individual females were recorded to nest on separate fire-free spots. Density of males was also marginal (17 per 100 ha), and their activity was very low. Apparently,
most of the birds moved from the inundated section to drier parts of the mire in the north where an increased density of males was observed in July. This is also corroborated by birds being found in sub-optimal sections of the mire where they had never been recorded before.

In 2005, the water level on Novoselki plot remained high until 20th May. As soon as the tops of tussocks were exposed, Aquatic Warblers started nesting. Dry old and well-developed green vegetation caused all the nests to be placed in a standard fashion under a canopy of dry and green vegetation. The timing of breeding was quite late, and the first clutch started in early June. During the second clutch in early July only 13% of the females were nesting.

4.4. Timing of the breeding and nest placement at Sporovo

At Sporovo, studies were carried out in 1998, 2000, 2002 and 2005. In 1998 and 2000, the timing of breeding was standard: the first clutch started in May, the second one in late June 2000 and early July 1998, respectively (Fig. 13A, 13B). As a result of rising water level in 1998, all nests built in July were inundated, and
the birds moved to a drier section of the mire 30 km away (KOZULIN et al. 1999). A rain flood also occurred in early July 2000, but at that time nestlings had fledged in most nests and only late clutches failed.

In 2001 and 2002, there were no spring floods on the mire and water did not rise above the soil. Besides, lack of fires caused an accumulation of last-year vegetation in 2002. Consequently, in May 2002 the lack of water and a layer of dry vegetation restricted the development of green vegetation to about 25% of conditions usually found at that time of the year. In addition, a low biomass of insects was present in that year. All these factors contributed to a situation of Aquatic Warblers nesting in low density and only in May (Fig. 13C). Already in June males virtually stopped singing, despite being present on the monitoring plot.

In 2005, a high water level caused by prolonged rains was observed from April to mid June. However, birds did not leave the mire: the density of singing males reached 20 birds per 100 ha and singing activity was very high. Due to a high water level from October 2004 through June 2005, virtually all dry vegetation was lying on the ground and birds could not build nests above water. Females started nesting immediately after the water level had decreased in mid June, and egg-laying finished in mid July (Fig. 13D). In 1998, 2000 and 2002, all nests were placed in a standard way and only in 2005, in the absence of dry grass, some nests were disguised mainly by green vegetation (Table 1).

The earliest date of the first egg laid in Belarus was recorded on 6th May 2000 at Peschanka plot, and the latest on 22nd July 1999 at Zvanets. The mean date of laying the first egg was 21st May in the first clutch and 28th June in the second clutch. The aggregated data on breeding phenology of the species did not show clear peaks of the first and second clutches (Fig. 14), because the timing of the first clutch can vary widely depending on nesting conditions.

**Table 1:** Patterns of nest placement during first and second clutches. – *Neststandorte bei Erst- und Zweitgelegen.*

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<th>sites and years – Gebiete und Jahre</th>
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5. Discussion

Comparison of the nesting phenologies of Aquatic Warblers in Belarusian mires and the Biebrza mire (Poland) reveals a considerable difference in the timing of breeding in the different populations. Probably owing to stable nesting conditions, birds of the Biebrza mire each year breed in the same time intervals, which are strongly synchronised and distinctly split. During the breeding season, 63–68% of the nests refer to the first and 32–37% to the second clutch (Dyrcz & Zdunek 1993). In Poland, again probably because of the stable nesting conditions, no unusual nest placement patterns have been observed. Unstable nesting conditions on the fens in Belarus allowed to detect a wide range of adaptation mechanisms, which are mainly related to the ability to vary both timing of breeding within a long period from May to late July and nest placement. In normal years, birds also have two clutches within the
breeding season. However, when nesting conditions are not suitable, females can vary the timing of breeding quite freely, and in certain years all the females nest within a single short period. Notably, in such years the number of nesting females is close to the total amount of females nesting during the first and second clutches in normal years. It appears that birds attempting to breed in late June and July (during the period of the second brood) are mostly females which did not breed earlier in the season, but in part also females with a second clutch.

Major factors contributing to the timing of breeding and the way of nest placement of the Aquatic Warbler are fluctuations in water level and changes in the composition of the vegetation due to fires and water levels. For the Polesian fens, wide fluctuations in the water table (floods and draughts) during nesting seasons (KOZULIN et al. 2003) are a typical phenomenon occurring twice per decade (KALININ & OBODOVSKI 2003). Most of the Polesian mires are located in river floodplains (e.g. Sporovo) or along the periphery of a floodplain (e.g. Zvanets), therefore the level and duration of spring floods determine the hydrological regime of the rivers. Over the last 40 years the hydrological regime of the mires was also enormously influenced by the practice of water use in the catchments of the mires (KOZULIN et al. 2003). Fires are also quite frequent on the Belarusian fen mires. Since the start of fen mire monitoring in 1995 (for 11 years), fires occurred in eight years at Zvanets and in five years at Sporovo, whereas no fires occurred at Dikoe. Fire occurrence is connected with the tradition of the local population to burn old grass to improve the productivity of hayfields. Spring burning of grass usually takes place in March and early April before the start of the spring flood. In the absence of water virtually all dry vegetation burns out and tussocks burn partially. In the past all fen mires were scythed by the local population by hand, therefore old vegetation was scythed by the local population by hand, therefore old vegetation did not accumulate in large amounts, and spring fires covered few spots. At present in the absence of water, any local grass burning results in the burning out of the whole mire. In the presence of water only the upper layer of vegetation burns out and this only improves habitat conditions for the Aquatic Warbler.

The Aquatic Warbler is a species which breeds exclusively on fens, therefore it has developed adaptation capacity to changing conditions at such sites. Other species associated with fen mires, such as Sedge Warbler Acrocephalus schoenobaenus and Reed Bunting Emberiza schoeniclus, can move to other habitats (drained lands, reed beds) when breeding conditions become unfavourable. These species do not considerably change the timing of their breeding. In contrast, the Aquatic Warbler must either adapt to nesting in unfavourable conditions or wait for the conditions to improve.

The ability of the Aquatic Warbler to shift the timing of breeding is explained by the unique reproductive system of the species, i.e. partial promiscuity, when birds do not form couples for breeding. With such a reproductive system, males keep singing during the whole breeding season (from early May to early August) and preserve the ability to mate throughout the entire period (SCHULZE-HAGEN 1991). The female is also able to start breeding from early May to late July. Besides, birds with such a breeding system have other adaptations to unstable habitat conditions:

- Aquatic Warblers are more mobile than monogamous species and able to move to more favourable breeding places any time from May to early June (KOZULIN et al. 1999; WAWRZYNIAK & SOHNS 1977).
- The absence of strict territorialism allows females to nest on more favourable plots with increased density (DYRČZ & ZDUNEK 1993).

Situations and factors, to which birds are not adapted, and which therefore cause a decline in the species abundance should be noted, particularly:

- Birds cannot nest in places where a high water level is preserved from May until early July. By late June, they move from such areas altogether, as observed on Peschanka monitoring plot (Sporovo) in 1999 and Povitie monitoring plot (Zvanets) in 2005.
- Birds do not nest at all or nest at extremely low density on mire plots where both spring floods and vegetation burning were lacking for two or more years. In such areas, accumulation of old vegetation or lack of water result in under-development of green vegetation. This probably causes a decline in the whole productivity of vegetation and brings about a decrease in the abundance of insects.

Based on adaptation studies on the Aquatic Warbler, key recommendations have been developed regarding habitat management of this globally threatened species. If properly implemented, they will allow to support the largest density of the Aquatic Warbler and preserve the ecosystems of open sedge fen mires in their natural condition.

**Hydrological regime.** It is needed to ensure a near-natural hydrological regime of habitats. The water level should be above tussock level in early spring (March to April), near the soil surface from mid May to mid/late June and lower than soil level in July and August. A high water level in early spring is required to ensure a high productivity of fen mire ecosystems, based on nutrients entering the mire together with flood waters, the development of water stages of insects and a rapid development of grass vegetation and sedge. Besides, lasting high water in early spring helps to maintain the normal vegetation structure – most of the old vegetation lies on the soil and decomposes quickly ensuring the normal development of green vegetation. Maintaining the water level near the soil level during the nesting
period enables the Aquatic Warbler and other ground-nesting birds to nest on the soil, as well as ensures the normal development of most of the insects. A low-water period in July–August is necessary to prevent succession processes to avoid predominance of Cattail Typha spec. and Reed Phragmites australis.

Vegetation structure. In order to support the normal vegetation structure when there is no scything going on, it is necessary to carry out controlled burning or scything. The best time for burning old vegetation is in late autumn or winter, when old vegetation and moss cover would not be burnt out completely. Burning yields the best results when the water freezes at tussock level. As a result, only part of old vegetation burns out, leaving normal conditions for early nesting disguises. Controlled winter burning is the only method to prevent unwanted spring fires when there are no or late spring floods.

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6. Zusammenfassung


7. References


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Lyubov Vergeichik, Institute of Zoology NANB, 220072 Minsk, Akademichnaya str. 27, Belarus.
E-Mail: lyubasha@tut.by
Alexander Kozulin, Institute of Zoology NANB, 220072 Minsk, Akademichnaya str. 27, Belarus.
E-Mail: kozulin@biobel.bas-net.by