

Rapid deterioration of Aquatic Warbler *Acrocephalus paludicola* habitats at the western margin of the breeding range

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Abstract In the last German breeding area of the rapidly declining “Pomeranian” population of the Aquatic Warbler (*Acrocephalus paludicola*), the Lower Oder Valley National Park, we investigated changes in habitat suitability between 1993 and 2006 by combining monitoring results with repeated assessments of vegetation structure and composition, site conditions, and land use. Sites with recent Aquatic Warbler records showed shorter and sparser vegetation, a thinner litter layer, and a higher total plant

species richness and cover of small and least competitive (CSR) species than abandoned or unoccupied sites. On a long-term study plot, during a period of late mowing and subsequent cessation of land use, vegetation height increased, the cover of CSR species decreased, and the site became abandoned by Aquatic Warblers. The probability of Aquatic Warbler occurrence was dependent on elevation and increased with the proportion of early mown or grazed area in the preceding year, with early use being most important on slightly higher elevated sites. This rapid deterioration of eutrophic habitats by delayed or discontinued land use is atypical for the majority of Aquatic Warbler breeding habitats. We conclude that both late or no land use and land use during the breeding season negatively affect the Pomeranian breeding sites and that a more sophisticated and flexible land management is urgently needed.

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Introduction

The Aquatic Warbler *Acrocephalus paludicola* formerly occurred throughout Central and Western Europe as an abundant breeding bird of mires dominated by sedges or grasses (Schulze-Hagen 1991; AWCT 1999). Since 1900, the species has lost most of its breeding range west of the current Polish–German border due to large-scale habitat destruction (AWCT 1999) and has become the only globally threatened songbird species of the European mainland. This has led to increased conservation efforts and conservation-related research since 1990. Birds breeding in

Germany and Western Poland at its current western range margin can be distinguished genetically from all other populations (Giessing 2002) and apparently occupy a different wintering area (Pain et al. 2004). Unlike the stable core population, which occupies large mires in Eastern Poland, Belarus and Ukraine, this small “Pomeranian population” has undergone a rapid decline since c. 1991 and is nowadays restricted to management-dependent secondary habitats (Tanneberger et al. 2005; Flade et al. 2006). About 10% of this population are found in the Lower Oder Valley National Park, the last remaining breeding site in Germany (Fig. 1).

In general, the ongoing loss of breeding habitat for the Aquatic Warbler has mainly been caused by reclamation and intensified use of wetlands. On many legally protected breeding sites, the cessation of traditional low intensity grassland use resulted in the overgrowing of meadows with reed *Phragmites australis* or willows *Salix* spp. and the local decline of the Aquatic Warbler (Krogulec and Kloskowski 1999; AWCT 1999). In the Lower Oder Valley National Park area, land use and vegetation have changed substantially since 1975 and the number of Aquatic Warblers has decreased by more than 80% (Helmecke et al. 2003; Fig. 2). The current critical situation of the Aquatic Warbler in the national park area, however, cannot be sufficiently explained by land reclamation and intensified

grassland use which caused the declines during the 1980s, as these processes stopped after 1990. Furthermore, overgrowing with reed or bushes rarely occurred in the national park.

In this paper, we test the hypothesis that habitat deterioration is attributable to late mowing and the cessation of land use.

Methods

Study area

In the Lower Oder Valley National Park (105 km²), Aquatic Warblers occur in three polders in an area of approx. 36 km² dominated by wet meadows and pastures (Fig. 1). Vegetation consists of stands dominated by tall slender tufted-sedge *Carex acuta* (“sedges”), stands dominated by reed canary grass *Phalaris arundinacea* (“reed canary grass vegetation”), mixed stands of meadow grasses, sedges and herbs (“meadow vegetation”), and mixed stands of low meadow grasses and herbs in moist depressions (“low meadow vegetation”). The area is flooded from winter until mid-April and heavily drained afterwards. From late May onwards, surface water is extremely rare and a large proportion of the grassland is mown or grazed (Dittberner and Dittberner 1976; Helmecke et al. 2003; Tanneberger et al. 2005). Since 1991, agricultural use on an increasing part of the area has stopped. A long-term 127-ha large study plot is situated in the northernmost part of the northern polder (Fig. 1).

Aquatic Warbler data

Numbers and distribution of Aquatic Warblers have been recorded annually in the long-term study plot since 1977,

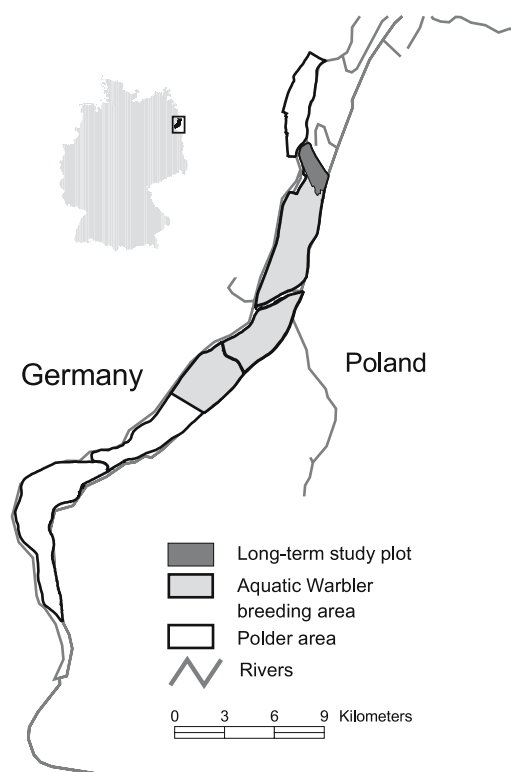


Fig. 1 Location of Lower Oder Valley National Park, including the long-term study plot in the northern polder

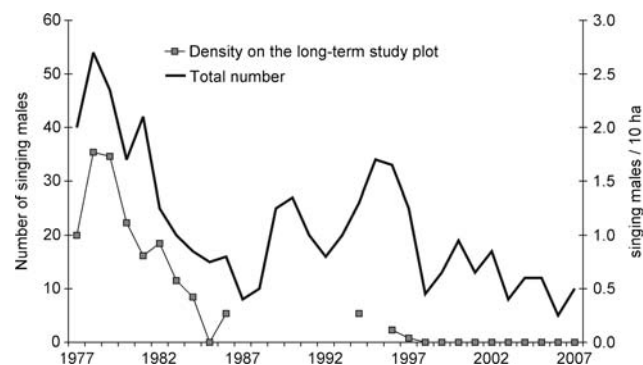


Fig. 2 Total number of Aquatic Warbler *Acrocephalus paludicola* singing males in the Lower Oder Valley National Park and density of singing males on the long-term study plot (own observations, and Dittberner and Mädlow 1998)

and in the entire area since 1994, by counting singing males. The study sites were subdivided into sites with records of Aquatic Warblers in the year(s) of vegetation assessment (“recent records”), sites abandoned by Aquatic Warblers up to 5 years before vegetation assessment (“abandoned”), and sites without Aquatic Warbler records (“not occupied”).

Habitat data

We focussed our analysis on the following habitat parameters, which have earlier been identified as crucial in Aquatic Warbler habitat selection: soil moisture, nutrient availability, mean vegetation height, and vegetation density at 60–80 cm height (Leisler 1981; Schulze-Hagen 1991; Kozulin and Flade 1999).

Soil moisture was estimated in four classes (dry, fresh, moist, wet; after AG Boden 2005) in early to mid-May. In the analysis, the classes moist and wet were combined to moist.

As a proxy for nutrient availability, total carbon (C) and total nitrogen (N) were determined in 2005 in soil samples from a depth of 5–10 cm (cf. Succow and Joosten 2001). The samples were stored for 1 week in polyethylene bags at 5°C, dried for 12 h in an oven at 105°C, and after Dumas digestion measured with a C/N-analyser (Element vario EL).

Vegetation height was measured with a vertical board (Sutherland and Green 2004) or a measuring stick. Data on maximum vegetation height from 1993 were decreased by 10% to make them comparable with the mean vegetation height assessed in all other years (difference between mean and maximum vegetation height in 2002: 22.1%) and to account for the temporal difference (mid-June in 1993 versus July or later in all other years) (mean increase of *Carex acuta* between mid-June and mid-July + 10% on the long-term study plot; Schumann et al. 1999). Vertical vegetation density was measured in 2004 and 2005 by clipping layers of 30 × 30 × 20 cm at 0–20 cm, 20–40 cm, 40–60 cm, etc., height using a vegetation frame (modified after Bibby et al. 1992). The fresh plant material was stored in polyethylene bags and its volume was determined by water displacement after 5 days.

Information on the time and technique of land use was recorded from 1994 onwards and completed by interviews with farmers. We distinguished between early mowing or grazing (until 31 July), late mowing or grazing (after 31 July) and no mowing or grazing in the respective year. As parameters related to land use, we analysed the total plant species number (Jensen and Schrautzer 1999; Pfadenhauer et al. 2001; Hodgson et al. 2005), the cover of small and

medium-sized, least competitive plant species (CSR species = intermediate strategy type, combination of competition, stress, and ruderal strategies; after Grime 1974; Grime et al. 1988; Hodgson et al. 1999; Moog et al. 2005; species list in Frank and Klotz 1990), and the thickness of the litter layer (Billeter et al. 2003). Plant species cover was estimated in 1993 and 1998–2002 in modified Braun-Blanquet scale (Dierschke 1994) and in 2004–2006 in Londo scale (Londo 1984). Braun-Blanquet values were transformed into percentage values following Dierschke (1994): $r = 0.1\%$; $+$ = 0.5%; $1 = 2.5\%$; $2m = 2.5\%$; $2a = 8.8\%$; $2b = 20.0\%$; $3 = 37.5\%$; $4 = 62.5\%$; $5 = 87.5\%$. For the analysis, we combined the cover of all CSR plant species to total “Cover of CSR species (%)”. These species are characteristic of meadow and low meadow vegetation and indicate a sparser growth of highly competitive species such as reed or tall sedges. Thickness of the litter layer was measured on 1 × 1 m subplots in 2002 and 2004–2006 and the geometric mean of minimum and maximum litter height was calculated.

We used a digital elevation model (5 × 5 m resolution) of the “Landesvermessung und Geobasisinformation Brandenburg” to calculate median elevation for an area of 100 m around positions of Aquatic Warbler records, and for 13 meadows for which information about the occurrence of Aquatic Warblers and the timing of land use during the study period was available.

To identify differences between sites of different Aquatic Warbler occurrence (= presence, abandoned, absence), multiple (ANOVA with Scheffé test and Kruskal–Wallis H -test) and pairwise tests (t -test and Mann–Whitney U -test) were used. Changes in vegetation height and cover of CSR strategy type in the period 1993–2006 were assessed by linear regression against year (with year 1993 as 1). Significance levels were Holm corrected (Quinn and Keough 2002) where appropriate. The influence of elevation and land use in the preceding year on Aquatic Warbler occurrence was analysed using logistic regression (software R v. 2.5.0). Area under the curve statistic (AUC) and Nagelkerke’s R^2 were used to evaluate the predictive power of the model.

The study was carried out on 25-m² plots in 1993 (Jehle and Pankoke 1999; $n = 37$; sampled in June), on plots of 20–40 m² in 1998–1999 (Mammen et al. 2005; $n = 20$; June and July) and 2002 (Just 2005; $n = 58$; June), and on 25-m² permanent plots (marked with magnets) in 1998–2002 ($n = 11$; 8 plots sampled again in 2006; July or later) and 2004–2006 ($n = 27$; May, June and July). Plots situated on the same meadow were regarded as pseudoreplicates and combined for the comparison of sites with different Aquatic Warbler occurrence. If plots were sampled for more than 1 year, the mean for the study period was calculated.

Results

Aquatic Warbler occurrence in relation to habitat parameters

Soil was generally moist or wet in early/mid-May without significant differences between sites with recent records (91% moist in 1998–2002 and 92% in 2004–2006) and abandoned sites (64 and 81%, respectively). Stagnant water above ground level was only present in small patches in both categories. All sites showed C/N ratios between 10 and 14, with a mean of 11.5 ± 1.1 .

Vegetation height was lowest at sites with recent Aquatic Warbler records, being lower than 1 m in June in all study periods (Table 1). In May, when Aquatic Warblers establish their home ranges and start egg-laying, mean vegetation height at occupied sites was 0.4–0.8 m (data from 1998–1999 and 2004–2006). In all layers, vegetation was denser in abandoned sites than in sites with recent Aquatic Warbler records (Fig. 3, Table 1). Thickness of the litter layer was significantly lower in sites with recent records than in abandoned sites. Cover of CSR plants and mean total plant species number were significantly higher in sites with recent records than in abandoned

sites. Values from sites with recent records in 1993 were similar to the respective values from later study periods.

Long-term changes in Aquatic Warbler numbers and habitat

Total numbers of singing Aquatic Warbler males in the study area showed a steep decline during the 1980s followed by a slight increase until the mid-1990s, decreased again steeply and fluctuated since 1998 between 6 and 19 singing males (Fig. 2). Since 1994, males (especially in the northern polder) shifted to meadows with lower elevation (northern polder: $r = 0.295$, $n = 100$, $P = 0.003$; equation of the line: $y = 0.342 - 0.017x$; central and southern polder: $r = 0.204$, $n = 115$, $P = 0.029$; equation of the line: $y = 0.483 - 0.008x$).

Aquatic Warbler density on the long-term study plot was relatively high in the late 1970s with >1 singing male/10 ha and up to 13 breeding females ringed in one breeding season. The density declined strongly in the early 1980s and the species vanished in 1998. During this period, land use intensity decreased: until 1989, the plot was annually mown with a first cut between mid-June and mid-July

Table 1 Site and vegetation structure parameters in different vegetation study periods for sites of different Aquatic Warbler *Acrocephalus paludicola* occurrence

| | Recent records | Abandoned | Not occupied | Test statistic | <i>P</i> |
|--|-------------------|-------------------|-------------------|------------------|----------|
| 1993 (mid-June) | | | | | |
| Number of plots | 13 | – | – | | |
| Mean vegetation height (m) | 0.70 ± 0.17 | – | – | – | – |
| Strategy type CSR (%) | 12 ± 18.3 | – | – | – | – |
| Number of plant species | 13 ± 7 | – | – | – | – |
| 1998–1999 (mid-June) | | | | | |
| Number of plots | 5 | 6 | 9 | | |
| Maximum vegetation height (m) | 0.95 ± 0.05 * | 1.02 ± 0.10 | 1.09 ± 0.03 * | $F_{2,17} = 8.1$ | 0.003 |
| 2002 (mid-June) | | | | | |
| Number of plots | 14 | 22 | 22 | | |
| Mean vegetation height (m) | 0.74 ± 0.11 | 0.75 ± 0.11 | 0.83 ± 0.10 | $\chi^2_2 = 7.5$ | 0.044 |
| Thickness of litter layer (cm) | 1.4 ± 2.8 * | 5.1 ± 6.7 | 10.7 ± 15.8 * | $\chi^2_2 = 7.6$ | 0.044 |
| 2004–2006 (early June) | | | | | |
| Number of plots | 12 | 15 | – | | |
| Mean vegetation height (m) | 0.65 ± 0.07 | 0.86 ± 0.08 | – | $t = 6.905$ | 0.005 |
| Cover of CSR species (%) | 14.84 ± 10.2 | 2.57 ± 3.55 | – | $t = -3.969$ | 0.005 |
| Number of plant species | 10 ± 4 | 6 ± 2 | – | $t = -3.887$ | 0.005 |
| Thickness of litter layer (cm) | 4.4 ± 6.55 | 10.33 ± 7.26 | – | $t = 2.224$ | 0.035 |
| Vegetation density in 60–80 cm height (dm^3 1,000 dm^3) ^a | 12.07 ± 11.24 | 35.94 ± 19.72 | – | $t = 3.861$ | 0.005 |

1993 vegetation data are derived according to 1994 records

^a Measured in 2004–2005 on 12 and 15 plots

* Significant pairwise differences at $P < 0.05$, Scheffé test for ANOVA and multiple Mann–Whitney tests with Holm correction for Kruskal–Wallis test, respectively

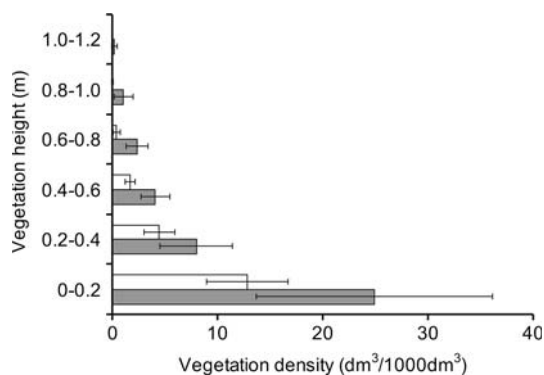


Fig. 3 Vegetation density in early June 2004–2005 in sites with recent Aquatic Warbler records (white bars, $n = 12$) and in sites abandoned by Aquatic Warblers (grey bars, $n = 15$)

(except the lower elevated parts in years with high precipitation) and a cut in September or October. In the late 1970s, the plot was used for honey production, indicating a high proportion of flowers. Deepening of shallow ditches in 1982 and nitrogen fertilisation from aircraft caused the local extinction of fen mire plant species such as bogbean *Menyanthes trifoliata*. After 1989, land use intensity gradually decreased: Following 2 years without mowing, the plot was mown early in 1992–1994 and subsequently mown in end-August to early-September until abandonment in 2001.

During 1993–2006, mean vegetation height increased on the long-term study plot from 0.9 to 1.26 m (Fig. 4, upper panels; plot centre: $r = 0.858$, $n = 21$, $P < 0.001$, equation of the line: $y = 0.872 + 0.024x$, plot margin: $r = 0.518$, $n = 50$, $P < 0.001$, equation of the line: $y = 0.567 + 0.023x$), while the cover of CSR strategy type decreased from 8.51 to 0.7% (plot centre: $r = 0.872$, $n = 21$,

$P < 0.001$, equation of the line: $y = 0.092 - 0.007x$; plot margin: $r = 0.523$, $n = 50$, $P < 0.001$, equation of the line: $y = 0.285 - 0.015x$). In 1993, sedges (50%), reed canary grass (30%), and meadow vegetation (20%) prevailed in the mown plot. In 2006, the unmown plot was dominated by tall sedges. On sites occupied by Aquatic Warblers during the study period, no significant changes could be observed (Fig. 4, lower panels). These sites were characterised throughout the study period by low meadow vegetation (40%), reed canary grass (30%), and meadow vegetation (20%).

Aquatic Warbler occurrence in relation to land use

The probability of Aquatic Warbler occurrence during 1998–2006 on 13 selected meadows was dependent on elevation and the proportion of area used early in the preceding year (AUC = 0.73, Nagelkerke’s $R^2 = 0.228$; Table 2). Land use early in the year was most important for Aquatic Warbler occurrence on higher sites (Fig. 5).

Discussion

Long-term Aquatic Warbler habitat deterioration

The Aquatic Warbler was a common breeding bird in the Lower Oder Valley in the first half of the twentieth century (Robien 1920 and unpublished reports) when mosses and sedges prevailed in the floodplain (Weber 1907). In the years until 1976, when Aquatic Warbler numbers in the study area were high (30–50 singing males according to

Fig. 4 Mean vegetation height and proportion of strategy type CSR in July 1993–2006 on sites which became abandoned by Aquatic Warblers during the study period (upper panels, circles = long-term study plot margin, triangles = long-term study plot centre) and on sites which were occupied by Aquatic Warblers throughout the study period (lower panels, circles = southern polder, triangles = central polder). Filled symbols indicate Aquatic Warbler occurrence during or up to 3 years after the study year

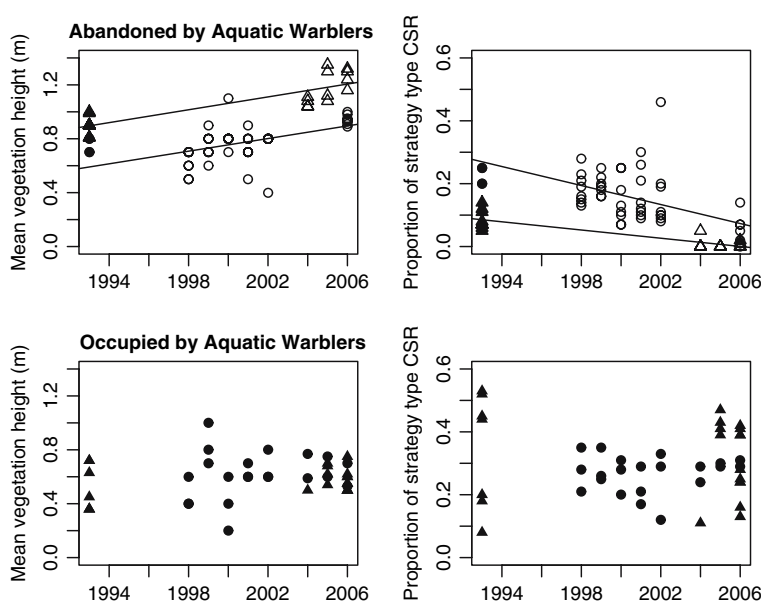
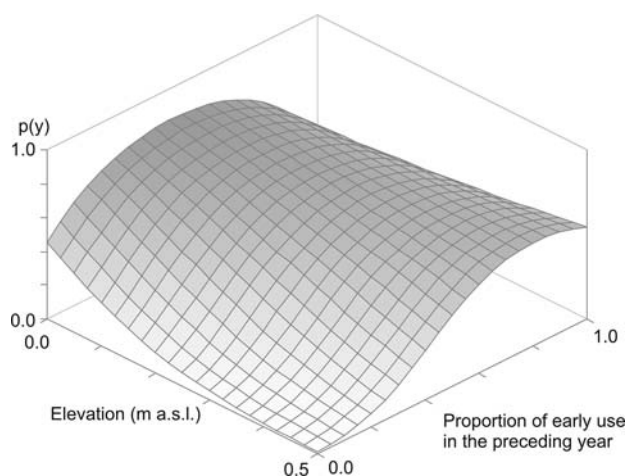


Table 2 Results of the logistic regression model to predict Aquatic Warbler occurrence from elevation and land use in the preceding year

| Parameter | Coefficient | SE | Wald statistic | <i>P</i> |
|--------------------------------------|-------------|--------|----------------|----------|
| Intercept | -0.1913 | 0.6904 | -0.28 | 0.7817 |
| Elevation | -8.9123 | 3.7472 | -2.38 | 0.0174 |
| Proportion of early use | 7.1423 | 2.7225 | 2.62 | 0.0087 |
| Proportion of early use ² | -7.6919 | 2.6329 | -2.92 | 0.0035 |
| Elevation × proportion of early use | 10.7371 | 4.7937 | 2.24 | 0.0251 |

**Fig. 5** Predicted Aquatic Warbler occurrence, $p(y)$, from the model in Table 2 in relation to elevation and the proportion of area mown or grazed early in the preceding year

incomplete counts), their breeding habitat was described as sedge with transitions to reed canary grass and meadow vegetation (Dittberner and Dittberner 1976). Small and least competitive meadow herbs such as *Caltha palustris*, *Galium palustre*, *Lysimachia nummularia*, *Ranunculus repens*, grasses *Agrostis stolonifera*, *Alopecurus geniculatus*, and sedges *Carex vulpina* occurred with high constancy (Schalitz 1970). Wawrzyniak and Sohns (1977) described for the Lower Oder Valley in 1974 a nesting site in meadow vegetation. The mix of sedges and meadow vegetation persisted on drier parts by mowing and grazing and on wet parts by mowing from July onwards or without land use (Dittberner and Dittberner 1976; G. Schalitz, personal communication).

From 1976 onwards, large scale early pumping of the polders and nitrogen fertilisation partly from aircraft with up to 150–360 kg N/ha (Schalitz et al. 1984) favoured the development of monotonous reed canary grass vegetation and facilitated earlier and more complete mowing. Whereas typical reed canary grass vegetation yield in 1966 still contained 44% sedge biomass, this proportion was

only 1% in 1983 (Schalitz et al. 1997). With the ongoing homogenisation of the vegetation, Aquatic Warbler numbers also declined (Fig. 2). Typical habitats of the remaining Aquatic Warblers in the 1980s (e.g. the long-term study plot) were structurally rich sites with sedges, reed canary grass and meadow vegetation, similar to important breeding sites in 1993 and today. Since the mid-1980s, the population has increased slightly (Fig. 2). Less intensive mowing due to the designation of protected areas and the changes in the east-German rural economy might have improved habitat conditions temporarily.

In 1993, Aquatic Warblers in the northern polder occupied regularly mown sedge stands, comprising small and least competitive meadow plants such as *Caltha palustris*, *Carex vulpina*, and *Ranunculus repens* with high constancy. When water levels allowed, they were partly mown early. Aquatic Warblers also occupied the adjacent early mown reed canary grass and meadow vegetation. In the central and southern polder, a patchy mosaic of sedges, reed canary grass, meadow and low meadow vegetation was occupied. Regularly mown sedges had a slightly lower vegetation height and cover than rarely mown sedges, thus allowing a larger diversity of species in the herb layer with a mean number of 19 plant species per relevé (Jehle and Pankoke 1999).

In the mid-1990s, Aquatic Warbler numbers decreased again severely and in 1998 the birds had already left the late mown meadows that had turned into tall, dense and homogeneous stands of sedge and reed canary grass. The mosaic of early mown sedges, reed canary grass, meadow and low meadow vegetation was maintained by early mowing in other parts.

The rapid habitat deterioration resulting from mowing at increasingly later dates and eventual cessation of land use is illustrated by vegetation changes on the long-term study plot in the northern polder (Fig. 4, upper panels), which was left by Aquatic Warblers in 1998. The effects of abandonment (increase in vegetation height, decrease of CSR species) can already be seen during the period of gradually reduced mowing intensity from 1995 to 2001. Where land use remained almost unchanged and Aquatic Warbler occurrence continued during the study period no similar change in vegetation structure could be observed (Fig. 4, lower panels). Taller vegetation and relatively low cover of CSR species in the centre of the long-term study plot as compared to sites not abandoned might indicate that the process was already ongoing on the former site in 1993. The high CSR species cover at the margins of the long-term study plot especially in 1998–2002 was characteristic for the species-rich *Cnidion dubii* plots studied at that time.

Such successional patterns—an increase of tall sedges and grasses at the expense of small or medium-sized herbs, altogether leading to a decrease in the cover of CSR

species, a reduced overall plant species number, and a thicker litter layer—have been reported in numerous long-term studies of abandoned meadows all over Central Europe (among others: Rosenthal and Müller 1988; Leyer 2002 for floodplain sites including fens; and Jensen and Schrautzer 1999; Falińska 1999; Bakker et al. 2002; Wagner et al. 2003; Güsewell and Le Nédic 2004; Hodgson et al. 2005 for other fens and grasslands). In the Elbe river floodplains, that are similar to the study site, sporadically mown or abandoned *Carex acuta* stands developed a thick litter layer, which inhibited colonisation of other plants for many years. “Light plants” such as *Carex vulpina*, a CSR species occurring with high constancy on current Aquatic Warbler sites in the Lower Oder Valley, became quickly displaced by fast-growing tall plants (Leyer 2002).

Current Aquatic Warbler habitats in the Lower Oder Valley National Park

Due to the lack of recent vegetation studies in the Lower Oder Valley National Park, we combined data from a study focussing on Aquatic Warbler habitats (Tanneberger et al. 2005) with older data collected for different purposes. Therefore, study plots until 2002 were either chosen randomly with respect to Aquatic Warbler occurrence or were situated at the margins of potential Aquatic Warbler breeding sites in the case of the *Cnidion dubii* plots. Vegetation structure and composition parameters, however, were measured in many cases with the same methods. The repeatability of differences in up to three independent studies (Table 1) together with changes tracked over 14 years (Fig. 4) presents a strong argument for the relevance of our results.

The following conditions indicate Aquatic Warbler habitat suitability in the study area during early breeding season:

1. soil moisture: moist or wet;
2. mean vegetation height: 0.4–0.8 m;
3. mean thickness of the litter layer: <5 cm;
4. mean cover of CSR species in early June: >10%;
5. total plant species number: $\geq 10/25 \text{ m}^2$.

The observed vegetation changes are all driven by the same process (land use change) and the values on abandoned sites (Table 1) reflect unfavourable conditions for Aquatic Warblers. Taller and denser vegetation may impede the bird's foraging mobility inside the vegetation, which distinguishes the species from all other European *Acrocephalus* species (Leisler 1975; 1981). Low foraging efficiency in tall and dense meadow vegetation has also been shown for other songbird species (Wilson et al. 2005). Although the litter layer is a preferred nesting substrate on

flooded meadows in former German breeding sites (Heise 1970) as well as in the Biebrza Valley (Dyrz and Zdunek 1993) this was not the case in the Lower Oder Valley. Here, the meadows inhabited are drained in spring and no surface water is left when Aquatic Warblers start nest building in May. Nests in this kind of meadows are often placed close to the ground (Wawrzyniak and Sohns 1977; Vergeichik and Kozulin 2006; own observations). A thick litter layer probably adds to the hindrance of foraging movements (Wawrzyniak and Sohns 1977) and, in addition, has a negative effect on Aquatic Warbler prey abundance (F. Tanneberger, unpublished data) as microclimatic conditions on the ground are less favourable for arthropod larval development (e.g. due to retarded warming of the soil in spring) and because the growth of food plants (CSR species) is reduced. For Orthoptera, contributing >50% to Aquatic Warbler diet in a nest observed by Heise (1970) at Rietzer See/Brandenburg, this was shown by Fartmann and Mattes (1997). Reduced prey abundance is particularly detrimental for the Aquatic Warbler as its breeding success relies strongly on sufficient food sources for the female raising the offspring in uniparental care (Heise 1970; Schulze-Hagen et al. 1999).

The process described here is most pronounced on higher sites because lower sites may maintain sparse vegetation even without land use due to higher water levels. This might explain the recent shift of Aquatic Warbler males to lower sites. During the study period, however, most Aquatic Warbler males and broods were still recorded on higher sites (>0.2 m) where early land use is most important.

Rapid habitat deterioration after the cessation of land use is an important threat for Aquatic Warblers in floodplain polder habitats in Germany and Lithuania, but less so in the groundwater-fed percolation mire habitats in Poland, Ukraine, and Belarus. The latter hold approximately 97% of the current world population and are therefore regarded as typical Aquatic Warbler habitats (AWCT 1999; Kozulin and Flade 1999). The two habitat types are similar with respect to vegetation height and cover of CSR species, but differ substantially in thickness of litter layer, cover of mosses and site conditions (Table 3). A medium or thick litter layer and the oscillating moss layer allow nest placement above water level and provide typical nesting sites in the percolation mire habitats (Vergeichik and Kozulin 2006). In the floodplain polder habitats, the litter layer is thin, mosses and water above ground level are absent and nests are placed close to the soil surface in old vegetation. The eutrophic conditions of these habitats (according to mire typology in Succow and Joosten 2001) are mainly caused by inundation with nutrient-rich river water and enhance biomass production and succession speed. In contrast, the mesotrophic percolation mire

Table 3 Comparison of floodplain polder and percolation mire habitats with regard to Aquatic Warbler density, vegetation and site conditions during early breeding season

| | Density (sm/10 ha) | Vegetation structure | | | Site conditions | | |
|--|-----------------------|--------------------------|-----------------------------|-----------------------------------|---------------------|--|--|
| | | Similar | | Different | Different | | |
| | | Vegetation height (m) | Cover of CSR species (%) | Thickness of litter layer (cm) | Water level (cm) | Water level amplitude April-August (cm) | Nutrient availability ^a (soil C/N ratio) |
| Floodplain polders | | | | | | | |
| Germany, Lower Oder Valley polders ^b | 0.9–1.7 | 0.4–0.8 | 5–34 | Low (0–8) | 0 | High (>50) | Eutrophic (10–14) |
| Lithuania, Nemunas delta polders ^c | 0.7–1.7 | 0.4–0.6 | 10–54 | Low (0–10) | 0 | High (>50) | Eutrophic (11–18) |
| Percolation mires | | | | | | | |
| Poland, Biebrza Valley ^d | 1–11 | 0.6–0.8 | 5–21 | High (29–39) | 0–25 | Low | Mesotrophic (mean \pm SD: 21.45 \pm 2.2) |
| Belarus, fen mires ^e | 1–13.5 | 0.6–0.7 | 3–20 | Medium to high (10–35) | 0–10 | Low (0–20) | Mesotrophic (mean: 20.2) |
| Ukraine, fen mires ^f | 3.3–11.5 | 0.6–0.7 | 9–11 | Medium | 0–20 | Low (< 20) | Mesotrophic |

Data are given as range, if not indicated otherwise

^a Nutrient availability classes after Succow and Joosten (2001)

^b This study (density data for long-term study plot before population decline; vegetation height data from May, all other vegetation data from June)

^c Tanneberger and Preiksa (unpublished), density: Sysa polder for 2004 and 2006; all other: for 2006

^d Sellin (1989), Dyrz and Zdunek (1993) and Marczakiewicz (unpublished), for 2006; soil C/N ratio: Wassen and Joosten (1996) for Biebrza Upper Basin

^e Kozulin and Flade (1999), Vergeichik and Kozulin (2006); CSR and litter: Stepanovich (personal communication); soil C/N ratio: Bambalov (personal communication)

^f Poluda (unpublished), for key habitats 2003 and Tanneberger (unpublished), for 2005

habitats are characterised by a smaller biomass production and a slower succession speed. Therefore, the cessation of land use in the latter results in a slower deterioration of habitat suitability than in the floodplain habitats. To maintain suitable habitats for Aquatic Warblers, the mesotrophic habitats are also dependent on land use, yet a lower mowing or burning frequency is sufficient. This might soon change with increasing nitrogen deposition in Eastern Europe (cf. Schöpp et al. 2003; HELCOM 2006).

Management implications

Although effective in preventing overgrowth with bushes or reed, permanent late mowing proved to be an inappropriate management method for Aquatic Warbler habitats under highly eutrophic conditions and with artificial drainage early in the breeding season in the Lower Oder Valley (Fig. 5). The low efficiency of late mowing in the conservation of wet meadows could also be shown by Kratz et al. (2001) for grasshopper communities. The reintroduction of early mowing on abandoned fen meadows led to an increase of plant species, especially small- and medium-sized herbs, from 3 to 16 within 6 years (Pfadenhauer et al. 2001). Unfortunately, early mowing is also a serious threat to breeding birds and without additional nest protection the early mown areas might act as an ecological trap (Battin 2004) for the birds. Successful broods have been recorded every year since 1998, but a part of the potential breeding sites is still destroyed by mowing or grazing in June or July.

In order to reverse the changes in vegetation caused by late or no mowing which are detrimental to Aquatic Warbler habitats we recommend an alternating management with late mowing in years when Aquatic Warblers are present and earlier mowing in the absence of Aquatic Warblers. Low intensity grazing may present an alternative which should also be tested. Given the constantly decreasing number of Aquatic Warblers in Pomerania, it is urgent to increase both habitat management and brood protection at the current breeding sites, including a continuous monitoring of its actual effects on Aquatic Warbler habitat structure and breeding success.

Zusammenfassung

Schnelle Verschlechterung von Habitaten des Seggenrohrsängers *Acrocephalus paludicola* am westlichen Rand des Verbreitungsgebietes

Im letzten deutschen Brutgebiet der stark gefährdeten ‘Pommerschen’ Population des Seggenrohrsängers (*Acrocephalus paludicola*), dem Nationalpark ‘Unteres Odertal’,

haben wir anhand von Daten zu Populationsgröße, Vegetationsstruktur und -zusammensetzung, Standortbedingungen und Landnutzung Veränderungen der Habitateignung zwischen 1993 und 2006 untersucht. Flächen mit aktuellem Seggenrohrsänger-Vorkommen wiesen niedrigere und weniger dichte Vegetation, eine dünnere Streuschicht, eine höhere Anzahl von Pflanzenarten sowie einen höheren Deckungsgrad von kleinen und konkurrenzschwachen (CSR) Arten auf als aufgegebene und nie besiedelte Flächen. In einem Zeitraum mit Spätmahd und anschließender Aufgabe der Landnutzung nahm die Vegetationshöhe auf einer Langzeit-Beobachtungsfläche zu, während sich der Deckungsgrad der CSR-Arten verringerte und die Seggenrohrsänger verschwanden. Die Wahrscheinlichkeit der Besiedlung durch Seggenrohrsänger war von der Geländehöhe und dem Anteil von im Vorjahr früh (vor dem 1.8.) gemähten oder beweideten Flächen abhängig, wobei die Bedeutung der Frühnutzung auf den höher gelegenen Flächen am größten war. Diese rapide Verschlechterung eutropher Habitate durch späte Nutzung oder Nutzungsaufgabe ist untypisch für die meisten Seggenrohrsänger-Habitate. Sowohl späte oder keine Landnutzung als auch Landnutzung während der Brutzeit gefährden die Pommersche Population, deshalb ist ein gezielteres und flexibleres Management der Brutgebiete dringend nötig.

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