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## Short communication

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# Optimal habitat conditions for the globally threatened Aquatic Warbler *Acrocephalus paludicola* in eastern Poland and their implications for fen management

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To identify optimal habitat for the Aquatic Warbler *Acrocephalus paludicola*, a flagship species of fen mires, we related numbers of singing males to habitat variables in all core breeding sites in eastern Poland. The density of male Aquatic Warblers increased with increasing ground cover by water and mosses and litter layer height, and was highest where vegetation was 60–90 cm tall. Male densities also increased with the biomass of arthropods > 10 mm length, estimated by sweep netting, and with the abundance of spiders, estimated by pan trapping. We suggest that habitat management should take into account species-specific morphological adaptations, nest safety and arthropod productivity. Prevention of vegetation succession is a conservation priority for open fen mires. However,

modern management practices to achieve this, especially mowing using tracked vehicles, should be evaluated and optimized to ensure that such practices do not adversely affect the long-term development of moss cover and litter structure.

**Keywords:** arthropods, fen mires, habitat requirements, management regime, vegetation structure.

Once widespread in European fen mires, the Aquatic Warbler *Acrocephalus paludicola* is at present the rarest and the only globally threatened migratory passerine bird on the continent (Flade & Lachmann 2008). The species has evolved adaptations to allow both the climbing of stalks (in common with other *Acrocephalus* warblers) and running (in common with *Locustella* warblers). Thus, it has been able to occupy a habitat niche that is extreme for *Acrocephalus* species – sedge fen mires and similarly structured wetland habitats with low vegetation (Leisler *et al.* 1989, Schulze-Hagen 1991). The promiscuous mating system with uniparental female care, atypical of *Acrocephalus* species, also implies specific habitat requirements, such as a high abundance of food during breeding (Schulze-Hagen *et al.* 1989, Dyrz & Zdunek 1993).

Measures for Aquatic Warbler conservation are required across the breeding range (Flade & Lachmann 2008). Many breeding areas have suffered from draining, land conversion, eutrophication and the resulting acceleration of vegetation succession. There is an urgent need to identify key characteristics determining habitat quality and the responses of Aquatic Warbler populations to land use practices. In many breeding sites, traditional scything and low-intensity grazing of fens has changed to machine-mowing in the framework of agri-environment programmes (Kotowski *et al.* 2013). Previous research on the species in core breeding sites has shown that it occurs in mesotrophic to slightly eutrophic sedge fens with water levels up to a few centimetres above the soil surface, with reed or bush succession adversely affecting habitat suitability (Kłoskowski & Krogulec 1999, Kozulin & Flade 1999).

The aim of this study was to quantify habitat characteristics, including estimates of arthropod prey abundance, associated with high densities of breeding Aquatic Warblers in eastern Poland, where over 95% of the Polish and approximately 25% of the global population breed (Flade & Lachmann 2008). Based on this, we aimed to describe ‘optimal’ habitat conditions for the species and to derive guidelines for improved fen mire management from assessment of remaining high-quality habitats.

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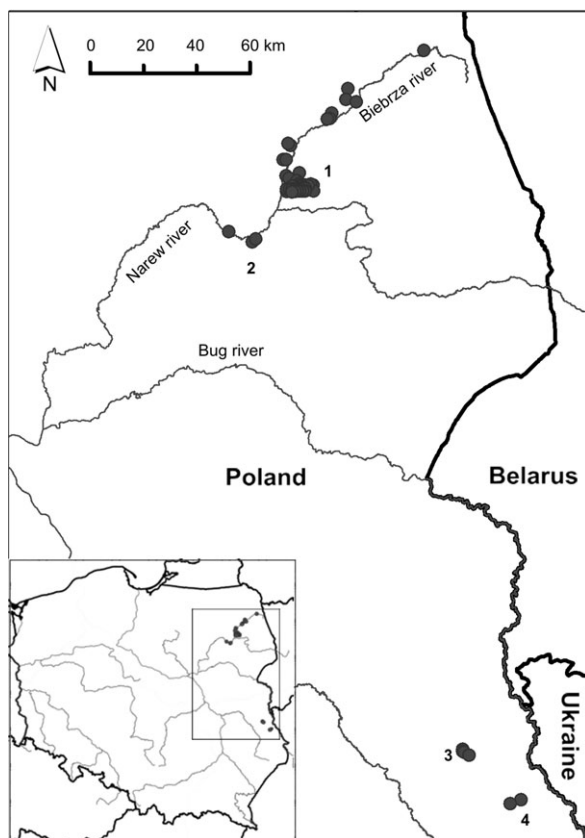
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## METHODS

### Study areas

The study was carried out between 2007 and 2010 in four main Aquatic Warbler breeding areas in eastern Poland (Fig. 1). Most birds breed in the Biebrza river valley in northeastern (NE) Poland in mainly mesotrophic fen mires characterized by species-rich Magnocaricion and Caricion nigrae communities. A small subpopulation occupies floodplain meadows in the valley of the lower Narew River, approximately 50 km south of the southern basin of the Biebrza River. In southeastern (SE) Poland, most Aquatic Warblers breed in the Polesie fen mires (Polesie National Park) dominated by Magnocaricion communities. The other important population occurs near Chelm in calcareous *Cladietum marisci* fen mires interspersed with sedge



**Figure 1.** Location of the Aquatic Warbler breeding areas covered in this study. (1) Biebrza valley (53°15'–44'N, 22°27'–23°19'E); (2) Narew valley (53°05'–09'N, 22°09'–23°17'E), both NE Poland; (3) Polesie National Park (51°20'–22'N, 23°15'–20'E); (4) Chelm mires (51°08'–11'N, 23°31'–40'E), both SE Poland.

meadows (Fig. 1; see also Dyrzc 2010, the classification of plant communities follows Matuszkiewicz 2001). We divided the areas of Aquatic Warbler occurrence into 100 × 1000 m transects. For our study, 60 transects were randomly selected using a stratification scheme to allow all populations to be represented proportional to densities of Aquatic Warbler males estimated during surveys conducted 1–3 years earlier and including only transects occupied by the species to increase the proportion of transects with high male densities: 51 transects in Biebrza valley, three in Narew valley, four in Polesie National Park and two in the Chelm mires.

### Aquatic Warbler counts

We based estimates of breeding numbers on counts of singing males. Male density is correlated with both nest density and fledgling production (Kubacka *et al.* 2014). Singing males were mapped in the field from 1 h before to 1 h after sunset when singing activity peaks (Dyrzc & Zdunek 1993). Small teams of observers experienced in Aquatic Warbler identification located singing males as described by Kloskowski and Krogulec (1999) in larger patches of suitable habitat containing the transects. Positions of singing males were recorded in a geographical information system (ESRI ARCGIS 9.2) and male numbers within transects were later extracted. If the study transects were adjacent to each other, they were sampled in a haphazard sequence in different years to ensure that males moving within their home-ranges (Dyrzc & Zdunek 1993) were not repeatedly counted in different transects.

Because Aquatic Warbler females are commonly double-brooded with egg-laying peaks around late May and late June (Dyrzc & Zdunek 1993), the counts were usually conducted twice per season, in late May and in late June, during the main mating periods. For analyses we used the maximum count from the two visits. In 16% of transects only one count was performed and this was used in data analysis.

### Habitat characterization

Habitat data were collected between 1 and 20 June, between the first and the second Aquatic Warbler count. We focused on parameters suggested to be important for Aquatic Warbler habitat selection (Dyrzc & Zdunek 1993, Kloskowski & Krogulec 1999, Tanneberger *et al.* 2008, 2010). Most habitat measurements were collected from four to five plots of 5 × 5 m distributed approximately evenly along each of two transects within heterogeneous habitats (mosaics of open and bush-covered areas), but omitting uncommon habitat elements (e.g. ditches, patches trampled by ungulates). Specifically, herbaceous vegetation height and cover were recorded

from four 1-m<sup>2</sup> subplots in the corners of each of these plots, and water and litter depth and cover were recorded in the four corners of each plot. Measures of cover were estimated using the Londo scale, with four replicates per plot and transformed to proportions (after Dierschke 1994). The number of bushes along each transect and their height were recorded. In the analyses, we first calculated the mean for each plot, and then means of plots (see Table S1 for detailed habitat variable descriptions).

To assess the relative abundance of invertebrate prey for Aquatic Warblers, we used two methods. Sweep-netting was conducted with a 33-cm-diameter sweep-net. Five series of 50 sweeps were made at intervals of 2–3 m along each transect using marked habitat sampling plots as orientation points. Sampling was carried out between 10:00 and 14:00 h on sunny and windless days. Sweep-netting is considered the most practical technique for real-time sampling of foliage-dwelling invertebrates but may vary with plant structure, weather and between individual field surveyors (Doxon *et al.* 2011). As a complementary method, we therefore used yellow pan traps of 18.5 cm diameter and 6 cm depth, each half-filled with a liquid glycol solution. Along each transect, five to six traps were placed on the ground at approximately even intervals for 10 days. To adjust for different numbers of traps retrieved (2% of the traps were flooded or lost based on a target amount of five traps per transect), trap results were standardized to a per-trap basis. This technique provides time-integrated estimates. Yellow pan traps were chosen because they are the most effective in capturing a high diversity of insects (Leong & Thorp 1999), although this may have resulted in some selective attraction of insects (Cooper & Whitmore 1990).

Invertebrates were identified to at least order level and assigned to five size classes (1–5 mm, 6–10 mm, 11–15 mm, 16–20 mm, > 20 mm). Based on body length–dry weight regressions established for Aquatic Warbler habitats in Belarus (A. Kozulin & F. Tanneberger unpubl. data), the mean abundance per size class was transformed into biomass averaged per five sweep series or per trap. For the analyses we pooled larval and adult stages.

### Statistical analysis

We modelled predictors of variation in Aquatic Warbler density between transects using generalized linear mixed models with Poisson errors and a log link. As well as main effects, we also considered the interactions of VEG HEIGHT and LITTER HEIGHT (see Table S1) with WATER COVER or WATER DEPTH (cf. Tanneberger *et al.* 2008). Quadratic terms (after being centred) were included for VEG HEIGHT and WATER DEPTH in order to model possible curvilinear relationships. We

allowed quadratic terms and interactions into the model only if the corresponding linear and main terms, respectively, were also included.

Due to adverse weather conditions during the sampling periods, sweep-netting was only performed in 38 transects and pan-trapping in 54 transects. We therefore first modelled relationships between Aquatic Warbler density and habitat characteristics only, using the full dataset. Using the models with good fit, we then separately modelled the two subsets of transects, adding the following food variables: the estimated biomasses of arthropod groups most abundant in the samples (> 20% by estimated biomass) (see Results), the biomass of arthropods > 10 mm (cf. Schulze-Hagen *et al.* 1989) and total arthropod biomass. To avoid multicollinearity we reduced the number of explanatory variables by censoring one member of any pair of strongly correlated variables (the one that yielded a weaker univariate model; see also Appendix S1). We considered the study year as a random term and the geographical location of sampling (NE vs. SE Poland) as a fixed factor.

We selected the best predictive models using Akaike's information criterion corrected for small sample size (AIC<sub>c</sub>; Burnham & Anderson 2002). We followed the convention that the model with the lowest AIC<sub>c</sub> represents the best compromise between goodness-of-fit and model complexity and that models with  $\Delta\text{AIC}_c$  (the difference between the AIC<sub>c</sub> for a particular model and that of the best model) < 2 fit almost as well as the most parsimonious (Whittingham *et al.* 2006) model, while models with  $\Delta\text{AIC}_c > 2$  and < 6 might be considered informative (Symonds & Moussalli 2011). We used all-subsets selection; however, for parsimony, we excluded (*post-hoc*) from the candidate set those models that were more complex versions of any model with a lower AIC<sub>c</sub> value ( $\Delta\text{AIC}_c > 2$ ) (Burnham & Anderson 2002, Richards 2008). We then calculated an Akaike weight ( $w_i$ ) for each model. Model averaging to account for model uncertainty was not used because the different response types (linear and quadratic) that were modelled would confound parameter averages (Burnham & Anderson 2002, Blums *et al.* 2005).

To evaluate goodness-of-fit of the most parsimonious model based on the entire dataset we used an internal cross-validation technique (Boyce *et al.* 2002). We performed a fourfold cross-validation by dividing our sample randomly into four equal groups and training our model iteratively on 75% of the subsets. Predictions were generated at the remaining 25%. We summarized our results using Spearman's rank correlation coefficients between predicted and observed bird densities (Boyce *et al.* 2002).

Model selection was performed using the R package lme4 (Bates *et al.* 2014; R version 3.1.1, R Foundation for Statistical Computing, Vienna, Austria).

## RESULTS

Aquatic Warblers were detected in all but two transects. The maximum density of singing males was 33/10 ha (median = 5, lower and upper quartiles 3–9). In the full dataset, Aquatic Warbler density increased with WATER COVER, MOSS COVER and LITTER HEIGHT. VEG HEIGHT showed a peaked (negative quadratic) relationship (Table 1), with maximum male densities occurring at intermediate levels of VEG HEIGHT (approximately 60–90 cm). The best models ( $\Delta AIC_c < 2$ ) also contained a negative interaction between LITTER HEIGHT and WATER COVER (Table 1). Predictions from the most parsimonious model are shown in Fig. 2. The fourfold cross-validation provided a mean Spearman's rank correlation between predicted and observed densities of Aquatic Warbler of 0.736 ( $P < 0.002$ ;  $r_S$  range: 0.618–0.915) for the most parsimonious model, indicating that the model performed well.

We then evaluated the good-fit habitat models (all those with  $\Delta AIC_c < 6$ ) on the subsets of transects for which food measures were available. Diptera was the

most abundant taxon in the sweep-net samples in terms of biomass (23.5%), followed by Coleoptera (20.3%) and Araneida (13.3%). In the traps, Araneida were most abundant (33.3%), followed by Diptera (24.3%) and Coleoptera (22.6%). For both subsets, the top models contained similar habitat variables as those obtained by the selection process on the entire dataset (Table 1). The biomass of arthropods > 10 mm was an additional strong positive predictor of Aquatic Warbler density in the subset with sweep-netting data, and Araneida biomass was an important predictor in the subset including data from pan traps (Table 1).

## DISCUSSION

### Optimal habitats

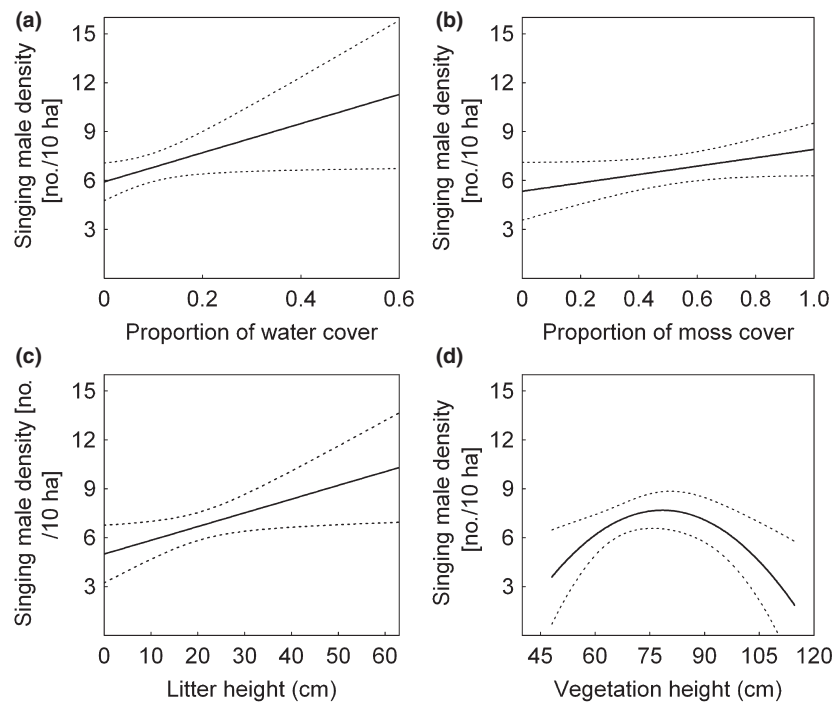
Habitats with a high proportion of the ground covered by water and mosses, a thick litter layer and with intermediate vegetation height supported high densities of Aquatic Warblers. Water levels in most transects were <20 cm and within the range used by the species (Schulze-Hagen 1991). The presence of surface water

**Table 1.** The top candidate models predicting densities of Aquatic Warblers in their best remaining habitats in Poland. The number of parameters ( $k$ ), Akaike's information criterion with small-sample bias adjustment ( $AIC_c$ ), the difference between the lowest  $AIC_c$  and  $AIC_{ci}$  ( $\Delta AIC_c$ ) and the model weight ( $w_i$ ) are shown. The signs in parentheses indicate the direction of the relationship. Only models with  $\Delta AIC_c < 6$  are included. Separate analyses were run on (a) the entire set of transects ignoring prey availability variables, (b) the subset of transects for which sweep netting data were available and (c) the subset of transects with pan trapping data.

Candidate model	$k$	$AIC_c$	$\Delta AIC_c$	$w_i$
<b>a. All transects, food variables not considered (<math>n = 60</math>)</b>				
LITTER HEIGHT <sub>(+)</sub> + MOSS COVER <sub>(+)</sub> + VEG HEIGHT <sub>(-)</sub> + VEG HEIGHT <sup>2</sup> <sub>(-)</sub> + WATER COVER <sub>(+)</sub> + LITTER HEIGHT*WATER COVER <sub>(-)</sub>	9	185.80	0.00	0.231
LITTER HEIGHT <sub>(+)</sub> + MOSS COVER <sub>(+)</sub> + VEG HEIGHT <sub>(-)</sub> + WATER COVER <sub>(+)</sub> + LITTER HEIGHT*WATER COVER <sub>(-)</sub>	8	186.12	0.32	0.196
LITTER HEIGHT <sub>(+)</sub> + MOSS COVER <sub>(+)</sub> + VEG HEIGHT <sub>(-)</sub> + VEG HEIGHT <sup>2</sup> <sub>(-)</sub> + WATER COVER <sub>(+)</sub> + LITTER HEIGHT*WATER COVER <sub>(-)</sub> + BUSH COVER <sub>(-)</sub>	10	187.69	1.69	0.090
<b>b. The subset of transects with sweep netting data (<math>n = 38</math>)</b>				
LITTER HEIGHT <sub>(+)</sub> + MOSS COVER <sub>(+)</sub> + VEG HEIGHT <sub>(-)</sub> + WATER COVER <sub>(+)</sub> + LITTER HEIGHT*WATER COVER <sub>(-)</sub> + Arthropoda > 10 <sub>(+)</sub>	9	128.20	0.00	0.220
LITTER HEIGHT <sub>(+)</sub> + MOSS COVER <sub>(+)</sub> + VEG HEIGHT <sub>(-)</sub> + WATER COVER <sub>(+)</sub> + LITTER HEIGHT*WATER COVER <sub>(-)</sub>	8	128.72	0.52	0.169
LITTER HEIGHT <sub>(+)</sub> + MOSS COVER <sub>(+)</sub> + VEG HEIGHT <sub>(-)</sub> + WATER COVER <sub>(+)</sub> + LITTER HEIGHT*WATER COVER <sub>(-)</sub> + Coleoptera <sub>(+)</sub>	9	130.69	2.49	0.063
<b>c. The subset of transects with pan trapping data (<math>n = 54</math>)</b>				
LITTER HEIGHT <sub>(+)</sub> + MOSS COVER <sub>(+)</sub> + VEG HEIGHT <sub>(-)</sub> + VEG HEIGHT <sup>2</sup> <sub>(-)</sub> + WATER COVER <sub>(+)</sub> + LITTER HEIGHT*WATER COVER <sub>(-)</sub> + Araneida <sub>(+)</sub>	10	175.99	0.00	0.396
LITTER HEIGHT <sub>(+)</sub> + MOSS COVER <sub>(+)</sub> + VEG HEIGHT <sub>(-)</sub> + VEG HEIGHT <sup>2</sup> <sub>(-)</sub> + WATER COVER <sub>(+)</sub> + LITTER HEIGHT*WATER COVER <sub>(-)</sub>	9	176.80	0.81	0.264
LITTER HEIGHT <sub>(+)</sub> + MOSS COVER <sub>(+)</sub> + VEG HEIGHT <sub>(-)</sub> + WATER COVER <sub>(+)</sub> + LITTER HEIGHT*WATER COVER <sub>(-)</sub> + Araneida <sub>(+)</sub>	9	177.40	1.41	0.196
LITTER HEIGHT <sub>(+)</sub> + MOSS COVER <sub>(+)</sub> + VEG HEIGHT <sub>(-)</sub> + WATER COVER <sub>(+)</sub> + LITTER HEIGHT*WATER COVER <sub>(-)</sub>	8	178.12	2.13	0.136

Abbreviations as in Table S1. Arthropoda > 10 = total biomass of arthropods > 10 mm per five sweep-net series/pan trap; Araneida = total biomass of Araneida, Coleoptera = total biomass of Coleoptera.





**Figure 2.** Predicted abundance of singing Aquatic Warbler males in relation to (a) WATER COVER, (b) MOSS COVER, (c) LITTER HEIGHT and (d) VEG HEIGHT. The predictions are based on the most parsimonious generalized linear mixed model. Predicted values were assessed for each variable when other variables were held constant at their mean values. Broken lines show 95% confidence intervals.

seems to be a prerequisite for Aquatic Warblers, presumably ensuring sufficient arthropod abundance (e.g. of spiders; Kajak *et al.* 2000) and providing protection against some predators. However, high water levels may cause flooding of nests (Vergeichik & Kozulin 2006, Kubacka *et al.* 2014), which are built either directly on or close to the ground (typically on tussocks). A rich moss layer is likely to indicate a strong oscillation of the mire surface, which buffers any sudden changes in the water table. Also, a well-developed litter layer provides structure for nest construction with better concealment (Schulze-Hagen 1991), protecting it from flooding and possibly also from some ground-dwelling predators such as shrews or snakes (Dyrz & Zdunek 1993, Vergeichik & Kozulin 2006). The interaction between litter height and water cover (positively correlated with water depth) was negative. One possible explanation is the potential development of a dense layer of decaying ground litter, hampering foraging opportunities at sites with long-term high flooding. The optimal vegetation height of 60–90 cm, as indicated by our modelling results, corresponds to the species' habitat niche breadth and the morphological adaptations of the feet of Aquatic Warblers for walking in and climbing on stalks of intermediate height (Leisler *et al.* 1989). The quadratic

relationship between vegetation height and male density perhaps reflects a trade-off between high predation risk in low vegetation and the strong hindrance of foraging movements and arthropod accessibility in tall vegetation (cf. Whittingham & Evans 2004). The broad range of male densities indicated that the habitat suitability gradient was not as short as might have been expected from the limitation of study transects to the least disturbed habitats. Vegetation succession indicators, such as reed cover or bush cover (Kloskowski & Krogulec 1999, Dyrz 2010), did not feature strongly in our best-fit models. However, this can be explained by the overall low reed and bush cover in the study transects located in well-preserved fen mires, as a consequence of our strategy of focusing on high-quality habitats in the first place. Still, we believe that inference about habitat quality based on sampling of the 'best' remaining habitats avoids trivial conclusions derived from the inclusion of entirely unsuitable habitats. This is important in the case of Aquatic Warbler, where two very basic indicators of habitat quality (habitat fragmentation and habitat succession to scrub) may overshadow more subtle but nonetheless important habitat attributes (cf. Simberloff 1995, Watters *et al.* 2002, Zuckerman & Vickery 2006).

Positive relationships between Aquatic Warbler density and both arthropods > 10 mm and spider biomass accord with earlier suggestions that Aquatic Warblers feed on larger arthropod classes and that spiders may be an important nestling food source (Schulze-Hagen *et al.* 1989). It also indicates that food supply is likely to be a key aspect of habitat selection by breeding Aquatic Warblers (Schulze-Hagen *et al.* 1989, Dyrzc & Zdunek 1993). However, considering arthropod productivity in conservation strategies can prove difficult due to broader methodological problems of obtaining relevant estimates of prey abundance for insectivorous birds because of the disparity between sampling methods and forager perception (Cooper & Whitmore 1990). As in our study, total arthropod biomass estimates may show no relationship to bird densities and more complex indices of prey availability may need to be examined. Nonetheless, evaluation of the effects of habitat structure and particularly of land use practices (cf. Swengel 2001, Schmidt *et al.* 2008) on the abundance of the arthropod prey of Aquatic Warblers remains an urgent research task.

### Management recommendations

The study areas show many similarities to other mesotrophic fen mires in Belarus and Ukraine (Tanneberger *et al.* 2008) and our results may be transferable to these other core population areas. Guidance on Aquatic Warbler habitat management has focused on hydrological and nutrient conditions and removal of bushes and mowing to halt succession (Kloskowski & Krogulec 1999, Flade & Lachmann 2008, Tanneberger *et al.* 2010). However, modern machine mowing practices may significantly affect plant communities by reducing soil aeration and promoting superficially rooting species (Schrama *et al.* 2013). Early results of vegetation monitoring accompanying mowing with tracked vehicles in Biebrza valley indicate that the cover of hummock mosses and of tussock species decreases, while the cover of hollow mosses and semi-aquatic, clonal species increases (Kotowski *et al.* 2013). The recognition of the role of mosses and litter in high-quality habitats for Aquatic Warblers may help determine management practices. In particular, the rate of moss and litter layer recovery after heavy machinery use in particular requires further investigation. Flattening of the ground and destruction of vegetation and litter structure is likely to limit the availability of safe nest-sites in years with high water levels (Kubacka *et al.* 2014). Reduction of habitat heterogeneity may also make nests more vulnerable to predation (cf. Whittingham & Evans 2004). By showing the importance of a high litter layer, our results favour longer than annual mowing intervals. Diversifying mowing operations in space and time is often recommended to reduce unwanted effects on plant and invertebrate

communities (Swengel 2001, Buchanan *et al.* 2006). While benefits from increasing mowing intervals on Aquatic Warbler breeding production have recently gained empirical support (Kubacka *et al.* 2014), effects of diversification in space (mowing executed in mosaic-like manners with strips or blocks of cut and temporarily uncut sward) are less well understood, although they may mitigate impacts on arthropods (Buchanan *et al.* 2006, Schmidt *et al.* 2008).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Means  $\pm$  standard errors (se) and ranges of habitat variables.