IBIS The International Journal of Avian Science

BOU

Ibis (2010), **152**, 347–358

Habitat selection of the globally threatened Aquatic Warbler *Acrocephalus paludicola* at the western margin of its breeding range and implications for management

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The globally threatened Aquatic Warbler *Acrocephalus paludicola* is an umbrella species for fen mires and is at risk of extinction in its westernmost breeding population due to severe habitat loss. We used boosted regression trees to model Aquatic Warbler habitat selection in order to make recommendations for effective management of the last remnant habitats. Habitat data were collected in the years 2004–2006 in all remaining breeding sites in Pomerania (eastern Germany and western Poland) as well as in recently abandoned sites. Models were validated using data from similar Aquatic Warbler habitats in Lithuania. The probability of occurrence of Aquatic Warblers in late May/early June was positively associated with low isolation from other occupied sites, less eutrophic conditions, a high proportion of area mown early in the preceding year, high availability of vegetation 60–70 cm high, high prey abundance and high habitat heterogeneity. Early summer land management is needed in the more productive sites to prevent habitat deterioration by succession to higher and denser vegetation. As this also poses a serious threat to broods, management that creates a mosaic of early and late used patches is recommended to preserve and restore productive Aquatic Warbler sites. In less productive sites, winter mowing can maintain suitable habitat conditions. Aquatic Warbler-friendly land use supports a variety of other threatened plant and animal species typical of fens and sedge meadows and can meet the economic interests of local land users.

Keywords: *Acrocephalus paludicola*, fen mires, land use mosaic, species distribution model, vegetation structure.

The Aquatic Warbler *Acrocephalus paludicola* breeds in fen mires and similarly structured habitats (Leisler 1981, Schulze-Hagen 1991) and was formerly an abundant breeding bird throughout Central and Western Europe (Wawrzyniak & Sohns 1977, Schulze-Hagen 1991, AWCT (Aquatic Warbler Conservation Team) 1999). Since 1900, the species has lost most of its breeding range west of the Polish–German border due to large-scale habitat destruction (AWCT 1999, Flade & Lachmann 2008) and has become the only globally threatened songbird of the European mainland, with a world population of only 10 200–14 200 singing males (Flade & Lachmann 2008). The Pomeranian Aquatic Warbler population (Fig. 1) is the smallest in Europe, and historical breeding records from Germany, the

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Netherlands, Belgium and France (Schulze-Hagen 1991) suggest that the remaining birds are the last survivors of a large western population (AWCT 1999). Unlike the core populations further east, the Pomeranian population has undergone a rapid, though not fully understood, decline since 1990 (Flade *et al.* 2006), recognized in a Memorandum of Understanding under the Convention on Migratory Species (CMS).

In this study, we developed species distribution models (also called habitat models or environmental niche models) based on presence–absence data using boosted regression trees (Leathwick *et al.* 2006, Elith *et al.* 2006, 2008) to identify key factors (Pearce *et al.* 1994, Oppel *et al.* 2004) and to analyse highly localized habitat change in the restricted and fragmented Pomeranian population (McCulloch & Norris 2001). Because of the small dataset and the importance of our models for future Aquatic Warbler management in Pomerania, we used both internal and external validation. To arrive at reliable guidance for habitat management, we used data from all current and recently abandoned Aquatic Warbler sites and thus worked along a short, yet informative, gradient of habitat data. We use the results of these analyses to develop recommendations on habitat management, integrating conservation and socio-economic interests.

METHODS

Fieldwork

Study areas

The study was carried out in the eight known Aquatic Warbler breeding regions in Pomerania, comprising protected areas in Poland and Germany (Fig. 1, Table 1) located along the Baltic Sea coast and in river valleys, mostly on peat soil. The more northerly regions contained sites (i.e. unconnected land use units of variable size and habitat suitability) dominated by reed *Phragmites australis* ('reed sites') and the regions close to the Oder River contained sites dominated by sedge, mainly *Carex acuta* and *Carex disticha* ('sedge sites'; Tanneberger *et al.* in press). The binary variable VEGETATION distinguishes between reed and sedge sites. The study sites for spatial validation were located in Lithuania. With *Carex disticha* and *Phalaris arundinacea* as dominant plant species, these regions are, among all remaining breeding regions, those most similar to sites in Pomerania (Table 1).

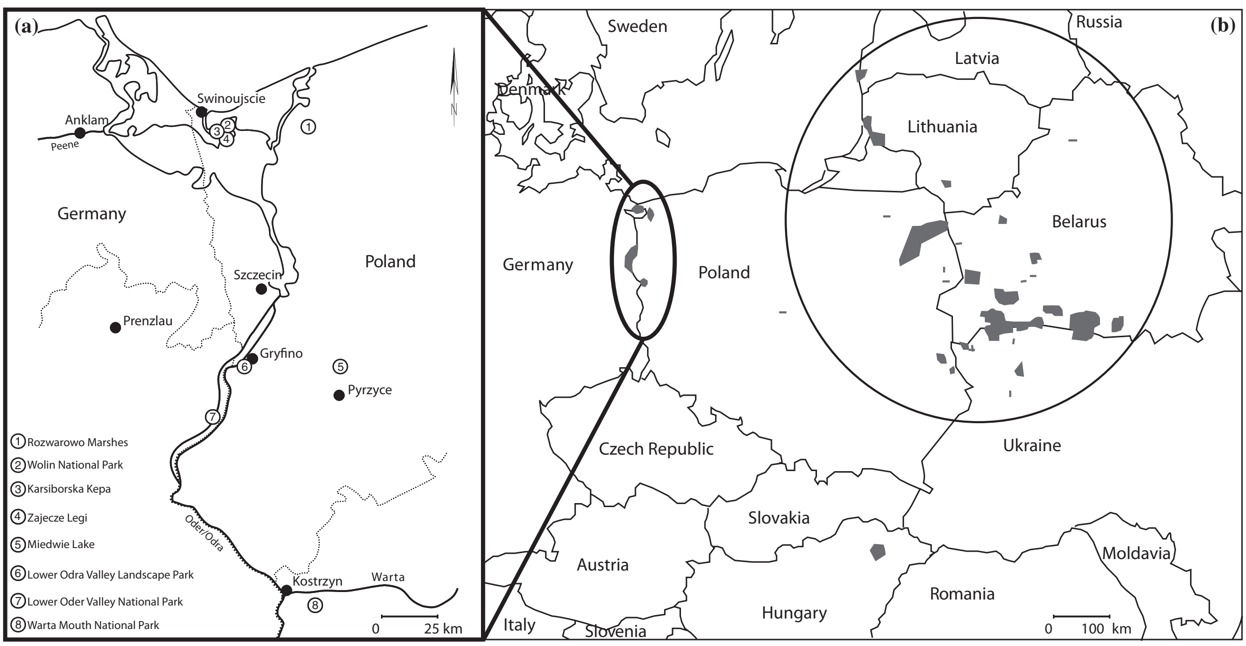

Figure 1. (a) Location of the eight protected areas with Aquatic Warbler breeding sites in Pomerania. (b) Global distribution of Aquatic Warbler breeding sites, showing the Pomeranian population (small oval) and the core population (large circle). The West-Siberian breeding sites (no permanent breeding) are not depicted. Data: Members of Aquatic Warbler Conservation Team (pers. comm.).

Table 1. Characteristics of the Pomeranian (a) and Lithuanian (b) Aquatic Warbler breeding sites.

	Name of breeding region	Location of breeding region	Main soil type	Trophic class	Dominant plant species	Main land use type	Aquatic Warbler population (singing males) 2004–2006	Number of sites
a								
1	Rozwarowo Marshes	small river valley (partly dikes)	peat	eutrophic – mod. rich	reed	WM	22–37	16
2	Wolin National Park (Warnie Kepy)	islands in Świna delta (no dikes)	peat	eutrophic – mod. rich	reed	WM, SM, GR	8–18	9
3	Karsiborska Kępy	island in Świna delta (with dikes)	peat	eutrophic – mod. rich	reed	WM, SM, GR	12–21	9
4	Zajęcze Łęgi	island in Świna delta (with dikes)	peat	eutrophic – mod. rich	reed	WM, SM, GR	0 (but records before 2004 and in 2007)	3
5	Miedwie Lake	lake shore (no dike)	peat	eutrophic – mod. rich	sedge	SM, GR	0–8	6
6	Lower Odra Valley Landscape Park and surroundings	Oder polder area (with dikes)	peat	eutrophic – rich	sedge	SM	5–7	11
7	Lower Oder Valley National Park	Oder polder area (with dikes)	mineral soil	eutrophic – rich	sedge	SM, GR	4–9	45
8	Warta Mouth National Park	Warta floodplain (no dike)	peat	eutrophic – rich	sedge	SM, GR	2–10	18
b								
1	Minija	ox-bow in Nemunas delta	peat	eutrophic – mod. rich	sedge	SM, GR	0	6
2	Rusne	island in Nemunas delta (with dikes)	peat	eutrophic – rich	sedge	SM, GR	2	6
3	Sakuciai	polder area N of Nemunas Delta (with dikes)	peat	eutrophic – mod. rich	sedge	SM, GR	0	3
4	Sausgalviai	polder area in Nemunas Delta (with dikes)	peat	eutrophic – rich	sedge	SM, GR	14	12
5	Svencele	Curonian lagoon shore (partly with dikes)	peat	eutrophic – mod. rich	sedge	no land use	6	3
6	Sysa	polder area (with dikes)	peat	eutrophic – mod. rich	sedge	SM	50–60	18

Land use types: WM, winter mowing; SM, summer mowing; GR, grazing. The number of sites refers to the total number studied in 2004–2006. Habitat data are from Tanne-berger *et al.* (in press), Aquatic Warbler data (Lithuanian sites: 2006 only) from OTOP pers. comm. and own observations.

Aquatic Warbler data

Information on the occurrence of singing males was obtained by full synchronous counts of singing males (Südbeck *et al.* 2005) in all current and recently abandoned breeding sites in 2004–2006 (unpublished data and OTOP BirdLife Poland monitoring reports). Information on Aquatic Warbler occurrence in previous years was obtained from the OTOP BirdLife Poland monitoring report 2003 and directly from the surveyors who conducted the monitoring in previous years. The sites were divided into those with records of Aquatic Warbler in the year(s) of assessment (presence sites) and those abandoned by Aquatic Warbler up to 5 years before assessment (absence sites). All records were stored in a Geographic Information System (ESRI ArcGIS 9.2), where the distance to the nearest confirmed Aquatic Warbler occurrence in respective years (DISTANCE) and the size of the site represented by the study plots and transects (AREA) were measured.

Habitat data

Habitat data were collected on one plot (25 m^2) and two transects (each 100 m) per site located where singing males had been observed in the year of sampling (current sites) or in previous years (abandoned sites). Data were collected in 2004–2006 at the time of arrival of Aquatic Warblers (late April/early May), at the peak of the first brood (late May/early June) and at the peak of the second brood (late June/early July). We focused our analysis on parameters that had earlier been identified as crucial in Aquatic Warbler habitat selection (Table 2): water level/soil moisture, soil nutrient availability, vegetation height, potential prey biomass (Leisler 1981, Schulze-Hagen 1991, Kozulin & Flade 1999) and land-use-related parameters (Tanneberger *et al.* 2008).

Water level (WATERHEIGHT) was measured with a measuring stick and soil moisture (SOILMOIS) was estimated in six classes (AG Boden 2005, Schäffer 1999) with three replicates per plot. As a proxy for nutrient availability, we determined the total carbon/total nitrogen (C/N) ratio in mixed soil samples from a depth of *c.* 5 cm using an Element vario EL C/N-analyser (C/N; Succow & Joosten 2001). Vegetation height (VEGHEIGHT) was measured with a measuring stick with 5–10 replicates per plot. To assess food resources for Aquatic Warbler (PREY), we collected samples by sweeping a net along transects of 100 sweeps (Mühlenberg 1993, Robel *et al.* 1995) under standardized wind and weather conditions (Southwood 1978). The dry weight was determined after drying in an oven at 60 °C (fresh weight < 10 mg) or at 105 °C (fresh weight > 10 mg) for 3 h.

Information on the time and technique of land use was recorded from 2003 onwards and completed by information provided by farmers and surveyors who conducted Aquatic Warbler monitoring. We distinguished between early summer mowing or grazing (until 31 July, LANDUSEEARLY), late summer mowing or grazing (after 31 July), winter mowing (i.e. reed cutting) and no mowing or grazing in the preceding year (LANDUSE). As parameters related to land use, we analysed the total plant species number per plot (SPECIESNUMBER; Jensen & Schrautzer 1999, Pfadenhauer *et al.* 2001), the cover of the lower and upper herb layer (Hodgson *et al.* 2005), and the thickness of the litter layer (Billeter *et al.* 2003). Plant species cover was estimated on the Londo scale (Londo 1984) and transformed to percentages: 0.1 = 0.5; 0.2 = 2; 0.4 = 4; 1 = 10; 2 = 20; 3 = 30; 4 = 40; 5 = 50; 6 = 60; 7 = 70; 8 = 80; 9 = 90; 10 = 97.5 (after Dierschke 1994). The nomenclature follows Wisskirchen and Haeupler (1998) for angiosperm and Frahm and Frey (1992) for moss species. For the analysis, we combined the cover of all plant individuals lower than 30 cm to 'cover of herb layer 1 (HERBCOVER1)' and those of 30 cm or higher to 'cover of herb layer 2 (HERBCOVER2)'. The thickness of the litter layer (LITTER) was measured on three 1 × 1-m subplots per plot and expressed as the geometric mean of minimum and maximum litter height.

To describe the spatial heterogeneity of the sites (HETEROGENEITY), we assessed vegetation height, litter height, soil moisture and the dominant plant species every 10 m along two 100-m-long transects that crossed each other perpendicularly in the centre of the study plot. We calculated the coefficient of variation for the first three parameters and the frequency of occurrence of a species as dominant in the lower herb layer. A measure of heterogeneity was derived by calculating the mean of all four values.

Statistical analysis

Univariate screening and hierarchical partitioning

Differences between current and recently abandoned sites were tested using Mann–Whitney

Table 2. Overview of predictors recorded in late May/early June 2006 to explain Aquatic Warbler occurrence in recently abandoned and current breeding sites.

			All sites			Sedge sites (VEG = 1)		Reed sites (VEG = 2)	
Abbreviation	Variable	Unit/Categories	Abandoned	Current	*P*	Abandoned	Current	Abandoned	Current
n			75	23		59	6	16	17
DISTANCE	Distance to nearest other Aquatic Warbler	m	900 ± 963	300 ± 119	***	805 ± 867	275 ± 267	1500 ± 815	300 ± 104
AREA	Area of this habitat type	ha	5.0 ± 3.0	5.0 ± 3.0	n.s.	5.0 ± 3.0	4.5 ± 2.2	5.0 ± 5.9	5.0 ± 3.0
WATERHEIGHT	Water level	cm	0 ± 0	0.25 ± 0.37	n.s.	0 ± 0	0.13 ± 0.19	2.42 ± 3.59	2.33 ± 3.45
SOILMOIS	Soil moisture	3 = moist 4 = moist to wet 5 = wet 6 = open water	3 = 21 4 = 36 5 = 9 6 = 18	3 = 3 4 = 8 5 = 4 6 = 8	n.s.	3 = 15 4 = 26 5 = 7 6 = 11	4 = 4 5 = 2	3 = 6 4 = 10 5 = 2 6 = 7	3 = 3 4 = 4 5 = 2 6 = 8
C/N	Nutrient availability measured in soil samples	–	15.3 ± 3.3	19.8 ± 4.8	*	14.1 ± 3.6	15.2 ± 2.8	17 ± 0.3	22.5 ± 7.1
VEGHEIGHT	Vegetation height	cm	81.7 ± 18.5	66.3 ± 15.5	**	74.4 ± 18.3	58.4 ± 8.2	111.8 ± 30.8	69.6 ± 19.8
PREY	Potential prey biomass	mg per 100 sweeps	390 ± 167	366 ± 274	n.s.	388 ± 139	422 ± 237	403 ± 292	330 ± 309
LANDUSE	Land use in previous year	0 = no land use 1 = any land use	0 = 34 1 = 41	0 = 3 1 = 20	***	0 = 28 1 = 31	0 = 0 1 = 6	0 = 6 1 = 10	0 = 3 1 = 14
LANDUSEEARLY	Proportion of early used area in preceding year	–	0 ± 0 (quartiles: 0;0)	0 ± 0 (quartiles: 0;1)	***	0 ± 0 (quartiles 0;0.5)	1 ± 0 (quartiles: 0;1)	0 ± 0 (quartiles: 0;1)	0 ± 0 (quartiles: 0;1)
SPECIESNUMBER	Number of vascular plant species per 25 m^2	–	6 ± 3	7 ± 3	n.s.	6 ± 3	9 ± 3	6 ± 4	6 ± 3
HERBCOVER1	Cover of the lower herb layer (< 30 cm)	%	2.0 ± 3.0	18.0 ± 17.8	***	2.0 ± 3.0	19.0 ± 4.7	2.3 ± 3.5	16.7 ± 17.8
HERBCOVER2	Cover of the upper herb layer (> 30 cm)	%	71.6 ± 12.4	53.3 ± 24.7	***	71.7 ± 12.4	55.0 ± 27.2	71.7 ± 12.4	53.3 ± 24.7
LITTER	Thickness of the litter layer	cm	12.6 ± 16.0	7.5 ± 3.8	*	10.5 ± 15.5	0.6 ± 0.8	16.0 ± 13.2	8.2 ± 2.7
HETEROGENEITY	Habitat heterogeneity	0 = lowest heterogeneity; 0.81 = highest heterogeneity	0.19 ± 0.08	0.23 ± 0.09	*	0.20 ± 0.07	0.21 ± 0.05	0.17 ± 0.07	0.25 ± 0.10

Median ± MAD (median absolute deviation) are given in the case of continuous variables and counts of zeros and ones in the case of binary variables. For LANDUSEEARLY, the 25% and 75% quartiles are also given. Asterisks indicate significant univariate differences (*U*-test; $^{***}P \leq 0.001$, $^{**}P \leq 0.01$, $^{*}P \leq 0.05$).

U-tests with Holm corrections (Quinn & Keough 2002). In the case of Spearman rank correlations of or exceeding 0.7, either one predictor was excluded from further analysis or, if both predictors were used, both were treated with particular care (Green 1979, Fielding & Haworth 1995).

Boosted regression tree modelling

We analysed the relationships between the occurrence of Aquatic Warblers and the habitat parameters using boosted regression trees (BRT; Friedman 2002, Elith *et al.* 2008). As a response variable, we used the occurrence of Aquatic Warbler in at least one of the three study years 2004–2006, and for the analysis of changes during one breeding season we used the occurrence of Aquatic Warbler at the time of habitat data sampling. We chose this technique because of: (1) its outstanding predictive power in model comparison (Elith *et al.* 2006) and its robustness in variable selection, (2) the small dataset with a non-negligible proportion of missing values and the method's ability to accommodate missing values, (3) its immunity to the effects of extreme outliers and the inclusion of irrelevant predictors, and (4) its facility for fitting interactions between predictors (Friedman & Meulman 2003). BRT consist of a (usually large) set of simple classification or regression trees, i.e. rule-based classifiers that partition observations into groups having similar values for the response variable, based on a series of binary rules (splits) constructed from the predictor variables (Hastie *et al.* 2001). The boosting algorithm uses an iterative method for developing a final model in a forward stage-wise fashion; starting with a first tree, additional trees are progressively added to model the residuals of the previous trees. This intrinsically yields a 're-weighting' of the data by emphasizing cases poorly predicted by the previous trees.

We calculated BRT models using a set of predictors resulting from univariate screening. We used comparatively small learning rates of 0.005–0.0001. The learning rate determines the rate at which model complexity is increased, with smaller values resulting in the fitting of a larger number of trees, each of lower individual influence and generally giving superior predictive performance in the ensemble model (Friedman 2001). Tree complexities of 1, 2 and 5 were used, thus allowing for two-way and higher interactions (Leathwick *et al.* 2006). Other settings were left at the defaults recommended in the R package 'gbm' (see below).

We used the area under the receiver operating characteristic (ROC) curve (AUC), i.e. a threshold-independent measure, to assess discrimination (Swets 1988). AUC values above 0.7 describe an acceptable discrimination, values between 0.8 and 0.9 indicate a good discrimination and values above 0.9 an excellent discrimination (Hosmer & Lemeshow 2000). As spatial autocorrelation violates the model assumption of independency (e.g. Legendre 1993, Lichstein *et al.* 2002), model residuals were tested for spatial autocorrelation by calculating Moran's I and spline correlograms (Dormann *et al.* 2007, Schröder 2008).

To test the accuracy and transferability of the final models and to get an unbiased estimate of the models' predictive performance, we applied internal and external validation techniques (Verbyla & Litvaitis 1989, Guisan & Zimmermann 2000). During the model building, BRT are internally validated by 10-fold cross-validation. For the external validation, we used data collected in the same year (2006) in Lithuania. Following Bonn and Schröder (2001), we applied the significance test according to Beck and Shultz (1986) to verify the transferability, whereby the evaluation is deemed successful if the AUC values of the model transferred significantly exceed a critical AUC value (here: AUC_{crit} = 0.9; Hosmer & Lemeshow 2000, *cf.* Binzenhöfer *et al.* 2005, Hein *et al.* 2007).

Software

All statistical analyses were performed with R 2.7.0 (R Core Development Team, http://www.r-project.org). We used the packages 'gbm' (Ridgeway 2006) and a custom code written by Elith *et al.* (2008) for fitting BRT, 'PresenceAbsence' (Freeman & Moisen 2008) for constructing calibration plots and 'spdep' (Bivand *et al.* 2005) and 'ncf' (Bjørnstad & Falck 2001) for testing spatial autocorrelation.

RESULTS

Abundance and spatial characteristics of Aquatic Warbler occurrence

In 2004–2006, Aquatic Warblers occurred in seven breeding regions in Pomerania with between one and 37 singing males per region (Table 1).

Effect of single environmental factors

Nine parameters showed significant univariate differences between current and recently abandoned sites (Table 2): DISTANCE, C/N, VEGHEIGHT, LANDUSE, LANDUSEEARLY, HERBCOVER1, HERBCOVER2, LITTER and HETEROGENEITY. Spearman rank correlations between LANDUSE and LITTER, HERBCOVER1 and LITTER, and C/N and PREY were ≥ 0.7 (Appendix).

Table 3. Contributions to the boosted regression tree (BRT) models of selected parameters for 2006. The BRT without the predictor PREY was used for external validation.

Parameter	Contribution in BRT (%)	Contribution in BRT without PREY (%)
C/N	3.0	2.6
DISTANCE	29.2	32.2
HERBCOVER1	2.4	2.8
HERBCOVER2	3.8	3.8
HETEROGENEITY	6.7	6.3
LANDUSEEARLY	6.5	6.9
LITTER	6.4	6.1
PREY	8.5	–
VEGETATION	2.0	3.2
VEGHEIGHT	31.5	36.3

Multivariate effects of environmental factors

The BRT model obtained from 10 predictors (DISTANCE, C/N, VEGHEIGHT, LANDUSEEARLY, HERBCOVER1, HERBCOVER2, LITTER, HETEROGENEITY with univariate significance as well as PREY with high importance in other breeding areas and VEGETATION indicating the two main vegetation types) includes 700 trees at a tree complexity of 3 and a learning rate of 0.005 (Table 3). The probability of occurrence of Aquatic Warblers is high when VEGHEIGHT is small (positive effect at below 80 cm), DISTANCE is small, PREY and LANDUSEEARLY are large, HETEROGENEITY is intermediate, LITTER and HERBCOVER2 are small, C/N is high, and HERBCOVER1 is intermediate (Fig. 2). The predictive performance and accuracy of the model is outstanding (AUC = 0.98; Fig. 3). The model shows no autocorrelation in the residuals (Moran's I deviate and P value: 0.452 (0.326)).

Models for the 2004 ($n = 22$) and 2005 ($n = 63$) datasets gave similar results, with DISTANCE (50%), VEGHEIGHT (26.1%) and LITTER (11.1%) the most important predictors in 2005 (PREY and HETEROGENEITY were not sampled).

Transferability of model results

To test transferability of the BRT model to the external dataset from Lithuania, we used a BRT with the same specifications, but without the pre-

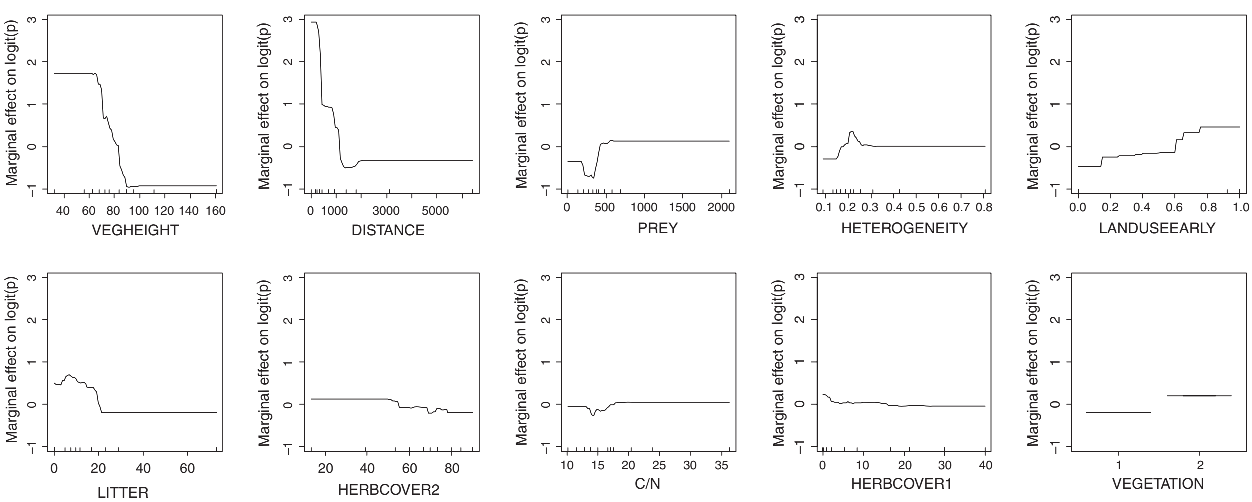

Figure 2. Partial dependence plots for the 10 most influential predictors in the boosted regression tree. Values above zero on the *y*-axis indicate a positive influence on Aquatic Warbler occurrence. For explanation of variables and their units see Table 2. *y*-axes are on the logit scale and are centred to have zero mean over the data distribution. Rug plots on the *x*-axes show distribution of sites across that variable, in deciles.

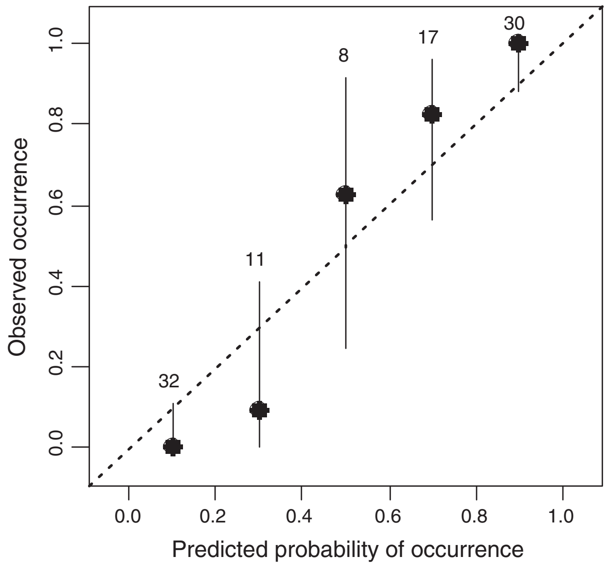

Figure 3. Calibration plot of the boosted regression tree model (Table 3). Predicted probabilities of occurrence are grouped into five bins (black dots). To be well calibrated, the dots should lie on the 1 : 1 line. The model is quite good at predicting the clear presences and absences; uncertainty is naturally highest for intermediate occurrence probabilities (0.3–0.7) with lowest predicted probabilities available (11; 8; 17).

dictor PREY, which could not be sampled in Lithuania due to strong winds (Table 3). The transfer was significant with AUC values exceeding AUC_{crit} = 0.9 with $P < 0.01$.

Changes during the breeding season

Throughout the breeding season from late April to early July, DISTANCE and C/N were of high importance for the occurrence of Aquatic Warblers (Fig. 4). At the beginning of the breeding season, LANDUSEEARLY and related vegetation features (HERBCOVER2 and LITTER) were important. With the first brood in late May/early June, VEGHEIGHT became more important. At the time of the second brood (late June/early July), HERBCOVER1 had a high contribution to the model.

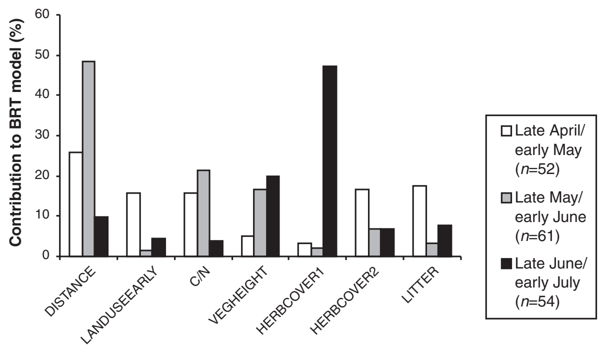

Figure 4. Contributions of selected parameters to the BRT model for three different time periods during the breeding season of 2005. PREY was sampled only in some sedge sites (sites 6 and 7, Table 1) and was therefore excluded. When included, this parameter has a high contribution of *c.* 55%. HETEROGENEITY had, when sampled and included, a high contribution (41% in late June/early July). During the last sampling period, many sedge sites without Aquatic Warblers had already been mown and were not sampled.

DISCUSSION

Habitat modelling of a specialist species

As a habitat specialist (Leisler 1981, Schulze-Hagen 1991), the Aquatic Warbler relies on a set of highly specific habitat parameters. Information about temporal changes is important, as Aquatic Warblers move breeding sites between the first and the second brood (data from colour-ringed Aquatic Warblers, G. Kiljan pers. comm.). The BRT model gives a high accuracy due to its flexibility in modelling non-linear response curves (Fig. 2) and its ability to accommodate missing values (e.g. parameters C/N, PREY and HETEROGENEITY). Logistic regression models of several predictor subsets yielded models with slightly lower accuracy, but nonetheless gave similar results and thus provide additional evidence for the importance of predictors used in the BRT model (Tanneberger 2008).

Description of optimal Aquatic Warbler habitat in Pomerania

The probability of occurrence is higher in sites with low isolation from other Aquatic Warbler sites. The tendency to form clusters is known, e.g. from telemetry studies by Schaefer *et al.* (2000), and can be explained by the mating system varying between promiscuity and polygyny (Heise 1970, Schulze-Hagen *et al.* 1999). Current sites cover a minimum of 5 ha of favourable habitat (Table 2) within a larger suitable wetland area.

Among the abiotic habitat parameters, the soil C/N ratio is of high importance. Its large independent effect (Table 3) can be explained by the higher proportion of presence among the less eutrophic reed sites than among the more eutrophic sedge sites in the dataset. As shown in Table 3 and Figure 2, this parameter contributes smaller yet important effects to the multivariate model and the probability of occurrence is higher on less eutrophic sites. This corresponds with findings from Belarus, where Aquatic Warbler density is highest on mesotrophic sites and decreases at a higher trophic level (Kozulin & Flade 1999). Neither water height nor soil moisture differed between current and recently abandoned Pomeranian sites. With minimum values in late May/early June of *c.* 0.5 cm, the water level was much lower than in the core population habitats (5–10 cm; Dyrcz & Zdunek 1993, Kozulin & Flade 1999).

Land-use-related parameters such as the proportion of early used land in the preceding year and the thickness of the litter layer are especially important in the sedge sites (Tanneberger *et al.* 2008) and during the early breeding period. For a high probability of Aquatic Warbler occurrence, at least a part of the site needs to have been mown early in the preceding year and the thickness of the litter layer should not exceed 10 cm. This is in complete contrast to the core population sites, where early land use is currently not important and the litter layer has to be thick, as it is needed for building nests above water level (Dyrcz & Zdunek 1993, Vergeichik & Kozulin 2006).

The vegetation structure parameters are closely related to land use and their importance for Aquatic Warbler occurrence in Pomerania increases during the breeding period. Optimal conditions during late May/early June include a vegetation height of < 70 cm, lower herb layer cover of *c.* 20% and upper herb layer cover of < 60% (Table 2), i.e. rather sparse vegetation. This is connected to the frequent use of the vegetation by Aquatic Warblers for climbing and foraging (Leisler 1981, Leisler *et al.* 1989). It is also related to prey supply – the biomass of potential prey is probably strongly influenced by the microclimatic conditions for larval development (which is reduced by a thick litter layer) and by the abundance of flowering plants for nectar-collecting insects (reduced by a thick litter layer and a strongly developed upper herb layer).

In contrast to the rather homogeneous core population habitats (Dyrcz & Zdunek 1993, Kozulin & Flade 1999), habitat heterogeneity plays an important role in Pomerania (Table 3). The positive effect of high habitat heterogeneity is possibly related to better foraging conditions along edges.

Implications for Aquatic Warbler conservation

Land use in the previous year has generally a strong influence on Aquatic Warbler occurrence, as already shown by Tanneberger *et al.* (2008) for the Lower Oder Valley National Park (site 7 in Table 1). Management should therefore focus on adapted land use, the timing and frequency of which depends on the nutrient conditions of the site.

Such land use systems in Pomerania are models for the land use that is needed in future in the Aquatic Warbler breeding sites in eastern Poland, Belarus and the Ukraine, being subject to increasing nutrient depositions (HELCOM 2006).

In the more productive sedge sites, the proportion of land used early in the preceding year is particularly important, especially on sites of higher elevation (Tanneberger *et al.* 2008). As early mowing is also a serious threat to broods, effective management needs to safeguard both currently occupied nesting sites by delayed mowing and the following year's habitat condition by early mowing (i.e. alternating land use).

In the less productive sites, winter mowing is currently sufficient to keep the vegetation suitable. Here, eutrophication is a serious threat (Tanneberger *et al.* 2009) and needs to be reduced to a minimum. The effects of grazing in addition to mowing are considered positive, but not yet sufficiently specified. On abandoned sites that are heavily overgrown with reed, summer mowing can improve habitat conditions.

Generally, land use should aim at creating a habitat mosaic, thus favouring habitat heterogeneity and probably the abundance of potential prey. Such land use will also benefit other threatened species (Habitats Directive Annex II species such as Large Copper *Lycaena dispar* and Birds Directive Annex I species Corncrake *Crex crex*) and it can meet the interests of local land users (e.g. reed cutters; Tanneberger *et al.* 2009). For the long-term perspective, such land use forms need to be further developed (e.g. by the energetic use of late mown biomass from sedge sites; Wichtmann & Joosten 2007) and to be supported by agri-environment schemes. These management recommendations are currently being implemented in conservation activities in Pomerania, especially in the EU Life project 'Conserving *Acrocephalus paludicola* in Poland and Germany (LIFE05NAT_PL_000101)' (2005–2011). Continued monitoring of breeding areas is therefore crucial to determine their success.

We thank all persons providing Aquatic Warbler monitoring data and the Wolin National Park, Lower Odra Valley Landscape Park, Lower Oder Valley National Park, Warta Mouth National Park, Nemunas Delta Regional Park, OTOP and the owners of Rozwarowo Marshes for sampling permission. F. Tanneberger thanks all helpers from Greifswald University, K. Mudinaite, G. Mozgeris, and Deutsche Bundesstiftung Umwelt (AZ 20004/852) as well as Landesumweltamt Brandenburg for financial support. We also thank J. Bellebaum and H. Joosten as well as three anonymous reviewers for valuable comments on the manuscript.

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Received 9 May 2009;
revision accepted 1 February 2010.

APPENDIX

Bivariate Spearman-rank correlations between predictor variables used for explaining the occurrence of Aquatic Warblers in the dataset from late May/early June 2006. Upper triangle: correlations, lower triangle: number of observations. Correlation coefficients $\rho_S \geq 0.7$ are shaded in grey.

	VEG	LAND USE	LANDUSE EARLY	DISTANCE	AREA	VEGHEIGHT	SPECIES NUMBER	C/N	WATER HEIGHT	SOIL MOIS	HERB COVER1	HERB COVER2	LITTER	PREY	HETERO GENEITY
VEGETATION		0.18	−0.27	−0.46	0.23	0.33	−0.37	0.53	0.33	0.29	0.04	−0.18	−0.12	−0.59	−0.15
LANDUSE	98		0.35	0.05	0.24	−0.29	0.01	−0.03	−0.36	−0.41	0.48	−0.04	−0.70	0.20	0.47
LANDUSEEARLY	98	98		0.02	0.00	−0.62	0.28	−0.35	−0.40	−0.41	0.54	−0.23	−0.51	0.47	0.44
DISTANCE	98	98	98		0.09	0.04	0.22	−0.40	−0.29	−0.27	−0.04	0.37	−0.11	0.49	−0.02
AREA	98	98	98	98		−0.06	0.26	0.18	0.13	0.09	0.22	0.19	−0.40	0.03	−0.10
VEGHEIGHT	98	98	98	98	98		−0.12	0.32	0.43	0.48	−0.42	0.18	0.40	−0.52	−0.33
SPECIESNUMBER	98	98	98	98	98	98		−0.06	0.10	−0.04	0.45	−0.15	−0.29	0.23	0.13
C/N	70	70	70	70	70	70	70		0.39	0.32	−0.02	−0.15	0.04	−0.79	0.02
WATERHEIGHT	98	98	98	98	98	98	98	70		0.90	−0.22	−0.18	0.39	−0.60	−0.24
SOILMOIS	98	98	98	98	98	98	98	70	98		−0.33	−0.16	0.50	−0.56	−0.29
HERBCOVER1	98	98	98	98	98	98	98	70	98	98		−0.31	−0.79	0.18	0.34
HERBCOVER2	98	98	98	98	98	98	98	70	98	98	98		0.08	0.19	−0.26
LITTER	98	98	98	98	98	98	98	70	98	98	98	98		−0.28	−0.42
PREY	88	88	88	88	88	88	88	66	88	88	88	88	88		0.09
HETEROGENEITY	72	72	72	72	72	72	72	62	72	72	72	72	72	66	