Habitat selection of Aquatic Warbler *Acrocephalus paludicola* in Poland: consequences for conservation of the breeding areas

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In parallel to the countrywide census of Aquatic Warblers *Acrocephalus paludicola* in Poland in 1997, data on breeding habitat characteristics were collected. Using multivariate statistics, the habitat features could be ordered along two gradients: from open areas with rare, coarse-grained patches of shrubs to those dominated by scattered shrubs, and from flat grass fen with shallow water to distinctly tufty, deeper flooded, and reed-dominated areas. These two gradients generally correspond to two successional processes in wetlands occupied by Aquatic Warblers: (a) colonisation by shrubs due to lowering of the water table and abandonment of agricultural use, and (b) invasion of reed associations in the vicinity of drainage channels. Densities of singing Aquatic Warbler ♂ were negatively correlated with the first gradient, but there was no significant relationship with the second. Reed associations are inhabited by Aquatic Warblers in Western Pommerania, where reeds are harvested every year, whereas singing ♂ were only occasionally recorded in this habitat in other parts of Poland, where no industrial reed exploitation occurs. Areas occupied by Aquatic Warbler and unoccupied, closely associated habitats differed with regard to both gradients. This indicates that breeding habitat suitability may be the most important factor limiting Aquatic Warbler populations. We conclude that overgrowing of open wetlands by shrub and reed vegetation is the principal reason for breeding habitat loss in Poland. Conservation measures are discussed, including those associated with low-intensity agricultural use of the wetlands comprising Aquatic Warbler breeding grounds.

Key words: *Acrocephalus paludicola*, habitat selection, vegetation structure, successional changes, conservation measures.

1. Introduction

Human-induced habitat alterations, mainly those associated with reclamation of wetlands and transformation of agricultural practices are among the major factors responsible for the dramatic decline of the Aquatic Warbler in most of its breeding range (BAUER & BERTHOLD 1997). There is an urgent need to describe the parameters of the species' preferred habitat, as these data constitute the basis for conservation programmes and models predicting future population trends on the basis of predicted habitat changes. While it is generally acknowledged that habitat destruction may be a limiting factor to Aquatic Warbler populations, little quantitative data characterising breeding habitats are available. LEISLER (1981) focused on habitat segregation between sympatric *Acrocephalus* species while the study of SELLIN (1989a, b) refers mainly to the Greifswald (NE Germany) population breeding in reed associations of brackish water, a rather marginal habitat of the Aquatic Warbler in Poland (KROGULEC 1995; this study). However, SELLIN's comparisons of breeding habitats in Greifswald and in Biebrza Marshes (NE Poland) demonstrated that structural vegetation aspects are presumably more important than the species composition of the local vegetation cover. Consequently, in this study, which aims at the description of habitats occupied by Aquatic Warbler in Poland, we concentrated on structural characteristics, although data on plant communities were collected as well.

To assess the role of habitat availability in the breeding areas, most studies compare patches occupied by the species of interest versus randomly chosen (usually adjacent) habitat patches (PRESCOTT & COLLISTER 1993; SEAMANS & GUTIERREZ 1995). Similarly, we predicted that if lack of breeding habitat is a factor limiting Aquatic Warbler populations, there should be differences in habitat features of occupied versus unoccupied areas. The research was conducted during the most recent 1997 census of the entire known population of the species throughout Poland (KROGULEC & KLOSKOWSKI 1997).

2. Study area and methods

Habitat measurements were carried out as a part of the census of singing ♂. All important breeding sites were surveyed from 19 May to 2 June 1997 with the exception of the upper course of Narew River valley, where a population of ca. 60 singing ♂ was recorded previously (KROGULEC & KLOSKOWSKI 1997). In most breeding areas a second survey followed between 3 and 18 June 1997. The sites were visited at intervals of at least two weeks. Trained surveyors searched all potentially suitable habitat patches working in groups of usually 4-5 individuals walking ca. 50 m apart from each other. These patches of 60-300 ha within natural boundaries were censused between 19:00 and 21:00 h, when the ♂ sing most persistently (DYRCZ & ZDUNEK 1993). The locations of ♂ were mapped at a scale of 1:25,000, and their density per km^2 of the National Grid squares was calculated. When any inaccuracies in assigning the recorded ♂ to squares were suspected or when the measurements might not have been representative because of pronounced heterogeneity of the habitat within a square, the squares were excluded from the statistical analysis.

Measurements and surveys of singing ♂ were performed on the same days. Five habitat variables were measured for each 1 km^2 square:

1. Water level (the depth of water level above the soil surface) was obtained as the mean of five measurements at random points by leaning a measure stick on the ground, not piercing the layer of vegetation.
2. Numbers of reed stalks counted on two randomly chosen 0.5 m^2 areas were summed to give the "reed density" per 1 m^2.
3. Four degrees of complexity of "ground profile" with regard to herbaceous vegetation were chosen visually, using a qualitative scale: 1 - flat, grass dominated fen; 2 - flat areas, vegetation with no grass; 3 - mosaic of flat and tufty patches; 4 - tufty.
4. Shrub number was estimated by counting all shrubs on four 100 x 0.5 m transects radiating in compass directions from a point constituting an approximated centre of the habitat patch occupied by singing ♂ in the given square. The four counts were averaged to give the mean number per 100 m. Shrubs were defined as such when exceeding 0.5 m in height. Total length of stretches covered by shrubs along four 100 m transects was measured for the approximated area of greatest singing activity inside the square.
5. A shrub cover index was calculated by multiplying the proportion of shrub layer per unit distance by the modal height of shrubs estimated by eye in four 100 m x 0.5 m transects. The ‘patchiness’ of the shrub layer was assessed summing up the number of shrub ‘patches’ (including trees) in the four transects and dividing it by their total length. A ‘patch’ was defined as at least one shrub/tree of height > 0.5 m at a distance of >1 m from another.

Records of dominating plant species were made and later compared with phyto-sociological cards (where available) of the surveyed areas. Subsequently, the data on plant associations was categorised into four habitats: *Carex* marshes (including both pure sedge mires and moss mires); wet meadows; reedbeds; calcareous *Cladium* marshes. However, as no quantitative estimate was made of

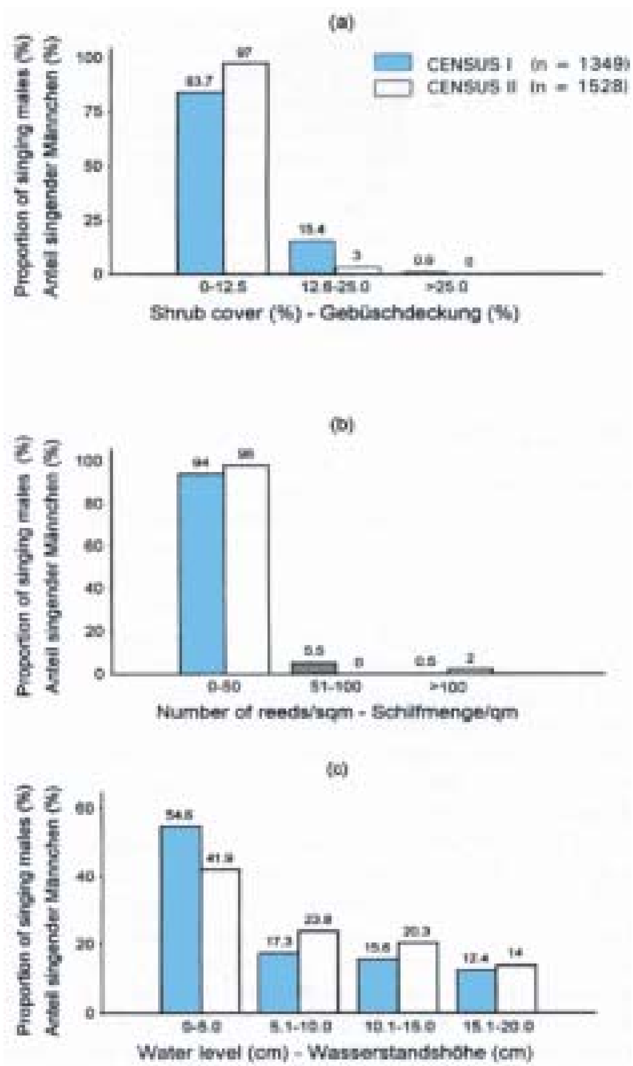

Fig. 1: (a) Occurrence of singing ♂ of Aquatic Warbler in areas of different shrub cover index. – *Vorkommen singender Seggenrohrsänger-♂ in Flächen mit unterschiedlichem Gebüschdeckungsindex.*
(b) Occurrence of singing ♂ of Aquatic Warbler in areas of different reed density. – *Vorkommen singender Seggenrohrsänger-♂ in Flächen mit unterschiedlicher Schilfdichte.*
(c) Water depth and occurrence of singing ♂ of Aquatic Warbler. – *Wasserstands-*

Table 1: Correlations of Aquatic Warbler breeding habitat features with the first two principal components of the PCA. – *Korrelationen der Strukturmerkmale des Bruthabitates des Seggenrohrsängers mit den ersten beiden Hauptkomponenten der Hauptkomponenten-Analyse.*

habitat variables	PC1	PC2
shrub cover	0.95	0.10
shrub 'grainnes'	0.91	0.04
water level	0.33	0.67
reed density	0.06	0.70
ground profile	-0.38	0.62

Table 2: Correlations of habitat features of occupied and unoccupied 1 km² squares with the first two principal components. – *Korrelationen der Strukturmerkmale der besetzten und unbesetzten Quadratkilometer-Gitterfelder mit den ersten beiden Hauptkomponenten.*

habitat variables	PC1	PC2
shrub cover	0.69	0.23
shrub 'grainnes'	0.81	-0.16
water depth	0.58	0.32
reed density	-0.10	0.80
herbaceous layer structure	0.15	0.81

the ground cover of plant associations belonging to these habitat, the integration of vegetation data into the statistical analysis was not attempted. In addition, data on the current conservation status and agricultural land-use like mowing, cattle grazing etc. were collected, although no quantitative estimates were attempted.

3. Statistical analysis

Principal component analysis (PCA) was performed on the correlation matrices of the habitat variables to transform the original sets of habitat variables into uncorrelated sets of factors comprising the interrelated variables. For this multivariate statistical analysis we used only squares where at least one singing ♂ was recorded during the first census. VARIMAX rotation was used in order to obtain a clear-cut interpretation of the factors. To determine the associations between the habitat features and Aquatic Warbler densities, the principal components were related to the estimated numbers of ♂ singing per 1 km² square.

To compare characteristics of occupied versus unoccupied areas, squares where at least one singing ♂ was recorded, were classified as 'positive', those without Aquatic Warblers as 'negative'. To describe the common gradient of habitat characteristics PCA was conducted on both 'positive' and 'negative' squares. Data from the maritime region, where Aquatic Warblers breed in a very specific habitat of harvested reed, were excluded. The principal components were derived from a correlation matrix of the transformed original variables. The axes were VARIMAX rotated. Subsequently, the principal component scores referring to the occupied and unoccupied habitats were compared using an analysis of variance (ANOVA). Additionally, untransformed original variables describing the occupied and unoccupied habitats were compared using the MANN-WHITNEY-U test.

It must be noted that the unoccupied squares used in our study were not taken at random, but were surveyed as apparently suitable breeding habitats. These areas were closely associated and visually similar to occupied habitats or/and breeding of Aquatic Warbler was previously documented there. However, these squares were distributed within all the most important Aquatic Warbler breeding areas in Poland. Furthermore, as the species appears to be a habitat specialist, it would have been difficult to obtain a representative sample by selecting random plots in the vicinity of the occupied sites.

4. Results

4.1. Breeding habitat description

Two independent habitat gradients were determined by PCA performed on the data from 83 squares. The first PCA component ordered the Aquatic Warbler breeding areas along a gradient from open, shrubless places, to areas dominated by high and abundantly scattered shrub patches. It accounted for 40.2% of total variance; the second, independent component ordered the counted squares from flat, reedless areas with shallow surface water to more deeply flooded and tufty areas with high reed density. It explained 25.6 % of the total variation in habitat complexity (table 1). Singing ♂ density was inversely related to the first principal component (PC 1: $F = 4.0$, $p < 0.05$), but no significant relationship was found with the second (PC 2: $F = 1.34$, ns). Frequencies of occurrence of singing ♂ in relation to shrub cover, reed density and water depth in the squares are presented in the Fig. 1a-c.

From 1,251 singing ♂ for which data on plant associations in the breeding habitat were available, 658 (52.6 %) were recorded in *Carex* marshes, 255 (20.4 %) in carbon marshes (exclusively in the breeding grounds near Chelm), 135 (10.8 %) in wet meadows and 203 (16.2 %) in reedbeds. However, 176 singing ♂ from the latter total were recorded in one breeding area in the maritime region whereas in all other parts of the country only 55 ♂ (4.4 %) were observed in reeds (mainly small patches inside of other vegetation types).

4.2. Occupied versus unoccupied habitats

A total of 65 'positive' and 27 'negative' squares was used for this analysis. The first component of PCA axis ordered the habitat features along a gradient from open fens without any shrubs to areas dominated by densely scattered shrub patches. It accounted for 35.1 % of total variance. The second component ordered the investigated squares from flat turf of grass to markedly tufty reedbeds and explained 24.5 % of the total variation in habitat complexity (Tab. 2). The PCA scores for the 'positive' and 'negative' squares differed; Aquatic Warbler apparently avoids areas overgrowing with shrubs and reeds and distinctively avoids areas with a tufty ground profile (Fig. 2; the first principal axis of ANOVA: $F = 3.92$, $p < 0.05$; the second axis: $F = 10.44$, $p = 0.002$). From the original habitat variables only "ground profile" ($U = 499.0$, $p = 0.001$) and "shrub cover" index ($U = 390.5$, $p < 0.001$) differed significantly between the occupied and unoccupied squares.

5. Discussion

5.1. Breeding habitat selection of Aquatic Warbler

Our results show that the species occurs in areas limited by succession of shrubs and reeds. Wetlands subjected to water extraction and drainage are influenced by two successional processes, generally represented by the two PCA factors in our analysis: (1) overgrowing of the open fen by bushes (mainly *Salix* spp.) due to water table depression brought about by drainage systems (PALCZYÑSKI 1985) and (2) local encroachment of reed communities associated outside the flooded zones of rivers with drainage ditches. These two processes seem to pose the major threats to habitat suitability for Aquatic Warbler in Polish wetlands. Although no negative association was found between the second habitat gradient of the increasing reed density and numbers of singing ♂, Aquatic Warblers were only exceptionally recorded in squares with reed density exceeding 100 stalks/m². Apparently, breeding of Aquatic Warblers in reedbeds in Western Pommerania contrasts with the rare occurrence of singing ♂ in reed associations in other parts of the country. However, this may be attributable to the fact that our records did not discriminate between high previous-year dead stems and low, newly grown green shoots. In fact only in Western Pommerania regular reed exploitation took place, thus ensuring predominance of young stalks. In the Narew valley small numbers of Aquatic Warblers were recorded after burning the reedbeds (KROGULEC & KLOSKOWSKI 1997). Apparently Aquatic Warblers occupy reed associations only in their earliest successional phases. This suggestion is confirmed by the colonisation of brackish water grasslands near Greifswald by Aquatic Warblers after invasion of weak and low reed vegetation due to reduction of the grazing intensity in the 1970s (SELLIN 1989). Remarkably, in our research no singing ♂ were recorded at reed densities of 200-300 stems/m², regarded by SELLIN (1989) as optimal conditions for breeding Aquatic Warbler.

Although Aquatic Warblers inhabit various plant associations, the range of structural characteristics of the habitat is relatively narrow. The fact that no areas were occupied when the average depth of water above the soil surface exceeded 20 cm may be explained by the female's way of foraging by collecting large arthropods from the ground (SCHULZE-HAGEN 1991) and the danger of flooding of the nests, as has been recorded in the Chelm *Cladium* marshes (pers. obs.).

5.2. Does breeding habitat availability limit Aquatic Warbler populations?

Although the differences in structural features of occupied and unoccupied habitat patches were significant for only two univariate habitat variables, they were clear in terms of multivariate combinations of the original variables. Bearing in mind the fact that most of the unoccupied squares had earlier been inhabited by the species, the character of the differences indicates that the main reason for the short supply of suitable breeding habitats in Poland are successional changes toward formations dominated by shrubs and locally by reeds. The Aquatic Warbler is presumably unable to colonise the areas due to a lack of relevant morphological adaptations relative to other *Acrocephalus* species

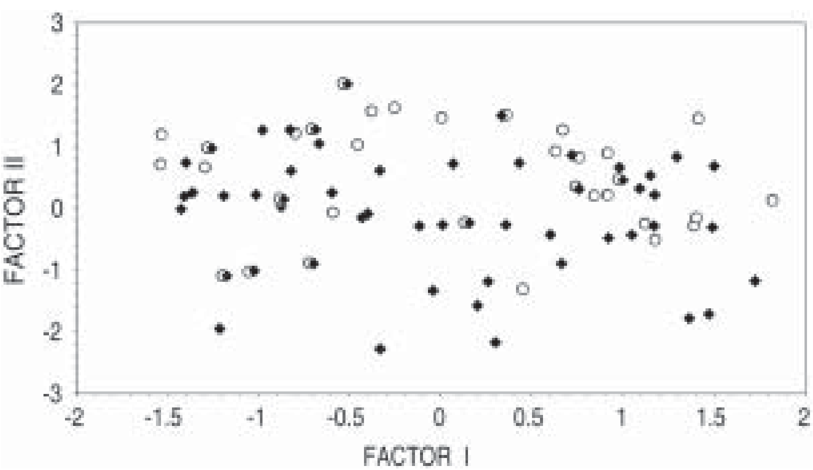

Fig. 2: Scores for 1 km² squares occupied (◆) and unoccupied (○) by Aquatic Warbler on the first two principal-component axes. – *Einordnung der vom Seggenrohrsänger besiedelten (◆) und unbesiedelten (○) Flächen nach den zwei Hauptachsen der Hauptkomponenten-Analyse.*

Fig. 3: Aquatic Warbler habitat in the calcarious Chelm marshes (E-Poland) with dominating *Cladium mariscus*. – *Seggenrohrsänger-Habitat in den Kalksümpfen von Chelm (Ost-Polen), mit dominierender Binsenschneide* Cladium mariscus. Photo: Authors.

Fig. 4: Open sedge fen with Cotton grass *Eriophorum angustifolium* in the southern basin of Biebrza marshes, where breeding density of Aquatic Warbler is high. – *Offenes Seggenmoor mit Schmalblättrigem Wollgras* Eriophorum angustifolium *im Süd-Becken des Biebrzatales; hohe Brutdichte des Seggenrohrsängers.* Photo: Authors.

Fig. 6: Sedge fen with high tussocks of *Carex appropinquata* are only a suboptimal habitat for Aquatic Warbler; southern basin of Biebrza marshes, June 1992. – *Seggenriede mit hohen Bulten der Schwarzschopfsegge* Carex appropinquata *sind nur ein suboptimaler Seggenrohrsänger-Lebensraum; südliches Biebrza-Becken, Juni 1992.* Photo: M. FLADE.

Fig. 7: Male Aquatic Warbler at his singing post. – *Seggenrohrsänger-♂ auf der Singwarte.* Photo: A. BALINSKI.

Fig. 5: Habitat loss caused by vegetation succession due to abandonment and (probably) changes in water regime: shrubs and reed are overgrowing open sedge fens in the southern basin of Biebrza marshes. – *Habitatverlust durch Sukzession als Folge von Nutzungsauflassung und (wahrscheinlich) Veränderungen des Wasserhaushaltes: Gehölze und Schilf überwachsen ein offenes Seggenmoor im südlichen Biebrza-Becken.* Photo: Authors.

which are competitively superior in such habitats (LEISLER *et al.* 1989).

Another argument for the importance of suitable habitat is the rapid increase of the relatively isolated Aquatic Warbler population in the Hortobágy Puszta (Hungary) after an accidental improvement of habitat quality (KOVÁCS & VÉGVÁRI 1999). Establishment of smaller populations clearly associated with changes in habitat characteristics were observed in other breeding sites, e.g. Greifswald (D. SELLIN), Sloñsk (JERMACZEK). In fact, all breeding grounds in Europe from which Aquatic Warbler disappeared, suffered pronounced habitat alterations (BAUER & BERTHOLD 1997).

Our findings do not diminish the possible importance of other causes for the species decline, especially those acting away from the breeding grounds. Accelerated habitat alterations in the wintering quarters, even if not decisive now, may become decisive soon. However, at the present stage of knowledge, breeding habitat destruction appears to be the crucial factor responsible for the Aquatic Warbler global population decline.

While under negative anthropogenic impacts for decades, Aquatic Warbler habitat availability also seems to be regulated by human-independent stochastic environmental factors like floods and droughts. Short-term seasonal changes in breeding habitat availability may be important with regard to the second broods. In most Aquatic Warbler breeding areas in Poland surveyed twice at intervals of >2 weeks, densities of singing ♂ increased after 3rd June (the assumed second brood period) relative to densities during the first census, indicating that density of late (often second) broods may even exceed that of early (first) broods. These differences are apparently not attributable to inaccuracies in the counts, as they were clear in all major breeding areas of the country. We have not tried to quantify the differences, but they seem to be linked to changes in habitat characteristics like depression of water table in the flooded zone of the Biebrza river (pers. observ.). Observations of DYRCZ & ZDUNEK (1993) on the Biebrza fen mires indicate that most ♀ Aquatic Warblers change the place for laying the second clutch. Distribution of ♀ is presumably determined by seasonal changes in food abundance (DYRCZ & ZDUNEK 1993). Considering the high proportion of second broods (WAWRZYNIAK & SOHNS 1977), sometimes (presumably subtle) changes in habitat structure and composition during the interval between first and second brood may be crucial for the population recruitment and deserve further work, using a larger set of variables and smaller-scale habitat units.

Theoretically, any species constrained by rapidly changing landscape dynamics should have extensive dispersal tendencies (PROBST 1986), as selection pressures favour flexible exploratory behaviour (FAHRIG & MERRIAM 1994). This seems to be confirmed by the extremely low return rate of Aquatic Warblers ringed as nestlings (DYRCZ & ZDUNEK 1993). As the interplay between the rate of landscape alterations and rate of change in dispersal behaviour is crucial for the species survival (FAHRIG & MERRIAM 1994), further research is urgently needed on dispersal characteristics of the species.

5.3. Recommendations for management of breeding areas

The stenotopic character of the Aquatic Warbler in regard to rapid successional changes of some of the breeding areas in Poland implicates the need of flexible ways of habitat conservation, based on monitoring of year-to-year habitat changes and suited to the local hydrological, successional and socio-economical regimes. Considering the factors mentioned above, some disturbance like mowing, controlled burning or cattle grazing, when not taking place during the nesting period, may be beneficial for the species, impeding the succession of shrubs and contributing to removal of dead top-growth of reeds. In fact, abandonment of mowing in the Biebrza valley is probably responsible for the expansion of bushes (PALCZYÑSKI 1985). In the southern Biebrza basin, at a few sites which were burnt down at least one year before the 1997 census, an increase in numbers of Aquatic Warbler was observed compared to the 1995 survey (KROGULEC 1995). However, an experimental approach at a scale large enough to affect birds within a whole local population (GREEN 1994) is needed to verify and specify this relationship. Such manipulative experiments are possible in Poland, where outside Biebrza marshes Aquatic Warblers breed in relatively small, discrete populations.

The traditional forms of agricultural land-use of the Aquatic Warbler breeding sites should be promoted and as most of them have been abandoned due to economical reasons, schemes of financial support for the agriculture practices, which may increase the habitat suitability for the species, should be worked out. Still these activities, although recommended for areas under low-intensity human use where Aquatic Warbler occur, cannot replace long-term hydro-technical programmes of improving water management of large wetland areas affected by prior drainage. Only in this way will it be possible to maintain such wetlands at the optimal stage of succession for the warbler. Locally such projects already exist. These works should aim both at the increase in water retention abilities in breeding areas independent of rivers and widening the range of floods in river valleys occupied by Aquatic Warblers.

As Aquatic Warblers inhabit various plant communities, an understanding of the various successional processes is urgently needed for reliable simulations of future population trends. In addition, population trends within discrete breeding areas should be described in relation to local habitat changes. Further research is also needed regarding the relations between habitat characteristics and warbler breeding productivity on different breeding grounds, because the complex social organisation of the species (DYRCZ 1989) may constitute a factor limiting its distribution to high productivity marshland ecotones (LEISLER & CATCHPOLE 1992).

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6. Zusammenfassung

Kloskowski, J. & J. Krogulec 1999: Habitatwahl des Seggenrohrsängers *Acrocephalus paludicola* in Polen: Folgerungen für Schutzmaßnahmen in den Brutgebieten. Vogelwelt 120: 113 – 120.

Vom 19. Mai bis 2. Juni 1997 wurden parallel zur Bestandsaufnahme des Seggenrohrsängers in Polen Daten zur Struktur der Bruthabitate gesammelt. Aufgrund der Messungen wurden fünf Habitatvariable definiert: Gebüschverteilung („patchiness“), Gebüsch-Bedeckungsgrad, Wasserstand, Schilfhalmdichte und Bodenrelief (Bultigkeit). Als Grundeinheit wurde für diese Untersuchungen ein Quadrat (Gitterfeld) von 1 km^2 mit mindestens einem singenden ♂ definiert. Eine Hauptkomponentenanalyse (PCA) wurde angewendet, um mehrere korrelierte Variablen zu wenigen voneinander unabhängigen Faktoren zu transformieren. Die untersuchten Bruthabitate wurden mit Hilfe der folgenden zwei Gradienten geordnet: Von offenen, gebüschfreien Arealen zu Flächen, die durch hohe, zerstreut stehende Büsche dominiert sind, sowie von homogen flach strukturierten, schilffreien Gebieten mit seichtem Wasserstand zu höher überfluteten, dichten Röhrichten mit stark bultigem Bodenrelief. Die beiden Gradienten entsprechen in etwa den zwei Sukzessionsrichtungen in den Brutgebieten des Seggenrohrsängers: Fortschreitende Verbuschung infolge von Wasserentzug sowie Schilfsukzession in der Nähe von Meliorationsgräben. Die Anzahl der singenden ♂ pro 1 km^2 war signifikant negativ korreliert mit der ersten PCA-Hauptkomponente, keine signifikante Korrelation bestand mit der zweiten. In Polen wurde der Seggenrohrsänger nur sehr selten in verschilften Teilen der untersuchten Gebiete registriert, mit Ausnahme von Westpommern, wo in den entsprechenden Gebieten jedes Jahr das Schilf für industrielle Zwecke gemäht wurde und die Vögel die niedrigen und schmächtigen diesjährigen Schilfbestände besiedelten.

Die von Seggenrohrsängern besiedelten (65 Quadrate) und unbesiedelten Gebiete (Auswahl von 27 optisch geeigneten und/oder früher besiedelten, jedoch aktuell nicht besetzten Quadraten in Nachbarschaft zu besiedelten Brutgebieten) unterschieden sich in den strukturellen Komplexmerkmalen der PCA. In den unbesiedelten Flächen war die Sukzession weiter fortgeschritten. Da alle entsprechende Habitate besiedelt waren, scheint die Qualität des Bruthabitats ein Hauptfaktor der Begrenzung der Populationsgröße zu sein. Die Ergebnisse zeigen, daß der Seggenrohrsänger ein schmales Habitatspektrum beansprucht und daß die größte Bedrohung für seine Bruthabitate in Polen von der sukzessiven Verbuschung ausgeht. Im Kontext der Ergebnisse werden Managementmaßnahmen zum Schutz der Bruthabitate diskutiert, insbesondere hinsichtlich extensiver Pflege- und Bewirtschaftungsmaßnahmen wie Beweidung, Mahd oder kontrolliertem Abbrennen.

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