REED DIE-BACK, WATER LEVEL MANAGEMENT AND THE DECLINE OF THE GREAT REED WARBLER *ACROCEPHALUS ARUNDINACEUS* IN THE NETHERLANDS

JAAP GRAVELAND

Graveland J. 1998. Reed die-back, water level management and the decline of the Great Reed Warbler *Acrocephalus arundinaceus* in The Netherlands. Ardea 86: 187-201.

Several species of migratory marsh birds have declined in Central and Western Europe. An important question is whether this decline is primarily caused by loss of wetlands on the wintering grounds in Africa or by a decline in habitat quality in the breeding areas. Significant losses of Reed *Phragmites australis* beds have been reported in many European countries, presumably as a result of unnatural water level regimes and eutrophication. We studied the reed requirements of nesting Great Reed Warblers *Acrocephalus arundinaceus* in relation to reed availability in The Netherlands. Numbers of Great Reed Warblers have declined dramatically but the species is less dependent on marshland in its winter quarters than most other migratory marsh birds. Great Reed Warblers nested almost exclusively in reed standing in water and this type of reed has become scarce in The Netherlands. The present distribution of water reed indicates that the man-induced reduction in natural fluctuations of the water level has been an important factor in its decline. Water reed represents the first stage of the succession in a reed marsh. Eventually, loss of water reed will therefore affect the entire marsh bird community. Restoration of natural water level fluctuations seems the most effective course for remedial action, but will be difficult to accomplish because of the conflicting interests of nature and agriculture.

Keywords: *Phragmites australis* - *Acrocephalus arundinaceus* - eutrophication - water management - hydrodynamics - succession

Institute for Forestry and Nature Management (IBN-DLO), P.O. Box 23, 6700 AA Wageningen, The Netherlands; Present address: National Institute for Coastal and Marine Management (RIKZ), P.O. Box 8039, 4330 EA Middelburg, The Netherlands, e-mail: j.graveland@rikz.rws.minvenw.nl

INTRODUCTION

Populations of several species of migratory marsh birds have been declining in Central and Western Europe over the last decades (Baillie & Peach 1992; Cramp 1992; Marchant 1992). Many of the species concerned winter in Africa. Large parts of Western Africa, particularly the Sahel region, suffered from severe periods of drought in the early 1970s and early 1980s. Analyses of survival and rainfall data have shown that drought in the wintering areas has been a major cause in the decline of the Purple Heron *Ardea purpurea* and the Sedge Warbler *Acrocephalus schoenobaenus* (Cavé 1983; Peach *et al.* 1991).

For other migratory marsh birds a relationship with rainfall in Africa is less evident. Populations of Great Reed Warblers *Acrocephalus arundinaceus* have declined more than 50% (e.g. France, Germany, Denmark, Czech Republic) and 20-50% (e.g. Greece, Italy, Switzerland) from 1970 to 1990 (Cramp 1992; Hagemeijer & Blair 1997). However, numbers in eastern Europe and Russia appear to be stable (Tucker & Heath 1994). The

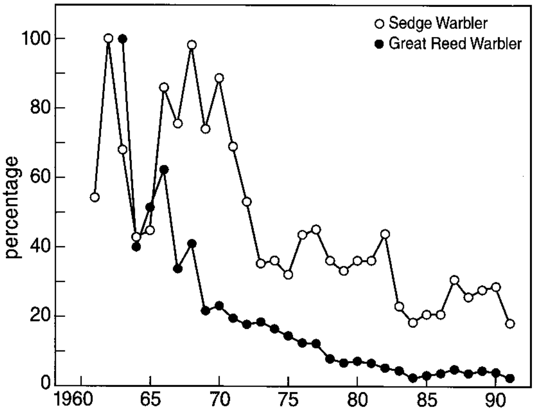

Fig. 1. Population trends of Great Reed Warbler and Sedge Warbler in The Netherlands (% of numbers present in 1962 and 1963). Trends were calculated from counts in 30 former and current breeding areas (R. Foppen and SOVON, unpublished results), using loglinear Poisson regression, adapted to deal with incomplete time series for areas (Ter Braak *et al.* 1994).

Dutch population has declined from more than 10 000 territorial males in the 1950s to approximately 350 males at present (Fig. 1; SOVON 1988). Great Reed Warblers utilise marshy areas in Africa to a lesser extent than the Sedge Warbler, and winter outside the Sahel zone (Cramp 1992). However, the Great Reed Warbler population in The Netherlands has declined even more than that of the Sedge Warbler, and it has not shown periods of population recovery, coincident with years of heavy rainfall in the Sahel, as is the case of the Sedge Warbler (Peach *et al.* 1991; R. Foppen, unpublished data; Fig. 1). These findings imply that the decline of the Great Reed Warbler is not primarily caused by low rainfall in Africa, but rather by changes in the breeding area.

Great Reed Warblers breed in stands of pure Reed *Phragmites australis* close to the water (Leisler 1981; Cramp 1992). Such reed stands have declined in most Western and Central European countries (Ostendorp 1989). Habitat destruction and drainage, for industrial and housing developments or for agricultural purposes, are important causes of the decline. However, the quality of reed stands is also declining ('reed die-back' or 'Schilff-Sterben') at protected sites without any apparent direct human influence. This die-back has been the subject of numerous studies in recent years and is primarily attributed to a combination of unnatural, stable water tables and eutrophication: the nutrient enrichment of water bodies by agricultural run-off and municipal waste (reviewed in Van der Putten 1997; see also Den Hartog *et al.* 1989; Ostendorp 1989).

Unnatural water level regimes and eutrophication are characteristic of most Dutch waters. The aim of this study was to determine whether a possible decline in the availability of reed suitable for nesting has been an important factor in the decline of the Great Reed Warbler in The Netherlands and to find possible evidence for a causal role of unnatural water level regimes and eutrophication in the decline of reed beds. I investigated which type of reed Great Reed Warblers preferred, the availability of this reed at present and in the past, and the spatial distribution of this reed. Nutrient availability, organic matter accumulation and the degree of exposure to wind and waves are important environmental variables affecting reed growth (Weisner 1987). In eutrophic lakes, the vigour of the reed stand and the ability to expand into deeper water are greater at exposed than at sheltered sites, where organic matter accumulates, and results in anaerobic conditions in the substrate that impede reed growth (Weisner 1991). The spatial distribution of reed beds along the shore might therefore provide information about the role of unnatural water level regimes and eutrophication in the decline of reed beds.

The reed requirements of nesting Great Reed Warblers were also compared with those of the Reed Warbler *A. scirpaceus*. Since the habitat requirements of Reed Warblers overlap considerably with those of Great Reed Warbler (Leisler 1981), this species is more suitable for comparisons than the Sedge Warbler. The Dutch population of the Reed Warbler has increased considerably during the last three decades and is at present estimated at 120 000-150 000 territorial males (SOVON 1988).

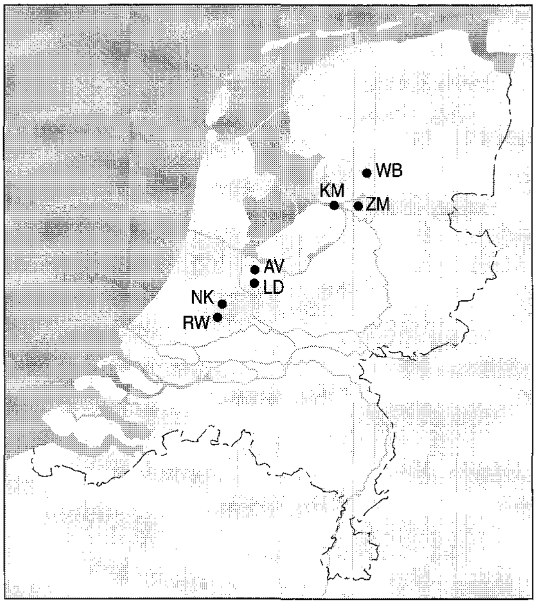

Fig. 2. Map of The Netherlands with study areas: De Weerribben (WB), Zwarte Meer (ZM), Ketelmeer (KM), Ankeveen (AV), Loosdrecht (LD), Nieuwkoop (NK) and Reeuwijk (RW).

METHODS

Study areas

The main study areas were De Weerribben (52°57'N, 5°57'E) and Zwarte Meer (52°38'N, 5° 55'E; Fig. 2). These two areas differ in substrate, extent of eutrophication, size of water bodies, degree of exposure to the wind, and type of reed. They represent two types of wetlands still common in The Netherlands that serve as the main breeding habitat of the Great Reed Warbler: excavated peat bogs (Weerribben) and large shallow lakes with a mineral substrate (Zwarte Meer). Reed harvesting is a common practice in both areas and almost all reed is cut each year, except in parts that are managed for wildlife only.

De Weerribben (3500 ha) was created by the excavation of peat in the 19th century. It consists of narrow, 30 m wide lakes ('broads') and narrow strips of land where the peat was dried. The water is mesotrophic (Van Wirdum 1991). The water level may fluctuate with an amplitude of 5 cm per week. Reed-dominated vegetation consist of two types: almost pure stands of reed in water or along edges of lakes and canals, and reed interspersed with herbs further inland. The reed in De Weerribben has thin stems and a high stem density (> 300 stems m^{-2}, 'peat type'; Van der Toorn 1972). About 20 territories of Great Reed Warbler and 500 territories of Reed Warbler were present in this study area.

Zwarte Meer is a large, shallow lake of 2700 ha, which was formed when the Noordoostpolder was reclaimed (Fig. 3). The substrate mainly consists of sand, with some clay in the sheltered parts; the water is eutrophic (Van Wirdum 1991). Due to the size of the lake and the open nature of the surrounding land, variation in wind speed and

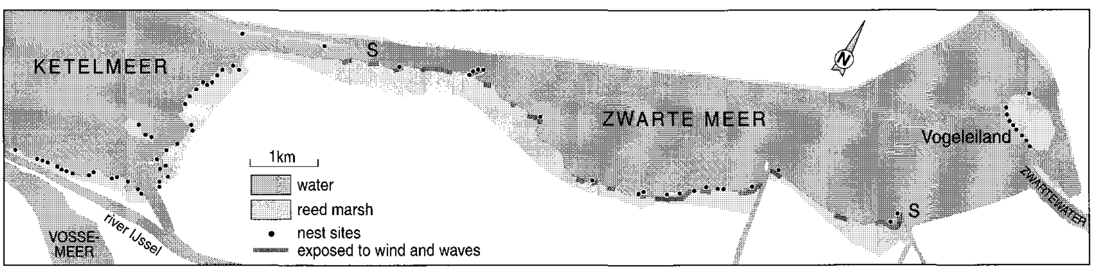

Fig. 3. The study areas Zwarte Meer and Ketelmeer. Dots indicate Great Reed Warbler nest sites in 1996. Relatively exposed (to wind and waves) parts of the shoreline along the southern shore of Zwarte Meer are indicated. 'Exposed' is defined here as facing to the west (compass angle 180-360°). The reed measurements in Zwarte Meer were conducted in the area between the two 'S'.

wind direction may cause changes in the water level of up to half a meter during the day. The south shore is fringed by a 50-300 m wide reed bed over a length of twelve kilometres. The reed has tall and thick stems and a low stem density (< 300 stems m^{-2}, 'river reed'; Van der Toorn 1972). The study area was located along the southern shore over a length of ca. eight km and had about 20 territories of Great Reed Warblers and 400 territories of Reed Warblers.

A preliminary analysis of the data from De Weerribben in 1994 indicated that the presence of water reed (reed standing in water) was an important determinant for the choice of nest sites. To examine whether that finding also applied to other marshes and lakes, the density of Great Reed Warblers and the presence of water reed was determined in five other areas in 1995 and 1996 (Fig. 2). The lake complexes of Ankeveen, Loosdrecht, Nieuwkoop and Reeuwijk were similar to De Weerribben; Ketelmeer was similar to Zwarte Meer.

Nest site choice and reed availability in Weerribben and Zwarte Meer

There were large differences in the density of Great Reed Warblers between and within study areas (Fig. 3). Reed characteristics such as stem density and stem length also varied considerably between sites along the shore. Great Reed Warblers prefer reed with tall and thick stems and tend to nest close to the water where the reed is highest (Leisler 1981). Reed characteristics were measured around the nests and at randomly chosen locations along the shoreline. The measurements at the random locations were carried out in the outer 5 m of the reed bed, where the Great Reed Warblers preferred to nest (Fig. 4). The measurements were taken haphazardly within this zone, but in Zwarte Meer not in the outermost 1-1.5 m. Great Reed Warblers avoided this reed bed edge, where nests would be strongly exposed to wind and waves, the reed density was much lower and the stems much shorter than further into the reed. The measurements (± SD) at the random locations and the nests were made at 0.61 ± 0.26 m

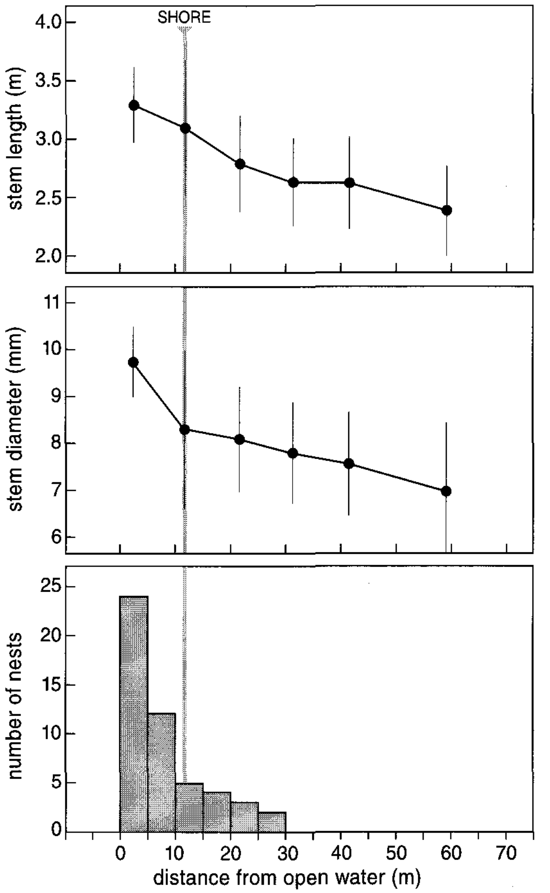

Fig. 4. Changes in reed characteristics (mean ± SD, 1995) and number of Great Reed Warbler nests (1994 + 1995) along the water-land gradient in Zwarte Meer. Reed measurements were taken along transects at nine randomly chosen locations at ca. 1, 10, 20, 30 40 and 60 m from the open water (position of markers along *x*-axis refers to mean of the distances at the nine transects).

(n = 63) and 1.45 ± 2.40 m (n = 32), respectively, from open water in Weerribben and 2.39 ± 0.28 m (n = 22) and 6.52 ± 6.23 m (n = 43), respectively, from open water in Zwarte Meer. By this procedure the potential role of stem height (and stem diameter) in the nest site choice was underestimated. However, effects of this on the results of the analysis were probably limited since most nests were located in the tallest reed along the land-water transect and the variation in reed characteristics between sites along the shore was higher than along the land-water gradient (Fig. 4).

Data on nest site selection were collected in De Weerribben (Great Reed Warbler and Reed Warbler) and Zwarte Meer (Great Reed Warbler) in 1994 and 1995. Nests were located by mapping the song posts of males, by recording long song and short song (short song indicates presence of female, Cramp 1992), by observing females during nest building and by systematic searching at sites where pairs were present. A comparison between the number of pairs present and the number of located nests, indicated that all the Great Reed Warbler nests and about 90% of Reed Warbler nests were found.

At each location, the following measurements were carried out within a 0.50 by 0.50 m square: (1) density of the new shoots and of previous year's shoots at 70 cm above the water or above land, (2) the diameter (in 0.1 mm) at the middle of the second internode above water or land of the five tallest stems, (3) reed stem length; the distance between the base of the stem (often under water) and the base of the sheath of the highest sideward pointing leaf for the five tallest stems, (4) number of herbs in the square, the most important herbs being Lesser Pond Sedge *Carex acutiformis*, Bittersweet *Solanum dulcamara*, Hedge Bindweed *Calystegia sepium* and Water Mint *Mentha aquatica*. The presence of these plant species indicates the position of the vegetation in the hydroseral succession, (5) water depth; mean of three measurements within the square, (6) width of the reed zone standing in water, referred to as 'water reed' (for the analyses log-transformed to provide normally distributed data), and (7) distance of nest from both the shore and open water.

Measurements at random sites were done on the same days as measurements at the nests. To avoid disturbance of the birds, the measurements at the nests were carried out in July and August, after the young had fledged (except from a few late nests). The measurements in Zwarte Meer were carried out on days with little wind, to minimise variation in the measurements caused by differences in water level between days. On each measuring day, I also measured the water level at a reference point in the centre of the study area in Zwarte Meer. These measurements were used to correct the data on water depth. Stem density and stem diameter hardly change in the course of the growing season. However, the stem length continues to increase until late August. Therefore, the analyses were carried out with the length as measured, and with the residuals of the regression of stem length on day. Since the results were the same, I present the results of the analyses with the stem length as measured.

Measurements of reed and presence of Great Reed Warblers in other study areas

The presence of reed along the shores, in the land or in the water, was investigated at 25 or more randomly chosen sites along the shore in each area. Data on numbers of Great Reed Warbler territories were obtained from bird counts carried out by volunteers under the auspices of, and with the standardized methods developed by, SOVON (1985). Each area was visited at least twice between June 1 and July 10. Males that were counted at two or more visits were regarded as territorial. Reed data from De Weerribben were divided into two groups: data from the two locations where Great Reed Warblers nested and data from the rest of the study area (referred to as Weerribben I and II, respectively).

Analysis of reed data

Many reed characteristics were correlated. For instance, reed in vigorous, expanding reed beds tended to have thick and tall stems and a low stem density. To determine which reed characteristics were most important in the choice of nest sites by Great Reed Warblers, a two-group discriminant analysis was carried out (Green 1978; Flury & Riedwyl 1985). With such an analysis a new variable is created from a linear combination of other variables in such a way that a maximum segregation of the two groups of data - e.g. nest sites and random sites - is accomplished along the axis representing this variable (discriminant axis). The contribution of the original variables to the new variable indicates the discriminative power of this variable for the two groups. An important feature of two-group linear discriminant analysis is that the calculations and the presentation of results are the same as in conventional multiple linear regression analysis (Green 1978). Significant variables were found by backward elimination of the non-significant variables ($P > 0.05$) from a model with all the variables of which the effect was investigated: stem length, stem diameter, stem density, proportion of old stems, the number of herbs, the width of the zone of water reed and water depth. Separate analyses were carried out for De Weerribben and Zwarte Meer, since reed characteristics and environmental conditions greatly differed between these areas.

Changes in reed characteristics

Aerial photographs were used to determine whether the type of reed that Great Reed Warblers preferred had declined. Data from Zwarte Meer and De Weerribben could not be used since it was impossible to recognize water reed as such on the pictures. Instead, photographs of Reeuwijk Lakes (1,600 ha) were used (Fig. 2). Reeuwijk was selected because photographs were available from the period 1926-1929, allowing a comparison over a long period, and because interpretation of the pictures was greatly facilitated by the detailed mapping of reed and other vegetation during the last two decades (Van Gemeren 1993). These lakes have a stable water level, are strongly eutrophied (Van Gemeren 1993) and so are typical of many lakes in The Netherlands. The population of Great Reed Warblers at Reeuwijk has declined from several hundred territorial males in the 1940s to about 35 males at present (Van Zinderen Bakker 1948; Van Gemeren 1991; J. van Gemeren pers. comm.).

For 1926-1929, low-angle photographs were available with a scale of approximately 1 : 5000. The photographs for 1967 and 1995 were taken from an angle of approximately 90° on a scale of 1 : 17 600 and 1 : 20 000, respectively. The outlines of reed stands and other vegetation types on the photographs were transferred to transparents and subsequently digitized with the program AUTOCAD (Autodesk 1994). The program ARCINFO (ESRI 1994) was used to correct the data for differences in scale and tilt between the pictures and to calculate changes in the size of reed beds.

Spatial variation in reed characteristics and density of Great Reed Warblers

To determine whether accumulation of organic matter and exposure to wind and waves might affect reed growth in the lakes examined in this study, water reed coverage was compared between exposed and sheltered sites in Reeuwijk, Zwarte Meer and Ketelmeer. Since wind direction is primarily south west in The Netherlands, eastern and northern shores were considered to be exposed, and southern and western shores sheltered.

RESULTS

Choice of nest site by Great Reed Warbler and Reed Warbler

Great Reed Warbler nests in De Weerribben were built in reed with thicker stems (diameter 6.2 ± 0.3 versus 5.5 ± 0.1 mm, $t_{80} = 2.72$, $P < 0.01$) and a lower stem density (335 ± 169 versus 486 ± 270 stems m^{-2}, $t_{80} = 2.82$, $P < 0.01$) than Reed Warbler nests. There were no differences in stem length (2.26 ± 0.33 and 2.13 ± 0.34 m, $t_{80} = 1.34$, $P = 0.18$) or proportion of old stems (21 ± 30 and $28 \pm 28\%$, $t_{80} = 1.01$, $P = 0.32$, data arcsin transformed). Great Reed Warblers nested at sites with much fewer herbs (14 ± 27 and 75 ± 114 stems m^{-2}, Mann Whitney U-test, $t_{80} = 2.59$, $P < 0.01$) and at much greater distances from the shore (2.54 ± 1.80 and 0.28 ± 0.43 m, $t_{80} = 5.17$, $P < 0.001$) than Reed Warblers. Great Reed Warbler chose much wider belts of water reed (3.92 ± 2.36 and 0.49 ± 0.87 m, $t_{80} = 4.92$, $P < 0.001$) and placed their nests much more often over water (16 out of 16 versus 15 out of 65, $\chi^2_1 = 32.2$, $P < 0.001$) than Reed Warblers.

Table 1. Reed characteristics contributing to the discrimination between nest sites of Great Reed Warbler, Reed Warbler and randomly chosen sites in 1994 and 1995. Results of two-group linear discriminant analysis. A) Nest sites of Great Reed Warblers ($y = 2$) versus Reed Warblers ($y = 1$) in reed beds in De Weerribben ($n = 143$ nests). B) Nest sites of Great Reed Warblers ($y = 1$) versus randomly selected sites ($y = 0$) in reed beds in De Weerribben ($n = 105$ sites). C) Nest sites of Great Reed Warblers and randomly selected sites in Zwarte Meer ($n = 96$ sites). Denoted are partial R^2 values: increase in explained variance by adding variable to model with other variables. Only significant results are given. The variables were selected by backward elimination of non-significant variables from the model with all measured reed characteristics. Coefficients (in C x 1000) and P-values refer to effects of variables in model with all significant variables.

Model with interaction	R^2 (%)	Coefficient ± SE	P
A			
Width water reed	17.7	1.422 ± 0.160	***
Water depth	4.5	0.015 ± 0.003	***
Old reed	1.4	-1.478 ± 0.560	**
Width water reed x Old reed	1.8	0.775 ± 0.261	**
R^2 selected model	68.5		***
Model without interaction			
Width water reed	29.8	1.639 ± 0.146	***
Water depth	5.3	0.016 ± 0.003	***
Old reed	1.2	0.169 ± 0.069	*
R^2 selected model	66.7		***
B			
Width water reed	25.3	0.746 ± 0.096	***
Water depth	5.1	0.008 ± 0.002	***
R^2 selected model	56.2		***
C			
Density	22.1	2.33 ± 0.348	***
Stem length	19.1	4.90 ± 0.79	***
Water reed	1.8	180 ± 84	*
Year	1.8	164 ± 77	*
R^2 selected model	53.6		***

A two-group discriminant analysis showed that the width of the water reed zone was the most important reed characteristic disciminating between nest sites of Great Reed Warblers and Reed Warblers (Table 1a). Water depth was the second most important factor. The small positive effect of old reed indicated that Great Reed Warblers were slightly more closely associated with old reed than Reed Warblers. Adding the interaction between old reed and width of the water reed to the model revealed a positive effect of this interaction and a negative effect of old reed. These results might imply that Great Reed Warblers seldom occur at sites with little water reed, and that the

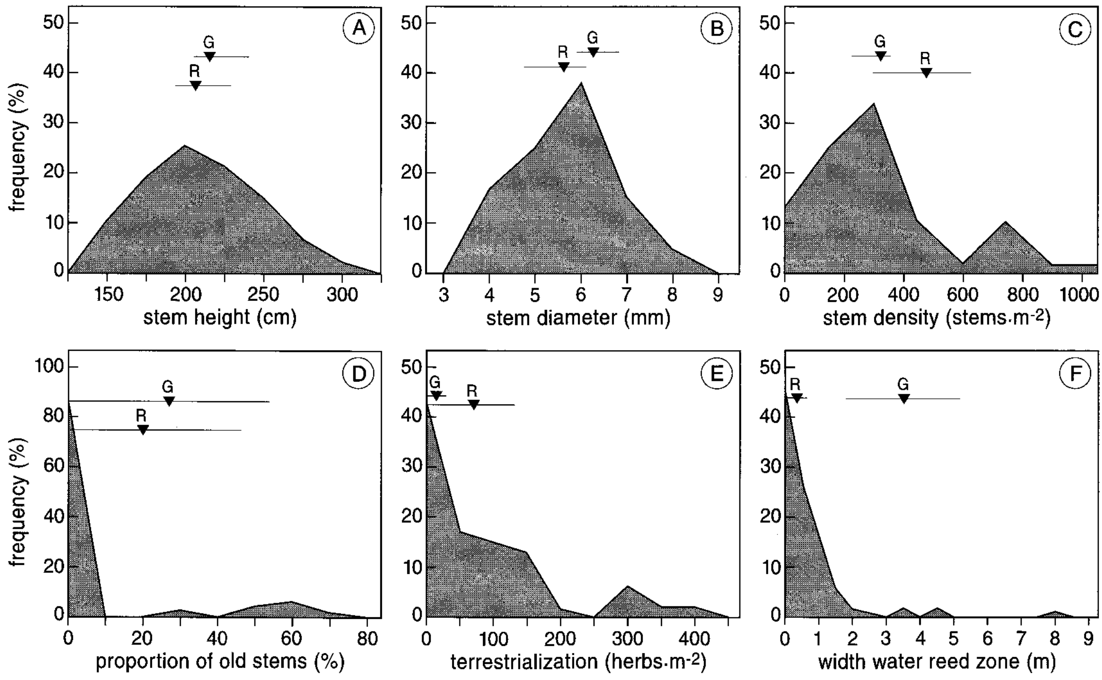

Fig. 5. Comparison of reed chosen for nesting by Great Reed Warbler (G) and Reed Warbler (R) and reed availability in De Weerribben. The shaded areas represent frequency distributions of the type of reed available. The arrows and bars indicate the mean and 25% and 75% quartiles of reed characteristics at nest sites.

close association between Great Reed Warblers and old reed is therefore only evident at sites with water reed.

Choice of reed and reed availability

Reed with the stem length and diameter that Great Reed Warblers and Reed Warblers chose was widely available in De Weerribben (Fig. 5a, b). Reed with the stem density and presence of herbs that Reed Warblers preferred was less common than that preferred by Great Reed Warblers (Fig. 5c, e). Reed with old stems was scarce (Fig. 5d). However, both species preferred reed with old stems to approximately the same extent. It seemed therefore unlikely that, if reed characteristics might explain the differences in abundance of Great Reed Warbler and Reed Warbler in De Weerribben, lack of old reed was the main explanatory factor. The type of shoreline where Reed Warblers nested without, or with only narrow zones of, water reed was quite common in De Weerribben (Fig. 5f). The opposite was true for the wide belts of water reed where Great Reed Warblers preferred to nest. The results of a discriminant analysis confirmed that nest sites of Great Reed Warblers in De Weerribben differed in particular from randomly chosen sites by the presence of water reed (Table 1b). Other factors did not significantly contribute to the discrimination between the two groups, with the exception of small effects of the presence of old reed stems and of water depth. Thus, with respect to the reed characteristic where the nest site choice of Great Reed Warblers and Reed Warblers differed most, Great Reed Warblers preferred a type of reed that was very scarce and Reed Warblers a reed type that was common in De Weerribben.

Reed in Zwarte Meer was taller (2.72 ± 0.84 versus 2.11 ± 0.36 m, Mann Whitney *U*-test, t_{74} = 5.20, $P < 0.001$), had thicker stems (8.0 ± 1.2 ver-

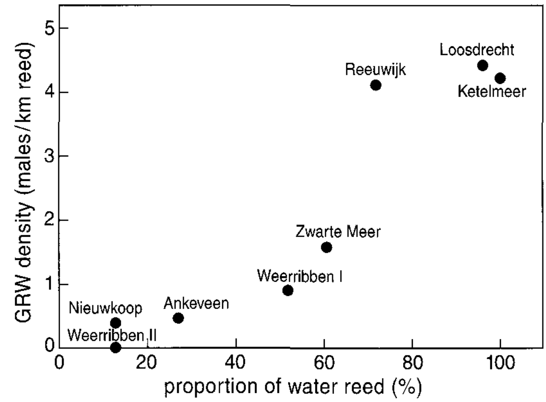

Fig. 6. Relation between proportion of reed standing in water and the density of Great Reed Warbler territories in Dutch marshes ($r_S = 0.97$, $n = 8$, $P < 0.001$). The *x*-axis denotes the proportion of the shore with reed, where water reed occurred.

sus 5.6 ± 1.0 mm, $t_{74} = 6.19$, $P < 0.001$) and a lower stem density (213 ± 84 versus 320 ± 173 stems m^{-2}, $t_{74} = 2.83$, $P < 0.01$) than reed in De Weerribben. The proportion of reed with old stems was five times as high as in De Weerribben (22 out of 28 sites versus 7 out of 47; $\chi^2_1 = 30.0$, $P < 0.001$). The proportion of shoreline that was lined with water reed was three times (17/28 and 24/113, $\chi^2_1 = 17.0$, $P < 0.001$) and the width of this zone eight times as high (8.1 ± 4.7 and 1.0 ± 1.2 m, $t_{93} = 3.77$, $P < 0.001$) as in De Weerribben. The reed in Zwarte Meer was therefore much more suitable for nesting Great Reed Warblers than that in De Weerribben. The results of the discriminant analysis showed that in Zwarte Meer nest site choice was mainly determined by density and stem length of the reed, with Great Reed War-

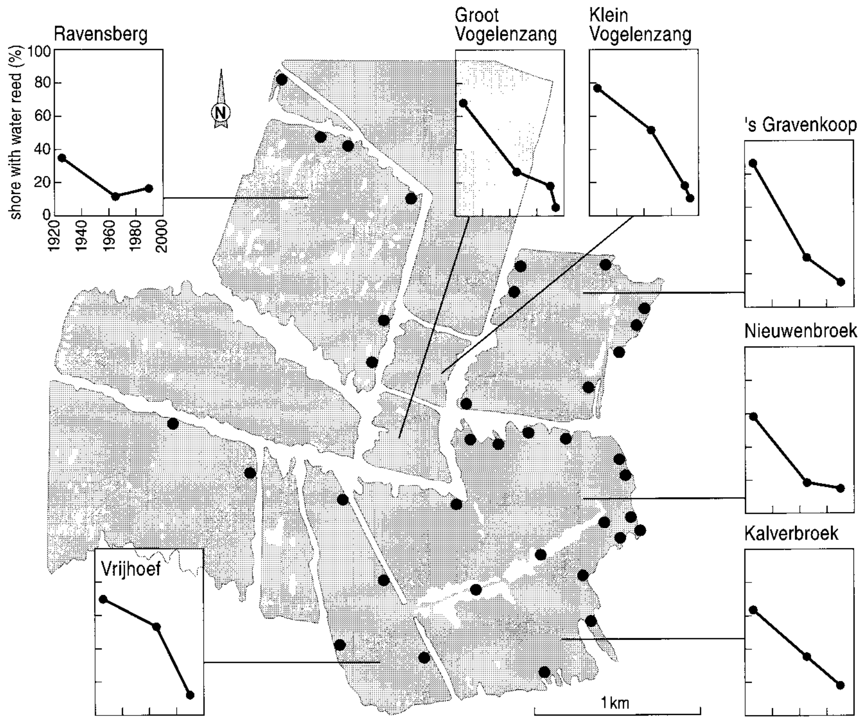

Fig. 7. Territorial males of Great Reed Warbler in 1985 (after Van Gemeren 1991) and the decline in the amount of water reed in the Reeuwijk Lakes complex. Note the high number of males along the northern and eastern shores, as compared to the southern and western shores (see Table 2).

Table 2. Presence of water reed and density of Great Reed Warblers at southern and western (sheltered) and northern and eastern (exposed) shores in Reeuwijk. Comparison by Mann-Whitney *U*-test.

	Sheltered			Exposed			
	Mean	SD	*n*	Mean	SD	*n*	*P*
Shoreline with water reed (%)	26	8	15	66	7	15	***
Territorial males km^{-1}	0.57	0.85	14	2.29	2.47	12	*

blers preferring reed with tall stems and a higher than average density (Table 1c). As in De Weerribben, Great Reed Warblers preferred sites with wide zones of water reed.

In summary, the presence of water reed determined nest site choice, where this type of reed is scarce (De Weerribben), and reed length and density mainly determined nest site choice where water reed was common (Zwarte Meer). The results obtained in the five other marshes corroborated that water reed was an important factor determining the presence of Great Reed Warblers. Among the marshes, the number of males per km shoreline with reed was highly correlated with the proportion of water reed in the total amount of reed (Fig. 6).

Changes in presence of water reed

Photographs, information from local people and field visits in 1995 indicated that almost all the reed in Reeuwijk was standing in water, both in the past and at present. However, the proportion of the shoreline that was lined with water reed had declined from 65 ± 16% (n = 7 lakes) in 1926-1929 to 32 ± 16% in 1967 ($t_{12} = 3.85$, $P < 0.01$) and 13 ± 4% in 1995 (1967 versus 1995: $t_{12} = 3.12$, $P < 0.05$, Fig. 7). The reed that was lost was replaced by open water. The 13% coverage in 1995 was lower than that measured in the field (table 2). This apparent discrepancy was caused by the fact that reed belts had also become narrower in time and reed belts of only 1-3 m wide were often not visible on the pictures.

Spatial variation in reed characteristics and density of Great Reed Warblers

The amount of water reed along exposed shores at Reeuwijk was 2.5 times higher than along sheltered shores (Table 2). The difference in presence of water reed between exposed and sheltered shores was reflected in the distribution of the Great Reed Warblers. The number of territorial males on northern and eastern shores was four times as high as along southern and western shores (Table 2, see also Fig. 7). Similar results were obtained from Zwarte Meer and Ketelmeer. These lakes have an almost identical shoreline vegetation with a wide zone of water reed at the water edge and extensive stands of dry reedland and scattered trees on the land side. However, there is a great difference in exposure to waves and wind. Wave attack and water level changes in Zwarte Meer are less pronounced than in Ketelmeer since water passing to and from Zwarte Meer has to pass through a narrow channel to the west side of the lake (Fig. 3). Also, the shore in Ketelmeer is mostly exposed to the west, in Zwarte Meer to the north. Reed stems around nest sites in Ketelmeer were longer (3.14 ± 0.40 m vs. 2.71 ± 0.26 m, $t_{64} = 2.89$, $P < 0.01$) and thicker (8.8 ± 0.1 mm and 8.1 ± 1.0 mm, $t_{64} = 3.20$, $P < 0.01$) than in Zwarte Meer. The density of Great Reed Warblers in Lake Ketelmeer was 2.6 times higher than along the southern shore in Zwarte Meer (Fig. 6). In Zwarte Meer, the island Vogeleiland (Fig. 3) with its fully exposed western shore, had a much higher density of Great Reed Warblers than the southern shore. Even along the southern shore of Zwarte Meer, where variation in exposure was small, there was an association between exposure and the presence of Great Reed Warblers. Reed stems in the 'exposed' part (dark hatching in Fig. 3) tended to be taller (2.52 ± 0.46 m versus 2.41 ± 0.44 m, *t*-test, $P > 0.05$) and were thicker (8.9 ± 1.1 mm versus 8.2 ± 0.9 mm, $t_{56} = 2.89$, $P = 0.006$) than at sheltered sites (facing north or east). At exposed sites, the density of Great Reed Warbler nests was six times as high (32 nests per 3.6 km) as in sheltered sites (11 nests per 7.8 km).

DISCUSSION

The importance of water reed for Great Reed Warblers

The width of the zone of reed standing in water was the most important reed characteristic explaining nest site choice of Great Reed Warblers in De Weerribben, where water reed was scarce, and also was the main factor discriminating between nest sites of Great Reed Warblers and Reed Warblers. The presence of water reed even affected nest site choice in Zwarte Meer, where water reed was widely available. The proportion of water reed was a good predictor of the density of Great Reed Warblers in the seven marshes examined in this study (Fig. 6). Similar results have been obtained by other observers. Leisler (1981) reported that Great Reed Warblers nested in deeper water than Reed Warblers and Mildenberger (1984) found that birds even deserted their nests when the water level dropped during nesting.

The close association of Great Reed Warblers with water reed cannot be explained by the availability of food in the reed belt. Great Reed Warblers in Zwarte Meer collected most of their food behind the water reed zone, where large prey were much more common than in the water reed (Graveland 1996). Land reed contained more insects than water reed (Graveland, unpublished results), presumably because it is less exposed to the wind, and because its higher density and the presence of other plant species provide insects with more cover and food.

Nests in water suffer a lower predation risk than nests on land because predators are less likely to reach the nests (Dyrcz 1986; Picman *et al.* 1993). The question arises as to why Reed Warblers do not nest in water reed as well. The nests of Reed Warblers are much smaller and constructed from finer material than Great Reed Warbler nests. The stem density in water reed may be too low for female Reed Warblers to build a nest or the combination of thick stems and wind might damage their nests. Also, Reed Warblers prefer denser reed with thinner and shorter stems than Great Reed Warblers (Leisler 1981; this study) and water reed has thicker and taller stems than land reed (Fig. 4). However, competition from Great Reed Warblers is probably the main cause of the low density of Reed Warblers in water reed. Great Reed Warblers do not tolerate Reed Warblers in their territories and are dominant in antagonistic interactions (Hoi *et al.* 1991; Cramp 1992).

Decline of water reed

The few data on changes in the size of reed beds along lakes and water courses in the Netherlands (De Nie & Jansen 1988; Graveland & Coops 1997) suggest that the decline of reed beds observed in Reeuwijk is representative for a general decline of water reed in the Netherlands, which is in line with large-scale declines observed elsewhere in Europe (Ostendorp 1989; Van der Putten 1997).

The die-back appears mainly to be caused by two factors: unnatural water tables and eutrophication. The die-back usually commences with a retreat from deep water (Van der Putten 1997). Reed grows poorly on substrate rich in organic material, including its own litter. The formation of toxic by-products of decomposing organic matter under the anoxic conditions of water bottoms affects the vitality of the reed and therefore seems to be the main cause of the poor growth of reed on organic substrates (Armstrong *et al.* 1996ab; Van der Putten 1997). Litter accumulation is accelerated by the increase in productivity in the water layer and in the reed belt as a result of eutrophication. The role of litter accumulation in

Fig. 8. Former and present water level fluctuations in lakes and canals in the province of Friesland in The Netherlands (source: Provincie Friesland). The year 1976 was taken as the summer of 1976 was the driest recorded in this century and without water level management water levels in summer would have been much lower than in winter.

the die-back may also explain why reed die-back hardly occurs in southern Europe (Van der Putten 1997), where the break-down of litter proceeds more rapidly at higher temperatures.

The natural fluctuation in water level, with high levels in summer and low levels in winter, impedes litter accumulation since it promotes the export of organic matter from the reed by water movement in winter (Boschker 1997), and allows rapid breakdown of litter in the presence of oxygen under low water levels in summer. Most marshes in The Netherlands now have stable water levels, as water level management is directed by the needs of agriculture in summer and prevention of flooding in winter (Fig. 8). Stable water tables may also affect reed belts due to an increase in bank erosion by the concentration of wave action at one elevation along the shoreline (Ferguson & Wolff 1984; Coops *et al.* 1991). Finally, low water tables in winter may cause damage to the reed rhizomes by exposing them to frost and ice, and to the reed belt in general by increasing the risk of infestation of important pest species such as the herbivorous Stemborer *Rhizedra lutosa* that lays its eggs at the base of the reed stems in autumn (Mook & Van der Toorn 1985). It is still under debate as to how large the relative contributions of water table management and eutrophication are to the die-back phenomenon, and which aspect of a stable water table affects water reed most. However, there is little doubt that the combination of stable water tables and eutrophication is the main cause of the large-scale decline of reedbeds observed in Western and Central Europe (Van der Putten 1997).

The die-back of water reed is not the only reed-related cause of decline of the Great Reed Warbler. Unnatural water table management and eutrophication affect water reed from the water side, but the presence of water reed is also affected by hydroseral succession from the land side. Succession is a natural phenomenon but its impact on the amount of water reed in the Netherlands would have been much smaller if the natural conditions that create new marshes, through the changing of river courses or other large scale events such as the flooding of valleys, still prevailed.

Implications for water and reed management

The loss of water reed will eventually affect also the occurrence of later phases in the succession of a reed marsh. In that sense, the decline of the Great Reed Warbler is an 'early' indicator of gradual changes that are taking place in marsh ecosystems that may affect the entire reed bird community in the future. There are four courses for remedial action. The first possibility is to cut the reed in parts of the reedbelt to slow down the hydroseral succession. However, this measure reduces the density and nesting success of most reed-dwelling species in the short term (Graveland 1999), so it has to be balanced against the long term benefit. That is particularly the case for birds that are dependent on the first stages of the hydroseral succession, such as the Great Reed Warbler, the Bittern *Botaurus stellaris*, and the Savi's Warbler *Locustella luscinioides*. The second course of action is to recreate early successional stages through various forms of nature restoration such as excavating peat bogs or filled-up floodplains, or removal of accumulated organic material. The effectiveness of these measures is probably limited without changes in the water level management. The third measure is to reduce the nutrient load of the water. Some success can already be claimed in this respect, in particular by the arrival of water treatment plants and the introduction of detergents without phosphates during the last two decades. The fourth and probably most effective measure is to restore natural water level fluctuations. It will be difficult to accomplish, because of agricultural interests and the expensive adaptations that may be needed in the hydrological infrastructure. It may also be controversial among conservationists, since in many areas restoration of natural water tables can only be accomplished through artificial means. For instance, nature reserves in peat areas tend to lie higher than the surrounding land, due to the oxidation of the peat as a consequence of the lowering of the water table for agricultural purposes in the past. In the Netherlands, the debate about the restoration of water levels for nature conservation has only recently started.

ACKNOWLEDGEMENTS

I want to thank Eric Janssen, Symen Deuzeman, Erik Bouma, Hendrik Smedes and Patrick Martens for their assistance in the field and Hilco Van der Voet for statistical advice. Herbert Hoi, Will Peach, Arie Spaans, Maarten Platteeuw and Jan Veen provided helpful comments on previous versions of this paper.

REFERENCES

Armstrong J., F. Afreen-Zobayed & W. Armstrong 1996a. *Phragmites* die-back: sulphide- and acetic acid-induced bud and root death, lignification, and blockages within aeration and vascular systems. New Phytol. 134: 601-614.

Armstrong J., W. Armstrong & W.H. Van der Putten 1996b. *Phragmites* die-back: bud and root death, lockages within the aeration and vascular systems and the possible role of phytotoxins. New Phytol. 133: 399-414.

Autodesk 1994. AUTOCAD User Guide Release 13. Autodesk Inc., New York.

Baillie S.R & W.J. Peach 1992. Population limitation in Palearctic-African migrant passerines. Ibis 134 suppl. 1: 120-132.

Boschker E. 1997. Decomposition of organic matter in the littoral sediments of a lake. Ph.D. Thesis, University of Wageningen.

Cavé A.J. 1983. Purple Heron survival and drought in tropical West-Africa. Ardea 75: 133-142.

Coops H., R. Boeters & H. Smit 1991. Direct and indirect effects of wave attack on helophytes. Aquatic otany 41: 333-352.

Cramp S. (ed.) 1992. The birds of the western Palearctic, 4. Oxford University Press, Oxford.

Den Hartog C., J. Kvet & H. Sukopp 1989. Reed. A common species in decline. Aquatic Botany 35: 1-4.

De Nie H.W. & A.E. Jansen 1988. De achteruitgang van de oevervegetatie van het Tjeukemeer tussen Oosterzee (Buren) en Echten. RIN-rapport 88/54, Rijksinstituut voor Natuurbeheer, Leersum.

Dyrcz A. 1986. Factors affecting facultative polygyny and breeding results in the Great Reed Warbler *Acrocephalus arundinaceus*. J. Orn. 127: 447-461.

ESRI 1994. ARC/INFO User's Guide. Environmental Systems Research Institute, Inc. Redland, California.

Ferguson H.A. & W.J. Wolff 1984. The Haringvliet-project: the development of the Rhine-Meuse estuary from tidal inlet to stagnant freshwater lake. Water Science and Technology 16: 11-26.

Flury B. & H. Riedwyl 1985. T2-tests, the linear two-group discriminant function, and their computation by linear regression. American Statistician 39: 20-25.

Graveland J. 1996. Watervogel en zangvogel: de achteruitgang van de Grote Karekiet *Acrocephalus arundinaceus* in Nederland. Limosa 59: 85-96.

Graveland J. 1999. Density and breeding success of Reed Warbler *Acrocephalus scirpaceus* and Sedge arbler *A. schoenobaenus* in relation to reed cutting. J. Avian Biol., in press.

Graveland J. & H. Coops 1997. Achteruitgang van rietgordels in Nederland. Landschap 14: 67-86.

Green P.E. 1978. Analyzing multivariate data. The Dryden Press, Hinsdale, Illinois.

Hagemeijer W.J.M. & M.J. Blair 1997. The EBCC Atlas of European breeding birds: their distribution and abundance. T & AD Poyser, London.

Hoi H., T. Richler & J. Dittami 1991. Territorial spacing and interspecific competition in three species of reed warblers. Oecologia 87: 443-448.

Leisler B. 1981. Die Ökologische Einnischung Mitteleuropäischen Rohrsänger (*Acrocephalus*, Sylviinae). I. Habitattrennung. Die Vogelwarte 31: 45-74.

Marchant J.H. 1992. Recent trends in breeding populations of some common trans-saharan migrant birds in northern Europe. Ibis 134 suppl. 1: 113-119.
Mildenberger H. 1984. Die Vögel des Rheinlandes, II. Kilda Verlag, Greven.
Mook J.H. & J. Van der Toorn 1985. Delayed response of common reed *Phragmites australis* to herbivory as a cause of cyclic fluctuations in the density of the moth *Archanara geminipunctata*. Oikos 44: 142-148.
Ostendorp W. 1989. 'Die-back' of reeds in Europe - a critical review of literature. Aquatic Botany 35: 5-26.
Peach W.J., S.R. Baillie & L.G. Underhill 1991. Survival of British Sedge Warbler in relation to West-African rainfall. Ibis 133: 300-305.
Picman J., M.L. Milks & M. Leptich 1993. Patterns of predation on passerine nests in marshes: effects of water depth and distance from edge. Auk 110: 89-94.
SOVON 1985. Handleiding broedvogelmonitoringproject. SOVON, Beek-Ubbergen.
SOVON 1988. Nieuwe aantalsschattingen van de Nederlandse broedvogels. Limosa 61: 151-162.
Ter Braak C.J.F., A.J. Van Strien, R. Meijer & T.J. Verstrael 1994. Analysis of monitoring data with many missing values: which method? In: Hagemeijer E.J.M. & T.J. Verstrael (eds.) Bird Numbers 1992. Distribution, monitoring and ecological aspects. Proceedings of the 12th International conference of IBCC and EOAC, Noordwijkerhout, The Netherlands, Statistics Netherlands, Voorburg/Heerlen & SOVON, Beek-Ubbergen.
Tucker G.M. & M.F. Heath 1994. Birds in Europe: their conservation status. Birdlife International, Cambridge, U.K.
Van der Putten W.H. 1997. Die-back of *Phragmites australis* in European wetlands: an overview of the uropean research program on reed die-back and progression. Aquatic Botany 59: 263-275.
Van der Toorn J. 1972. Variability of *Phragmites australis* (Cav.) Trin. ex Steudel in relation to the environment. Van Zee tot Land. Rapporten en mededelingen inzake de droogmaking, ontginning en sociaal-economische opbouw der IJsselmeerpolders, nr. 48. Rijksdienst voor de IJsselmeerpolders, Lelystad.
Van Gemeren C.A. 1991. De Grote Karekiet in het Reeuwijkse Plassengebied. IVN-Afd. IJssel en Gouwe, Gouda.
Van Gemeren C.A. 1993. De ontwikkeling van water- en oevervegetaties in enkele Reeuwijkse Plassen in relatie tot eutrofiëring, fosfaat-fixatie en visstandbeheer. Hoogheemraadschap Rijnland/Natuuractiviteitencentrum de Watersnip, Leiden/Reeuwijk.
Van Wirdum G. 1991. Vegetation and hydrology of floating rich-fens. Ph.D. Thesis, University of Amsterdam.
Van Zinderen Bakker E.M. 1948. De West-Nederlandse veenplassen: een geologische, historische en biologische landschapsbeschrijving van het water- en moerasland. Deel 1. Heemschut bibliotheek, Allert de ange, Amsterdam.
Weisner, S.E.B 1987. The relation between wave exposure and distribution of emergent vegetation in a eutrophic lake. Freshwater Biology 18: 537-544.
Weisner S.E.B 1991. Within-lake patterns in depth penetration of emergent vegetation. Freshwater Biology 26: 133-142.

SAMENVATTING

Sommige in Afrika overwinterende moerasvogelsoorten nemen in Midden- en West-Europa sterk in aantal af. Een belangrijke vraag is in hoeverre deze aantalsvermindering wordt veroorzaakt door verlies aan *wetlands* in Afrika of door verslechterde omstandigheden in de broedgebieden. In veel Europese landen wordt een sterke achteruitgang gemeld van de omvang van rietvelden, die vooral wordt toegeschreven aan het verminderen van natuurlijke fluctuaties van het waterpeil (met een hoog winter- en een laag zomerpeil) en aan eutrofiëring. Deze processen leiden tot een ophoping van organisch materiaal in de rietkraag, waar riet slecht tegen kan. De afname van waterriet begint aan de waterzijde van een rietkraag, en staat los van het verlies aan rietvelden door bebouwing, drooglegging van moeras en dergelijke. Onnatuurlijke waterpeilen en eutrofiëring kenmerken de meeste Nederlandse wateren. Onderzocht werd welke eisen nestelende Grote Karekieten *Acrocephalus arundinaceus* aan het riet stellen, en hoeveel geschikt riet nog aanwezig is in vergelijking met het verleden. De Grote Karekiet werd gekozen, omdat deze soort sterk is afgenomen en minder afhankelijk lijkt van *wetlands* in het overwinteringsgebied dan bijvoorbeeld de Rietzanger *Acrocephalus schoenobaenus*. De nestplaatskeuze van de Grote Karekiet werd vergeleken met die van de zeer talrijke Kleine Karekiet *Acrocephalus scirpaceus*, een soort met vergelijkbare biotoopeisen.

Grote Karekieten verkozen wat zwaarder riet dan Kleine Karekieten, maar de aanwezigheid van dit riet was niet beperkend voor de Grote Karekiet. Grote Karekieten broedden echter, in tegenstelling tot Kleine Karekieten, bijna uitsluitend in riet dat in het water stond (waterriet). Juist het areaal van dit type riet is

sterk in omvang achteruitgegaan. Vitaal waterriet bleek vooral te staan op plaatsen waar door op- en afwaaiing nog peilfluctuaties voorkwamen, zoals de Randmeren en de oost- en noordoevers van grote laagveenplassen. Waterriet vormt het eerste stadium in de successie van een rietmoeras. Het verlies van waterriet zal daarom op wat langere termijn gevolgen hebben voor de gehele moerasvogelgemeenschap. Herstel van de natuurlijke waterpeildynamiek lijkt de meest effectieve maatregel om waterrietkragen te behouden en te herstellen, maar dit herstel staat op gespannen voet met de eisen die de moderne landbouw en waterbeheerders stellen aan het waterpeil. Met de discussie over een mogelijk herstel van de natuurlijke peildynamiek in Nederland is onlangs een begin gemaakt.

Received: 18 February 1998, accepted 25 October 1998
Corresponding editor: Mardik (F.) Leopold