Habitat selection by the Corncrake *Crex crex*: importance of ecotope distribution and landscape composition in river floodplains.

Corncrake distribution along the Dutch Rhine branches
in the period 2001-2005.

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Contents

Preface

This report is the product of a three months research project carried out at the Department of Environmental Science of the Radboud University Nijmegen, in collaboration with the Dutch Centre for Field Ornithology (SOVON). It deals with the spatial distribution of the Corncrake *Crex crex* in the Dutch Rhine floodplains in the period 2001-2005. This distribution is related to landscape characteristics and ecotope availability.

I would like to thank my supervisors, Rob Leuven and Kees Koffijberg, for advice and guidance. Also thanks to Aafke Schipper for her additional suggestions. And finally of course I would like to thank SOVON and the volunteer bird watchers, who provided the data that formed the basis for this study.

Abstract

Distribution of Corncrake *Crex crex* in the floodplains of the Dutch Rhine branches was studied. Data on male singing sites from the period 2001-2005 were used. Occurrences and numbers of singing sites were related to ecotopes and inundation frequency. Landscape characteristics of floodplains with different occupation frequencies were compared.
The ecotopes "production meadows" (41%) and "pastures" (28%) are preferred habitat for the Corncrake. Reference densities for the most important ecotopes varied from 0.1 to 0.62 singing males / ha. Results proof that a shift in ecotope preference occurs when the season proceeds: production meadows become less favourable and natural pastures and herbaceous grasslands more. This is probably caused by mowing activities in the middle of June.
There were no significant differences in amount of suitable habitat between floodplains that were occupied in one, two, three or more of the years. Floodplains with a higher occupation frequency show a higher Shannon Index score. Also, these floodplains contain less different patch types. This suggests a preference of the Corncrake for heterogenic landscapes with a limited number of different ecotopes that are represented equally in the area. However, based on these results it can not be concluded that habitat availability is a key factor in settlement of the Corncrake in the floodplains. Probably other factors like land use are of more importance.

1. Introduction

The Corncrake (*Crex crex*) is a migratory bird that is threatened throughout the world and has the status of 'Near Threatened Species' (Schäffer & Green, 2001; Schoppers & Koffijberg, 2001). It is included in Red Lists of most European countries and it is a Species of European Conservation Concern (EU SPEC1 species). It is also a target species for nature conservation in river floodplains in the Netherlands (Duel *et al*., 1996). Intensification of land use and loss of suitable breeding habitat are the main factors responsible for the decline of the Corncrake (Gerritsen *et al*., 2001; Schäffer & Green, 2001; Keišs, 2005).

1.1 Species description

The Corncrake is a member of the family of rails (*Rallidae*) and is related to species such as the Water rail (*Rallus aquaticus*), the Common moorhen (*Gallinula chloropus*) and the Eurasian coot (*Fulica atra*). It has a breeding range from Ireland to the Baikal Lake in Siberia, extending from 62° N to Southern France, Italy and the Caucasus (Schäffer & Koffijberg, 2004; figure 1).
The Corncrake is only present in Eurasia during the spring and summer months (April – September) to breed. In autumn it migrates to the east and southeast of Africa, using two different migration routes (see figure 1).

Figure 1.
Distribution of *Crex crex* (Adapted from: www.kwartelkoning.nl).

The Corncrake is a species that has some specific demands concerning breeding habitat. Vegetation should be at least 20-30 cm high and offer sufficient cover. However, too dense vegetation typically found in fertilized or unmanaged grasslands, does not provide sufficient breeding space, is difficult to move through and is therefore avoided (Green *et al.*, 1997; Schäffer & Koffijberg, 2004).

Original Corncrake habitats were lowland marshes with *Carex* and the mosaic like landscape of the river floodplains (Flade, 1997). The Corncrake needs an open vegetation structure; periodic removal of vegetation is a key factor for Corncrake habitat to remain intact. In the historic landscape forces like flooding, ice rafting and fire played an important role in this (Flade, 1997). Nowadays, original habitat has become scarce in Europe due to cultivation. Open or half open grasslands (less intensively used hay lands, production meadows) that are mown seasonally are now very important as a secondary habitat (Keišs, 1997; Schäffer & Green, 2001).

The species has a remarkable breeding strategy. Two broods are raised, in between which both male and female change partners. The breeding season starts in May and flightless chicks might still be found as late as September (Schäffer & Koffijberg, 2004). The first nest is usually in the end of May or the beginning of June which is very late in comparison to other meadow birds. A brood typically consists of 8 – 12 eggs. These hatch after 16 – 19 days, after which the female will stay with the juveniles for about two weeks. Then she will leave in search of another male and a second brood.

1.2 Global status

Corncrake populations and trends are quite well documented in Western Europe (Green *et al.*, 1997; Williams *et al*., 1997; Schäffer & Green, 2001). Recently, several surveys in Central and Eastern European countries have shown that there are much more Corncrakes in this part of Europe than was estimated thus far. Current world population is estimated at 1.7 – 3.5 million singing males (Schäffer & Green, 2001; Schäffer & Koffijberg, 2004). The species' status as near threatened is not based on sheer numbers, but on trends observed in Western Europe. Recent declines have shown the Corncrake's sensitivity to changes in (agricultural) land use (Schäffer & Green, 2001), as several studies have found positive correlations between Corncrake numbers and changes in land use. A decline of Corncrake numbers over a five year period in Latvia was correlated with a decrease of cultivated and uncultivated meadow area (Keišs, 2005). Declines in Corncrake numbers in Britain and Ireland were associated with reductions in the area of hay-meadows (Green & Stowe, 1993). Abandonment of agricultural lands has been found to lead to the development of suitable habitat for Corncrake (Schäffer & Green, 2001; Keišs, 2005). It is thought that the species' sensitivity to the effects of agricultural and conservation management lies in its low annual survival rate (0.2 – 0.3; Green, 2004), i.e. a high reproduction rate is necessary to compensate for a high annual adult mortality.

The most important factor in the decline of the Corncrake is the combination of their habitat needs and the late breeding season. Today, their habitats are mostly agricultural lands that are subject to mowing. Most meadow birds breed in April – May. When mowing is adapted to meadow birds, juveniles will have fledged long before the mowing season starts mid June. The Corncrake's breeding period, however, is likely to coincide with the mowing season. This poses a serious threat to nests, chicks and possibly moulting adults. Indeed, in Western Europe populations have declined rapidly with the introduction of mechanized mowing (Schäffer & Green, 2001). In addition, improved land drainage allows for earlier mowing of meadows in river floodplains which had formerly been too wet. Faster machines make it possible to mow a large area of land in a shorter period of time, causing larger parts of Corncrake habitat to be mown early in the season. In addition, there is a trend in Europe from hay-production to silage-production, which leads to increased losses due to earlier mowing (Green & Stowe, 1993; Schäffer & Koffijberg, 2004).

Conservation measures as introduced in various Western European countries aim at reducing loss by mowing activities. Postponing mowing until the beginning of August can greatly enhance the survival of broods and chicks. Another effective conservation measure is changing the method of mowing. Meadows are typically mown from the outside inwards, creating isolated patches of vegetation in the middle that trap the fleeing chicks. A more Concrake-friendly mowing method, from the inside outwards, allows the birds to move to another meadow or to designated 'refuge borders' of vegetation (Broyer, 2003; Schäffer & Koffijberg, 2004; Schoppers & Koffijberg, 2006).

1.3 Situation in the Netherlands

Typically, the Corncrake is an inhabitant of grasslands. In the Netherlands, about half of the territories are found in grasslands, often hay lands that are subject to some sort of management measures with late mowing dates (after mid June). Besides, every year an important part of the Corncrake population is found in arable land with crops of the Oldambt area, in the northeast of the province of Groningen. Territories in crops are almost exclusively found in this region and account for 25-50% of the Dutch population annually (Schoppers & Koffijberg, 2001, 2003, 2004, 2005, 2006). Furthermore, ecological rehabilitation areas that are usually managed with low or moderate grazing regimes account for another 10-20% of the territories (Schoppers & Koffijberg, 2001, 2003, 2004, 2005, 2006). These areas are mostly found in the river floodplains, which originally are the Corncrake's natural habitat.

The Corncrake usually arrives in May - beginning of June. Nowadays first observations in April are rare (Schoppers & Koffijberg, 2006). Data from the 1950's shows that the birds arrived earlier then: from the 20th of April onwards, with a peak between the 18th of May and the 21st of June. (Braaksma, 1962). This is almost two weeks earlier than in recent years. The reason for this is not clear. One explanation is that there are two groups of Corncrakes: one that has the Netherlands as their home ground and one group that 'drifts in' from elsewhere later in the season (Schoppers & Koffijberg, 2006). It is possible that due to habitat deterioration and increased disturbance in the entire breeding range the group of drifters increases and are longer in search of suitable habitat, before settling.

The Netherlands is one of the few countries where detailed national surveys of Corncrake numbers are available (Schoppers & Koffijberg, 2001, 2003, 2004, 2005, 2006). Intensification of agriculture and loss of breeding habitat have had consequences for the number of Corncrakes in the Netherlands as much as in other European countries. The number of territories has decreased from an estimated 875 in 1968 to a minimum of about 60 territories in 1993-'94. From 1997 a recovery has been observed. In 1998, 586 territories were recorded. An underestimation of 10 – 20% was assumed (caused by bad weather conditions and the nocturnal singing activity of the species), which led to an estimated breeding population between 640 and 700 territories (Koffijberg & Van Dijk, 2001). In the following years the population remained at a high level with more than 200 territories in the years 1997-2003 (Schoppers & Koffijberg, 2006). A possible explanation for this sudden revival is that there has been an increased immigration from Eastern Europe (e.g. Russia). The collapse of communism, with a system of collective farms, caused an abandonment of large fields and grasslands. Vegetation could develop in such a way that area of breeding habitat expanded greatly and high reproduction rates were possible (Koffijberg & Van Dijk, 2001; Schäffer & Green, 2001).

The last two years have been a period of low Corncrake numbers with less than 150 territories (Schoppers & Koffijberg, 2006). Because these declines coincide with declines in other European countries it is believed they are caused by negative developments on population level rather than problems on country-scale. Conservation measures are being applied more and more on Dutch agricultural lands (e.g. postponing mowing until beginning of August, and Corncrake-friendly mowing methods). These measures ensure sufficient habitat throughout the breeding season.

1.4 Scope of research

Current knowledge on Corncrake ecology is heavily based on studies outside the Netherlands (Schoppers & Koffijberg, 2006). This study aims to assess habitat selection in relation to ecotope distribution and landscape composition in the Dutch Rhine floodplains. Information on factors that influence settlement of Corncrakes is one of the knowledge gaps specified in the national Species Action Plan Corncrake (Gerritsen *et al*. 2004). This study will be a first step in creating a multi-variable database that will link Corncrake occurrence in different years to landscape characteristics of the floodplains. This knowledge is essential to provide more insight into implications of river management measures that are being planned within the framework of 'Room for the River' on Corncrake habitat. Furthermore, information on Corncrake ecotope preference and reference densities can be used for validation of landscape ecological models such as BIO-SAFE (De Nooij, *et al.*, 2004) and MORRES (Duel *et al*., 1996). Bio-SAFE is a model developed for the floodplains of the rivers Rhine and Meuse. It links habitat requirements of a selection of species to present ecotopes in order to assess suitability of an area for these species as well as potential impacts of reconstruction measures on biodiversity of the area (De Nooij *et al.*, 2004). MORRES uses calculation rules and reference densities to quantify the development potential of target species based on the ecotope distribution of the area (Duel *et al*., 1996).

Existing data on numbers and distribution of singing males (2001 – 2005), obtained from the Dutch Centre for Field Ornithology (SOVON), are analyzed. Several environmental factors are included: land cover (ecotopes), landscape heterogeneity / diversity, height / inundation frequency. Distinctions are made between areas that were occupied in one, two, three, four or all of the years, in order to identify a relation with the spatial factors that may determine habitat selection. A distinction is also made between observation dates, to study changes in ecotope preference over the season. The research questions are:

- What were the geographical distribution and frequency of occurrence of the Corncrake at various sites in the floodplains of the Dutch Rhine branches in the period 2001-2005?
- Which ecotopes are preferred by the Corncrake and does ecotope preference change over the season?
- Does inundation frequency of the floodplains have an effect on Corncrake occurrence?
- Are there differences in ecotope distribution, landscape diversity and patchiness between floodplains that were occupied by Corncrakes in respectively 0, 1, 2, 3 or more of the years 2001-2005?

The outline of this study is shown in figure 2.

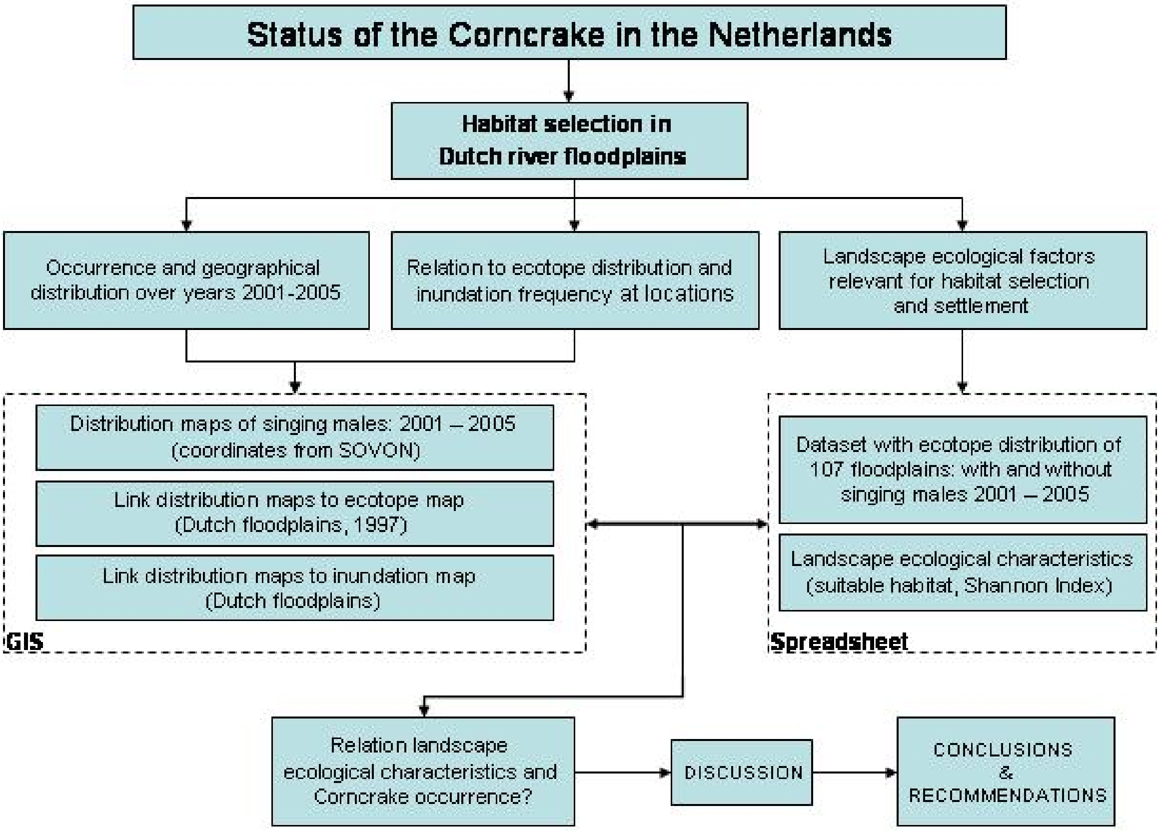

Figure 2. Flowchart of this study.

2. Methods

2.1 Field survey method

Every year, two simultaneous surveys are carried out by volunteer bird watchers from SOVON. These surveys take place at the beginning and the end of June, respectively and comprise at least all known core areas (mostly along the main rivers and in the Oldambt crop fields; Schoppers & Koffijberg, 2006). Surveys are carried out after sunset, when the birds begin to sing. Counting Corncrakes is done entirely by ear, because of the nocturnal singing activity of the animal. When a singing bird is heard the location is determined with the help of a topographic map of the area (1:25 000) and the coordinates are recorded. This is done with either 10 m, 100 m or 1000 m accuracy, using the lower left corner of the corresponding grid (km grid, 100x100 m or 10x10 m grid) on the map. Observers mark both their own location and the location of the singing site on the map and connect these with a dotted line. In this way, possible double recordings caused by misinterpretation of the singing site can be excluded afterwards (Schoppers & Koffijberg, 2001). However, the methods and conditions of the surveys are such that 100% accuracy can not be guaranteed. While direction of the sound can be determined quite exactly, distance is difficult to estimate and often a singing male is further away than estimated by the observer. Weather conditions can frustrate surveys, although this has only happened once during the simultaneous surveys. However, assessing Corncrake distribution from singing males is a widely accepted method (Green *et al.*, 1997) and a more exact method is not available. Hence a certain uncertainty in these data should be accepted.

Results from the simultaneous surveys are gathered by SOVON and included in the national survey of rare and colonial breeding birds. In addition, all other observations outside the surveys are gathered, to get as many data from the complete season (Schoppers & Koffijberg, 2006). Each observation is given a code (year and number) and put in a central database. This dataset, with all observations of the years 2001-2005, formed the basis for this study.

The dataset with singing sites contains a column 'territory'. All observations are clustered to territories, following the guidelines of SOVON's national survey of rare and colonial breeding birds (Van Dijk *et al.*, 2004). This specifies that singing males are only attributed a territory when observed between the 20th of May and the 31st of July. Territories of singing males are used as an indication for population size. However, studies on habitat and land use are based on singing sites and not territories (Schoppers & Koffijberg, 2006). Since a territory might include more than one singing site this approach is more practical and anticipates more on the Corncrakes breeding behaviour. In this study also singing sites will be used in the analyses.

2.2 GIS

Geographical coordinates of singing males in the Dutch river floodplains along the Rhine branches (over the years 2001 – 2005 and obtained from SOVON) were entered in a GIS environment (ArcGIS 9). Data consisted of in total 956 coordinates of singing males. First they were corrected for their accuracy. During the surveys, the coordinates are noted down with either 10 m, 100 m or 1000 m accuracy, using the lower left corner of the corresponding grid (1000 x 1000 m , 100X100 m or 10x10 m grid) on the map. The singing sites were centered in the grids. This was done by adding either 5, 50 or 500 meters to both the x and y coordinate. It was assumed that differences in accuracies would have no effect on the ecotope relation. Table I-1 in Appendix I shows the distribution of the singing sites over different ecotopes, for the whole dataset and for the 10m, 100m and 1000m data respectively. When comparing the separate data with the complete dataset, the distribution is very similar in the case of the 10m data. The data shows more discrepancies with lower accuracies. However, the major part of the dataset consists of 10m data, causing the whole dataset to be a good representation of the real spatial distribution. 10 meters means a 5m error in the x and y coordinate, which corresponds to the error margin in constructing GIS maps. Therefore, in the further analyses the complete dataset was used irrespective of accuracy.

A 1997 GIS ecotope map of the Rhine branches (Jansen & Backx, 1998) was used to relate the singing sites to ecotopes (following the River Ecotope System (RES); Rademakers & Wolfert, 1994). This is the most recent ecotope map of the river floodplains, but in nine years time ecotopes could have developed into others. However, in an earlier study an ecotope transition matrix was created based on literature and expert knowledge. This matrix predicted ecotope successions over periods of 8, 15 and 50 years.

In this model, most ecotopes had not changed into another one after 8 years and it was assumed that all cultivated ecotope types would remain unchanged (Atsma, 2006). Based on this information, it can be expected that the 1997 ecotope map will still provided reliable results. However, changes in land use or implementation of river management measures can also have occurred in the period of nine years. Based on the 1997 map, a list of 26 land ecotopes resulted that had contained at least one singing site in the period 2001-2005. The ecotope where the singing site was located was added in the attribute table of the singing sites.

A GIS map of inundation frequencies in the Dutch floodplains (Anonymous, 1997) was used to relate the singing sites to flooding. Inundation frequency was specified in six classes: 180-365 days/year, 50-180 d/y, 20-50 d/y, 2-20 d/y, <2 d/y and unknown. The class where the singing site was located was added to the attribute table of the singing sites.

A GIS map of all floodplains along the Dutch Rhine branches was used to study Corncrake distribution on floodplain scale. Singing sites were dispersed over 67 floodplains along the rivers Rhine, Waal and IJssel. An additional 40 floodplains that had not contained Corncrakes in the period 2001-2005 were selected for comparison. It was ensured that these were distributed over the whole extend of the Rhine branches. Thus, a total of 107 floodplains were used for analyses (table III-1, appendix III). For these 107 floodplains the ecotope distribution was determined in ArcGIS, by selecting the ecotope polygons that 'had their centre in' the floodplain.

2.3 Spatial distribution and relation to ecotopes and inundation frequency

Spatial distribution over the floodplains was determined. Density of singing males (per ha) was calculated for each of the 67 occupied floodplains and for each year they were occupied. A distinction was made between floodplains that contained Corncrakes in 1 year (N=22), 2 years (N=13), 3 years (N=17), 4 years (N=9) and all 5 years (N=6) in the period 2001-2005. For each of these five classes an average was calculated for all densities in the years that they were occupied, resulting in a mean yearly density of singing males (for the six floodplains that were occupied in all five years the sample size will be N=30).

For all five years together, as well as all years separately, the distribution of the singing sites over the types of ecotopes was determined. A distinction was made between the first simultaneous survey (beginning of June) and the second one (end of June), to see if shifts in habitat preference occur in the course of the season. Suitability of ecotopes probably changes during the season due to vegetation growth, mowing or inundation frequency.

To study preference of the Corncrake for areas with a certain inundation frequency, the number of singing sites per inundation class was determined. This resulted in a distribution of singing sites over the inundation classes that might show a certain preference.

2.4 Landscape characteristics

In addition to the specific locations of the singing sites, distribution of the Corncrake was also studied on floodplain scale and their occurrence linked to certain landscape characteristics. The share of suitable habitat, landscape diversity (Shannon Diversity Index) and patchiness (number of polygons) of the 107 floodplains were analyzed. A distinction was made between floodplains that held Corncrakes in 0 years (N=40), 1 year (N=22), 2 years (N=13), 3 years (N=17) or 4 / 5 years (N=15) in the period 2001-2005. 4 and 5 years were put together in this case, because the sample size would otherwise be too small.

The ecotopes that contained Corncrakes were classified as "suitable habitat" (the first six ecotopes in table II-1 in Appendix II) and "marginal habitat" (the rest). A third class, "unsuitable habitat", was formed by the ecotopes where Corncrakes were not found (e.g. the area of the floodplain that is not suitable or marginal). For each floodplain this resulted in percentages suitable, marginal and unsuitable habitat. The distinction between suitable and marginal is a little bit arbitrary. When going down in the list of 26 ecotopes, Corncrake occurrence becomes more and more sporadic. As a rule, it was decided that ecotopes with at least 50 singing sites in the whole period 2001-2005 (> 5% of the 956 singing sites) would fall in the class “suitable habitat”. Together these ecotopes harboured 69% of all singing sites. The other 20 ecotopes harboured 31% of all singing sites

The Shannon Diversity Index (SHDI) was calculated for each of the 107 floodplains. The SHDI is a measure for the patch diversity of an area. SHDI = 0 if there is only one patch present in the landscape (=no diversity). SHDI increases as the number of different patch types increases and/or the proportional distribution of area among patch types becomes more equitable (McGarigal & Marks, 1994). The formula for the Shannon Diversity Index was taken from McGarigal & Marks (1994):

$$SHDI = -\sum_{i=1}^{m} (P_i * LN\ P_i)$$

Where Pi = the proportional abundance of a certain patch type.

In an Excel spreadsheet the SHDI was calculated by dividing the area of one ecotope type by the total area of all ecotopes in the floodplain (resulting in a proportional abundance) and using the above formula to get an SHDI score.

In addition, for each floodplain the number of polygons and the number of different polygon types in the ecotope map were included in the dataset. These were expressed as patch density (number of patches / ha) and patch type density (number of different patch types / ha). Together with the SHDI this gives information about both the patchiness and the diversity of the area.

For each of the above characteristics, an average was calculated for floodplains that contained Corncrakes in 0, 1, 2, 3 or 4 / 5 of the years.

2.5 Statistical analysis

Statistical analyses of the results were done using a one-way ANOVA, with a *post-hoc* Games-Howell test for unequal variances. Sample sizes in the analyses were different (number of floodplains with different occupation frequencies). Games-Howell is also accurate when sample sizes are unequal (Field, 2000).
Analysis of shifts in habitat preference was done using a Pearson chi-square test. This test detects if there is a significant association between two categorical variables (Field, 2000). In this case the variables are ‘first or second survey’ and ‘Production meadow or Natural pastures / herbaceous’.

3. Results

3.1 Spatial distribution and relation to ecotopes and inundation frequency

Singing sites of the years 2001-2005 are shown in a map of the Dutch Rhine branches (figure IV-1 in appendix IV). Mean yearly density (per ha) was calculated for each of the 67 occupied floodplains. A distinction was made between floodplains with different occupation frequencies (figure IV-2 in appendix IV). This map shows that the floodplains along the rivers Waal and IJssel provide the most important Corncrake areas in comparison to the Lower Rhine and Lek. This is also shown by the difference in numbers of territories in table 1.

Table1. Number of territories in the Netherlands and the Rhine branches in the years 2001-2005.

Year	Number of territories				Percentages Rhine branches
	Rhine / Lek	Waal	IJssel	Netherlands	
2001	21	28	28	210	36.7
2002	19	37	38	348	27.0
2003	32	45	53	503	25.8
2004	11	27	15	113	46.9
2005	2	9	23	116	29.3
Average 1980-2005*	12.6	20.8	20.0	178.1	**35.2**

(*) Long-term data obtained from SOVON.

Table 1 illustrates the importance of the Dutch Rhine branches for harbouring the yearly Corncrake population in the Netherlands. In 2001-2005, one quarter to one third of all territories were found in the Rhine branch floodplains. In 2004 this percentage was even higher. Since 1980 these percentages varied from 12 to 78%. Overall, the Rhine branches account for about one third of all territories in the Netherlands. Please note that table 1 shows number of territories, where the map in Appendix III depicts the singing sites.

Figure 3 shows the mean yearly density of singing males in floodplains with different occupation frequencies (see figure IV-2 in appendix IV for the floodplains). Floodplains that were occupied in all 5 years show a significantly higher density per year that they were occupied, in comparison with floodplains that were occupied in 2 of the 5 years. Other differences are not significant, but densities are clearly lower.

Distribution of the 2001-2005 singing sites over ecotope types was determined. Figure 4 shows the mean yearly density of singing males for each of the six most important ecotopes. Density varies between 0.1 and 0.62 singing males / ha. Especially rich structured herbaceous natural levee has a much higher density, whereas high-water free production meadow has a much lower density. The first four ecotopes all have a density of around 0.2 – 0.3 singing males/ ha. Mean density in suitable habitat (‘total’) is around 0.23 singing males / ha.

Table 2 shows the numbers of singing sites per ecotope and per year. Table 3 shows the percentages. There are 27 different ecotopes that harboured Corncrakes in this five year period. The ecotopes are ranked from highest numbers of Corncrakes to lowest numbers. The term “Water ecotope” is a collective term for different ecotopes that are almost permanently inundated. Singing sites located in these ecotopes are considered incorrect coordinates. They could be a result of misinterpretation of the singing site during fieldwork. Another likely explanation is differences in water levels between the moment the surveys were carried out (June) and the moment the aerial photographs were taken the ecotope map is based on. June is typically the month of lowest water levels so this could be the reason why some singing sites are in locations that are under water any other time of the year. Because of the discrepancy this data was excluded and a final list of 26 (land) ecotopes was used for the analyses. Figure 5 shows the same data as tables 2 and 3, aggregated to six classes. See also table II-1 in Appendix II for additional data on minimum and maximum acreages of the occupied ecotope patches.

Figure 3. Mean yearly density (singing males/ha) of Corncrakes for floodplains with different occupation frequencies. Standard errors are shown. Significance was tested using a Games-Howell test for unequal variances ($p<0.05$). Different letters indicate the significant differences; identical letters indicate no significant differences between the classes. 1 year: N=22, 2 years: N=26, 3 years: N=51, 4 years: N=36, 5 years: N=30.

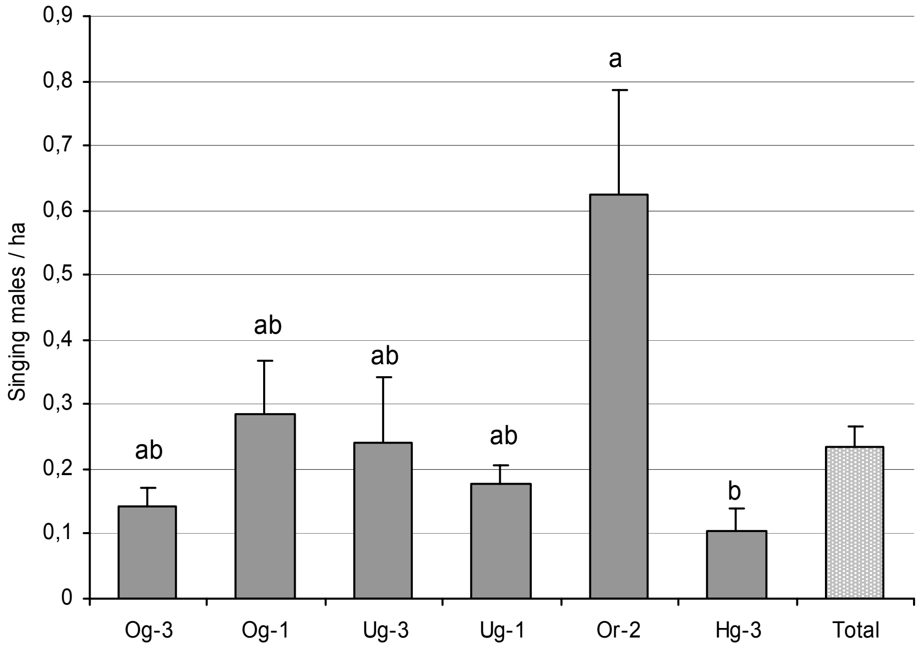

Figure 4. Mean yearly density (singing males/ha) of Corncrakes for the six most important ecotopes and for all six together. Standard errors are shown. Significance was tested using a Games-Howell test for unequal variances ($p<0.05$). Different letters indicate the significant differences; identical letters indicate no significant differences between the classes. Og-3=Natural levee production meadow (N=69); Og-1=Natural levee pasture (N=40); Ug-3=Floodplain production meadow (N=31); Ug-1=Rich structured floodplain pasture (N=25); Or-2=Rich structured herbaceous natural levee (N=21); Hg-3=High-water free production meadow (N=21).

Table 2. Numbers of singing sites per ecotope over the years 2001-2005.

Ecotope	All years	2001	2002	2003	2004	2005
Natural levee production meadow	238	47	50	78	45	18
Natural levee pasture	135	30	28	53	7	17
Floodplain production meadow	94	16	11	34	17	16
Rich structured floodplain pasture	77	3	22	39	7	6
Rich structured herbaceous natural levee	62	18	7	27	2	8
High-water-free production meadow	56	25	17	3	1	10
Water ecotope*	**46**	**7**	**4**	**7**	**14**	**14**
Rich structured herbaceous floodplain	46	7	13	11	15	0
Rich structured marshy floodplain pasture	36	3	2	3	21	7
Built up natural levee	29	11	2	9	6	1
High-water-free herbaceous rough	24	7	0	9	3	5
Herbaceous swamp	21	1	2	8	9	1
Bare high-water-free terrain	16	11	0	5	0	0
High-water-free natural pasture	16	4	8	4	0	0
Arable natural levee	15	1	0	3	6	5
Reed swamp	11	0	0	9	2	0
Natural levee production forest	7	0	0	5	2	0
Arable high-water-free terrace	7	0	4	3	0	0
Marshy floodplain production meadow	5	0	4	1	0	0
Pour structured herbaceous floodplain	5	0	5	0	0	0
Marshy floodplain softwood forest	2	0	0	2	0	0
Bare levee	2	0	2	0	0	0
Pour structured herbaceous natural levee	2	0	2	0	0	0
Floodplain seepage forest	1	0	1	0	0	0
Marshy floodplain shrubs	1	0	0	0	0	1
Natural levee softwood forest	1	1	0	0	0	0
High-water-free forest (softwood)	1	0	1	0	0	0
Total	**956**	**192**	**185**	**313**	**157**	**109**

(*) singing sites which were located in permanent water and therefore are excluded from further analyses.

Table 3. Percentages of singing sites per ecotope over the years 2001-2005.

Ecotope	All years	2001	2002	2003	2004	2005
Natural levee production meadow	25	24	27	25	29	17
Natural levee pasture	14	16	15	17	4	16
Floodplain production meadow	10	8	6	11	11	15
Rich structured floodplain pasture	8	2	12	12	4	6
Rich structured herbaceous natural levee	6	9	4	9	1	7
High-water-free production meadow	6	13	9	1	1	9
Water ecotope*	**5**	**4**	**2**	**2**	**9**	**13**
Rich structured herbaceous floodplain	5	4	7	4	10	0
Rich structured marshy floodplain pasture	4	2	1	1	13	6
Built up natural levee	3	6	1	3	4	1
High-water-free herbaceous rough	3	4	0	3	2	5
Herbaceous swamp	2	1	1	3	6	1
Bare high-water-free terrain	2	6	0	2	0	0
High-water-free natural pasture	2	2	4	1	0	0
Arable natural levee	2	1	0	1	4	5
Reed swamp	1	0	0	3	1	0
Natural levee production forest	1	0	0	2	1	0
Arable high-water-free terrace	1	0	2	1	0	0
Marshy floodplain production meadow	1	0	2	0	0	0
Pour structured herbaceous floodplain	1	0	3	0	0	0
Marshy floodplain softwood forest	0	0	0	1	0	0
Bare levee	0	0	1	0	0	0
Pour structured herbaceous natural levee	0	0	1	0	0	0
Floodplain seepage forest	0	0	1	0	0	0
Marshy floodplain shrubs	0	0	0	0	0	1
Natural levee softwood forest	0	1	0	0	0	0
High-water-free forest (softwood)	0	0	1	0	0	0
Total	**100**	**100**	**100**	**100**	**100**	**100**

(*) singing sites which were located in permanent water and therefore are excluded from the analyses.

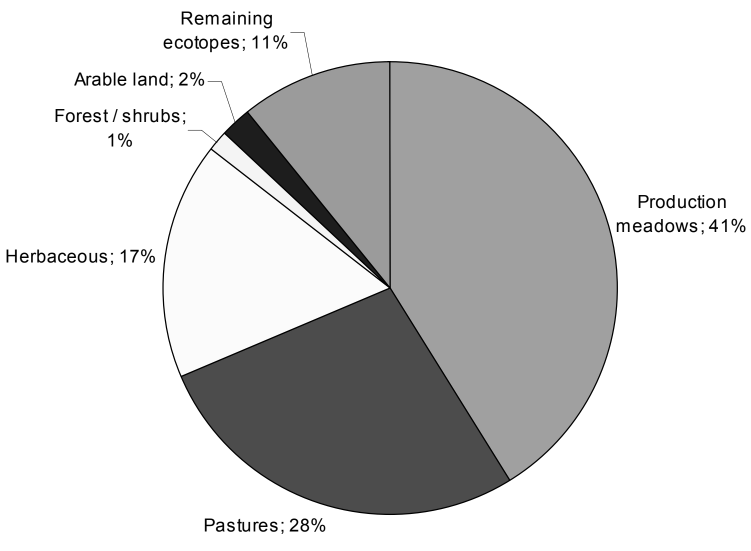

Figure 5. Ecotopes that contained Corncrakes, aggregated to six groups. Percentages singing sites are shown (N=956). The group 'Remaining ecotopes' contains ecotopes like bare and built-up terrain and water.

The ecotopes that are most important as Corncrake habitat appear to be production meadows and natural pastures (tables 2 and 3, figure 5): both are very abundant (see table II-1 in appendix II) and both are grasslands with some kind of mowing regime. This is in line with what is known about Corncrake habitat preferences. In addition, there are a number of ecotopes where Corncrakes were heard that would not be expected. However, numbers are much lower in these cases, suggesting a sporadic occurrence. Table II-1 further suggests that any patch larger than 0.3 ha is potentially suitable for harbouring an individual Corncrake.

In addition, a distinction was made between data from the first and from the second simultaneous survey (table 4). This was done in order to assess possible changes in ecotope preference in the course of the season.

Table 4. Comparison of numbers of singing sites per ecotope between the first (beginning of June) and the second (end of June) simultaneous survey (data of all five years).

Ecotope	All data	%	1st survey	%	2nd survey	%
Natural levee production meadow	238	25	46	29	45	23
Natural levee pasture	135	14	20	12	35	18
Floodplain production meadow	94	10	20	12	21	11
Rich structured floodplain pasture	77	8	12	7	14	7
Rich structured herbaceous natural levee	62	6	9	6	14	7
High-water-free production meadow	56	6	15	9	10	5
Water ecotope*	**46**	5	**8**	**5**	**11**	**6**
Rich structured herbaceous floodplain	46	5	9	6	10	5
Rich structured marshy floodplain pasture	36	4	3	2	8	4
Built up natural levee	29	3	1	1	5	3
High-water-free herbaceous rough	24	3	4	2	5	3
Herbaceous swamp	21	2	2	1	6	3
Bare high-water-free terrain	16	2	0	0	0	0
High-water-free natural pasture	16	2	4	2	2	1
Arable natural levee	15	2	0	0	3	2
Reed swamp	11	1	3	2	3	2
Natural levee production forest	7	1	1	1	1	1
Arable high-water-free terrace	7	1	2	1	2	1
Marshy floodplain production meadow	5	1	1	1	2	1
Pour structured herbaceous floodplain	5	1	0	0	1	1
Marshy floodplain softwood forest	2	0	0	0	0	0
Bare levee	2	0	0	0	0	0
Pour structured herbaceous natural levee	2	0	0	0	0	0
Floodplain seepage forest	1	0	0	0	1	1
Marshy floodplain shrubs	1	0	0	0	0	0
Natural levee softwood forest	1	0	1	1	0	0
High-water-free forest (softwood)	1	0	0	0	0	0
Total	**956**	100	**161**	100	**199**	100

(*) singing sites which were located in permanent water and therefore are excluded from the analyses.

Table 4 shows that there are relatively small differences in the ecotope occupation by the Corncrake between the beginning and end of June. Using a Chi-square test it was tested if the differences within production meadows and natural / herbaceous ecotopes are significant. Natural levee production meadow, floodplain production meadow and high-water free production meadow were classified as ‘Production meadow’. Natural levee pasture, rich structured floodplain pasture, rich structured herbaceous natural levee, rich structured herbaceous floodplain and rich structured marshy floodplain pasture were classified as ‘Natural pastures / herbaceous’. Shares of production meadows in harbouring Corncrakes show a strong significant decrease where the share of natural / herbaceous ecotopes significantly increases (Figure 6).

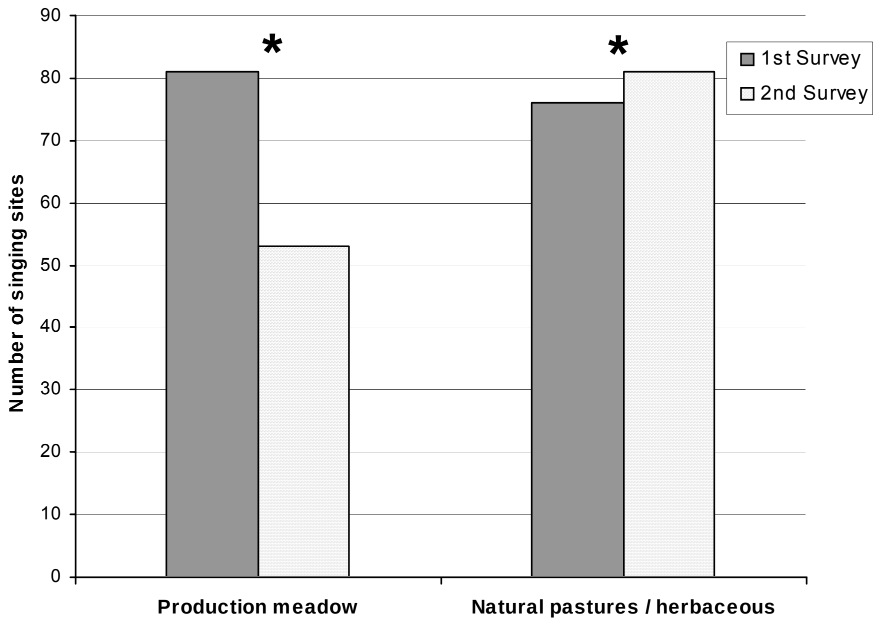

Figure 6. Difference in number of singing sites in production meadows and natural grasslands between the first and the second survey. The class 'Production meadow' consists of the ecotopes natural levee production meadow, floodplain production meadow and high-water free production meadow. The class 'Natural pastures / herbaceous' consists of the ecotopes natural levee pasture, rich structured floodplain pasture, rich structured herbaceous natural levee, rich structured herbaceous floodplain and rich structured marshy floodplain pasture (see table 4). Difference in distribution was tested using a Chi-square test ($p < 0.05$); significance is shown by the asterisk (*).

Singing sites were also related to inundation frequencies of the locations. Table 5 shows the numbers of singing sites per inundation class. The Corncrake mostly settles in areas that are inundated for a reasonably short period of time. Most singing sites (94%) are located in areas that are inundated for less than 50 days a year. On the other hand, these areas constitute more than 90% of the floodplains of the Dutch Rhine branches.
Figure 7 shows that inundations over the years 2001-2005 mainly occurred during the winter period (water discharges of more than 3000 m^3/s) and thus outside the Corncrake's breeding season. So rather than selecting its habitat based on inundation, the Corncrake seems to have adapted its entire life cycle to the cycle of the river; their late breeding season coincides with the period where water discharges (and thus water levels) are low.

Table 5. Inundation frequencies of locations were singing males were found.

Inundation frequency (+ % of floodplain area)	Number of singing sites	%
180 - 365 days/year (1.6%)	2	0.2
50 - 180 days/year (6.9%)	18	1.9
20 - 50 days/year (12.5%)	231	24.7
2 - 20 days/year (48.4%)	521	55.7
< 2 days/year (30.5%)	126	13.5
Unknown	37	4.0
Total	**935***	**100**

(*) total number differs from the total number in the ecotope tables, because of differences in the extend of the maps.

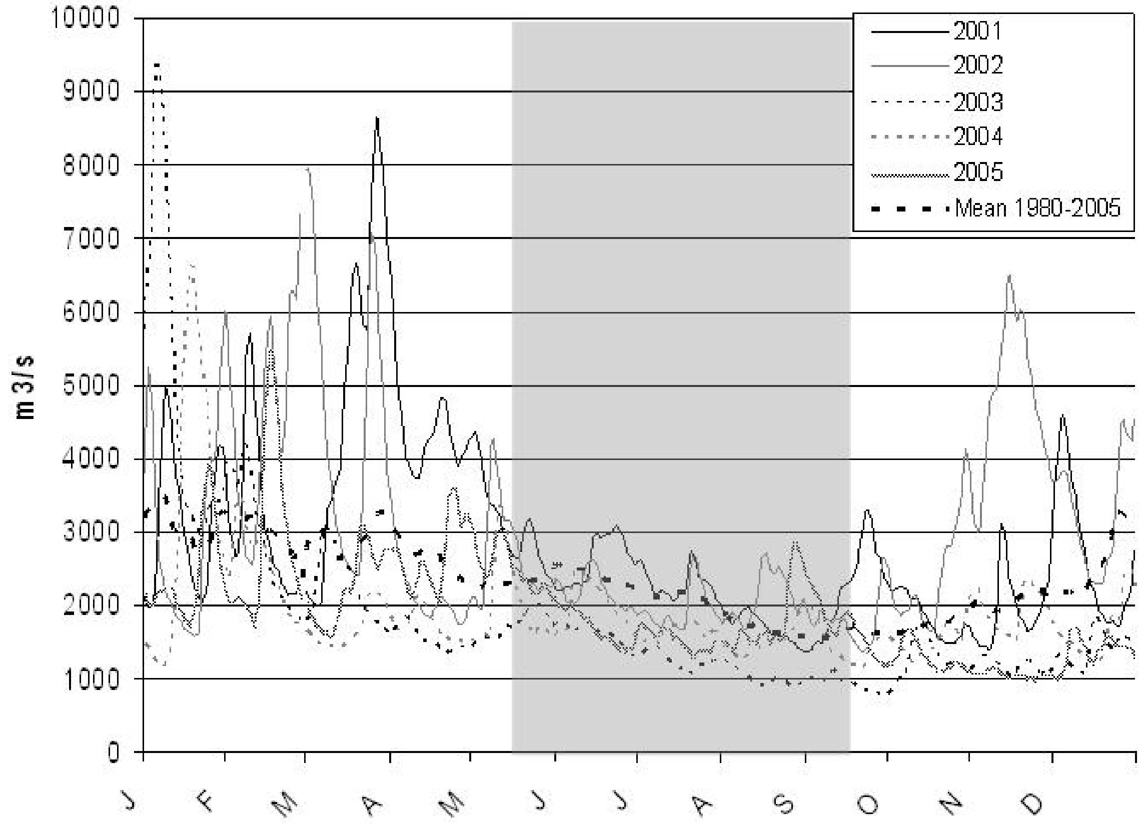

Figure 7. Monthly water discharge of the Rhine (measuring point Lobith) in the years 2001-2005, as well as an annual mean over 25 years (1980-2005). Data from: Rijkswaterstaat. The shaded area depicts the Corncrake's breeding period.

3.2 Landscape characteristics

3.2.1 Suitable habitat

Ecotope distributions in the 107 floodplains were analyzed and classified in area suitable habitat, area marginal habitat and area unsuitable habitat (see methods for a specification of the classes). Figure 8 shows percentages of these classes in relation to occupation frequency of the floodplains. The stacked graph shows an increase in available habitat (suitable and marginal) for floodplains that are occupied in more years, although floodplains that are occupied in 4 or 5 years in the period 2001-2005 show a smaller area of available habitat again, similar to the unoccupied floodplains. However, all differences are not significant.

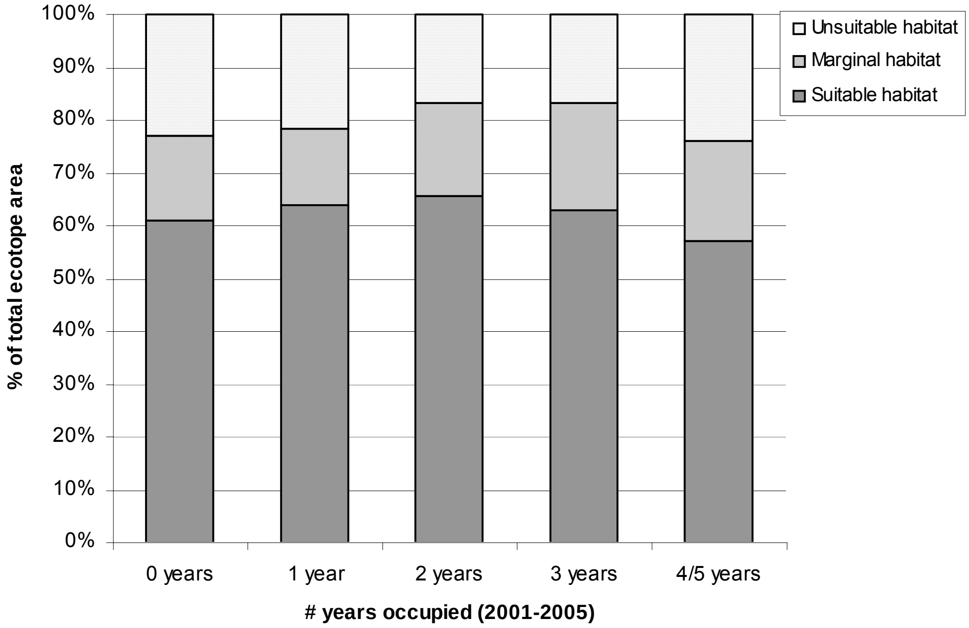

Figure 8. Mean percentages available habitat in relation to occupation frequency of the floodplain. Differences are not significant. Significance was tested using a Games-Howell test for unequal variances (p<0.05). 0 years: N=40, 1 year: N=22, 2 years: N=13, 3 years: N=17, 4/5 years: N=15.

3.2.2 Diversity of the landscape

The Shannon Diversity Index (SHDI) was calculated for all 107 floodplains (figure 9). The SHDI is a parameter for the diversity of the landscape: SHDI increases with an increasing number of patch types. In other words: a higher SHDI score means that the landscape has a higher degree of heterogeneity. Figure 6 shows that floodplains that have been occupied by the Corncrake in 3 or more of the 5 years have a significantly higher SHDI score than floodplains that were unoccupied in the period 2001-2005. This means that the landscape of frequently occupied floodplains have a higher heterogeneity than unoccupied floodplains.

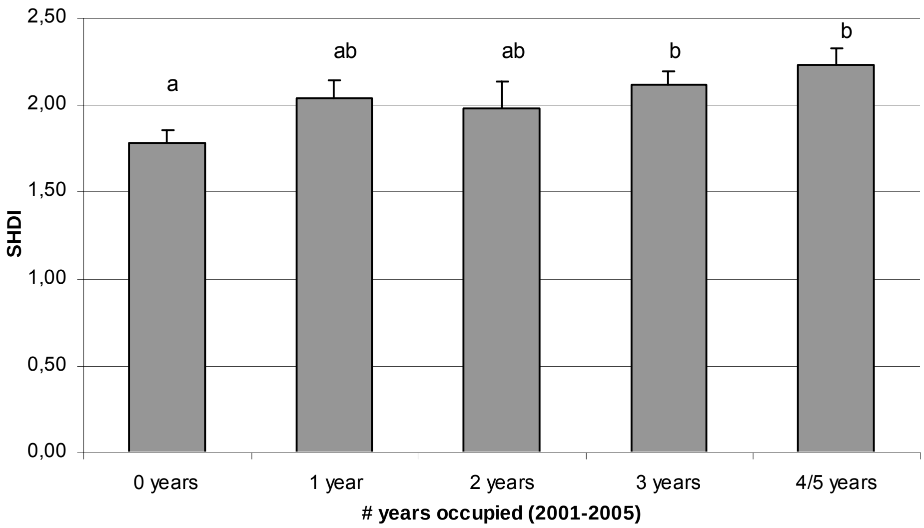

Figure 9. Mean SHDI score for floodplains that harboured Corncrakes for a different number of years. Standard errors are shown. Significance was tested using a Games-Howell test for unequal variances (p<0.05). Different letters indicate the significant differences; identical letters indicate no significant differences between the classes. 0 years: N=40, 1 year: N=22, 2 years: N=13, 3 years: N=17, 4/5 years: N=15.

In addition, patchiness of the floodplains was determined by counting the number of patches (polygons) per ha in every floodplain (patch density), as well as the number of different patch types per ha (patch type density). This gives additional information about the diversity of the landscape. The patch density does not differ significantly between floodplains with different occupation frequencies, but is slightly lower in the more frequently occupied floodplains (figure 10). The patch type density is significantly higher in the less frequently occupied floodplains. In combination with the SHDI results this means that, although there is no difference in patchiness, the more frequently occupied floodplains have less different types of ecotopes, resulting in a more equitable distribution of the area among the ecotopes and thus a higher SHDI.

Figure 10. Mean patch density and patch type density, in relation to occupation frequency. Standard errors are shown. Significance was tested using a Games-Howell test for unequal variances (p<0.05). Different letters indicate the significant differences; identical letters indicate no significant differences between the classes. 0 years: N=40, 1 year: N=22, 2 years: N=13, 3 years: N=17, 4/5 years: N=15.

4. Discussion

4.1 Spatial distribution

Originally, the typical Corncrake habitats are open riverine meadows and lowland marshes (Flade, 1997; Schäffer & Green, 2001; Schäffer & Koffijberg, 2004). As these deteriorated, cultivated grasslands where annual removal of vegetation occurs became an important secondary habitat. Apart from a large population in crops in the northern part of the Netherlands, river floodplains contain the largest area of important Corncrake habitat. In general, approximately one third of all Corncrake territories in the Netherlands are located in the floodplains along the Rhine branches (see table 1). In the period 2001-2005, 956 singing sites were reported along the whole extend of the Rhine branches: only one of the 15 river trajectories (the most downstream part of the Rhine) did not contain any singing sites.

Occurrence of Corncrakes in different floodplains was compared. A mean yearly density (singing males / ha) was determined for floodplains with different occupation frequencies (figure 3). Floodplains with a high occupation frequency show a higher mean density in comparison to floodplains with a lower occupation frequency. So floodplains that are occupied every year also harbour a higher density of Corncrakes. This indicates that these floodplains are favoured by the Corncrake. This fact should be taken into consideration when designing river management measures in such areas. Important Corncrake floodplains must be treated with special care to ensure suitable habitat. The question is which factors play a key role in habitat preference. In this study, effects of landscape composition of the floodplains on habitat selection are discussed.

The distribution of the singing sites from the period 2001-2005 was linked to an ecotope map to see which ecotopes were preferred by the Corncrake. Most singing sites were located in production meadows and natural pastures (tables 2 and 3, figure 5). This is in line with the Corncrake's documented habitat preference in the Netherlands (Braaksma, 1962; Schoppers & Koffijberg, 2006) but in most literature habitat characterization is limited to a general classification in grasslands, nature and crop fields. The results presented in this study give a more specific characterization based on the River Ecotope System (RES; Rademakers & Wolfert, 1994). The list in tables 2 and 3 also contains ecotopes with a very sporadic occurrence of Corncrakes. These should probably not be considered typical Corncrake habitat. Therefore, the top six ecotopes were classified as 'suitable habitat' and the rest of the list as 'marginal habitat'. The top six are also the most abundant ecotopes. This could be the very reason they are the most inhabited ones: lack of a better alternative. However, in table II-1 in Appendix II, the columns "# of patches occupied" and "% area occupied" show that the sporadic occurrence of Corncrakes in the lower 20 ecotopes is not due to a lack of these ecotopes. It is plausible that the top six ecotopes and especially the first two are indeed ecotopes that are favoured by the Corncrake. For these six ecotopes the mean density was calculated (figure 4). Density varies between 0.1 singing males / ha for high-water free production meadow and 0.6 for rich structured herbaceous natural levee. Mean density for all six ecotopes together is 0.23 singing males / ha. Duel *et al*. (1996) use for the MORRES calculation rule for the Corncrake a reference density of 60 breeding pairs per 100 ha. In the case of the Corncrake it is difficult to express its numbers in breeding pairs since it is unclear how well singing sites or territories relate to number of pairs (Green *et al.*, 1997; Schäffer, 1999; Schäffer & Koffijberg, 2004). However, when assuming that each singing male will eventually attract a female and form a breeding pair, numbers of singing sites can thus regarded as pairs (0.23pairs/ha). The present results then show a reference density of about 23 breeding pairs per 100 ha suitable habitat. This is considerably lower than the MORRES reference density. However, the latter is based on ideal, natural circumstances with high quality habitat. Dutch rivers and their floodplains are highly regulated and habitat quality can be expected to be lower, resulting in overall lower densities. Although Duel *et al*. (1996) give a good reference density for pristine habitats they have not made any distinction between various ecotopes for their reference value. However, regarding the partly significant differences shown in figure 4, it is recommended to apply different reference values for different ecotopes in the MORRES calculation rule for the Corncrake. More reliable reference densities for various ecotopes could be obtained by studying Corncrake habitat preference in a more natural, pristine river system.

By distinguishing between the singing sites found during the first (beginning of June) and the second (end of June) simultaneous survey, it was studied if a shift in ecotope preference would occur in the course of the season. Table 4 shows that the most important difference is the decrease in percentage singing sites in the production grasslands and the increase in natural levee pasture. Results from further analysis of these differences show a significant shift from production grasslands to pastures and herbaceous grasslands in the second half of June (Figure 6). This could be an indication that mowing in mid June causes production grasslands to become unsuitable for Corncrakes for the rest of the season. Habitat suitability is strongly correlated with vegetation height (Tyler, 1996; Schäffer, 1999). Disturbed Corncrakes could switch to more naturally managed ecotopes, like natural levee pastures or herbaceous levees. Similar shifts in habitat preference were found in Poland (Schäffer, 1999) and Germany (Just, 2005). In the area Unteres Odertal in Germany height of vegetation and total cover of grassland vegetation were the key variables for the occurrence of Corncrakes in the middle of May. In the middle of June this was land use. Mowing is the most probable explanation for this shift. Early in the season Corncrakes prefer meadows with high-grown grass which is cut once a year. By the middle of June most meadows are being mown. Preference then shifts to meadows with a later mowing date (Just, 2005).

Mechanisation of hay making, resulting in earlier mowing dates, has been identified as the most important factor for the decline of the Corncrake in Europe in the last decades (Broyer, 2003; Keišs, 2005; Schoppers & Koffijberg, 2006). Current conservation measures therefore aim to delay haymaking until the beginning of August, as well as using Corncrake friendly mowing methods (Broyer, 2003; Schoppers & Koffijberg, 2006). To get more insight into factors of disturbance and shifts in habitat preference of the Corncrake in the Netherlands, further studies will have to be carried out over a larger period in the season. For instance by comparing the initial settlement in May / June with Corncrake distribution at the end of July / beginning of August. Besides human-induced changes also the natural development of vegetation over the course of the season is important (Tyler, 1996; Schäffer, 1999; Schäffer & Koffijberg, 2004). Factors like vegetation height, vegetation density (penetration force) and amount of dead plant material should therefore be included in future studies.

Inundation is an important factor in river floodplains and therefore also affects the Corncrake's habitat. Figure 7 shows how the Corncrake seems to have adapted its life cycle to the cycle of the river: this is also the reason for its late breeding season. Originally, with riverside meadows being its natural habitat, the Corncrake was largely dependent on the periodic removal of vegetation and dead material by flooding and ice-rafting, preventing the system from developing into a climax stage with mainly bushes and trees (Schäffer & Green, 2001). For this reason, inundations in the winter period could have been important for the Corncrake and several studies claim that winter inundations are also in the present landscape an important factor in riverside habitats (Braaksma, 1962; Flade, 1997; Green *et al*., 1997). Nowadays however, in the cultivated meadows that dominate the floodplains, vegetation removal is often realized only by mowing activities since natural dynamics in water tables are largely regulated. In this respect there is another significant aspect to flooding. Areas that remain flooded for a longer period of time are mown later in the season due to poor accessibility for mowing machines (soft and moist soil). This is beneficial to Corncrakes, because these areas provide suitable habitat later in the season. Delayed hay-making is generally thought to be the most important effect of inundation (Van Den Bergh, 1991).
On the other hand, it is possible that flooding can also influence Corncrake settlement in a negative way. High water will halt vegetation development until the water retreats. Upon first arrival of the Corncrake in May and June, certain areas can still be flooded or provide poor vegetation cover. This is suspected to be the case in 2006, when first reports came in. Numbers of singing males in June were still very poor. Water levels in the Rhine branches were higher then normal; no singing males were reported along the river Waal until the 26^{th} of June and known singing sites along the river IJssel were even flooded (www.kwartelkoning.nl).

It is evident that flooding regimes have an effect on the Corncrake's habitat and this can both be in a positive and a negative way. Results in this study are not conclusive: at first sight there seems to be a preference for areas that are flooded less than 50 days a year. This could indicate that indeed a period of inundation in winter is necessary for the rejuvenation processes. However, it might also be caused simply by the fact that about 90% of the floodplain area falls within this class. To properly study the effects of flooding on habitat suitability it would be better to look at exact inundation dates rather than general inundation frequencies. The moment the water retreats is probably more determining for settlement of the Corncrake than the number of days a floodplain is flooded. Vegetation development and mowing dates in flooded areas are determined by water retreat. Moreover, this approach will take unusual flooding events into account, like summer highwaters. This could give insight into fluctuating Corncrake numbers in the Rhine floodplains.

4.2 Landscape characteristics

The results show that there are no significant differences in availability of certain specific ecotopes between floodplains with an occupation frequency of every year and those that were never occupied in the period 2001-2005. Figure 8 shows some minor differences, with floodplains that were occupied 2 or 3 years having a slightly higher proportion of suitable and marginal habitat. However, for yearly occupied floodplains this proportion is lower again. Based on these results it can not be concluded that floodplains that were never occupied in the years 2001-2005 have an unfavourable ecotope distribution. Of course, the classification in suitable, marginal and unsuitable habitat was based on the number of singing sites located in these ecotopes. As was said before, the six ecotopes that came out as favourable are also the ones that are most abundant in the floodplains of the Dutch Rhine branches. In almost every floodplain these ecotopes, and especially natural levee production meadow and natural levee pasture, are present. In a study in Latvia, Keišs (2003) also found that meadows are the most important habitat for Corncrakes. He even assumed that the number of Corncrakes in Latvia is directly related to the area of meadows. Considering the reasonably low annual numbers of Corncrakes in the Dutch Rhine floodplains and the abundance of these types of ecotopes, it is thought that habitat availability in terms of area is currently not a limiting factor for the population size in the Netherlands.

As for landscape diversity, results show some significant differences between the floodplains. Floodplains with a higher occupation frequency have a significantly higher SHDI score than unoccupied floodplains (figure 9). Patch density does not differ significantly between floodplains with a higher occupation frequency and unoccupied floodplains. However, patch type density is lower in more frequently occupied floodplains (figure 10). This means that the higher SHDI score is not a result of an increased number of different patch types, but rather of a more equitable proportional distribution of area among patch types. When a floodplain consists of a lot of patches of different size and type, the proportional distribution of area becomes more inequitable, resulting in a lower SHDI (McGarigal & Marks, 1994). These results suggest that the Corncrake favours floodplains which have a diverse, heterogenic landscape. This can be explained by the character of its original habitat: natural rivers are characterized by a very heterogenic landscape, created by the dynamics of the river. Results further show that the patchiness of the landscape does not seem to be a significant factor in determining Corncrake settlement.

4.3 Other factors

Overall it must be concluded that, although a heterogenic landscape is certainly favoured by the Corncrake, landscape composition does not seem to be a driving force behind habitat selection on a floodplain scale. What became clear during the analyses is that the different floodplains are not that different from each other in composition. The ecotopes that are favoured by the Corncrake are at the same time the most abundant. It seems that the majority of all floodplains are potentially suitable for harbouring Corncrakes. However, this is apparently not the case. Maybe the scale level, floodplains, is already too large. An ecotope is defined as a spatial ecological unit of which the composition and development are determined by their abiotic, biotic and anthropogenic factors (Rademakers & Wolfert, 1994). However, regional and local differences have not been incorporated in the classification (Rademakers & Wolfert, 1994). Also, a degree of homogeneity still exists within ecotopes. For these reasons a clear detection of Corncrake's habitat preferences may be hindered by the scale level of the study. Some analyses were also done on an even larger scale level – river trajectory - to see if this would give other results. This produced insignificant data, because the scale level is too large. With increasing scale, landscape dynamics decrease and local processes become invisible (Geerling *et al.*, 2006). Possibly there are factors on a smaller scale level that are more determining, but do not become clear in this analysis, such as food availability and vegetation type and structure. Because Corncrakes are quite opportunistic feeders and principal prey items also occur in habitats not inhabited by Corncrakes, it is generally thought that vegetation structure is the key factor explaining distribution (Schäffer & Koffijberg, 2004). However, prey density might differ between areas, so studying food availability could still provide useful information. One other factor that is generally thought to be of importance is clustering. Corncrake males have the tendency to choose their singing location in such a way that their call is being amplified: close to an echoing structure for example (Schäffer & Koffijberg, 2004). For the same reason males seem to be attracted by the presence of an already settled male.

This has the advantage that their combined calls can be heard over a much larger area, attracting females from further away. Also, settling in the vicinity of another male can have the advantage that females attracted by the neighbour can be lured away, into the own territory. Sklíba & Fuchs (2004) have shown that males deliberately visit neighbouring territories during the day, probably to seek for females. No studies have been conducted yet that specifically prove a cluster effect. However, when looking at the singing sites superficially, one cannot but suspect that such an effect does indeed exists (see Appendix III). Of course, when it does, this will have consequences for this study: floodplains will remain unoccupied simply because the first arriving males have not settled here. This will not mean that these floodplains are unsuitable to settle. To really study which landscape ecological factors are important for habitat selection it is recommended to look at the settling sites of the early arriving birds. However, to do this correctly this will require a simultaneous survey earlier in the season, before clustering takes place.

On a floodplain scale it is thought that type of land use and changes herein is a stronger driving force in habitat selection by the Corncrake than ecotope availability. Several studies have shown this for other European countries (Green & Stowe, 1993; Schäffer & Green, 2001; Keišs, 2005). Corncrake habitats in Europe are mostly managed lands (Schäffer, 1999). When agricultural land changes into property of nature conservation foundations the management of the area will change. Suitability for Corncrakes can increase or decrease, depending on the type of management applied. On the other hand increased or decreased use of pesticides, fertilizer and fast-growing grasses on agricultural lands will be of negative influence on habitat suitability. Vegetation density is increased by these applications, while Corncrakes prefer less dense fields (Tyler, 1996). It is recommended to do further research in which land use within the floodplains is included. Function (agriculture versus nature), mowing regime, pesticide and fertilizer use and management agreements can all be taken into account. A multi-variable dataset will give insight in Corncrake occurrence in relation to landscape characteristics and in which factors play a key role in habitat selection. This information can be used to harmonise river management measures in the floodplains with Corncrake habitat requirements.

Nature development plans that are being implemented along the rivers can also be an important factor explaining Corncrake population dynamics. The landscape can change in such a way that the area becomes either more or less suitable for Corncrake settlement. Including these measures in future studies, as well as the number of years after implementation could explain new settlements and disappearance in certain areas.

4.4 Implications for management

The present study shows the ecotope preference of the Corncrake. When looking at this in the light of the 'Room for the River' alternatives that are planned, it becomes clear that Corncrake habitat will be affected by these measures. Figures presented in the environmental impact assessment report "Room for the River" (Anonymous, 2005) show that the area of production grasslands and natural levee pastures will decrease in Special Protection Areas along the rivers Waal, Lower Rhine / Lek and IJssel, as a result of either of the alternatives. These ecotopes constitute the most important habitats for the Corncrake in the Rhine floodplains. Whether this decrease in suitable area will affect the carrying capacity of the floodplains for Corncrakes is not clear, because production grasslands and pastures are quite abundant along the rivers. However, for a number of important floodplains that harboured Corncrakes in four or five of the years, management plans were formulated. For the floodplains Millingerwaard (Waal), Meinerswijk (Lower Rhine) and Stiftsche Uiterwaarden (Waal) for instance, excavation plans are included in the alternatives or already being executed. This will have implications in the short term for the quality of these floodplains for the Corncrake. Overall, floodplains that are known to be important Corncrake areas (e.g. the ones with high occupation frequencies; table III-1, appendix III) must be treated with care when management measures are being planned, and Corncrake habitat requirements must be considered in the plans.

When translating the figures on densities of singing males to densities of breeding couples, this results in a different reference value than the one used by Duel *et al*. (1996) in the MORRES rule for the Corncrake. The MORRES reference density is based on high quality natural habitats, whereas the reference densities from this report are based on Dutch floodplain habitats. The MORRES reference provides a target density for ideal situations and is more useful for setting conservation goals. However present results also suggest that different reference densities apply for different ecotopes. When calculating the carrying capacity of an area for the Corncrake these differences should be considered.

Including this distinction in the calculation rules will result in a more reliable output and is therefore recommended.

Validating the BIO-SAFE species - ecotope relation for the Corncrake shows that the ecotopes that are most important according to this study - natural levee production meadow and natural levee pasture - are actually not included. Rich marsh grassland and floodplain hayfield are the only ecotopes linked to the Corncrake as being suitable habitat. These are indeed suitable Corncrake habitats. However present results suggest that some additions and specifications might be in order to make the model more complete for this species.

5 Conclusions

1. River floodplains provide important habitat for the Dutch Corncrake population; one third of all territories are located in the floodplains of the Rhine branches annually.
2. In general production meadows and pastures are typical Corncrake habitat. The ecotopes natural levee production meadow and natural levee pasture are the most favoured by the Corncrake. Both are not identified as suitable habitat in BIO-SAFE.
3. Mean densities for the six most important ecotopes ("suitable habitat") vary between 0.1 singing males / ha for high-water free production meadow and 0.6 for rich structured herbaceous natural levee. The reference density currently used in MORRES (60 breeding pairs / 100 ha) is a lot higher than an overall reference density derived from current results (46 pairs / 100 ha). The lower number is most likely caused by the lower quality of Dutch floodplain habitats.
4. Densities are also significantly higher in floodplains that are occupied every year. Apparently these floodplains are preferred by Corncrakes.
5. There is no significant difference in surface area of suitable habitat between floodplains that were not occupied in the years 2001-2005 and floodplains that were occupied for a number of years. Hence, ecotope distribution alone is not sufficient for explaining apparent preference of the Corncrake for certain floodplains.
6. Based on the SHDI and patch type density results, Corncrakes seem to favour floodplains which have a diverse, heterogenic landscape, with a relatively limited number of different ecotopes that are evenly represented. SHDI score is higher because the area of the floodplain is distributed more evenly among the different ecotopes. Patchiness (patch density) of the area does not seem to influence suitability of the landscape.
7. Results suggest a shift in habitat preference in the course of the breeding season, from production grasslands to pastures and herbaceous grasslands. It is assumed that this shift is caused by mowing activities in the middle of June.
8. Based on these results, it can not be concluded that landscape composition (in terms of present ecotopes and diversity) has a significant influence on the presence or absence of Corncrakes in a floodplain.
9. Results on inundation frequencies are not conclusive. Most singing sites are located in floodplains that are inundated less than 50 days a year. However, these constitute 90% of the floodplains.
10. The floodplains of the Dutch Rhine branches contain extensive areas of potentially suitable landscape for the Corncrake. However, analysis on the level of ecotopes is probably too coarse: there is still a lot of heterogeneity within ecotopes. Factors on a smaller scale (vegetation structure and cover, land management, clustering) are probably of more importance for distribution of the Corncrake.

6 Recommendations

1. Aspects of land use (nature reserves versus agriculture, mowing regime, grazing regime, management agreements, years since management measures) should be included in further studies to see if this can explain Corncrake preference for certain areas.
2. Because results show different reference densities for different ecotopes, distinguishing between ecotopes in calculation rules (e.g. MORRES) is recommended. Conducting a study in a pristine river system might provide better 'ideal situation' reference densities for various ecotopes.
3. The species - ecotope relation in BIO-SAFE can be improved by adding the important grassland ecotopes. This will enhance the models output reliability for this species.
4. To study influence of flooding frequency on Corncrake settlement, more accurate data on flooding is necessary: which areas were flooded during which days of the breeding season. For the winter months, the number of days flooded will be sufficient, as this will indicate rejuvenation of herbaceous vegetation.
5. A study on a possible cluster effect in settlement by male Corncrakes will be interesting. This can reveal how important presence of other males is in habitat selection in comparison to landscape characteristics. At the same time the early arriving birds will be expected to show an even stronger correlation with landscape and vegetation. Habitat preference can then be studied without influence of the cluster effect.

6. Comparing habitat preference over a larger period of time might give insight in changes in suitability of ecotopes over the season. Combined with data on land use and vegetation development this will enhance understanding of habitat selection and disturbance.
7. Repeating this study when the new Ecotope map becomes available will present more up to date results and can give insight in ecotope transitions that have occurred over the period of nine years, as well as in Corncrake distribution in relation to turnover of ecotopes.

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Appendix I. Test of coordinate accuracy

Table I-1. Distribution of singing sites over the ecotopes, with different accuracies separated.

Ecotope	All data	%	10m coordinates	%	100m coordinates	%	1000m coordinates	%
Natural levee production meadow	238	25	176	25	62	27	0	0
Natural levee pasture	135	14	111	16	21	9	3	14
Floodplain production meadow	94	10	73	10	17	8	4	19
Rich structured floodplain pasture	77	8	65	9	11	5	1	5
Rich structured herbaceous natural levee	62	6	56	8	6	3	0	0
High-water-free production meadow	56	6	36	5	12	5	8	38
Water ecotope*	**46**	5	**20**	**3**	**22**	**10**	**4**	**19**
Rich structured herbaceous floodplain	46	5	37	5	9	4	0	0
Rich structured marshy floodplain pasture	36	4	33	5	3	1	0	0
Built up natural levee	29	3	13	2	16	7	0	0
High-water-free herbaceous rough	24	3	19	3	5	2	0	0
Herbaceous swamp	21	2	12	2	9	4	0	0
Bare high-water-free terrain	16	2	16	2	0	0	0	0
High-water-free natural pasture	16	2	9	1	7	3	0	0
Arable natural levee	15	2	10	1	5	2	0	0
Reed swamp	11	1	5	1	6	3	0	0
Natural levee production forest	7	1	7	1	0	0	0	0
Arable high-water-free terrace	7	1	5	1	2	1	0	0
Marshy floodplain production meadow	5	1	5	1	0	0	0	0
Pour structured herbaceous floodplain	5	1	0	0	5	2	0	0
Marshy floodplain softwood forest	2	0	0	0	2	1	0	0
Bare levee	2	0	0	0	2	1	0	0
Pour structured herbaceous natural levee	2	0	0	0	2	1	0	0
Floodplain seepage forest	1	0	0	0	1	0	0	0
Marshy floodplain shrubs	1	0	0	0	0	0	1	5
Natural levee softwood forest	1	0	1	0	0	0	0	0
High-water-free forest (softwood)	1	0	0	0	1	0	0	0
Total	**956**	100	**709**	100	**226**	100	**21**	100

(*) singing sites which were located in permanent water and therefore are excluded from the analyses.

Appendix II. List of Corncrake ecotopes

Table II-1. Additional information on abundance of the 26 ecotopes specified as 'potential suitable habitat' in the Dutch Rhine area. The table specifies the number of polygons in the ecotope map and the number of these with singing sites, the smallest and largest polygon and the smallest occupied. Ecotopes are sorted in order of number of singing sites that occur in the ecotope.

Ecotope	# of patches	# of patches occupied	Total area of patches (ha)	Min area (ha)	Max area (ha)	Total area occupied (ha)	% Area occupied	Min area occupied (ha)
Natural levee production meadow	732	48	8549.21	0.01	430.86	2759.87	32.28	0.76
Natural levee pasture	524	24	1531.70	0.20	45.74	300.57	19.62	0.32
Floodplain production meadow	687	25	2721.80	0.09	143.41	579.98	21.31	0.33
Rich structured floodplain pasture	447	15	1142.92	0.12	28.05	147.04	12.87	1.51
Rich structured herbaceous natural levee	428	18	469.26	0.07	21.14	80.73	17.20	0.30
High-water-free production meadow	593	15	5397.99	0.16	773.46	1478.38	27.39	1.67
Rich structured herbaceous floodplain	399	10	373.84	0.12	14.22	30.64	8.20	0.92
Rich structured marshy floodplain pasture	166	9	280.31	0.13	21.63	46.14	16.46	0.64
Built up natural levee	101	1	110.39	0.12	32.47	32.47	29.41	32.47
High-water-free herbaceous rough	230	9	290.24	0.08	14.96	69.82	24.06	0.31
Herbaceous swamp	540	9	486.64	0.05	11.42	24.75	5.09	0.41
Bare high-water-free terrain	113	1	161.04	0.15	6.17	4.80	2.98	4.80
High-water-free natural pasture	260	8	675.35	0.21	53.50	102.81	15.22	1.45
Arable natural levee	187	4	868.91	0.14	87.27	16.46	1.89	1.12
Reed swamp	357	4	294.96	0.05	18.86	32.21	10.92	2.04
Natural levee production forest	75	1	68.09	0.09	12.77	10.05	14.76	10.05
Arable high-water-free terrace	216	3	1386.22	0.18	87.39	103.92	7.50	7.38
Marshy floodplain production meadow	106	3	319.14	0.15	43.02	7.30	2.29	0.91
Pour structured herbaceous floodplain	51	1	41.13	0.10	3.19	0.74	1.80	0.74
Marshy floodplain softwood forest	230	1	259.74	0.06	20.95	0.24	0.09	0.24
Bare levee	129	1	226.47	0.12	29.03	4.29	1.89	4.29
Pour structured herbaceous natural levee	94	1	100.93	0.12	13.07	13.07	12.95	13.07
Floodplain seepage forest	8	1	7.21	0.42	1.84	0.54	7.49	0.54
Marshy floodplain shrubs	239	1	187.22	0.07	10.93	1.83	0.98	1.83
Natural levee softwood forest	396	1	232.93	0.04	7.75	2.82	1.21	2.82
High-water-free forest (softwood)	203	1	109.69	0.05	6.23	0.07	0.06	0.07

Appendix III. List of floodplains included in analyses

Table III-1. The 107 floodplains that were used in this study: 67 with and 40 without Corncrake singing sites.

Branch	Trajectory code	Trajectory name	Floodplain	Area (ha)	# of years occupied
R	B1	Bovenrijn	Lobberdensche Waard	316,04	0
R	R1	omgeving splitsingspunt Pannerdense Kop	Pannerdensche buitenwaard	119,68	0
Y	R2	omgeving splitsingspunt IJsselkop	Westervoort	32,62	0
Y	R2	omgeving splitsingspunt IJsselkop	Hondsbroeksche pleij	11,51	0
R	R3	Doorwerthse Nederrijn	Drielsche uiterwaarden	121,86	0
R	R3	Doorwerthse Nederrijn	Doorwerthsche waarden	192,78	0
R	R4	Gestuwde Nederrijn en Lek	Honswijkerwaarden	97,80	0
R	R4	Gestuwde Nederrijn en Lek	Elster buitenwaarden	157,43	0
R	R4	Gestuwde Nederrijn en Lek	Schalkwijker buitenwaard	165,57	0
R	R4	Gestuwde Nederrijn en Lek	Lunenburgerwaard	131,89	0
R	R4	Gestuwde Nederrijn en Lek	Koornwaard	132,32	0
R	R4	Gestuwde Nederrijn en Lek	Rijswijcksche buitenpolder	263,42	0
R	R4	Gestuwde Nederrijn en Lek	Schoutenwaard	71,45	0
R	R4	Gestuwde Nederrijn en Lek	Middelwaard	105,94	0
R	R5	Boven-Lek	t Waalsche waard	60,18	0
R	R5	Boven-Lek	Bossenwaard	60,33	0
R	R5	Boven-Lek	Heerenwaard	51,61	0
R	R5	Boven-Lek	Polder de Eendragt	327,95	0
R	R5	Boven-Lek	Vogelzang	73,08	0
R	R5	Boven-Lek	Lekwaard	85,73	0
W	W2	Middenwaal	Loenensche buitenpolder	167,69	0
W	W2	Middenwaal	Gouverneursche polder	334,29	0
W	W2	Middenwaal	Drutensche waarden oost	164,54	0
W	W2	Middenwaal	Afferdensche en Deestsche waarden	305,47	0
W	W2	Middenwaal	Ewijcksche waard	87,63	0
W	W3	Waal omgeving St. Andries	Heeseltsche middenplaat	100,14	0
W	W3	Waal omgeving St. Andries	Rossumsche waard	30,71	0
W	W4	Benedenwaal	Kerkenwaard	191,57	0
W	W4	Benedenwaal	Ruyterwaard	115,06	0
W	W4	Benedenwaal	Groesplaat	7,80	0
W	W4	Benedenwaal	Gamerensche waarden	100,09	0
Y	Y1	Boven-IJssel	Rheden en de Steeg	82,16	0
Y	Y1	Boven-IJssel	Zuiderwaard	319,09	0
Y	Y2	Midden-IJssel	Wilpse klei	676,09	0
Y	Y2	Midden-IJssel	Gelderhoofdsche waard	34,13	0
Y	Y2	Midden-IJssel	Brummensche waarden	430,60	0
Y	Y4	Sallandse IJssel, noordelijk deel	Harculosche buitenwaarden	118,86	0
Y	Y4	Sallandse IJssel, noordelijk deel	Herxer uiterwaarden	80,48	0
Y	Y5	Beneden-IJssel	Kampen	87,68	0
Y	Y5	Beneden-IJssel	Spoolderwaard	13,87	0
W	B1	Bovenrijn	Tolkamer	72,89	1
R	R1	omgeving splitsingspunt Pannerdense Kop	Loowaard	225,06	1
R	R3	Doorwerthse Nederrijn	Renkumse benedenwaarden	127,27	1
R	R3	Doorwerthse Nederrijn	Randwijcksche uiterwaarden	192,71	1
R	R3	Doorwerthse Nederrijn	Rosandepolder	211,32	1
R	R4	Gestuwde Nederrijn en Lek	Mauriksche- en Ecksche waarden	303,62	1
R	R4	Gestuwde Nederrijn en Lek	Beusichemse waard	235,10	1
R	R4	Gestuwde Nederrijn en Lek	Lazaruswaard	73,93	1
R	R4	Gestuwde Nederrijn en Lek	Rhenen	77,00	1

Branch	Trajectory code	Trajectory name	Floodplain	Area (ha)	# of years occupied
W	W1	Waalbochten	Bemmelsche waarden	406,74	1
W	W1	Waalbochten	Buiten Ooy	235,84	1
W	W2	Middenwaal	Willemspolder	475,12	1
W	W4	Benedenwaal	Breemwaard	128,43	1
Y	Y1	Boven-IJssel	Noordingsbouwing	224,92	1
Y	Y1	Boven-IJssel	Fraterwaard	300,93	1
Y	Y1	Boven-IJssel	Velperwaarden	168,09	1
Y	Y2	Midden-IJssel	Epseweerdse polder	225,59	1
Y	Y2	Midden-IJssel	Olburgsche waard	153,75	1
Y	Y3	Sallandse IJssel, zuidelijk deel	Welsumvelder buitenwaarden	201,07	1
Y	Y3	Sallandse IJssel, zuidelijk deel	Deventer	122,91	1
Y	Y4	Sallandse IJssel, noordelijk deel	Wijher buitenwaarden	119,30	1
Y	Y5	Beneden-IJssel	Bentinkswellen	128,35	1
R	R1	omgeving splitsingspunt Pannerdense Kop	Doorneburgsche buitenwaard	92,25	2
W	W1	Waalbochten	Gendtsche waarden	408,05	2
W	W2	Middenwaal	Hiensche uiterwaarden	293,86	2
W	W2	Middenwaal	Winsensche waarden	231,32	2
W	W3	Waal omgeving St. Andries	De Kop	190,34	2
W	W3	Waal omgeving St. Andries	Hurwenensche uiterwaarden	415,12	2
Y	Y1	Boven-IJssel	Havikerwaard	1147,51	2
Y	Y2	Midden-IJssel	Bolwerksweide	235,48	2
Y	Y2	Midden-IJssel	Ravenswaarden	227,70	2
Y	Y2	Midden-IJssel	Rammelwaard	199,16	2
Y	Y2	Midden-IJssel	Reuversweerd	294,62	2
Y	Y5	Beneden-IJssel	Onderdijksche waard	79,93	2
Y	Y5	Beneden-IJssel	Zalkerbos en de Welle	253,59	2
R	R4	Gestuwde Nederrijn en Lek	Amerongsche bovenpolder	424,24	3
R	R4	Gestuwde Nederrijn en Lek	Wageninger benedenwaarden	186,52	3
R	R4	Gestuwde Nederrijn en Lek	Rhenensche buitenwaarden	232,75	3
W	W1	Waalbochten	Groenlanden	143,31	3
W	W2	Middenwaal	Wamelsche uiterwaard	186,54	3
W	W3	Waal omgeving St. Andries	Rijswaard	205,23	3
W	W3	Waal omgeving St. Andries	Heesseltsche uiterwaard	286,62	3
W	W4	Benedenwaal	Munnikenland	192,62	3
Y	Y1	Boven-IJssel	Vaalwaard	212,06	3
Y	Y2	Midden-IJssel	Stokebrandsweerd	95,98	3
Y	Y3	Sallandse IJssel, zuidelijk deel	Olster waarden	166,47	3
Y	Y3	Sallandse IJssel, zuidelijk deel	Keizers- en Stobbenwaard	300,37	3
Y	Y3	Sallandse IJssel, zuidelijk deel	Terwolderdorpenwaarden	134,35	3
Y	Y4	Sallandse IJssel, noordelijk deel	Scheller en Oldener buitenwaarden	166,27	3
Y	Y4	Sallandse IJssel, noordelijk deel	Gelderdijksche waard	79,99	3
Y	Y4	Sallandse IJssel, noordelijk deel	Vorchter waarden	129,35	3
Y	Y5	Beneden-IJssel	Vreugderijker waard	138,09	3
W	B1	Bovenrijn	De Bijland	597,06	4
R	R1	omgeving splitsingspunt Pannerdense Kop	Huissensche waarden zuid	479,36	4
W	W1	Waalbochten	Oosterhoutsche weilanden	247,21	4
W	W1	Waalbochten	Millingerwaard	583,76	4
W	W3	Waal omgeving St. Andries	Stiftsche uiterwaarden	254,23	4
W	W4	Benedenwaal	Brakelsche benedenwaarden	213,68	4
Y	Y3	Sallandse IJssel, zuidelijk deel	Duursche waarden en Fortmond	404,70	4
Y	Y3	Sallandse IJssel, zuidelijk deel	Oenerdijker- en Weelsumerwaarden	218,26	4
Y	Y5	Beneden-IJssel	Scherenwelle en Koppelerwaard	258,84	4

Branch	Trajectory code	Trajectory name	Floodplain	Area (ha)	# of years occupied
R	R2	omgeving splitsingspunt IJsselkop	Meinerswijk	329,47	5
W	W1	Waalbochten	Klompenwaard	89,76	5
W	W3	Waal omgeving St. Andries	Passewaaij	57,35	5
W	W3	Waal omgeving St. Andries	Dreumelsche waard	338,02	5
Y	Y3	Sallandse IJssel, zuidelijk deel	Ossenwaard	107,74	5
Y	Y4	Sallandse IJssel, noordelijk deel	Hoenwaard	712,25	5

Appendix IV. Maps of singing sites distribution (2001-2005)

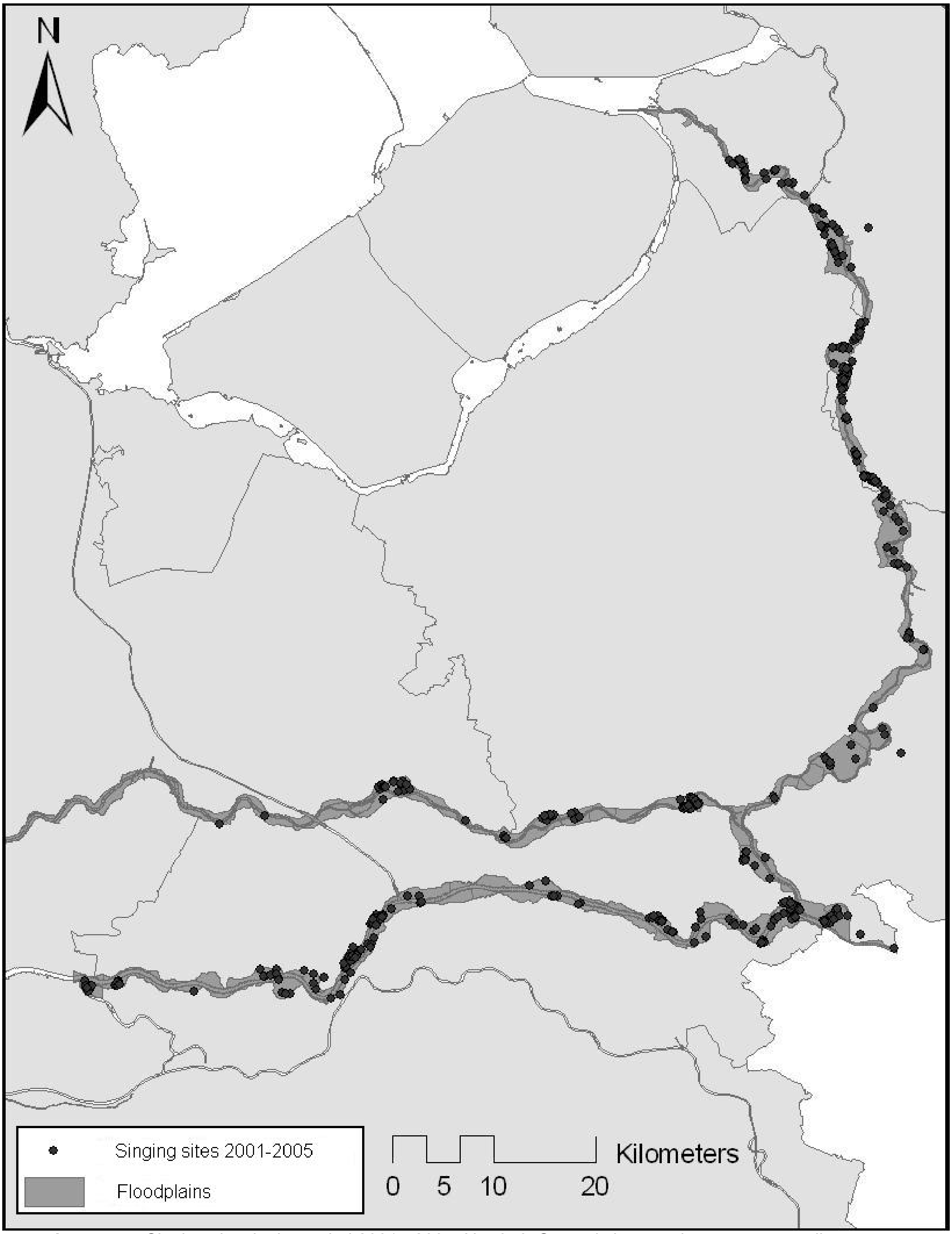

Figure III-1. Singing sites in the period 2001 - 2005: N = 956. Several sites can have same coordinates.

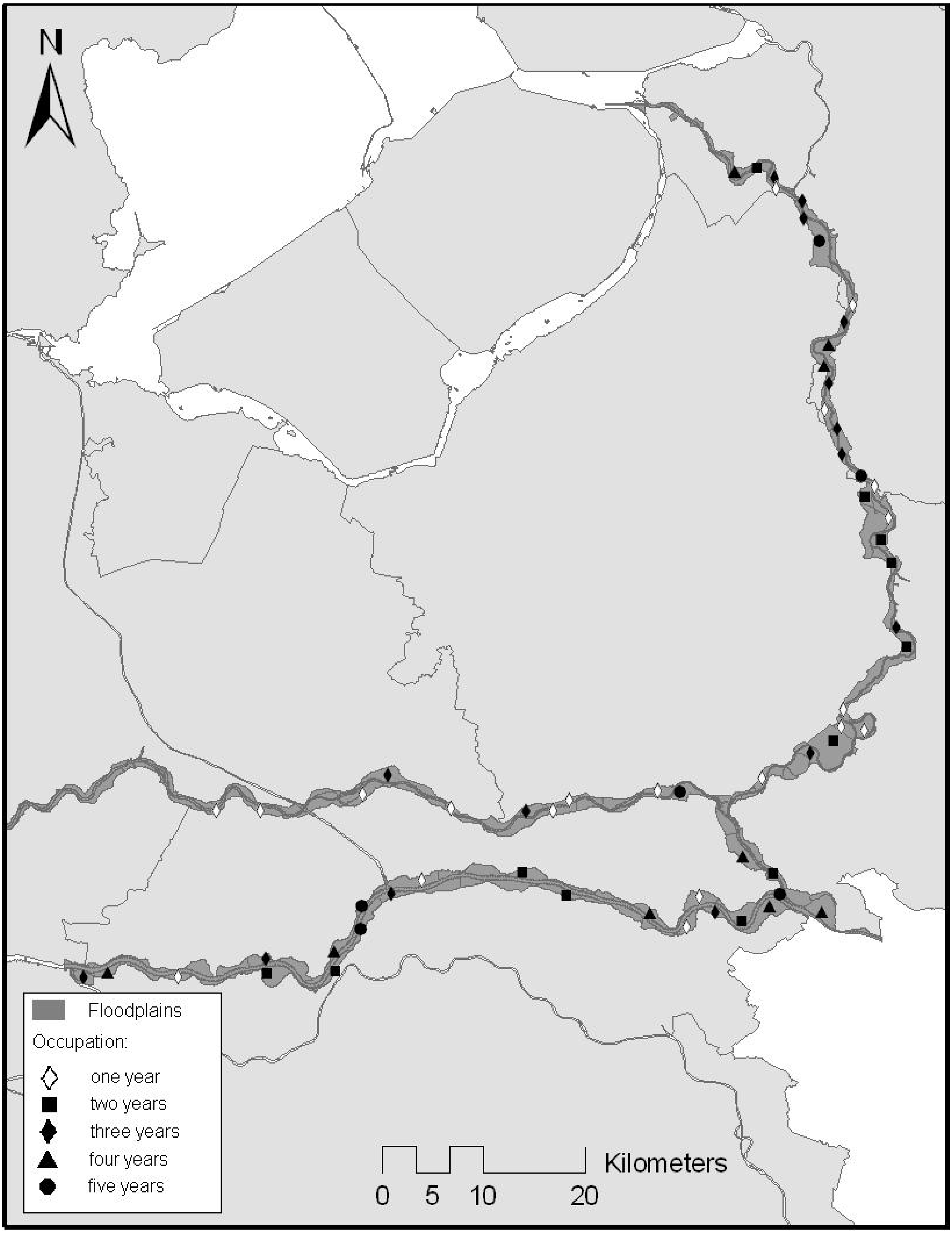

Figure III-2. Occupation frequencies of floodplains in the period 2001 – 2005.