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Viability of meta-populations of wetland birds in a fragmented landscape: testing the key-patch approach

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Abstract The key patch approach assumes that metapopulations in fragmented landscapes are likely to be viable with at least one “key” sub-population that is sufficiently large to ensure re-colonization of surrounding minor habitat patches. It is based on a minimum viable number of breeding pairs and within-breeding season dispersal distance, linked to size of the animal and longevity. It was tested using census data of 15 wetland bird species (bearded tit, bluethroat, great reed warbler, sedge warbler, Savi’s warbler, grasshopper warbler, spotted crake, water rail, common snipe, common teal, garganey, little bittern, night heron, great bittern and marsh harrier) in 14 wetland complexes of variable size (3–55 km²) spread across the Netherlands (distances ranging 4–156 km). First, for each species it was assessed whether a wetland harbored a key subpopulation, which was the case for the sedge warbler (7 key subpopulations), grass-hopper warbler (2), water rail (2), bearded tit, bluethroat, Savi’s warbler, common teal, garganey, great bittern and marsh harrier (all one key subpopulation). Together with the adjacent sub-populations present within breeding season dispersal distance, 10 out of the 15 studied species formed viable meta-populations. This was compared with the trend in the census data of 13 species for 1990–2000 and was found to correspond significantly (likelihood ratio test, $P = 0.003$): species without a viable meta-population had declined (2 out of 4) or remained stable (2 out of 4), whereas viable meta-populations had increased (6 out of 9) or remained comparatively stable (2 out of 9). One wetland complex, the Oostvaardersplassen, stood out in that it harboured key sub-populations for 9 out of the 15 species studied. Variation in quantity of specific habitat (area or perimeter marshland, woodland or open water) in a wetland complex was of limited importance explaining abundance patterns, since all covaried strongly with total area among the wetland complexes, with the exception of water perimeter. Apparently, these wetlands on peat harbour largely similar landscapes. Indeed, population sizes of most birds covaried strongly and in a PCA two distinct clusters of species were identified that shared high numbers of breeding pairs in the

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same, larger, wetland complexes, the first (3 species) including the great reed warbler, and the second (9 species) the water rail.

Keywords Meta-population · Habitat quality · Bird census data

Introduction

With the development of the meta-population approach (e.g. Hanski 1999), the spatial dimension of island theory became quantitatively incorporated in population ecology (Leibold et al. 2004). Based on the meta-population concept, Verboom et al. (2001) developed a practical ‘key patch’ approach to estimate whether a fragmented population would have chances to survive. Briefly, the key patch approach predicts long-term meta-population viability when one or more subpopulations are sufficiently large to allow frequent, but transient re-establishment of new subpopulations where suitable patches of habitat have become unoccupied. These larger subpopulations have also been labelled ‘source’ populations that feed the smaller ‘sink’ populations through colonization (e.g. Pulliam and Danielson 1991; Dias 1996; Foppen et al. 2000; Leibold et al. 2004).

For most wetland birds, habitat availability in the Netherlands has become increasingly patchy, due to e.g. expansion of urban areas, increased road density, agricultural intensification and enhanced recreative pressure (e.g. Verhoeven 1992; Reijnen and Foppen 1994; Barendregt et al. 1995; Graveland 1998; Jongman 2002; Vermaat et al. 2007). Across the Netherlands, a range of wetland complexes forms a patchy habitat network for these birds of variable extent, habitat quality and prevalence as well as mutual proximity (cf Foppen et al 2000; Vermaat et al. 2007). This habitat network allows us to approach wetland bird populations as potential meta-populations. Using high quality census data of at least 15 years since 1990, we here formally test the key-patch approach. We hypothesise that species maintaining a viable metapopulation with at least one source or “key-patch” subpopulation would not have declined in number over this period. A considerable range exists in estimates of minimum viable population sizes for vertebrates: from around 7,000 proposed by Reed et al. (2003; based on 99% survival chance and 40 generations) to 120–200 pairs employed by Verboom et al. (2001; 95% survival, 100 year). Our census data cannot cover such a time span, and also the Dutch landscape has gone through major changes between 1930 and 1980 (e.g. Bakker et al. 1994; Knol et al. 2003). We recognize that our data are comparatively short-term to allow firm conclusions on longer term population viability, but at the same time also need a comparatively short window of observation to ensure a steady state in habitat distribution over the landscape as well as a limited impact of climate change (e.g. Opdam and Wasscher 2004; Both et al. 2006). Thus we take the time span covered by the recent bird censuses as an acceptable compromise for our purpose (Brawn and Robinson 1996).

A confounding effect of habitat quality over mere habitat size, patch proximity and spatial configuration is possible since different wetland birds have specific habitat preferences (e.g. Foppen et al. 2000; Henle et al. 2002). The studied wetland complexes could differ in the proportion of water and forested land, in shoreline density (line per area, km km^{-2}), intensity of recreation and adjacent agriculture as well as overall productivity due to differences in soil and geomorphological setting (Vermaat et al. 2007). We addressed this by analysing covariance patterns in bird density and habitat distribution among the wetland complexes studied. Also, climate-change-related changes in habitat

suitability could lead to variable responses among species with a more northern or southern distribution range (e.g. Opdam and Wasscher 2004; Both et al. 2006). For example, a species with sparse and small subpopulations will appear to lack long-term viability but may well be observed to increase in numbers due to continuous immigration and range expansion from the south.

Materials and methods

We included the following 14 wetland complexes (cf. Fig. 1; here listed approximately from NE to SW, including area in km²): Fochteloerveen (23.0), Alde Feanen (18.0),



Fig. 1 Location of the 14 wetland complexes across The Netherlands. Ankeveense plassen and Kortenhoefse plassen are closely adjacent and therefore only the former is printed here

Rottige Meenthe (13.2), Weerribben (42.1), Wieden (49.2), Zwarte Meer (18.6), Oostvaardersplassen (52.2), Naardermeer (6.3), Ankeveense Plassen (4.4), Kortenhoefse Plassen (3.1), Loosdrechtse Plassen (34.4), Vinkeveense Plassen (13.8), Nieuwkoopse Plassen (15.9), and Reeuwijkse Plassen (10.9). All are complexes of open water, reedland, woodland (mainly alder carr and some willow stands) and meadowland. All but Zwarte Meer and Oostvaardersplassen are on peat soils. At first we purposefully limited ourselves to the 12 wetlands on peat, to prevent complex and potentially confounding interactions with differences in productivity, food availability, or other aspects of habitat quality. However, this led to the exclusion of large subpopulations for quite some species in these two wetland complexes, which would reduce the validity of our spatial metapopulation analysis. Distances between the complexes ‘as the crow flies’ range between 4 (Ankeveense and Kortenhoefse Plassen) and 156 km (Reeuwijkse Plassen and Fochteloerveen). We limited our subsequent analysis of habitat quality to the 12 wetland complexes on peat, for reasons just given. Areas and perimeters of the wetland complexes and of major habitat types within these complexes were obtained from the database of Vermaat et al. (2007). In the raw digital topographic map, line elements and shapes of open water bodies contained a range of erroneous elements, for example several stone dams or administrative boundaries in open water had been classified as ditches and banks. These have been removed by the third author.

Bird census data from the Dutch Breeding Bird Atlas of 2002 were obtained from the open access data depository of SOVON (www.sovon.nl). These data have a high spatial resolution (1 km²) and a coverage of at least 15 years since 1990. Census data are collected by numerous volunteers and professionals using a standard protocol and a central quality-control at SOVON (see also Soldaat et al. 2007). We selected 15 species (Table 1) out of 30 potentially useful wetland species because (a) maps of variable density were available (some species are only recorded as present/absent, such as the reed bunting), (b) abundance should be distinctly higher inside the wetlands studied than outside (this was not the case for the hen harrier), and (c) species distribution should not be limited to a few colonies (as in the purple heron). Geo-referencing of the bird distribution maps was carried out against known points on the digital 1:10,000 land use map of the Netherlands (CBS 2000). Bird population data are reported on a 5 × 5 km grid and in six density classes with the following class limits 1–3, 4–10, 11–25, 26–100, 101–500 and >500 breeding pairs per grid cell. Wetland complexes are delineated as complex shapes, hence do not match up with the grid lay-out. Minimum and maximum grid cell breeding pairs were therefore summed for each wetland complex across the 5 × 5 km grid cells covered, and the values of partly overlapping cells were area-weighted. Then the median of these two sums was taken to reflect the breeding population in a complex. Our approach combines larger-scale wetland complex landscapes and a comparatively coarse grain imposed by the 5 × 5 km grid. Our resolution therefore will not allow us to cover the spatial pattern of finer-scaled landscape elements, as in for example Foppen et al. (2000). Still, it should allow the detection of pattern at the larger extent of 10–100 of km across the whole of the Netherlands (cf Bailey et al. 2002), as well as habitat preferences aggregated to the basis of individual wetland complexes, similar to the landscape scale, or rather extent, of Fahrig (2003).

The key patch approach of Verboom et al. (2001) assumes that minimally viable populations of vertebrates vary in size depending on longevity and body mass of the individual. Longer-lived, larger species require smaller populations in an apparent steady state. Meta-populations without a key population (occupying a key patch) are assumed to require a larger number of breeding pairs to remain viable. Verboom et al. (2001)

Table 1 Estimated population size, trend (from www.sovon.nl) and red list status of 15 wetland breeding bird species included in this study

Bird species	Size (cm)	Estimated size of Dutch population (breeding pairs)	Trend in population size since 1990 ^a	Red list
<i>Acrocephalus schoenobaenus</i> (sedge warbler)	13	20,000–25,000	[++]	No
<i>Locustella naevia</i> (grasshopper warbler)	13	4,000–6,000	[+]	No
<i>Locustella luscinioides</i> (Savi's warbler)	14	1,700–2,100	[+]	Yes
<i>Luscinia svecica</i> (bluethroat)	14	9,000–11,000	[+]	No
<i>Panurus biarmicus</i> (bearded tit)	16.5	1,200–2,000	No data	No
<i>Acrocephalus arundinaceus</i> (great reed warbler)	19	250–300	[]	Yes
<i>Porzana porzana</i> (spotted crane)	22–24	150–300	[0]	Yes
<i>Rallus aquaticus</i> (water rail)	22–28	2,500–3,200	[+]	No
<i>Gallinago gallinago</i> (common snipe)	25–27	1,200–1,500	[]	Yes
<i>Ixobrychus minutus</i> (little bittern)	33–38	10–30	[0]	Yes
<i>Anas crecca</i> (common teal)	34–38	2,000–2,500	[]	Yes
<i>Anas querquedula</i> (garganey)	37–41	1,600–1,900	[0]	Yes
<i>Circus aeruginosus</i> (marsh harrier)	48–55	1,300–1,450	[0]	No
<i>Nycticorax nycticorax</i> (night heron)	58–65	1–6	No data	Yes
<i>Botaurus stellaris</i> (great bittern)	70–80	200–250	[+]	Yes

The species are sorted according to size (beak to tail, from Jonsson 1998)

^a Trends are (% year⁻¹): [–] decline <5%, [0] no significant change, [+] increase <5%, [++] increase >5%

Table 2 Rule-of-thumb numbers of breeding pairs of key sub-populations and comprising meta-populations as suggested by Verboom et al. (2001)

Species group	Key sub-population or patch	Meta-population with key patch	Meta-population without key patch
Long-lived, large	20	80	120
Medium life span, medium-sized	40	120	200
Short-lived, small	100	150	200

discerned three body size/life span classes (Table 2) and allotted rule-of-thumb (cf Frank and Wissel 1998) numbers of breeding pairs for each class. We classified all reed warblers and their likes into the small category (bearded tit, bluethroat, great reed warbler, sedge warbler, Savi's warbler and grasshopper warbler), waders were allocated to the 'medium' category (spotted crane, water rail, common snipe) and herons (little bittern, great bittern, night heron), ducks (common teal, garganey) and the marsh harrier were considered 'large'. For the little bittern and the water rail, this allocation may be disputable, and we therefore also checked the alternative allocation, without great effect. Sub-populations in a fragmented meta-population are considered to be within reach when they are separated by less than 25 for smaller birds or 75 km for intermediate and large birds,

which is taken to reflect the maximum breeding season dispersal range (adopted from Verboom et al. 2001).

Results

Based on the maximum breeding season dispersal distances, the wetlands form one connected cluster for the larger birds (cf. Fig. 1 and 2a), and three clusters for the smaller species (Figs. 1 and 2b). Fochteloeveen and Alde Feanen were isolated, whereas Rottige

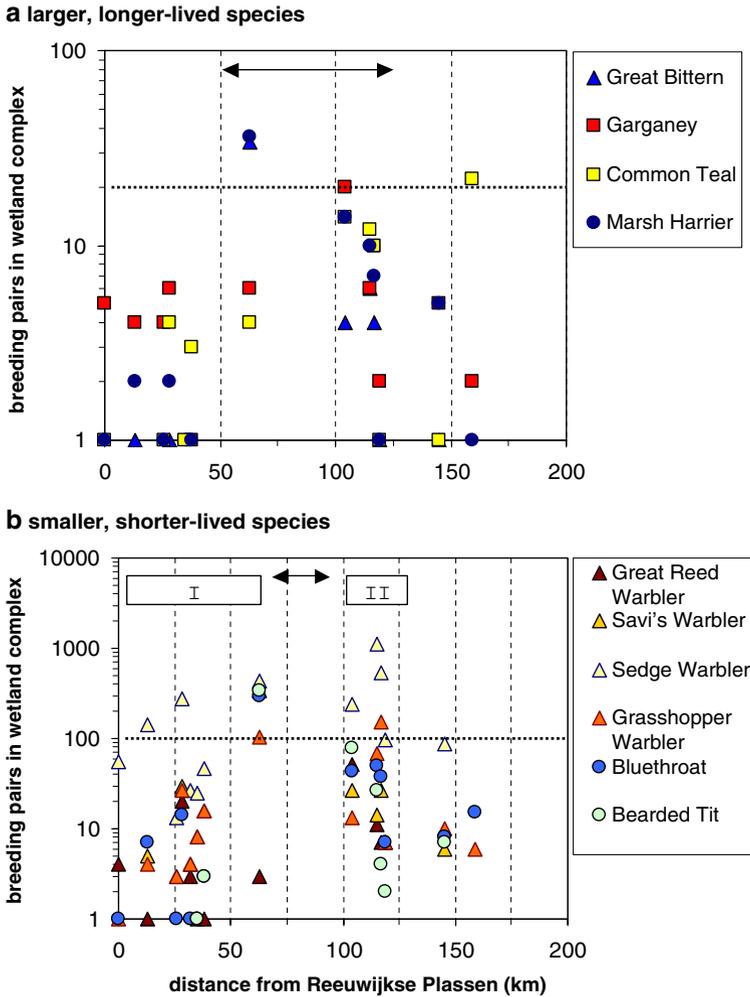


Fig. 2 Size of wetland bird subpopulations plotted against distance from the Reeuwijkse Plassen, which is used for graphical convenience as a proxy for the SW–NE axis that spaces out the major wetland complexes across The Netherlands (cf Fig. 1). Only the data for four larger-sized (a) and six smaller-sized (b) species are shown. Indicated are the minimum size of a key sub-population (horizontal broken line), the maximal breeding season dispersal distance (two-sided arrow, respectively 75 and 25 km), and two clusters of wetland complexes, I and II, where individual complexes are within reach of this distance in (b)

Meenthe, Weerribben Wieden and the Zwarte Meer formed a Northeastern cluster. Nardermeer, Ankeveense, Kortenhoefse, Loosdrechtse and Vinkeveense Plassen formed a cluster together with the Oostvaardersplassen to the Northeast and the Nieuwkoopse and Reeuwijkse Plassen to the Southwest (cf Fig. 1). For brevity, these clusters are labelled I and II, moving from SW to NE.

Applying the minimum key population sizes of Table 2 led to identification of several key sub-populations (Fig. 2): the sedge warbler (7 key subpopulations), grass-hopper warbler (2), water rail (2, or 4 with the lower minimum size). Several species had only one key subpopulation, most were in the Oostvaardersplassen: i.e. marsh harrier, great bittern, spotted crane, bearded tit, Savi's warbler, and bluethroat. Together with the adjacent subpopulations, these species also formed a viable meta-population in cluster I. For the sedge warbler, grasshopper warbler and the water rail, both clusters complexes were inhabited by viable meta-populations. Hence, we found at least one viable meta-population for 10 out of the 15 species studied. Also, we observed that number of species that have a key-patch subpopulation correlated with the size of a wetland complex, ($y = 0.11x - 0.86$, $r^2 = 0.55$, $P = 0.003$). For several species the estimated populations in our studied wetlands were very small (e.g. 2 pairs of little bittern in only one wetland and single pairs of night heron in three separate wetlands). Still, these species had persisted over the census period covered.

To test the outcome of the key-patch approach for the present set of bird species, we compared these results with the observed trends using a likelihood ratio correspondence test (Table 3). The correspondence was significant ($P < 0.003$). Hence most declining or fluctuating species had no viable meta-populations, whereas most viable metapopulations increased in number or were stable.

Using forward stepwise multiple regressions of population size versus habitat area and perimeter in the wetland complexes on peat (Table 4), we found significant relations for all species, and these explained a substantial proportion of the observed variation in breeding pairs (>70%) for 11 out of the 15 species. Some species correlated more strongly to perimeters, others to areas. However, five of the six habitat area and perimeter variables employed were highly correlated amongst each other and with total complex area (Table 4, footnote): only the perimeter of water bodies present varied independently from the others. Total complex area, however, only had a separate significant effect in three bird species, the bluethroat, the sedge warbler and the night heron (in the latter it explained only an additional 4% of the variance, in the former two this proportion explained was substantial). Thus, the 12 wetland complexes on peat formed landscapes of similar make-up, only differing in the total length of shorelines present quantified by water perimeter, and

Table 3 Cross-tabulation of predicted viability of meta-populations with observed trends in Dutch bird population size for the 13^a species analysed (from Table 1)

Trend?	Increase	Stable or fluctuating	Decline
<i>Viable metapopulation?</i>			
Yes	6	2	1
No	0	2	2

The correspondence is significant: likelihood ratio test, $P = 0.003$, so a higher proportion (6 out of 9) of the species with a key subpopulation is observed to increase than for those without a key subpopulation (0 out of 4)

^a No trend data were available for bearded tit and night heron

Table 4 Results of forward stepwise multiple regression of bird population sizes (not density) in 12 wetland complexes on peat and prevalence of habitat area and perimeter variables^a

	Variables included in model at step 1–3 (and r^2)			Significance
	1	2	3	
Marsh harrier	Marshland perimeter (+, 0.86)	Water area (+, 0.92)		$P < 0.001$
Bearded tit	Marshland perimeter (+, 0.51)			$P < 0.009$
Bluethroat	Total area (+, 0.88)	Marshland area (+, 0.96)		$P < 0.001$
Great reed warbler	Water area (+, 0.68)	Forest perimeter (+, 0.81)	Marshland area (–, 0.92)	$P < 0.001$
Sedge warbler	Total area (+, 0.74)			$P < 0.001$
Savi's warbler	Forest perimeter (+, 0.81)	Marshland area (+, 0.92)		$P < 0.001$
Grasshopper warbler	Forest area (+, 0.75)	Marshland perimeter (+, 0.84)	Marshland area (+, 0.92)	$P < 0.001$
Little bittern	Water area (+, 0.41)			$P = 0.025$
Night heron	Forest perimeter (+, 0.83)	Marshland area (+, 0.94)	Total area (+, 0.98)	$P < 0.001$
Great bittern	Marshland perimeter (+, 0.94)	Water area (+, 0.97)		$P < 0.001$
Spotted crane	Forest area (+, 0.83)			$P = 0.001$
Water rail	Forest perimeter (+, 0.93)	Marshland perimeter (+, 0.96)		$P < 0.001$
Common snipe	Marshland perimeter (+, 0.89)	Forest area (+, 0.94)		$P < 0.001$
Common teal	Forest area (+, 0.55)			$P = 0.005$
Garganey	Water perimeter (+, 0.86)			$P < 0.001$

Total area of the wetland complex was also included, to correct for possible area effects. For significantly contributing variables the sign of the effect (+ or –) and the resultant explained variance (r^2) after each step is also presented. Criteria in the stepwise were the probability of F to be entered $P \leq 0.05$, and to be removed $P \geq 0.10$

^a In a principal components analysis of these six habitat area and perimeter variables, forest area and perimeter, marshland area and perimeter and water area as well as total complex area were all found to covary significantly and correlated highly ($r > 0.88$) with the first principal component that explained 76% of the variation. Only water perimeter varied independently of the others and added a second principal component explaining another 15%

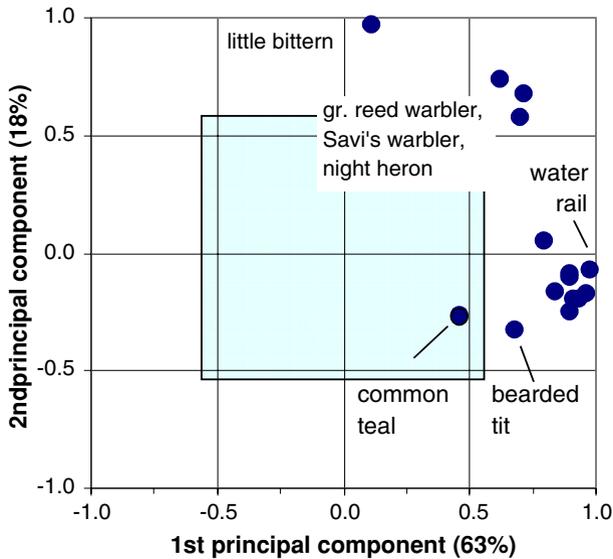


Fig. 3 Principal components analysis of 15 wetland bird densities in 12 major wetlands on peat in the Netherlands displaying the correlation of bird population size with the first two principal components. Two major clusters of co-varying species are apparent: (1), labelled by the water rail and including marsh harrier, bluethroat, sedge warbler, grasshopper warbler, spotted crake, great bittern, common snipe and garganey, and (2) the cluster of the great reed warbler, Savi’s warbler and the night heron. Three species, the little bittern, the bearded tit and common teal had a different spatial distribution of abundance among wetlands. Species in these clusters share sites of higher abundance. The third axis explained another 9% and correlated significantly with the bearded tit. Outside the blue transparent frame the correlations with a principal component were significant at $P = 0.05$

probably reflecting the density of ditches. The abundance of one single bird species, the garganey, correlated with water perimeter, confirming its association with ditches and vegetation-rich littoral zones.

We carried out a principal components analysis of the bird populations across the wetland complexes studied, to address covariance in their abundances. We found two apparent groups of species that displayed parallel abundance patterns, one composed of nine species including the water rail, and the other of three species including the great reed warbler (Fig. 3). The remaining three species displayed an individual pattern, with the common teal not correlating to any of the three principal components.

Discussion

Our test of the keypatch method suggests a reasonable correspondence between predicted and observed changes in population size (Table 3). Our hypothesis was that species maintaining a viable metapopulation with at least one “key-patch” or source subpopulation would not have declined in number over this period. Only one out of the nine species with a key subpopulation was observed to decline, the common teal. Six others had increased over the time span covered and two had remained stable. Thus we conclude that the keypatch method appears applicable to wetland birds in fragmented landscapes across a wide range of bird size (fivefold) and probably also life span, despite its important reliance

on rule-of-thumb estimates for meta-population sizes and breeding-season dispersal distances (Verboom et al. 2001). Based on the correlation found between number of species with a source subpopulation and total area of a wetland complex we can add another rule-of-thumb: a minimum area for a wetland complex in the Netherlands to potentially function as a key patch for at least one species of wetland bird would be 17 km².

For the larger species, the scattered wetland complexes can be seen as one common set of patches of suitable habitat all within travelling distance. For the smaller species, however, the Netherlands probably contains two separate clusters of habitat. However, the larger spatial extent applied here prevented the inclusion of all minor patches of scattered reedbeds and fringing wetlands outside the presently covered complexes. Still, as Foppen et al. (2000) demonstrated, these patches harbour transient ‘sink’-subpopulations that may form a substantial proportion of the total breeding population and thus contribute to its viability. Particularly sedge warbler, snipe and garganey occur also in considerable numbers in such small habitat patches.

Our attempt to analyse habitat preferences met with the unexpected strong collinearity among water, marsh and woodland areas, as well as the perimeters of the latter two. Apparently, the 12 studied wetland complexes on peat have similar relative distributions of these habitats, irrespective of their size, and probably they differ mainly in the presence of ditches, as witnessed from the deviating pattern observed for water perimeters. This similarity of landscapes must be an important reason for the close clustering in the distribution patterns of nine bird species (covarying with the water rail, Fig. 3): apparently all these species have the largest subpopulations in the same wetland complexes, and generally these are the largest wetland complexes, since population sizes of all species but one (little bittern) correlated with the area of the wetland (r^2 between 0.54 and 0.87, at least $P < 0.05$). The clustering in distribution of bird species (Fig. 3) suggests the existence of possibly two communities of wetland birds. Focusing protective measures on a surrogate, or umbrella species (Andelman and Fagan 2000) like for example the great reed warbler and the water rail, would then possibly be effective for other community members as well.

Most key subpopulations observed in this study were found in just a few wetland complexes and particularly the Oostvaardersplassen stand out with nine species, six of which only in this wetland complex. This area only became available to wetland birds after reclamation of the southern Flevoland polder in 1968 and has developed into a major source area for many wetland birds. Probably, extrapolating from our present analysis, it is crucial for the survival of six to nine meta-populations of wetland bird species in the Netherlands.

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