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The need for future wetland bird studies: scales of habitat use as input for ecological restoration and spatial water management

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All over Europe, wetlands have decreased in size, lost their original dynamics and became fragmented as the consequence of an ever increasing human land use. These processes have resulted in losses of nature values, among which declines in marshland bird populations. Ecological restoration of wetland systems follows from initiatives like EU Bird and Habitat Directives and Water Framework Directive, but may be, in itself, too costly to be widely applied. More promising perspectives to reinforce the wetland part of the ecological network Natura 2000 might come into focus when combined with spatial water management which is primarily aimed at more sustainable safety against flooding. In this way, the wetland network may acquire a wider public and political support. Knowledge on scale-related habitat use of wetland birds can play a role in the process of spatial planning. We illustrate this point by distinguishing four levels of spatial and temporal habitat use by wetland birds, and giving examples for each. The four levels are: (1) birds on stopover sites during migration, (2) territorial breeding birds, (3) colonial breeding birds, and (4) staging birds on wintering sites. This asks for ecological coherence on different scales, e.g. on the international level of migration flyways, on the regional level of landscapes and on the local level of individual wetlands. It is advocated that wetland ecologists dedicate themselves more specifically to quantifying the relevant data on habitat use of birds on each of these scale levels. Meanwhile, spatial planners should try to incorporate them into their efforts in realising combinations of ecological restoration or rehabilitation of wetlands and solutions for sustainable water management. These combinations might turn the tide for some seriously threatened species of marshland and wetland birds.

Key words: wetland birds, habitat requirements, scale levels, ecological coherence, spatial planning, water management

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Not until the beginning of the 20th century, nature conservation became an issue in Europe. However, up until the late 1980s, nature conservation has been primarily concerned with the preservation of nature reserves. Since then, the importance of large ecosystems, natural processes (e.g. erosion, sedimentation, tidal influences, hydrodynamics) and ecological coherence with the surrounding landscape have also been recognised. In particular, the importance of the interaction between scale and ecological processes has long been underestimated

(Wiens 1989). This is particularly true for wetland areas in which size and hydrological dynamics play a prominent role. The sizes of wetlands have decreased sharply and the original dynamics have been much reduced. Moreover, fragmentation by human activities, like urbanisation and infrastructure, has been increasing across the 20th century. Especially in The Netherlands, human activities have severely reduced and modified the original wetland habitats. Consequently, many marshland bird species have declined considerably



Eurasian Spoonbills nesting on the Wadden Sea island Texel, The Netherlands (14 April 2007). Photo by Bas van den Boogaard.

in population size and are currently considered threatened (den Boer 2000, van Turnhout & Hagemeijer 2010). Some of the most obvious examples are Blackcrowned Night Heron Nycticorax nycticorax, Purple Heron Ardea purpurea, Great Bittern Botaurus stellaris, Little Bittern Ixobrychus minutus, Red-crested Pochard Netta rufina, several species of rails and crakes, Black Tern Chlidonias niger, Great Reed Warbler Acrocephalus arundinaceus, Sedge Warbler A. schoenobaenus, Savi's Warbler Locustella luscinioides and Bearded Reedling Panurus biarmicus (den Held 1981, Cavé 1983, Bekhuis 1990, van der Winden et al. 1994, 1996, Graveland, 1996, 1998, Foppen et al. 1999, Beemster et al. 1999, 2010, Erhart & Kurstjens 2000, den Boer 2000, Bijlsma et al. 2001, Zwarts et al. 2009, van Turnhout et al. 2010). However, other species have increased (e.g. Great Cormorant Phalacrocorax carbo, Eurasian Spoonbill Platalea leucorodia, Bluethroat Luscinia svecica) or became settled (e.g. Greylag Goose Anser anser, Great Egret Casmerodius albus, Penduline Tit Remiz pendulinus) over the second half of the century (van den Bergh 1991, Voslamber 1992, Bekhuis et al. 1993, Voslamber 1994, Hustings et al. 1995, van Eerden & Gregersen 1995, van der Kooij & Voslamber 1997, Voslamber et al. 2010). All these changes are likely to have been caused by environmental factors operating at different scales.

Throughout the centuries, agricultural land use has become more and more dominant. At the same time safety against regular flooding from either the sea or the rivers became ever more important and was, accordingly, assured. The reduction of natural hydrodynamic processes was effectuated by reclamations of lakes and marshlands, draining of fen areas and by damming and transformation of estuaries. The natural courses of rivers and riverbeds are now artificially controlled, thus reducing drastically the surface area of land periodically flooded. All these measures have improved socio-economic conditions of the countryside (particularly with respect to agriculture), including a higher level of safety. The remaining wetlands and marshes, however, have become small and fragmented. Original levels of hydrodynamics are lost or can only be maintained at relatively high costs. Particularly in The Netherlands this increasing human control over hydrodynamics and land use has resulted in a spectacular change of the landscape. Originally a vast area of wetlands including all gradients between salt and fresh water, eutrophic and oligotrophic systems, tidal, streaming and still waters and extensive transitions between water and land, it supported a rich variety of wetland and marshland bird species (van Eerden et al. 2010). This has been transformed into a man-made cultural landscape with isolated wetlands in between.

Similar processes have operated on the majority of natural West European wetland systems.

Over the past fifteen years, concern has started to rise in The Netherlands about whether the strategy of complete hydrological control over water and wetland systems will continue to guarantee safety in the long run (Ministry of Transport and Public Works 2000). Predictions about sea level rise, soil subsidence over the north-western two-thirds of the country and wetter winter seasons throughout the river basins of Rhine and Meuse imply considerable risks. A series of exceptionally high water levels in the rivers in recent years (1993, 1995 and 1998) may be taken as a sign for overregulation and supports the view that more room should be given to natural hydrological processes. The extreme floods occurring in central European rivers in the summer and autumn of 2002, 2006 and 2010 have also been partly attributed to the reduction of natural floodplain areas downstream and a lack of natural water retention upstream, underlining that the problem is also becoming more acute in the rest of Europe.

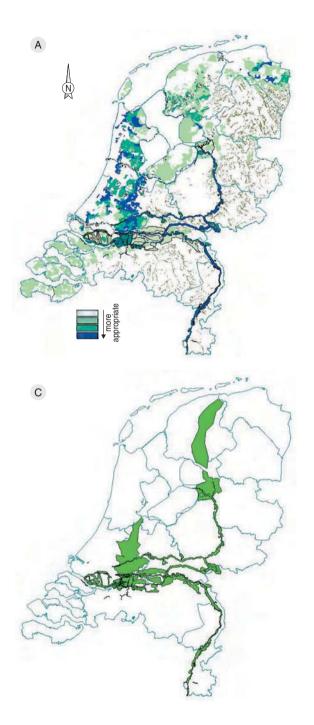
As a consequence, many large-scale projects are being planned across The Netherlands, aimed at designating considerable surface areas for retention and/or buffering of water. For safety reasons, retention alone would seem to be sufficient and, therefore, the possibilities of coupling wetland restoration schemes to spatial solutions for preventing flood risks would be limited. Nevertheless, since climate predictions also include drier summers, and desiccation is already a problem at present (Haasnoot et al. 1999, Runhaar 1999), the largescale buffering of fresh water during the wet season for use in summer is often considered as well (so called Delta Programme, Ministry of Transport Public Works and water Management 2010). This type of measures might be accompanied by ecological restoration of wetlands. Currently, investigations are being carried out to explore the possibilities for the coupling of wetland restoration (and their nature conservation values, e.g. in terms of avian biodiversity and ecological carrying capacity) to safety measures. These investigations are not only concerned with the situation in The Netherlands, but are extending across Europe (e.g. Ministerium für Umwelt und Verkehr 1997, Lohr & Walter 2000, Ministry of Transport and Public Works 2000).

This paper aims at identifying the relevant levels of scale (according to Wiens 1989) in time and space of habitat use in wetland and marshland birds. We will emphasise the need for studies concerning wetland conservation with a focus on spatial issues, in order to fit wetland restoration activities with other activities like spatial solutions for lowering flood risks.

Spatial settings

For The Netherlands maps have been prepared to show where surplus water may be retained or conserved (Fig. 1A). These spatial claims aim at providing safety against flooding and prevention of economical damage caused by possible excessive rainfall. Besides areas along the coast of the North Sea, this concerns the floodplains of the rivers Rhine and Meuse especially. Since these claims could very well lead to limitations in human land use, the possibilities to designate them to other uses, such as ecological restoration of wetlands, are being investigated. At the same time the distribution of wetlands with considerable ornithological and other natural values has been mapped (Fig. 1B). By combining these geographical datasets with knowledge on spatial requirements of wetland birds, suggestions come forth for adjusting spatial planning and design of future water management to the need for larger and more coherent wetland systems (Fig. 1C), among others for marshland birds. In this respect, knowledge about the spatial requirements of wetland and marshland birds becomes relevant if one is to unify existing data into modelling exercises (Verboom et al. 2001, Foppen 2001). Despite the numerous papers on habitat selection in birds, almost no studies exist that specifically deal with the importance of spatial configuration of habitat at a landscape scale, and many studies are descriptive and lack a clear use of semantics (Jones 2001). For marshland birds the situation is even worse, as many of these birds are secretive in a habitat that is not easily charted (e.g. Lor 2007 for American Bittern Botaurus lentiginosus, Puglisi et al. 2003 for Great Bittern). The use of GPS-transmitters is a step forward to describe the use of marshland and its surroundings by individual birds, also in the migratory context between continents as in Purple Heron (van der Winden et al. 2009, 2010).

Notwithstanding the lack of empirical data, the concept of combining spatial water management and ecological restoration of wetlands is considered a fruitful way ahead with regard to the conservation of marshland species. Locally (e.g. along the French/German stretch of the Rhine), projects are under way that aim at restoring natural flooding regimes in floodplains (Ministerium für Umwelt und Verkehr 1997). Thus, both ecological restoration and higher safety levels for economically important areas are strived for. However, spatial coherence over large scales (e.g. large catchment areas or even between different catchment areas), as expressed in the maps made for The Netherlands, has not been comprehensively elaborated as yet in other countries.



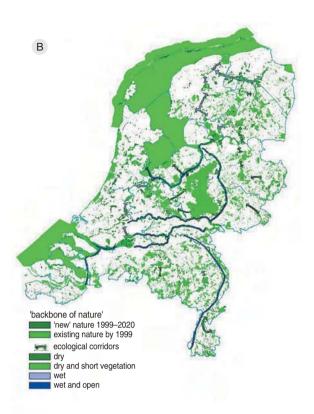


Figure 1. Maps of The Netherlands, (A) showing where spatial water management may be looked for (the darker, the more appropriate), (B) where actual nature reserves and ecological corridors are situated, and (C) where the most important large-scale combinations of spatial water management and wetland enforcement may be realised. Within map B, most of the large areas indicated refer to wetland systems, except for the large woodland in the centre of the country (Veluwe).

Scales of spatial use by wetland birds

The habitat requirements of wetland birds may operate on three scales: international (along flyway systems), regional (landscape), and local (within one particular wetland area). These scales are relevant for four different states in which the birds may find themselves:

(1) Staging or wintering (water)birds along their flyway; mainly determined by availability of suitable and accessible feeding areas within the reach of a non-stop migratory flight.

(2) *Territorial breeding birds of marshlands*; mainly determined by size of wetlands, size of suitable breeding and feeding habitats and the relationship between proximity of other wetlands and the dispersal capacities of the species concerned.

(3) Non-territorial, mainly colonial breeding marshland

birds; determined by a combination between safe and predator-free breeding sites within reach of a sufficient and often seasonally varied number of feeding areas. (4) *Staging or wintering (water)birds on the stopover or wintering site*; mainly determined by availability of feeding areas within reach of a safe roosting area.

For wetland areas of different sizes and with varying degrees of 'ecological coherence' (e.g. mutual distance, connectivity and, most importantly, vicinity of suitable feeding grounds), these spatial requirements result in varying degrees of species richness (Fig. 2). Also, the interdependence with agricultural areas becomes less as wetland size increases. Larger wetlands show more gradients (e.g. water–land, fresh–brackish–saltwater, eutrophic–mesotrophic–oligotrophic) and tend to have more coherence with their surroundings (feeding areas) than small, isolated patches (M.R. van Eerden & M. Platteeuw, unpubl. data). Therefore, they offer suitable life conditions to a wider array of wetland birds (Vulink 2001).

STAGING AND WINTERING WATERBIRDS ALONG THE FLYWAY

On the international level, many marsh- and wetland bird species are migratory, breeding at relatively high latitudes and wintering in milder climatic zones. During their seasonal migrations between breeding grounds and wintering quarters, these birds depend on the availability of staging areas at crucial points along their migration routes. These staging areas have to be sufficiently large and/or productive to serve as forage stopover and they cannot be further apart than the distance which may be covered by the birds in a single non-stop flight. This, in its turn, is determined to a large extent by the amount of fat the birds are able to store as 'fuel' at the previous stopover site (Piersma 1987, 1994, Ens *et al.* 1990, van Eerden 1997).

A qualitative model for the relationships between carrying capacity of stopover sites, satiation levels of the staging birds and migration decisions was proposed by van Eerden (1997) for the autumn flyway between breeding and wintering wetland areas (Fig. 3). This model assumes that, in general, the wetland areas in the north and east are larger and/or of higher carrying capacity than those further south and west, thus forcing the birds into higher densities while gradually migrating southwest in autumn. The birds that achieve the most profitable stopover sites may move on relatively straightforward towards the wintering areas. On the other hand, birds that encounter difficulties in 'refuelling' at stopover sites, either because of low quality of the site or due to depletion by preceding birds, have the option of moving on to lower quality sites closer by, before moving on. This model appreciates the importance of the relationships between size and quality of wetland patches along the flyway, their proximity, and timing of migration with respect to the seasonal availability of profitable food resources.

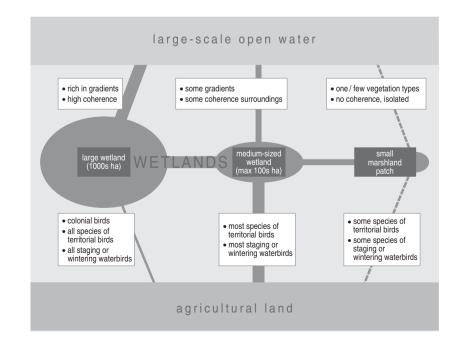


Figure 2. Hypothetical relationships between size and coherence of a wetland area and species richness in wetland birds. Larger wetlands would sustain birds that are less dependent upon agricultural land and show a higher ecological coherence, as a result attracting more wetland species.

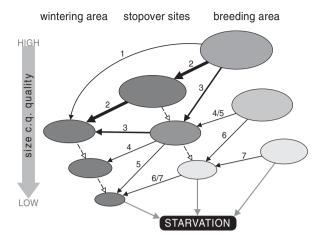


Figure 3. Qualitative model showing use of stopover sites by wetland birds during autumn migration. For three stages (breeding, stopover and wintering), wetlands are shown according to decreasing size and/or quality, and their usage by birds is indicated by the intensity of grey tone (the darker, the more intensively used). Migration routes (closed arrows) are indicated by numbers: 1 = long-distance migrants using no or few stopover sites, 2 = migrants using most rewarding stopover sites, 3-7 = cascade of use of sub-optimal stopover sites along the flyway. Instead of moving on to the next region, supposing a long migratory flight, individual (flocks of) birds that have not succeeded in storing sufficient fat reserves may decide to move to alternative, less profitable stopover sites in the same region which are closer by. These shorter 'dispersive' movements are indicated with dotted arrows. Model modified from van Eerden (1997).

TERRITORIAL MARSHLAND BREEDERS

Most of the traditional marshland bird species, such as rails and crakes, and most of the typical reedland passerines (e.g. Great Reed Warbler, Common Reed Warbler Acrocephalus scirpaceus, Sedge Warbler, Savi's Warbler and Bluethroat) can be considered to be territorial breeding birds, breeding and feeding within the same patch of wetland throughout the reproductive period. Individual pairs of these species do not need extensive surface areas to survive, but all of them are potentially vulnerable to habitat fragmentation. For self-sustaining breeding populations of these species, patches of suitable breeding and feeding habitat may become too small and too fragmented. Recolonisation of isolated, small patches of marshland that have become accidentally devoid of a certain species may be hampered by fragmentation (Foppen 2001). Therefore, by way of precaution, either wetlands should be large enough to compensate for accidental local extinctions, or the habitat network should be dense enough to allow for sufficient potentials for recolonisation after local extinctions.

It is a challenge for landscape ecologists to develop quantitative standards on the landscape level for (meta-)populations of target species to persist, for example minimum amount of typical habitat or minimum landscape cohesion. One of these standards that have been developed and applied is the key patch approach (Verboom et al. 2001). A key patch is a habitat patch in a network with a small probability of going extinct (<5% in 100 years), based on the assumption that from other parts in the network sufficient individuals disperse to allow for at least one immigrant per generation (Verboom et al. 2001). With these standards an a priori evaluation can be applied to studies concerning wetland and/or marshland restoration plans. A striking example of such an approach is presented in Fig. 4 (Verboom et al. 2001). For each of 16 of the larger wetlands in The Netherlands and 13 characteristic marshland breeding bird species the proportion of species is determined that would have viable populations at present and in a hypothetical future in which 50,000 ha of 'new' marshland would have been added, by enlarging existing marshlands. In this scenario the sustainability of marshland bird populations clearly improves. Indeed, based on empirical data (population trends) it has been demonstrated that marshland bird populations in key patches show more population stability than in marshland patches that are smaller (Vermaat et al. 2008).

COLONIAL BREEDING BIRDS

For many larger species of marshland and wetland birds, like cormorants, herons, gulls and terns, individual food requirements are high and the main food sources are unpredictable in their occurrence in space and time. In order to meet their needs throughout a breeding cycle, these birds cannot rely on a breeding territory of limited size, but have to cover a larger area on a regular basis. Breeding colonially may solve this problem by sharing information among individuals (such as food: Ward & Zahavi 1973, but possibly other parameters as well: see Bijleveld et al. 2010). Thus, individual birds may profit from each other in finding the best feeding sites over a larger area (van Eerden & Voslamber 1995, for Great Cormorant), while forsaking the expenses involved in defending a breeding and feeding territory large enough to cover their needs. But there is a price: colonies need to be better protected against disturbance by potential predators of eggs and chicks. A bird colony is impossible to hide and can thus only be situated in sites that are inaccessible to predators (e.g. islands or trees) and/or allow an unobstructed view to see predators from far away and chase them

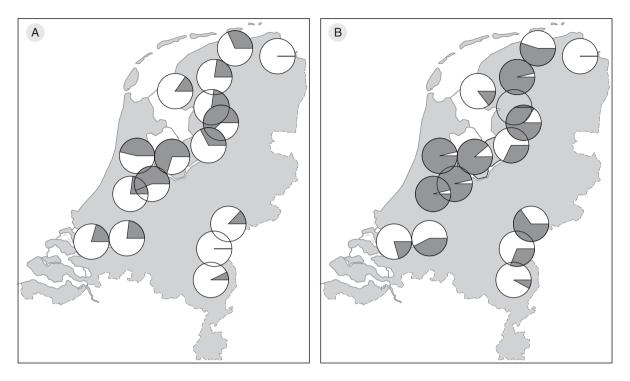


Figure 4. Results of a multi-species viability evaluation for 13 characteristic species of marshland birds in 16 representative large wetlands in The Netherlands. The circles indicate the locations, with the proportion of species (in dark grey) that have viable populations. (A) present situation, (B) scenario in which 50,000 ha of new marshland has been developed, divided spatially among the 16 keypatch sites (after Verboom *et al.* 2001).

off in time. Some other species, like Western Marsh Harrier *Circus aeruginosus*, Great Bittern and Bearded Reedling, also usually feed well away from the proximity of their nests (Schipper 1977, 1978, Gilbert *et al.* 2005, Beemster *et al.* 2010), but do not join in colonies. Generally, these species have smaller feeding ranges and more localised and specific feeding sites than colonial breeders.

Colonial birds tend to breed in safe and quiet spots and commute between breeding site and feeding grounds. In Europe, colonial marshland birds include pelicans, cormorants, herons, spoonbills and ibises and all species of gulls and terns. Throughout the breeding season, for at least three to four months, these birds need a spatially coherent combination of undisturbed and predator-free breeding sites, often close to or surrounded by water, in close proximity to profitable feeding grounds. In The Netherlands, most colonies of Great Cormorant and large wading birds (mainly Grey Heron Ardea cinerea and Eurasian Spoonbill) are found in and around the most extensive waterbodies and wetlands in the southwestern and northern parts of the country, as well as around the central freshwater Lake IJsselmeer and on the mostly predator-free Wadden Sea

islands (Fig. 5). Other colonial marshland bird species are either absent (pelicans, Squacco Heron Ardeola ralloides) or very scarce and local (Great Egret, Little Egret Egretta garzetta, Black-crowned Night Heron). The colonial breeding birds show a remarkable gap in their distribution in the mid-western part of the country, despite the abundance of water systems. Here, urbanisation, infra-structural works and other forms of human land use reach high densities and are likely to have a disturbing effect on wetland nature. The higher and drier eastern and south-eastern parts of The Netherlands, where wetlands are scarcer, smaller and more scattered, cormorants and herons have not established any significant colonies either (Fig. 5). Another striking pattern of distribution emerges from the hydrologically relatively undisturbed Danube Delta (Romania and Ukraine), where breeding colonies of fish-eating birds (pelicans, cormorants, storks) are concentrated close to the feeding areas in large-scale shallow waters and on the interface of water and land, avoiding areas with the most extensive dense reedbeds (Platteeuw et al. 2004). These findings indicate a spatial constraint on the choice of colony sites, connected with the need for nearby gradient-rich feeding grounds. The total number

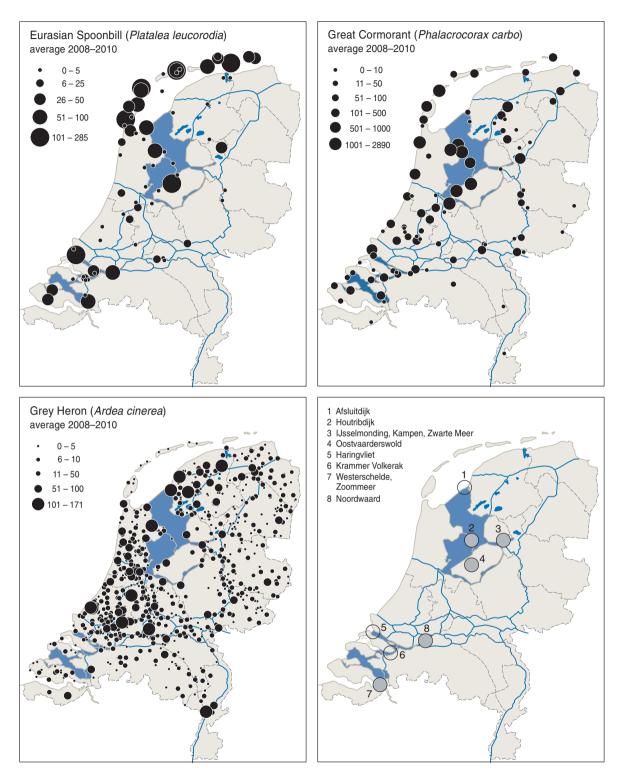


Figure 5. Breeding distribution of three colonially breeding wetland birds in The Netherlands (2008–2010): Eurasian Spoonbill, Great Cormorant and Grey Heron in relationship to abundance of freshwater areas. Maps are from the Network Ecological Monitoring, SOVON Dutch Centre for Field Ornithology. The chart indicates plans for major reconstruction of waterworks either affecting the flow, water quality and/or construction of major fish passageways (open symbols) or development of large-scale wetland habitat by specific management actions (filled symbols).

of colonies per 1000 km² proved to be 8 in The Netherlands and 4 in the Danube Delta, colony size in Romania being larger than in The Netherlands. Also, species diversity in the Danube Delta is far higher, with two species of pelican, two species of cormorant, seven species of heron, Eurasian Spoonbill and Glossy Ibis *Plegadis falcinellus*, much more reminiscent to the historical situation in The Netherlands (see van Eerden *et al.* 2010).

WATERBIRDS AT STOPOVER SITES OR ON WINTERING GROUNDS Huge flocks of ducks, geese and swans spend part of the winter in Dutch wetlands and equally large numbers of waders stop over during spring and autumn migration, particularly on the tidal flats of the Wadden Sea and in the southwestern estuaries. During their stay, these migratory waterbirds depend heavily on the availability in The Netherlands of profitable feeding grounds, e.g. (tidal) mudflats (waders) (Smit & Piersma 1989), productive shallow waters (swans and ducks) (van Eerden 1997) and extensive and productive agricultural lands (swans, geese and Eurasian Wigeon Anas penelope) (van Eerden et al. 1996, 2005). The presence of these feeding grounds within the delta of Rhine and Meuse is crucial to the survival of populations of these species, because of the unique geographical position of The Netherlands with respect to these birds' migratory flyways (Fig. 3). During their stay, the spatial requirements of staging and/or wintering birds mainly depend on the richness and attainability of food sources and is, therefore, directly related to the surface area of their favoured feeding grounds (van Eerden 1997). Depending on species they also need well-protected and quiet daytime or nighttime roosts. As many wetlands have become smaller in The Netherlands, the food provisioning function extends well beyond the borders of the reserve. Especially herbivorous waterbirds strongly depend on agricultural crops and merely use the wetlands as a roost. This, in turn, has consequences for the issue of possible damage that waterbirds may cause in winter (van Eerden 1990, van Eerden et al. 1996) and, recently, also in summer (van der Jeugd et al. 2006).

Implications of habitat needs for spatial water management

INTERNATIONAL SCALE

The challenge for ecologists working on migratory wetland birds is to establish general 'rules of thumb', i.e. quantitative tools allowing authorities and spatial planners to make ecologically relevant decisions on spatial configurations of new or rehabilitated wetlands. Relevant factors are size and productivity of the wetland, position with respect to other wetlands and positioning within the flyways of the birds. These rules would have to provide indications about the habitat types of wetland needed for stopover and staging sites, their size, their productivity with respect to food resources, seasonality in food availability (relative to timing of migration) and the distances from each other. There is, thus, a need to describe and quantify the required ecological state and conditions of the wetlands that are used as stepping stones along the flyways.

Ecological restoration of wetlands, and particularly river systems, is being planned and carried out all over Europe (Gereš 2004, Gumiero et al. 2008, see also http://www.ecrr.org/). All member states of the European Union, as well as most of the other European countries, have committed themselves to comply with the so-called Water Framework Directive, which will impose targets for ecological quality for all water systems and calls for catchment-based management in order to achieve these goals. Moreover, the member states of the European Union have also adopted the obligation to designate their most valuable nature areas the status of Special Protected Areas (SPAs) within the framework of either the EU Bird Directive or the EU Habitat Directive. The intention is that the Bird and Habitat Directive SPAs would function as a pan-European ecological network (Natura 2000), enhancing ecological coherence on an international level. Comprehensive mapping of the potentials and necessities of spatial water management and the intended distribution of Natura 2000 nature areas might prove valuable tools for assessing the possibilities within Europe. The role of natural vs. man-induced food sources remains to be identified for different stopover sites along the flyway.

REGIONAL SCALE

Studies have shown that in heavily fragmented wetlands or marshlands the occurrence, abundance and diversity of marshland bird species are less than expected (Foppen *et al.* 1999, Foppen 2001, Paracuellos & Tellería 2004, Naugle *et al.* 2001) and that population trends in key patch areas differ from those in smaller areas (Vermaat *et al.* 2008). Both size and spatial configuration of elements in the surrounding landscape (degree of isolation, distance to nearest other habitat elements) determine the number of breeding birds. Landscape ecological theory offers us a better understanding of how populations, for instance of a marshland bird, function in fragmented habitats. In small marshland patches, extinction chances are supposedly higher because of stochastic demographical processes. In fragmented sites the chances for recolonisation, once a habitat patch has become deserted, are smaller. However, migratory habits of many marshland birds limit the applicability of the original theory based on island biogeography (MacArthur & Wilson 1967, Simberloff & Wilson 1969). Moreover, in several instances isolation can also protect vulnerable key patches against predators or more aggressive competitors, thus enhancing the occupation of certain species (Lack 1971). The presence of water barriers may play an essential role here, as shown by the newly created island 'Kreupel' in Lake IJsselmeer (70 ha, in 2003), which in 2010 harboured over 7000 breeding pairs of Common Terns Sterna hirundo (Leon Kelder, pers. comm.).

Meta-population theory predicts that viability of spatially structured populations depends on the balance between local extinctions and recolonisations (Verboom et al. 2001). A spatially structured population can be viable even when partly fragmented. The population can be called a network population, and this is the basic idea behind the nature policy plans of the Dutch government (Ministry of Agriculture, Nature Management and Fisheries 2000). For a better insight in the quality of ecological connections among the socalled key patches, research on dispersion patterns of marshland birds in relation to quantified environmental parameters (such as food availability and disturbance) is needed for more reliable input in the spatial relationship models (see also Bowne & Bowers 2004, van der Windt & Swart 2008).

LOCAL SCALE

Individual birds breed, stage or winter in areas where they can find the right combination of breeding and/or roosting sites and suitable feeding opportunities within their daily range of activities. A demanding period in any bird's life is the breeding period (Drent & Daan 1980), when they are bound to the nest site for at least a couple of months. For wintering birds the spatial arrangement of roosting sites and feeding areas should last long enough to cover the winter period. Staging areas should meet these needs for periods of days to a couple of weeks during periods of seasonal migration. A general issue concerns the degree of ecological dynamics in wetland areas and measures to manage or improve these dynamics. As many wetland areas in The Netherlands are hydrologically closed systems with an often fixed watertable, succession tends to be in one direction, leading to a less dynamic habitat. This holds for vegetations, but also for prey populations. Areas with abundant seed production, large densities of invertebrates (crustaceans, molluscs, insects) or vertebrates (amphibians, fish, rodents), invariably are estuarine or coastal areas, connected to a larger river or lake. Management options to restore these characteristics in eutrophic wetlands include the introduction of a seasonally changing watertable, i.e. high in winter and spring, low in summer and early autumn. Connecting waterbodies by improving fish migration from one system to another is also considered of major importance for the functioning of wetlands.

Spatial planning of local restoration and water management projects should therefore consider the daily activities of targeted wetland bird species. It should include careful planning of quiet and undisturbed breeding and roosting sites, located strategically within daily range of profitable feeding areas of sufficiently large size. Ecologists and ornithologists should strive at providing the spatial planners with accurate data on the birds' habitat requirements for breeding, roosting and feeding, as well as on the commuting distances between the different components of their daily environment. Future ecological work on wetland birds should focus on filling in the knowledge gaps that still exist. For many species the feeding ecology (habitat use, food choice and intake rates) at the local level is still poorly understood. This needs emphasis in future studies, as well as the need for better field data on the exchange of individuals between patches of suitable habitat (Bowne & Bowers 2004).

EPILOGUE

Combining spatial information on water management and ecological restoration plans and wetland management (in terms of ecological coherence and networks), a perspective might be drawn for marshland birds. As pointed out by van der Windt & Swart (2008) rigorously applying an appealing theory based on scientifically weak grounds is a major risk to society on the longer term. These authors analyse the factors that contributed to the popularity of the concept of ecological corridors in The Netherlands. One of their conclusions is that, due to the vagueness of the concept, it was acceptable to many stakeholders. Therefore it is necessary to specify important gaps in knowledge in more detail. For the three levels of scale, the most relevant biological parameters of spatial habitat use by wetland birds are:

(1) Flight range during migration in relation to size and profitability of stopover sites, in order to determine

sizes of these sites and distances between them.

(2) Size of breeding and feeding territories in relation to size of the wetland, dispersal characteristics, population resilience in dependence of habitat quality features and degree of fragmentation, in order to establish effective networks for meta-populations.

(3) Daily attainable flight ranges between breeding (or roosting) sites and feeding grounds, in order to optimise the spatial arrangement of breeding and feeding habitats.

For spatial planners, important knowledge gaps in relation to water management include a better insight on river catchment and inter-catchment area levels of the spatial relationships, i.e. between size of floodable areas and sustainable safety levels for different forms of human land use.

The great challenge for both disciplines, spatial planning and ecology, will be to combine their skills and knowledge to ensure the most effective way of designing wetland landscapes on all relevant scales for sustainable use by Man and birds. In The Netherlands, the spatial planning for the 'backbone of nature' is being based on the concept of assuring key habitats and ecological corridors for viable meta-populations (Ministry for Agriculture, Nature Management and Fisheries 2000). For the wetland parts of the network a link is sought with flood protection activities along the rivers Rhine and Meuse as well as in the lowland polders (e.g. Ministry of Transport, Public Works and Water Management 2000, Wolters et al. 2001, Platteeuw & Iedema 2002). Elsewhere in Europe the opportunities involved in linking wetland restoration and reducing risks of flooding are also recognised (e.g. Ministerium für Umwelt und Verkehr 1997) and ecological restoration per se seems even more widely embraced (Lohr & Walter 2000, Buijse et al. 2002). However, the possibilities for establishing ecological networks of wetlands on larger scales have barely been touched so far. The EUfunded project 'EcoFlood' aimed at achieving a more comprehensive overview of what is going on in this field in a pan-European context, including socio-economic and ecological perspectives for wetland restoration and flood reduction (see http://levis. sggw.waw.pl/ ecoflood/ and references therein).

Our present knowledge underpinning the key patch approach focuses on understanding spatial processes but ignores effects of habitat quality on sustainability of a population. Only with an integrated approach the right assessments can be made for prioritising conservation actions. These should be based on theory, empirical evidence and experiments (Haddad *et al.* 2000). Also, the present key patch sizes are not 'climate proof', that is not buffered to changing conditions. If in the near future climate change is causing additional stress for species, i.e. steeper fluctuations due to the influence of extreme weather spells, population viability will decrease and standards need to be adapted (see e.g. Sæther et al. 2006, Watkinson et al. 2004). This appeals for action, experiments and measures, rather than just desk research and further debate. However, the present situation shows how difficult it is to maintain direction and develop an adequate answer to the increasingly man-used environment by empowering ecosystems. To illustrate this process of dealing with uncertainty we present examples of the IJsselmeer area in The Netherlands. Here, questions related to three levels of measures and management of large-scale wetland areas show up:

(1) In the case of Oostvaardersplassen, a newly developed wetland (6000 ha) in a Dutch polder, it shows that maintaining high waterlevels in marshland by active management can safeguard ground-breeding waterbirds (geese, egrets, spoonbills; Vulink et al. 2009) from mammalian predators. The question remains of how the necessary draw-down of the watertable, in order to restore the marshland vegetation, can be applied without losing this function - and thus the breeding birds – during the four years of time that are required (Vulink & van Eerden 1998). The grazing of Red Deer Cervus elaphus, Heck Cattle and Koniks in the dry border zone of the marsh (Vulink 2001) still causes a lot of – politically charged – debate, related to the management of the introduced populations of large herbivores.

(2) Plans to merge Oostvaardersplassen with the 4000 ha of broad-leaved forest of Horsterwold using a wide corridor of 1900 ha have been proposed to combine ecological empowerment of the region with recreation and housing. This measure, for which the first steps have already been taken by purchasing farmland, is now jeopardised because of political debate. The instalment of a new government in November 2010 have grinded the plans to a halt.

(3) Large-scale marsh restoration in Lake Markermeer is another attempt to boost wetland ecosystems in the IJsselmeer region, to ameliorate the hard ecotone of artificial shores: 6000 ha of marsh connected to Lake Markermeer (60,000 ha) are proposed to be developed. Such developments are likely to improve the wetland functions of the entire lake. The nearby Oostvaardersplassen wetland would benefit simultaneously, as the proposed distance between both key areas would be less than 15 km, a small distance for most marshinhabiting birds. After careful planning and stakeholder involvement at all stages, a pilot project is being set-up (Samenwerkingsverband TMIJ 2009).

These examples show that large-scale developments, either alternative management experiments or large scale changes in land use planning, need to be based on well-studied ecosystems and, perhaps more important, need to be well-anchored into society. A pitfall to be avoided would be, given the uncertainties associated with sweeping plans, to compromise the levels of scale that are needed to successfully circumnavigate ecological problems.

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SAMENVATTING

Over geheel Europa zijn wetlands in omvang afgenomen, hebben ze hun oorspronkelijke dynamiek verloren en zijn ze gefragmenteerd geraakt als gevolg van een geleidelijke toename van het menselijk landgebruik. Deze processen hebben geleid tot belangrijke verliezen in natuurwaarden, waarvan rijkdom aan moerasvogels er één is. Ecologisch herstel van wetlands is in principe een haalbare kaart, maar kan op zichzelf gemakkelijk als te duur worden beschouwd, ondanks initiatieven als de EU Vogel- en Habitatrichtlijn en de Kaderrichtlijn Water. Versterking van wetlands binnen het Natura 2000 netwerk (Speciale Beschermingszones onder Vogel- en Habitatrichtlijn) heeft betere kansen in combinatie met een ruimtelijke aanpak van het waterbeheer gericht op het voorkómen van overstromingen en wateroverlast. Onderzoek naar schaaleffecten in habitatgebruik door moerasvogels kan worden gezien als een essentieel onderdeel van de ruimtelijke planvorming met betrekking tot ecologisch herstel en waterbeheer (bijvoorbeeld ter voorkoming van ongewenste overstromingen). Met de opgedane kennis kan rekening worden gehouden in de ruimtelijke ordening. We onderscheiden vier niveaus van habitatgebruik door moerasvogels, en van elk geven wij voorbeelden van de consequenties voor de grootte en onderlinge samenhang van de habitats. Die vier niveaus zijn: (1) vogels op pleisterplaatsen langs de trekroute, (2) territoriaal broedende vogels, (3) in kolonies broedende vogels, en (4) vogels in hun overwinteringsgebieden. Dit vergt ecologische samenhang op drie verschillende schalen, te weten op het niveau van internationale trekroutes, op het regionale niveau van landschappen en op het lokale niveau van individuele wetlands. Wij propageren dat moerasvogel-ecologen zich zouden moeten wijden aan de kwantificering van relevante gegevens over habitatgebruik op elk van deze drie schaalniveaus, terwijl ruimtelijke planvormers zich zouden moeten beijveren om deze gegevens in te brengen in de realisering van duurzaam waterbeheer. Een dergelijke aanpak zou wellicht het tij kunnen doen keren voor ernstig bedreigde moerasvogelsoorten.