This thesis describes, quantifies and explains changes in breeding bird diversity in the Netherlands in the past decades. The analyses are based on large-scale, long-term and multi-species datasets on changes in distribution and abundance. A substantial part of these data is gathered by volunteers, people who go out into the field to count birds merely for the joy of it. Nevertheless, they are generally very skilled and use standard protocols for carrying out the field work. By confronting population trends with life-history and ecological traits of breeding birds, the characteristics that are primarily associated with successful and unsuccessful species in our rapidly changing environment are identified. This helps unraveling underlying mechanisms, prioritizing conservation research and developing management strategies.

Mechanisms and constraints in biodiversity conservation and restoration

5

Birding for science and conservation

Chris van Turnhout

Birding for science and conservation

Explaining temporal changes in breeding bird diversity in the Netherlands

Chris van Turnhout

Uitnodiging

Hierbij nodig ik u uit om de openbare verdediging bij te wonen van mijn proefschrift:

Birding for science and conservation

Explaining temporal changes in breeding bird diversity in the Netherlands

op dinsdag 15 maart 2011
om 15:30 uur precies

in de aula van de Radboud
Universiteit Nijmegen
Comeniuslaan 2 te Nijmegen

Aansluitend is er een receptie

Paranimfen:
Hein van Kleef
Marijn Nijssen

Chris van Turnhout
chris.vanturnhout@sovon.nl

Birding for science and conservation

Explaining temporal changes in breeding bird diversity in the Netherlands

FSC
www.fsc.org
MIX
Paper from
responsible sources
FSC® C014810

Van Turnhout C.A.M. 2011. Birding for science and conservation. Explaining temporal changes in breeding bird diversity in the Netherlands. Thesis, Radboud University, Nijmegen.

ISBN: 978-90-9025945-1

Cover: P. Eekelder
Layout: A.M. Antheunisse
Artwork: F. Hustings (cartoon) and J. Zwarts (all other drawings)
Printed by: Ipskamp Drukkers B.V., Enschede.

Birding for science and conservation

Explaining temporal changes in breeding bird diversity in the Netherlands

Een wetenschappelijke proeve op het gebied van de
Natuurwetenschappen, Wiskunde en Informatica

PROEFSCHRIFT

ter verkrijging van de graad van doctor
aan de Radboud Universiteit Nijmegen
op gezag van de rector magnificus prof. mr. S.C.J.J. Kortmann,
volgens besluit van het college van decanen
in het openbaar te verdedigen op dinsdag 15 maart 2011
om 15:30 uur precies

door

Christiaan Aloysius Maria van Turnhout

geboren op 17 april 1971
te Heerlen

Promotores:
Prof. dr. H. Siepel
Prof. dr. A.J. Hendriks

Copromotores:
Dr. R.S.E.W. Leuven
Dr. R.P.B. Foppen

Manuscriptcommissie:
Prof. dr. J.M. van Groenendael
Prof. dr. F. Berendse (Wageningen Universiteit)
Dr. G. van der Velde

Dit proefschrift is tot stand gekomen in samenwerking met SOVON Vogelonderzoek Nederland

Paranimfen:
Hein van Kleef
Marijn Nijssen

Voor m'n ouders

Contents

Chapter 1

General introduction

Chris van Turnhout

Abstract

This thesis describes, quantifies and explains changes in breeding bird diversity in the Netherlands in the past decades. The analyses are based on survey data on (changes in) distribution and abundance and ecological data on traits of breeding birds. A substantial part of these data is gathered by volunteers, people who go out into the field to count birds merely for the joy of it. Nevertheless, they are generally very skilled and use standard protocols for carrying out the field work, thus enabling scientifically sound analyses. The first paragraph of this general introduction focuses on birds as environmental indicators. The next two paragraphs deal with the merits of the contribution of volunteers to field ornithology. The fourth paragraph summarizes the most important historic changes in Dutch landscapes and breeding bird composition in the Netherlands, as a reference for the changes described in the following chapters. In the last two paragraphs the aim of this thesis and the research questions are described in more detail.

Breeding birds as monitors of environmental change

Boosting human populations, their increasing demands on natural resources and technological developments all result in a continuing increase in the impact of people on the natural environment. There is broad consensus that global biodiversity is declining more rapidly now that at any time in human history (Millenium Ecosystem Assessment 2005). At present, 13% of the known bird species in the world is threatened with extinction (Hoffmann *et al.* 2010). In 2002, at the United Nation's Convention on Biological Diversity (CBD), member states agreed to achieve by 2010 a significant reduction of the rate of biodiversity loss at the global, regional and national level (Carpenter *et al.* 2006). At the CBD conference in Nagoya in 2010 it was agreed to reduce the global loss of species by 50% in 2020 (www.cbd.int). The need for environmental monitoring has therefore never been greater.

Until quite recently, observational (or surveillance) monitoring had only little academic respectability, probably partly due to poorly-defined objectives and poorly-designed methodologies of monitoring programs (Furness & Greenwood 1993). Moreover, monitoring relies largely on correlative analyses rather than on manipulative experiments, thus weakening inferences (Nichols & Williams 2006). However, as ecological systems exhibit incredibly complex structures and dynamics, many scientific and conservation questions are hardly amenable to an experimental approach (Brown 1999). Although experiments are necessary to solve a part of the research questions, this is often only possible after observational and correlative monitoring studies have established the basic facts and backgrounds. Bart (2005) even states that it is difficult to think of a major wildlife issue for which monitoring has not provided essential information. Monitoring also generates hypotheses for underlying mechanisms (Nichols & Williams 2006). The appreciation that short-term and experimental approaches have their limits has, mainly in the past two decades, led to increased acceptability of long-term and broad-scale monitoring studies (Godfray & Hassell 1992, Wooler *et al.* 1992, Furness & Greenwood 1993). It has stimulated an explosive growth in the research field of macroecology, the study of distribution and abundance at large spatial and temporal scales (Greenwood 2007). This was also facilitated by the increasing availability of large, standardized and high-quality datasets, computer power and statistical techniques. Brown (1999) describes macroecology as 'the empirical exercise of detecting general patterns, the theoretical exercise of formulating mechanistic hypotheses to account for these patterns, and the empirical exercise of testing the hypotheses'. Due to limitations and practicalities, macroecology is often characterized by studying easily measured variables (such as counts of abundance), large numbers of species and individuals of well-studied groups of organisms, at relatively large spatial and temporal scales (Brown 1999).

The idea that birds can be used to monitor environmental changes is far from new, and dates back to the ancient times of Aristotle, when some aspects of bird behaviour were thought to predict changes in weather conditions (Furness & Greenwood 1993). More convincing historic examples are perhaps the presence of flocks of seabirds as indicators of the location of shoals of fish for fishermen, and caged canaries as indicators of the presence of methane or carbon monoxide gasses to alert coal miners (Figure 1). There are a number of reasons why birds are useful monitors of environmental change. They are regarded as good general indicators of the state of

Figure 1. Coal miner with caged canary (http://staff.kings.edu).

wildlife, although it is still to a large extent unclear how the spatial and temporal changes in bird numbers correspond with those of other taxa (Gregory *et al.* 2008; but see Thomas *et al.* 2004). Nevertheless, regional networks of sites selected as important for birds also capture a part of the other biodiversity (Brooks *et al.* 2001), birds appear to be good representatives of global species richness and endemism patterns (Stattersfield *et al.* 1998) and average population trends of Dutch breeding birds since 1990 resemble those of most other fauna groups with reliable data, ranging from dragonflies to mammals (Kalkman *et al.* 2010). Birds are positioned at the upper end of food chains and are relatively long-lived, and are thus sensitive to many diverse factors that affect (BirdLife International 2004, Newton 2004, Jetz *et al.* 2007, Lemoine *et al.* 2007), or accumulate through (Newton *et al.* 1993, Hendriks & Enserink 1996, Van den Burg 2009) the food chain. Birds use the landscape at different spatial scales, from less than a hectare in small sedentary birds to the entire globe in some long-distance migratory species, thus integrating the effects of environmental changes over huge areas (Gregory *et al.* 2008). Birds use both the aquatic and terrestrial components of ecosystems. Birds cover a moderate diversity of species (around 10,000 species world wide) and a broad scope of ecological and life-history traits. They occupy a large variety of habitats and are relatively abundant. Furthermore, birds are mostly diurnal, vocal or conspicuous, easy to identify and there is much knowledge available on their taxonomy, ecology, behaviour, ranges and numbers (Furness & Greenwood 1993). However, one of the most compelling reasons for using birds as biomonitors is that they have great public resonance, and are very suitable to raise awareness of biodiversity issues. Given the considerable interest in birds, there are many potential observers and volunteer efforts can be directed into useful and large-scale monitoring programs (Gregory *et al.* 2008).

To conclude, birds are regarded as sensitive and useful indicators of ecological integrity at the landscape scale. They are therefore increasingly used as monitors of specific environmental drivers, from drivers acting at the local scale, such as shrub encroachment in the Dutch coastal dunes (Van Strien *et al.* 2009), to processes at the global scale, such as climate change (Gregory *et al.* 2009, Jiguet *et al.* 2010a). They are also used as surrogates of changes in biodiversity more broadly (Furness & Greenwood 1993, Butchart *et al.* 2004, Gregory *et al.* 2005, Butchart *et al.* 2010). These latter composite 'state indicators' provide a simple way of measuring progress towards targets of reducing biodiversity loss at a number of spatial scales, and have been very successful in influencing policy and communicating to a wider audience (Gregory *et al.* 2008). This is of course no scientific argument for using birds as indicators, but to achieve the ultimate goal of improved management, monitoring must be embedded in a relevant socio-economic context to ensure that research findings on population declines will be used for priority setting, and translated into active conservation (Nichols & Williams 2006).

Birds, citizens and science

There are few fields of scientific research that approach ornithology in the extent of the contribution of volunteers. In the United States for example, there are 48 million 'birdwatchers', about 21% of the population (Carver 2009). To be counted as a birder in this enquiry, an individual must have either taken a trip of one mile or more from home for the primary purpose of observing birds or have tried to identify birds around the home. To further illustrate the socio-economic value of birding, trip- and equipment-related expenditures associated with birding generated over $82 billion in total industry output, 671,000 jobs, and $11 billion in tax revenues (Carver 2009). In the Netherlands, field work for the most recent national breeding atlas (SOVON 2002) was mainly carried out by volunteers. Their efforts were coordinated by a handful of professionals. Costs would have been over six times higher if field work was carried out by professionals (SOVON 2003). Levrel *et al.* (2010) estimated that the French administration saves between 678,523 and 4,415,251 euros per year thanks to efforts of volunteers in national biodiversity monitoring schemes.

Greenwood (2007) has written a thorough review on the history and merits of international collaborative research by networks of amateurs for ornithology and conservation. The word 'amateur' often suggests a negative qualification nowadays, associated with a lack of seriousness and reliability. Here, however, amateurs (further referred to as 'volunteers') are considered those who contribute to surveys or ornithological research for the joy of it, not for payment. The skills and expertise of volunteers are generally gained through extensive field experience, not from formal education. The first large-scale bird surveys based on the efforts of volunteers date from the 18th and 19th century, and focused on the collection of first arrival dates of migrants in spring. Fields of collaborate ornithological research that soon followed were migration counting (Figure 2) and bird ringing (from 1899 onwards). Large-scale distribution studies, relying mainly on the efforts of volunteers, were undertaken from the 1970s onwards. The first national multi-species grid-based atlases were from the UK (Sharrock 1976), France (Yeatman 1976), Denmark (Dybbro 1976) and the Netherlands (Teixeira 1979). More than 400 bird atlases have been published now worldwide, involving over 160,000 observers (Gibbons *et al.* 2007). 12% of those concern second or 'repeat atlases', which make it possible to quantify changes in distribution in time (see chapter 4). A pan-European atlas was published in 1997, in

Figure 2. Watching visible bird migration at Breskens, the most famous spring observation site in the Netherlands (photo Gerard Troost).

which the atlas data of separate countries were compiled in order to overcome differences in language, methodologies and organizations (Hagemeijer & Blair 1997). Other fields of research that have benefited from the input of volunteers are studies into habitat requirements, behaviour, demography (reproduction and survival) and population dynamics (Greenwood 2007).

The first annual surveillance of common and wide-spread birds was initiated in the United States in 1900, and the Christmas Bird Count is still the oldest and largest (66,000 participants) citizen bird survey in the world (G. Butcher, *pers. comm.*). More systematic programs, in which fieldwork methods and efforts were standardized, started in the 1960s in the United Kingdom (Common Bird Census) and United States (Breeding Bird Survey). Nowadays, 37 European countries have similar breeding bird schemes, although a variety of methods is used, ranging from territory mapping to transect and point counts (www.ebcc.info/pecbm.html). Most schemes have some kind of sampling strategy, and therefore produce relative indices of the true populations.

The availability of data on these different topics, gathered by efforts of volunteers, has allowed conservation work to be focused on identification of priority species, habitats and sites (e.g. BirdLife International 2004). It also enabled and refined research aimed at providing the understanding of underlying mechanisms for population changes, which is needed for evidence-based policy and management (Greenwood 2007). One of the best examples is the work on farmland birds in Britain. Collaborate work by volunteers proved to be essential in identifying the problems, diagnosing its causes, developing solutions and monitoring the success of the policies in which the solutions were implemented (Siriwardena *et al.* 1999, Siriwardena *et al.* 2000, Vickery *et al.* 2004). This work is most successful where there is a strong partnership between the volunteers and professional biologists. The participation of large numbers of volunteers not only enables work to be done that would otherwise be impossible at the same spatial and temporal scales, but also facilitates democratic participation in the decisions made by society.

Volunteers may sometimes be less experienced than professionals and fieldwork mistakes arise through a number of reasons. On the other hand, it is more likely that volunteers are motivated and familiar with their study sites than professionals. The magnitude of actual errors appears generally within an acceptable range in most types of survey work (Greenwood 2007). Moreover, competence of volunteers is generally assessed in monitoring programs and the data are validated both automatically and manually. Nevertheless, surveys must be organized in ways that take into account the skills and the diversity of motives of participants. The work has to be enjoyable, useful (also for the volunteers' own objectives), challenging, improving their knowledge and giving the idea of being part of a community. Surveys must include standardized methods and clear instructions, including registration of effort (although the prerequisites of the latter are being more relieved as new statistical methodologies become available; see chapter 8). Furthermore, surveys must have a careful design (see chapter 2), provide representative coverage, gather data that can easily be processed, and must provide continuity for the long term (Greenwood 2007).

A brief history of bird survey work in the Netherlands

The history of citizen ornithology in the Netherlands resembles the situation abroad: the counting activities of a handful of individual pioneers gradually evolved into regional and national cooperation of many volunteers in atlas studies, into standardization of field work methods adopted in national survey programs, and eventually into fine-tuning of monitoring efforts for optimal embedding in national policy-making processes. This paragraph is largely based on SOVON (1998), and focuses on the contribution of volunteers in studies on distribution and abundance of birds.

Reliable quantitative information on bird population numbers and distribution from the early 20th century is only available for a small selection of appealing breeding birds, such as White Stork *Ciconia ciconia*, Spoonbill *Platalea leucorodia* and Cormorant *Phalacrocorax carbo*. Other accounts on the occurrence of birds in the Netherlands in that period were mostly qualitative or anecdotal. In 1931 the first attempt was made to carry out a complete count of water birds in the Dutch Wadden Sea (Van Oordt 1932). It was not until the 1970s however, that such complete counts were carried out at a more regular basis (Ens *et al.* 2009). Haverschmidt (1942) published the first national overview on the occurrence of all Dutch birds that included substantial quantitative data, as well as some distribution maps. A publication of Tinbergen (1941) gave a boost to the more systematic survey of breeding birds, as he included a brief manual on how to carry out breeding bird surveys by means of territory mapping (still the prime method for monitoring breeding birds in the Netherlands nowadays), and promoted this among volunteers. Local and annually repeated inventories of breeding birds using standardized methods started from the 1950s onwards (see Chapter 3). Some of the study sites that were initiated in the 1960s are still counted to this date, sometimes even by the same observers. In the 1960s also the first nationwide censuses of a number of scarce breeding bird species and wintering geese were carried out, as well as the mid winter count of important wetlands, which were coordinated by a handful of professionals. Volunteers had then started to organize themselves in regional working groups, often aiming to produce a local or regional bird atlas. These activities cumulated to almost 250 working groups and approximately 17,000 published atlas pages by the end of the 20th century (Bijlsma *et al.* 2001). In 1973, SOVON was founded to organize the field work for the first national grid-based breeding bird atlas, coordinating the efforts of individual observers and regional working groups. Almost 3,000 volunteers participated, and the atlas presented hitherto unknown information on national distribution and population sizes of all breeding bird species (Teixeira 1979; see Chapter 4). This was soon followed by grid-based and year-round fieldwork for an atlas of breeding, migrating and wintering birds, this time coordinating the efforts of 5,000 participants (SOVON 1987). A second breeding bird atlas project was organized in 1998-2000 (SOVON 2002). This enabled the assessment of changes in distribution over a 25 year period (see Chapter 4). Again, around 5,000 participants were involved.

With the increase of the number of volunteers and their networks, the need to uniform and standardize field work increased as well. It was considered important that survey results were comparable in space and time. Hustings *et al.* (1985) described and harmonized field work methods, and included detailed guidelines which were largely based on detection probabilities of breeding birds. These guidelines were adopted, further specified and expanded with guidelines for interpretation of the fieldwork in the manual for the national breeding bird monitoring program, which started in 1984 (Van Dijk 2004; see Chapter 2). The main objective of this monitoring scheme, which is carried out in close collaboration with Statistics Netherlands (CBS), was to assess yearly changes in population sizes of common and scarce breeding birds at national and regional scale. The number of study sites grew from around 300 per year in the mid 1980s to a maximum of 1,900 around 2005. This has resulted in a total of over 4,000 plots surveyed in the period 1990-2008. Both volunteers and professionals contribute to this scheme (Van Dijk *et al.* 2010). It is the prime source of data for the analyses presented in this thesis (see Chapters 2, 3, 5, 6 and 7).

Bird monitoring in the Netherlands is not restricted to common breeding birds. Several surveys exist, also for rare breeding birds and non-breeding birds. Surveys are essentially differentiated by the period of the year in which species occur and by the abundance of the species that are monitored (Table 1). All surveys have their own background, history and objectives, but together they yield information on population changes of almost all regular birds occurring in the country, both breeding and non-breeding. Over 8,000 volunteers have participated in these surveys and in atlas studies (Figure 3).

Recently, the aims of most monitoring schemes have been extended. There is an increasing need for local and site-specific trends and fine-scale distribution data for planning and legislation issues (e.g. EU Bird Directive). Furthermore, the data are increasingly used to address specific research questions and management issues (Breeuwer *et al.* 2009, Grashof-Bokdam *et al.* 2009, Kraan *et al.* 2009, Klok *et al.* 2010,

Table 1. Operational national bird monitoring schemes in the Netherlands, differentiated by time of year and abundance of species. The rectangle indicates the schemes from which data are used in this thesis (together with data of the two successive national breeding bird atlases, which are not shown here).

Abundance	Sampling strategy	Category		
		breeding birds	*waterfowl and wintering birds*	*migrating birds*
rare	national coverage or large study sites	Rare Breeding Birds Monitoring program (LSB-Z) since 1990	Wetland Bird Survey (Meetnet Watervogels) since 1967	casual observations (BSP-nb) since 1989
scarce or clustered	medium-large study sites	Colonial Breeding Birds Monitoring Program (LSB-K) since 1990 Breeding Bird Monitoring Program (BMP-B/W/R/E) scarce species, precursor since 1985	Wetland Bird Survey Roosting Bird Survey (Meetnet Slaapplaatsen) since 2009	
abundant and widespread	small study sites	Breeding Bird Monitoring Program (BMP-A) all species, since 1984	Wetland Bird Survey	
	point counts	Monitoring Urban Species (MUS) since 2007 Monitoring Farmland Species (MAS) since 2009	Point-Transect-Counts (PTT) since 1978 Garden Bird Count (Tuinvogeltelling) since 2003	migration counts (LWVT/Trektellen.nl) since 1978

Jiguet *et al.* 2010b, this thesis). Our challenge is to innovate the schemes to fulfil these new demands as much as possible, without losing track of the main objectives (and continuity of methods!). Simultaneously, we have to guarantee and stimulate the commitment of volunteers, taking into account their changing preferences and time budgets (see Chapter 8).

Historic changes in Dutch landscapes and bird communities

The Dutch landscape has continually been on the move since prehistoric times as a result of changes in climate, sea level and, gradually, impact of man. Birds were forced to adapt to their changing environment, but not all succeeded. In this paragraph the most important processes behind changes in breeding bird diversity are briefly summarized, in order to put the more recent changes described in this thesis into a historic perspective. The occurrence of birds in the Netherlands until the Middle Ages is based on archeozoological records. Later, written accounts became increasingly available which, together with data from collections, enable a more reliable and semi-quantitative reconstruction (Vogel 2007).

Figure 3. Distribution of volunteers (number per postal code) participating in monitoring programs and atlas studies in the Netherlands.

In Roman times the Netherlands consisted largely of extensive (open) forests and marshlands. Locally however, forests were already being cleared to create arable land and meadows. Here, House Sparrow *Passer domesticus* successfully colonized as a new breeding bird (Vogel 2007). In the early Middle Ages the lower parts of the country were still dominated by the extensive and highly dynamic estuaries of Rhine and Scheldt, with mudflats, saltmarshes and dunes. More inland tidal marshlands dominated, where Dalmatian Pelicans *Pelecanus crispus* bred in colonies. Also present were forests, fens, mires and extensive freshwater marshlands, where large heron colonies occurred. The higher parts of the country still consisted of extensive primeval forests. Around 1000 A.D. most primeval forests had already been cleared, and were replaced by heathlands and inland drift sands. Tawny pipits *Anthus campestris* successfully colonized these areas, and populations of Black Grouse *Tetrao tetrix* thrived (both species are now at the verge of extinction; see Chapters 4 and 5). In the period 1600-1800 AD the human population increased strongly, and the cultivation of the landscape accelerated. In the lower parts of the country marshlands were drained and successively reclaimed, and fens were excavated. Temporarily, this resulted in a vast and very diverse marshland landscape, consisting of a variety of succession stages. The area of water reed stands increased. Black-tailed Godwit *Limosa limosa* and some other waders, originally breeding birds of fens and mires, colonized the polders and became meadow birds. Grazing by livestock intensified on heathlands, and many turned into drift sands. Together, these habitats accounted for 20% of the land around 1830 (Vogel 2007). Breeding bird diversity in the adjacent farmland increased strongly, as a result of its small-scale and heterogeneous use.

In the 19th century raptors, herons, gulls and terns were heavily persecuted, and some species were almost completely extirpated (Vogel 2007). The coastal dunes were actively fixed with grasses and forest plantations, and lost much of its original dynamics. Species inhabiting open dune habitats decreased, whereas birds of shrubs increased. Reclamation of marshlands continued and large heron colonies gradually disappeared. Most meadow bird populations increased as a result of farmland fertilization and favorable management. Blackbirds *Turdus merula* started to colonize the expanding cities. The area of forest reached its all time low around 1870, leaving only 3% of the country covered. Thereafter, the economic value of heathlands diminished, through a combination of the import of wool from Australia (around 1870) and the introduction of artificial fertilizers (around 1890). This was the onset of large-scale afforestation. Mostly exotic coniferous tree species were used. Data are sparse, but it can be expected that forest birds in general will have benefited. At the end of the 19th century the exploitation of mires started, as well as the intensification of farmland use.

These processes continued and accelerated during the 20th century, as described by Bijlsma *et al.* (2001) and Van Beusekom *et al.* (2005). The human population tripled, intensity of land use increased even faster, particularly since the 1960s. Dutch farmland, occupying 70% of the country, is now among the most productive of the world. Cattle densities are four times higher than the West-European average, yields per hectare are even five times higher (RIVM 2003). The countryside rapidly changed from small-scale, mixed and organic at the beginning of the century, to large-scale, uniform and industrialized, and no longer dependent of local soil and weather conditions. Massive application of fertilizers and pesticides, drainage, mechanization, earlier and more frequent mowing, introduction of monocultures, reduction of crop diversity and land consolidation were the key drivers. Successive reclamations increased the land size of the Netherlands with 6%. The saline Zuiderzee was turned into a freshwater lake (IJsselmeer) in 1932, and then its area was reduced with 42% by three large land reclamation projects (see Chapter 3). Similar embankments were carried out in other parts of the country, including the Dutch estuaries and floodplains (see Chapter 7). Most ecosystems, except the Wadden Sea, have now lost their natural dynamics. The area of woodland increased substantially (+29% since 1900, www.natuurcompendium.nl), now occupying almost 10% of the country. Other semi-natural habitats decreased in both quantity and quality, particularly heathlands and marshlands (–77% since 1900), as a result of cultivation, drainage and eutrophication (see also Chapters 3 and 4). The area of urban habitats has increased by 473% since 1900, now occupying around 15% of the country.

It will be clear that the landscape processes described above have had huge effects on breeding bird composition. In addition, migratory species are also affected by land-use changes abroad. Climate change is another potential major driver of population changes, particularly since the onset of global warming in the 1980s. After an evaluation of a large number of historical sources on Dutch breeding bird numbers, Parlevliet (2003) concluded that the number of species that had substantially increased in abundance (population at least tripled) since 1900 was larger (n=62) than the number of species that had decreased with the same rate (n=47). Whereas seven species disappeared as regular breeding birds during the 20th century (two of which returned later following reintroductions), at least 39 species became established as regularly breeding birds. The latter figure excludes at least seven introduced non-native species. Another eight species have become annual breeding birds since 2000. These results may be rather contra-intuitive, given the highly anthropogenic Dutch landscape where ecosystems have long been experiencing very strong human pressure (Kondoh 2001). However, changes in diversity at the national level might not correspond to changes at other spatial scales (McKinney & Lockwood 1999, Sax & Gaines 2003; see Chapter 4), and changes in taxonomic diversity might not correspond to changes in functional diversity among species in a community (Olden & Rooney 2006, Devictor *et al.* 2008; see Chapter 5).

Aim of this thesis

The main aim of my thesis is to quantify and explain changes in breeding bird composition in the Netherlands in the past decades. An integrated and quantitative analysis of population developments in all co-existing breeding bird species is not yet available for the Dutch situation in scientific literature, and international studies based on similar spatial scales and time periods are scarce. I want to explain these changes from life-history and ecological traits of individual species. Life-history traits are defined here as traits that affect the life course of an organism, and are directly related to various investments in reproduction, development, dispersal, and the synchronization between those (Verberk 2008). Ecological and behavioural traits compromise environmental preferences and associated behaviors (Vieira *et al.* 2006). Confronting population trends with species traits may clarify which sets of traits are primarily associated with successful and unsuccessful species in our rapidly changing environment, which is affected by multiple processes simultaneously. It may also identify and rank the most important environmental changes responsible, including changes in land-use, climate and habitat management.

This thesis therefore is primarily a macroecological study that describes general patterns based on empirical survey data (Brown 1999). Furthermore, I formulate and test hypotheses that account for these patterns, using comparative methods (Fisher & Owens 2004). By confronting unique large-scale, long-term and multi-species datasets on distribution and abundance with data from a large number of autecological species-specific studies, I will identify and rank traits that are correlated with population trend in Dutch breeding birds. By doing this, I will also illustrate and strengthen the value of large-scale survey data gathered by volunteers to address scientific questions, to prioritize conservation research and action and to identify and evaluate suitable management strategies.

Research questions and outline

The body of this thesis consists of chapters 4, 5 and 6. Chapter 2 addresses some specific methodological issues related to the monitoring design. Chapter 3 additionally describes long-term habitat-specific trends of marshland birds, and chapter 7 illustrates the value of the approach for a specific habitat management issue in river floodplains. The structure of this thesis is schematized in Figure 4. First, populations trends are reconstructed (chapters 2 and 3). Then, diversity patterns are described (chapters 3 and 4) and causes of changes are explored (chapter 5). Next, changes are explained using two case studies which focus on a specific environmental process (chapters 6) and management issue (chapter 7). Finally, the results are integrated, the merits of the methodologies used are discussed and the value of citizen ornithology for science and conservation is addressed (chapter 8).

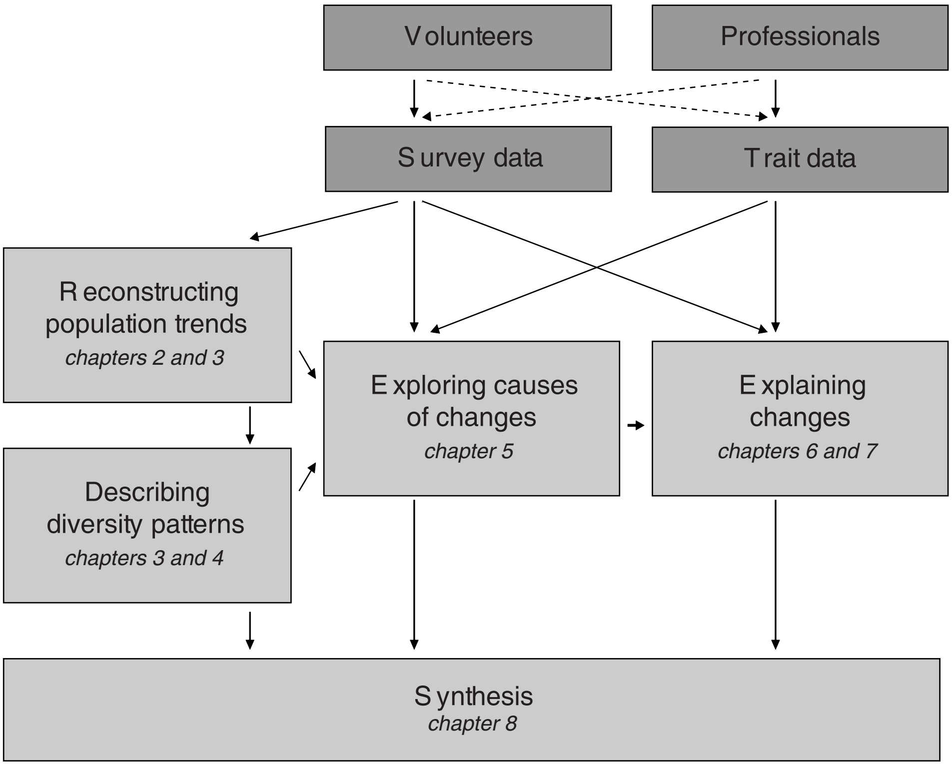


Figure 4. Structure of this thesis. For further explanation, see text.

Chapter 2. Monitoring common and scarce breeding birds in the Netherlands: applying a post-hoc stratification and weighting procedure to obtain less biased population trends.

Objective
The main aim of the Dutch Breeding Bird Monitoring Program (BMP) is to assess annual changes and trends at the national and regional level in common and scarce breeding bird populations. Because it is not possible to count all individual birds to calculate the true trend in species abundance, it is necessary to take samples. Since the participants, mainly volunteers, are free in choosing their study sites, plots are not randomly distributed over the Dutch regions and habitat types. If the trends between these strata differ, the estimates of population changes may be biased. The aim of this chapter is to describe and discuss a method to correct for unequal sampling, using an independently collected set of atlas data.

Research question
- How can the non-random sampling design of the Dutch Breeding Bird Monitoring Program, where participants are free in choosing there study sites, be corrected for in order to get unbiased population trends?

Data
Data used are from the BMP (1990-2004) and the second Dutch breeding bird atlas (1998-2000). Approximately 100 common and scarce breeding bird species are included.

Chapter 3. Long-term population developments in typical marshland birds in the Netherlands.

Objective
The main aim of this chapter is to reconstruct the long-term developments in the breeding populations of typical marshland bird species in the Netherlands, and to address and rank possible causes of these population trends in relation to environmental changes and habitat requirements as described in literature.

Research questions
- What are the long-term developments in the breeding populations of typical marshland bird species in the Netherlands?
- How do population trends of marshland birds relate to their broad habitat preferences and what are the underlying causes?

Data
Monitoring data used are from the BMP (1984-2008) for common and scarce breeding birds, LSB (1990-2008) for rare and colonial breeding birds, and their ancestor the Old Timeseries database (1950-1990). Distribution data are used from the first (1973-77) and second (1998-2000) breeding bird atlases. 23 typical marshland bird species are included, both common and rare species.

Chapter 4. Scale-dependent homogenization: changes in breeding bird diversity in the Netherlands over a 25-year period.

Objective
The main aim of this chapter is to describe and quantify changes in taxonomic diversity of breeding bird communities in the Netherlands over a 25-year period, by testing three hypotheses related to the loss of biodiversity worldwide. Changes in diversity are assessed at different spatial scales (local, regional and national), among species characteristic for different landscapes (farmland, woodland, heathland, wetland, coastal habitats and urban habitats), and in relation to the abundance of species.

Research questions
- How have species richness and diversity changed at different spatial scales?
- To what extent has biotic homogenization of the Dutch breeding bird community occurred?
- Have rare species declined more severely on average than abundant species?

Data
Data used are from the first (1973-77) and second (1998-2000) breeding bird atlas. All regular breeding bird species are included (approximately 200).

Chapter 5. Life-history and ecological correlates of population change in Dutch breeding birds.

Objective
In this chapter I use monitoring data of all Dutch breeding birds to investigate correlations between species characteristics and medium-term population changes, thereby examining which ecological, life-history and behavioral traits appear associated with successful and unsuccessful species in our rapidly changing and highly modified environment. The aim is to describe changes in functional diversity and to make a global ranking of traits to select the most relevant ones with respect to population changes and, indirectly, to address which environmental changes are most likely responsible for these effects.

Research questions
- Which life-history, ecological and behavioural traits are correlated with observed medium-term population changes in Dutch breeding birds?
- How are sets of traits related to the underlying environmental changes most likely responsible?

Data
Data used are from BMP (1990-2005) and LSB (1990-2005). All regular breeding bird species with reliable monitoring data are included (approximately 170), excluding non-native introduced species. A total of 25 species traits is included.

Chapter 6. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats.

Objective

In this chapter the focus is on the effects of climate change as a cause of changes in Dutch breeding bird diversity. One consequence of climate change may be an increasing mismatch between timing of food requirements and food availability, due to differences in advancement of phenologies. Such a mismatch is mostly expected in long-distance migrants (particularly those species that arrive relatively late at their breeding grounds), in habitats with a seasonal food peak, and in regions with most spring warming.

Research questions

- What are the differences in Dutch population trends of breeding birds between a seasonal and less seasonal habitat (woodland and marshland, respectively), and in relation to migratory strategy?
- Have woodland species declined more in Western Europe, where spring temperatures increased strongly, compared to Northern Europe where this happened less?

Data

Data used are from BMP (1984-2004). Population trends are differentiated between woodland and marshland. Also national monitoring data from eleven other countries in Northern en Western Europe are used. 42 species of insectivorous passerines are included. Traits included are migratory strategy, habitat preference and timing of arrival. Finally, data are used from arthropod sampling in woodland and marshland sites.

Chapter 7. Ecological strategies successfully predict the effects of river floodplain rehabilitation on breeding birds.

Objective

In this chapter changes in the breeding bird communities of the Rhine and Meuse river floodplains are evaluated in response to large-scale rehabilitation management, by comparing population trends in rehabilitated sites and non-rehabilitated reference sites. To understand these effects, population trends are related to ecological and life-history traits of species. Combining separate traits into strategies, thereby accounting for trade-offs, is used as an additional functional approach to predict the effects of floodplain rehabilitation, and to adapt the rehabilitation strategy if necessary.

Research questions

- What are the effects of large-scale floodplain rehabilitation on Dutch breeding bird populations?
- How are these rehabilitation effects related to traits and strategies of species?
- Is rehabilitation of vegetation succession or rehabilitation of hydrodynamics the key driver behind breeding bird changes in response to floodplain restoration?

Data
Data used are from BMP (1989-2007). Population trends are differentiated between rehabilitated and non-rehabilitated sites. 93 common and scarce breeding birds are included. Traits included are nest location, reproductive investment and migratory behaviour. These are combined into eight life-history strategies.

Chapter 8. Synthesis.

In this chapter the results of the studies presented in the earlier chapters are integrated, the merits of the used methodologies are discussed and the value of citizen ornithology for science and conservation is addressed.

References

Bart J. 2005. Monitoring the abundance of bird populations. *Auk* 122: 15-25.

BirdLife International 2004. Birds in Europe: population estimates, trends and conservation status. Cambridge, UK.

Breeuwer A., Berendse F., Willems F., Foppen R., Teunissen W., Schekkerman H. & Goedhart P. 2009. Do meadow birds profit from agri-environment schemes in Dutch agricultural landscapes? *Biological Conservation* 142: 2949-2953.

Brooks T., Balmford A., Burgess N., Hansen L.A., Moore J., Rahbek C., Williams P., Bennun L., Byaruhanga A., Kasoma P., Njoroge P., Pomeroy D. & Wondafrash M. 2001. Conservation priorities for birds and biodiversity: do East African Important Bird Areas represent species diversity in other terrestrial vertebrate groups? *Ostrich* 15: 3-12.

Brown J.H. 1999. Macroecology: progress and prospect. *Oikos* 87: 3-14.

Butchart S.H.M., Stattersfield A.J., Bennun L.A., Shutes S.M., Akcakaya H.R., Baillie J.E.M., Stuart S.N., Hilton-Taylor C. & Mace G.M. 2004. Measuring global trends in the status of biodiversity: Red list indices for birds. *PLoS Biology* 2: 2294-2304.

Butchart S.H.M., Walpole M., Collen B., *et al.* 2010. Global biodiversity: Indicators of recent declines. *Science* 5982: 1164-1168.

Bijlsma R.G., Hustings F. & Camphuysen C.J. 2001. Schaarse en algemene vogels in Nederland (Avifauna van Nederland 2). GMB/KNNV uitgeverij. Haarlem/Utrecht.

Carpenter S.R., DeFries R., Dietz T., Mooney H.A., Polasky S., Reid W.V. & Scholes R.J. 2006. Millennium Ecosystem Assessment: Research needs. *Science* 314: 257-258.

Carver E. 2009. Birding in the United States: A Demographic and Economic Analysis. Addendum to the 2006 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation. Report 2006-4. U.S. Fish and Wildlife Service.

Devictor V., Julliard R., Clavel J., Jiguet F., Lee A. & Couvet D. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography* 17: 252-261.

Dybbro T. 1976. De danske ynglefugles udbredelse. Dansk Ornitologisk Forening, Copenhagen.

Ens B.J., Van Winden E.A.J., Van Turnhout C.A.M., Van Roomen M.W.J., Smit C.J. & Jansen J.M. 2009. Aantalontwikkeling van wadvogels in de Nederlandse Waddenzee in 1990-2008. Verschillen tussen Oost en West. *Limosa* 82: 100-112.

Fisher D.O. & Owens I.P.F. 2004. The comparative method in conservation biology. *Trends in Ecology and Evolution* 19: 391-398.

Furness R.W. & Greenwood J.J.D. 1993. Birds as monitors of environmental change. Chapman & Hall, London.

Godfray H.C.J. & Hassell M.P. 1992. Long time series reveal density dependence. *Nature* 359: 673.

Grashof-Bokdam C.J., Chardon J.P., Vos C.C., Foppen R.P.B., Wallis de Vries M., Van der Veen M. & Meeuwsen H.A.M. 2009. The synergistic effect of combining woodlands and green veining for biodiversity. *Landscape Ecology* 24: 1105-1121.

Greenwoud J.J.D. 2007. Citizens, science and bird conservation. *Journal of Ornithology* 148: 77-124.

Gregory R.D., Van Strien A., Vorisek P., Meyling A.W.G., Noble D.G., Foppen R.P.B. & Gibbons D.W. 2005. Developing indicators for European birds. *Philosophical Transactions of the Royal Society B*: 269-288.

Gregory R.D., Vorisek P., Noble D.G., Van Strien A., Klvanova A., Eaton M., Meyling A.W.G., Joys A., Foppen R.P.B. & Burfield I. 2008. The generation and use of bird population indicators in Europe. *Bird Conservation International* 18: 233-244.

Gregory R.D., Willis S.G., Jiguet F., Vorisek P., Klvanova A., Van Strien A., Huntley B., Collingham Y.C., Couvet D. & Green R.E. 2009. An indicator of the impact of climatic change on European Bird Populations. *PLoS One* 4: e4678

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

Haverschmidt F. 1942. Faunistisch overzicht van de Nederlandse broedvogels. Brill, Leiden.

Hendriks A.J. & Enserink E.L. 1996. Modelling response of single species populations to microcontaminants as a function of species size with examples for waterfleas *Daphnia magna* and cormorants *Phalacrocorax carbo*. *Ecological Modelling* 88: 247-262.

Hoffmann M., Hilton-Taylor C., Angulo A., *et al.* 2010. The impact of conservation on the status of the world's vertebrates. *Science* DOI: 10.1126/science.1194442.

Hustings M.F.H., Kwak R.G.M., Opdam P.F.M. & Reijnen M.J.S.M. (eds.) 1985. Vogelinventarisatie. Natuurbeheer in Nederland, 3. Pudoc, Wageningen/Vogelbescherming, Zeist.

Jetz W., Wilcove D.S. & Dobson A.P. 2007. Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* 5: 1211-1219.

Jiguet F., Gregory R.D., Devictor V., Green R.E., Vorisek P., Van Strien A. & Couvet D. 2010a. Population trends of European common birds are predicted by characteristics of their climatic niche. *Global Change Biology* 16: 497-505.

Jiguet F., Devictor V., Ottvall R., Van Turnhout C., Van der Jeugd H. & Lindström A. 2010b. Bird population trends are linearly affected by climate change along species thermal ranges. *Proceedings Royal Society London B. Biological Sciences* 277: 3601-3608.

Kalkman V.J., Van Duuren L., Gmelig Meyling A.W. & Odé B. 2010. Veranderingen in de Nederlandse biodiversiteit. In: Noordijk J., Kleukers R.M.J.C., Van Nieukerken E.J. & Van Loon A.J. (eds.). De Nederlandse biodiversiteit. Nederlandse Fauna 10. Nederlands Centrum voor Biodiversiteit Naturalis & European Invertebrate Survey- Nederland, Leiden: pp. 339-354.

Klok C., Van Turnhout C.A.M., Willems F., Voslamber B., Ebbinge B. & Schekkerman H. 2010. Analysis of population development and effectiveness of management in resident Greylag Geese *Anser anser* in the Netherlands. *Animal Biology* 60: 373-393.

Kondoh M. 2001. Unifying the relationships of species richness to productivity and disturbance. *Proceedings Royal Society London B. Biological Sciences* 268: 269-271.

Kraan C., Van Gils J.A., Spaans B., Dekinga A., Bijleveld A.I., Van Roomen M., Kleefstra R. & Piersma T. 2009. Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. *Journal of Animal Ecology* 78: 1259-1268.

Lemoine N., Bauer H.G., Peintinger M. & Bohning-Gaese K. 2007. Effects of climate and land-use change on species abundance in a central European bird community. *Conservation Biology* 21: 495-503.

Levrel H., Fontaine B., Henry P.Y., Jiguet F., Julliard R., Kerbiriou C. & Couvet D. 2010. Balancing state and volunteer investment in biodiversity monitoring for the implementation of CBD indicators: A French example. *Ecological Economics* 69: 1580-1586.

McKinney M.L. & Lockwood J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* 14: 450-453.

Millennium Ecosystem Assessment 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

Newton I., Wyllie I. & Ahser A. 1993. Long-term trends in organochlorine and mercury residues in some predatory birds in Britain. *Environmental Pollution* 79: 143-151.

Newton I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* 146: 579-600.

Nichols J.D. & Williams B.K. 2006. Monitoring for conservation. *Trends in Ecology and Evolution* 21: 668-673.

Olden J.D. & Rooney T.P. 2006. On defining and quantifying biotic homogenization. *Global Ecology and Biogeography* 15: 113-120.

Parlevliet J. 2003. Breeding birds in the Netherlands in the 20th century. *Limosa* 76: 141-156.

RIVM 2003. Natuurcompendium 2003. RIVM, CBS, DLO, Bilthoven, Netherlands.

Sax D.F. & Gaines S.D. 2003. Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution* 18: 561-566.

Sharrock J.T.R. (ed.) 1976. The atlas of breeding birds in Britain and Ireland. T&AD Poyser, London.

Siriwardena G.M., Baillie S.R. & Wilson J.D. 1999. Temporal variation in the annual survival rates of six granivorous birds with contrasting population trends. *Ibis* 141: 621-636.

Siriwardena G.M., Baillie S.R. & Wilson J.D. 2000. The importance of variation in the breeding performance of seed-eating birds in determining their population trends on farmland. *Journal of Applied Ecology* 7: 128-148.

SOVON 1987. Atlas van de Nederlandse Vogels. SOVON, Arnhem.

SOVON 1998. Boeiende vogels of saaie pieten; 25 jaar SOVON Vogelonderzoek Nederland. KNNV, Utrecht.

SOVON 2002. Atlas van de Nederlandse Broedvogels 1998-2000. (Nederlandse Fauna 5). Nationaal Natuurhistorisch Museum Leiden, KNNV Uitgeverij & European Invertebrate Survey-Nederland, Leiden.

SOVON 2003. Interne evaluatie van het Atlasproject voor broedvogels 1998-2000. Intern document.

Stattersfield A.J., Crosby M.J., Long A.J. & Wege D.C. 1998. Endemic Bird Areas of the World: Priorities for Biodiversity Conservation. BirdLife International, Cambridge, UK.

Teixeira R.M. 1979. Atlas van de Nederlandse broedvogels. Natuurmonumenten, 's-Graveland.

Thomas C.D., Cameron A., Green R.E., Bakkenes M., Beaumont L.J., Collingham Y.C., Erasmus B.F.N., de Siqueira M.F., Grainger A., Hannah L., Hughes L., Huntley B., Van Jaarsveld A.S., Midgley G.F., Miles L., Ortega-Huerta M.A., Peterson A.T., Phillips O.L. & Williams S.E. 2004. Extinction risk from climate change. *Nature* 427: 145-148.

Tinbergen L. 1941. Vogels in hun domein. Thieme, Zutphen.

Van den Burg A.B. 2009. Limitations of owl reproduction in the wild: is there a role of food quality besides quantity? *Ardea* 97: 609-614.

Van Dijk A.J. 2004. Handleiding Broedvogel Monitoring Project. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Dijk A.J., Boele A., Hustings F., Koffijberg K. & Plate C.L. 2010. Broedvogels in Nederland in 2008. SOVON-monitoringrapport 2010/01. SOVON, Beek-Ubbergen.

Van Oordt G.J. 1932. Verslag van een tocht met Hr.Ms. Watervliegtuig L7 boven de Nederlandse Waddenzee op 5 october 1931. Jaarverslag Stichting Vogeltrekstation, Texel.

Van Strien A.J., Van Duuren L., Foppen R.P.B. & Soldaat L.L. 2009. A typology of indicators of biodiversity change as a tool to make better indicators. *Ecological Indicators* 9: 1041-1048.

Verberk W.C.E.P. 2008. Matching species to a changing landscape. Aquatic macroinvertebrates in a heterogeneous landscape. PhD thesis, Radboud University Nijmegen.

Vickery J.A., Bradbury R.B., Henderson I.G., Eaton M.A. & Grice P.V. 2004. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. *Biological Conservation* 119: 19-39.

Vieira N.K.M., Poff N.R., Carlisle D.M., Moulton II S.R., Koski M.L. & Kondratieff B.C. 2006. A database of lotic invertebrate traits for North America. U. S. Geological Survey Data Series 187.

Vogel R. 2007. De Nederlandse avifauna door de eeuwen heen. In: Saris F. Een eeuw vogels beschermen. KNNV, Utrecht.

Wooler R.D., Bradley J.S. & Croxall J.P. 1992. Long-term population studies of seabirds. *Trends in Ecology and Evolution* 7: 111-114.

Yeatman L. (ed.) 1976. Atlas des Oiseaux Nicheurs de France de 1970 à 1975. Paris.

Chapter 2

Monitoring common and scarce breeding birds in the Netherlands: applying a post-hoc stratification and weighting procedure to obtain less biased population trends

Chris van Turnhout, Frank Willems, Calijn Plate, Arco van Strien, Wolf Teunissen, Arend van Dijk and Ruud Foppen

Published in 2008 in Revista Catalana d'Ornitologia 24: 15-29

Abstract

The main objective of the Dutch Breeding Bird Monitoring Program (BMP) is to assess changes in population sizes of common and scarce breeding birds. Despite the large number of study plots, trends might be biased because plots are not equally distributed over the country. In this chapter we present a post-hoc stratification and weighting procedure to correct for this non-random sampling. Indices and trends are first calculated for a number of species-specific strata (combinations of region, main habitat type and bird density class). Thereafter, the indices per stratum are weighted by population sizes (derived from an independently collected set of atlas data) and sampling efforts per stratum. The procedure has a small but substantial effect on national trends, trends generally becoming less conservative. We believe that for the majority of breeding birds this procedure results in a substantial improvement of trends, and we will therefore continue the BMP in forthcoming years.

Introduction

Breeding birds are useful indicators of the state of the environment. Monitoring data therefore provide valuable information on the quality of nature and on the effectiveness of nature conservation policy. Furthermore, such data are useful for scientific research purposes, such as the evaluation of the effects of environmental changes, (local) conservation measures and habitat management (Furness & Greenwood 1993, Freeman *et al.* 2007).

In 1984, SOVON and Statistics Netherlands started the Breeding Bird Monitoring Program (BMP) in the Netherlands (Van Dijk 1992). The main objective of this monitoring scheme is to assess yearly changes and trends at national and regional scale in population sizes of common and scarce breeding birds, including nine species of the EU Bird Directive and 25 species of the Dutch Red List (Van Beusekom *et al.* 2005). Because it is not possible to count all individual birds to calculate the true trend in species abundance, it is necessary to sample. An ideal monitoring scheme, resulting in accurate and representative population indices and trends, would consist of a large number of randomly selected study plots, and a yearly participation of all observers from the beginning onwards. Despite the relatively large number of study plots, the BMP is not such an ideal scheme. Not all study plots are covered yearly, so it is necessary to cope with missing values (Ter Braak *et al.* 1994). Moreover, because participants (mainly volunteers) are free to choose their study areas, plots are not equally distributed over Dutch regions and habitat types. Also, within a specific habitat volunteers may have a preference for the most attractive sites, i.e. those which are relatively species-rich and have high bird densities. In particular, within farmland, wet grasslands with high densities of meadow birds are oversampled, in comparison to dry grassland areas poor in species and numbers. This is no problem as long as trends between these strata are identical. However, if trends differ, the estimates of population changes may be biased. Here we describe a method to correct for biased sampling, using an independently collected set of atlas data. First we carried out a pilot study on meadow bird population trends, on the basis of which we applied a simplified approach to all other breeding bird species.

Materials and methods

Breeding Bird Monitoring Program (BMP) data

The Dutch Breeding Bird Monitoring program is based on the method of intensive territory mapping in study plots (Hustings *et al.* 1985, Bibby *et al.* 1997). All common and scarce breeding birds in the Netherlands are covered. The scheme consists of five modules, focused on either all species or specified groups or habitats (scarce species, raptors, meadow birds, urban areas). Fieldwork and interpretation methods are highly standardized and are described in detail in a manual (Van Dijk 1985, Van Dijk 2004). Between March and July all plots (10-500 hectares each) are visited 5-10 times. Size of study plots, as well as exact number, timing and duration of visits, depend on habitat type and species coverage. All birds with territory- or nest-indicative behaviour (e.g. song, pair bond, display, alarm, nests) are recorded on field maps. At the end of the season, species-specific interpretation criteria are used to determine the number of territories per species (Van Dijk 2004). Interpretation criteria focus on the type of behaviour observed, the number of observations required (depending on species-specific detection probabilities), and the period of observations (to exclude non-breeding migrants).

All observers submit their data on standard forms. After a first check by the project coordinator at SOVON, Statistics Netherlands performs standardized checks using computer routines to detect possible errors. Observers check and if necessary

Figure 1. Location of BMP study plots in the Netherlands in 2000-2004. Only plots which are studied in at least two years are included.

correct these errors. Between 1984 and 2004 a total of 3,374 different study plots were covered, ranging from around 300 per year in 1984 to a maximum of around 1,750 in 1998-2000.

Atlas data

Independently collected data from the second Dutch breeding bird atlas (SOVON 2002) are used to correct the BMP results. Fieldwork for the atlas was carried out using a sampling design based on the Dutch national grid, which consists of 1,674 5×5 km squares (henceforth referred to as atlas squares). In every atlas square eight (out of 25) 1×1 km squares were systematically selected, in which presence/absence of all breeding birds was assessed during two standardized one hour visits. Fieldwork was carried out in 1998-2000. Using geostatistical interpolation techniques (*stratified ordinary kriging*; Burrough & McDonnel 1998) a relative density (probability of occurrence) was calculated for all 1×1 km squares, based on the observations in 12 surrounding squares with the same habitat. For further details, see SOVON (2002).

Calculation of indices and trends

Yearly changes in numbers of species are presented as indices. From 1990 onwards, sampling efforts are sufficient to calculate indices for approximately 100 species. Indices are calculated using TRIM-software (Pannekoek & Van Strien 2005). TRIM is specifically developed for the analysis of time series of counts with missing data, and is based on loglinear Poisson regression. The regression model estimates year and site factors using the observed counts. Subsequently the model is used to predict the missing counts. Indices and standard errors are calculated using a complete data set with the predicted counts replacing the missing counts. Overdispersion and serial correlation are taken into account.

The national indices are calculated using a post-hoc stratification and weighting procedure, to correct for the unequal distribution of study plots over Dutch regions (Figure 1) and habitat types (Figure 2). Indices and trends are first calculated for each stratum separately (stratified imputing of missing values). Thereafter, the indices per

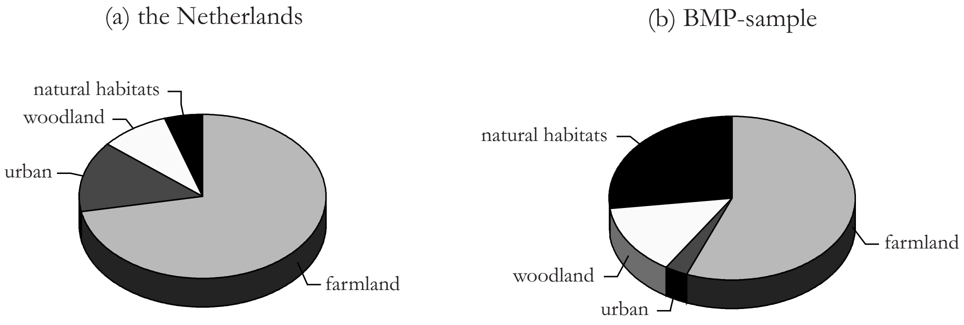


Figure 2. Relative distribution of main habitat types within (a) the Netherlands (relative area) and in (b) the BMP-sample (relative number of study plots).

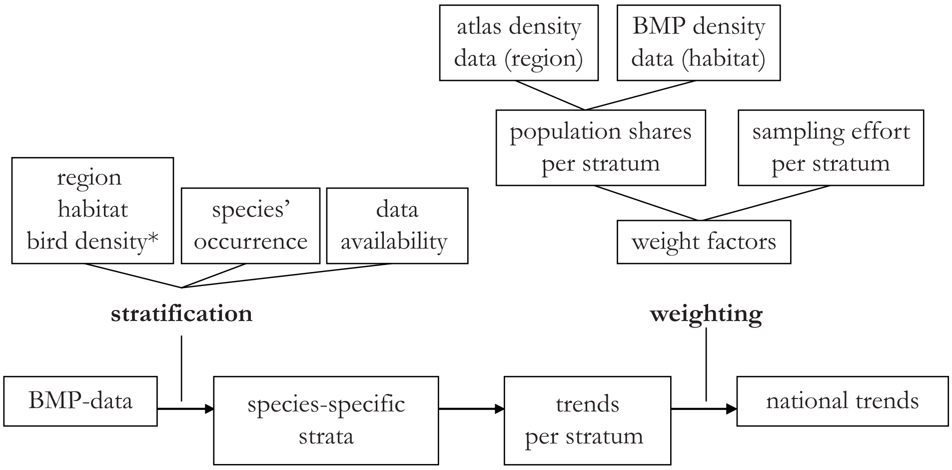


Figure 3. Flow chart of the post-hoc stratification and weighting procedure to obtain less biased population trends. For explanation see Materials and methods. (*: for meadow birds only).

stratum are combined into a national index, weighted by population sizes and sampling effort per stratum. If all strata were equally sampled according to the number of territories present, all weights would be similar. If a stratum is undersampled, the stratum index is given a higher weight in compiling the national index. A schematic overview of the procedure is presented in Figure 3.

Stratification

The following three variables are used in the stratification procedure, because these are thought to correlate most strongly with differences in breeding bird trends within the Netherlands: physio-geographic region, main habitat type and bird density.

The classification of 14 physio-geographic regions is based on main soil type, main landscape characteristics and location (Bal *et al.* 1995). The classification is independent of bird distribution. Main habitat types include farmland (arable land, grassland, hedgerows), woodland (deciduous, coniferous and mixed forest), heathland (dry and wet heathland, bog and inland drift sand), freshwater marsh, salt marsh, coastal dunes and urban habitats (city, suburb, industrial zone, park).

Species-specific bird density is used as a stratification variable because trends may differ between core areas with high densities (resulting from favourable habitat quality) and marginal areas with low densities (resulting from unfavourable habitat conditions). We distinguish three classes: areas with high, medium and low densities. For each species all 1×1 km squares are sorted according to relative density, based on atlas data. The top 15% squares are arbitrary classified as high-density areas, the next highest 30% as medium-density areas and the remaining 55% as low-density areas.

For all species, strata are defined where species occur in substantial numbers, with strata being the combinations of physio-geographic region, main habitat type and bird density (the latter for meadow birds only, see result section). The stratification is done based on the expert judgement of two breeding bird specialists at SOVON. Strata are lumped if the minimum number of positive plots per year since 1990 is less than five (based on experience of Statistics Netherlands). Strata are lumped according to either region or main habitat type, depending on which strata trends are expected to be most similar. A total of over 1,400 strata are defined for 102 species.

Weighting

To calculate relative population sizes per stratum, we returned to the relative densities in 1×1 km squares from the breeding bird atlas. The species-specific relationship between absolute densities in BMP-plots (studied in 1998-2000) and (mean) relative densities in the 1×1 km squares is quantified by regression analysis. Relative densities are converted into absolute densities per square. On average 749 records were available per species for the regression analyses. For further details see SOVON (2002).

Next, absolute numbers per square are summed to obtain population sizes per physio-geographic region (and also bird densities for meadow birds) (step 1). To assess the relative population sizes per habitat type within a region, we chose not to use the absolute densities per square, mainly because of considerable habitat heterogeneity within squares. Instead, for each habitat type we multiply the total area of habitat within a region (from GIS-assessment) by the average density in BMP-plots consisting of more than 75% of that habitat (step 2). The result of step 2 is divided by the population size per region as calculated in step 1. For example, if the calculated population size of Skylark *Alauda arvensis* in region X was 2,000 territories (step 1), the area of heathland and farmland in region X were 10,000 and 100,000 ha respectively (step 2), and the densities in heathland and farmland were 10 and 1 territories per 100 ha respectively (step 2), then the proportion of the population both in heathland and in farmland within region X is 0.5. If region X held 10% of the total Dutch population of Skylarks, then the proportion of the population in either heathland or farmland in region X is $0.5 \times 0.1 = 0.05$.

These proportions of population are used to assess weight factors. The weight factor for a particular stratum is the population proportion divided by the proportion of the number of territories counted in that stratum. All weights would be exactly one where no oversampling or undersampling occurs across strata. The weights are calculated for the atlas period 1998-2000 and then applied to all years from 1990 onwards, using the weight option in TRIM (Pannekoek and Van Strien 2005).

Results

Pilot study on meadow birds

Large differences in regional trends within farmland exist for nine species of meadow birds, as illustrated by Black-tailed Godwit *Limosa limosa* (Figure 4). In region ZKZ numbers have increased moderately between 1990 and 2004 (Wald test, $p<0.05$). Conversely, in region ZKN numbers show moderate declines, and in region LVN numbers have strongly declined (both Wald test, $p<0.05$). Regionally distinct trends also exist for the other meadow bird species. These results underline the necessity of a stratification and weighting procedure.

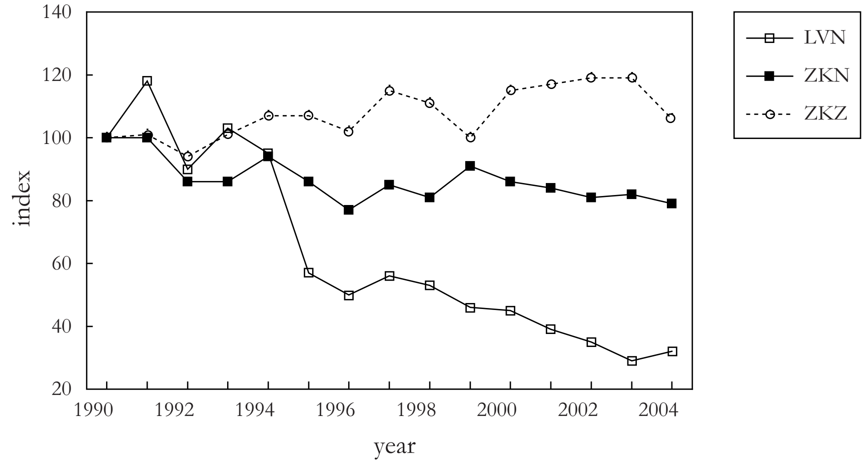


Figure 4. Population indices of Black-tailed Godwit *Limosa limosa* in three different regions within farmland in the Netherlands 1990-2004. Region ZKZ refers to polders on sea clay soils in the south-western part of the country, region ZKN refers to polders on sea clay soils in the northern part of the country, and LVN refers to polders on peat soils in the north-eastern part of the country.

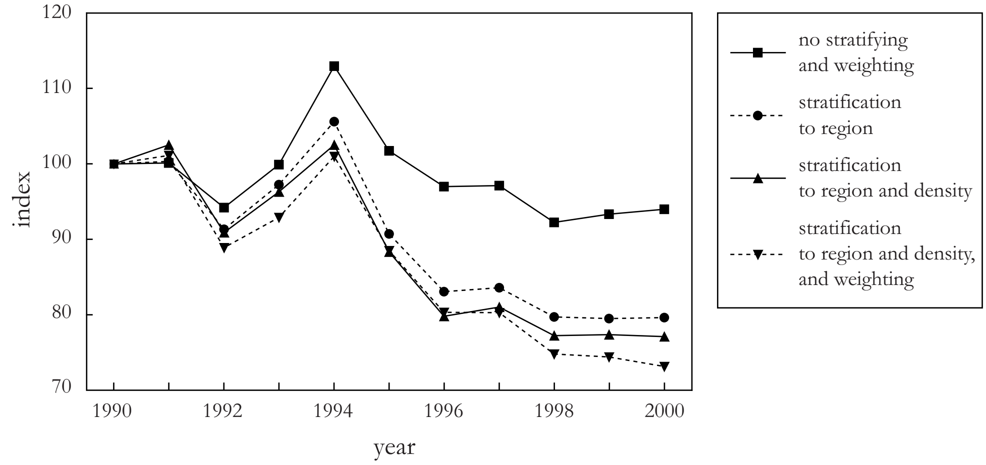


Figure 5. Population indices of Black-tailed Godwit *Limosa limosa* in farmland in the Netherlands 1990-2000. Presented are indices without stratifying and weighting (solid line and squares), with stratification according to region only (dotted line and circles), with stratification according to both region and bird density (solid line and upward triangles), and with stratification according to region and bird density and weighting (dotted line and squares).

Without stratification and weighting, national Black-tailed Godwit numbers seem to have decreased only slightly in the period 1990-2000 (Figure 5). Stratification according to physio-geographic region alone results in an evident decline. The index in 2000 is 15% lower compared to the 2000-index without stratification. This implies that regions with decreasing Black-tailed Godwit populations are undersampled. Stratification according to both region and bird density results in a 2000 index that is 20% lower. Stratification in combination with weighting reduces the 2000 index by another 2%. The effect of weighting therefore appears much smaller than the effect of stratification, and the effect of stratification according to bird density is less than of stratification according to region. Results are similar for other meadow bird species.

Other breeding birds

Based on the results of the pilot study, and the availability of data, we have based our stratification and weighting procedure for all other breeding birds only on the variables physio-geographical region and main habitat type.

This means that we only use bird density as a stratification variable for nine species of meadow birds. The effect of this variable on corrected trends appears minimal, even for the meadow birds for which we expected that bias due to unequal sampling of high density areas would be largest.

For most species substantial and significant differences in trends exist between regions (Figure 6), and between main habitat types within regions (Figure 7) (Wald tests, $p<0.05$). The stratification and weighting procedure has a small but substantial effect on linear trends of common and scarce breeding birds in the period 1990-2004, trends generally becoming less conservative. Mean absolute change over all species is 3.26% per year (*SE* 0.40%) for corrected trends, and 2.88% per year (*SE* 0.29%) if trends are not corrected for unequal sampling, a difference which is significant (paired t-test, $p=0.04$). For 52 species, stratification and weighting results in a more positive (or a less negative) trend (Figure 8a). This implies that strata with increasing numbers are undersampled. For 47 species, trends are more negative (or less positive) after stratification and weighting (Figure 8b), which means that strata with decreasing numbers are undersampled. In the case of the Linnet *Carduelis cannabina*, numbers are increasing in the heavily oversampled coastal dunes, whereas numbers in most other

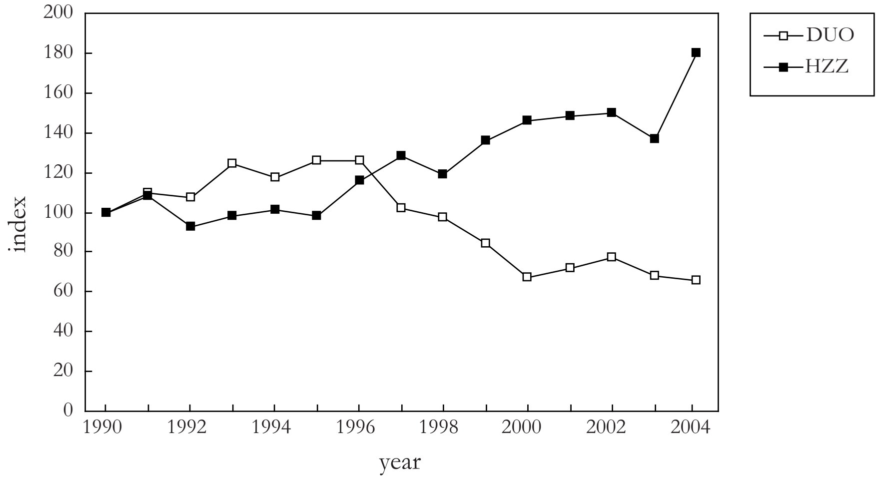


Figure 6. Population indices of Green Woodpecker *Picus viridis* in two different regions in the Netherlands 1990-2004. Region DUO refers to coastal dunes on the mainland and region HZZ refers to sandy soils in the southern part of the country.

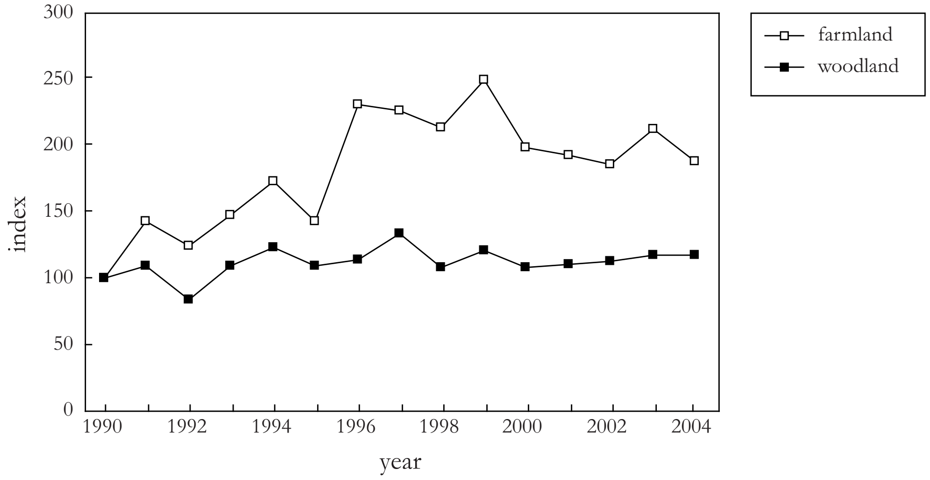


Figure 7. Population indices of Great Spotted Woodpecker *Dendrocopos major* in farmland and woodland in region HZN (sandy soils in the northern part of the country) 1990-2004.

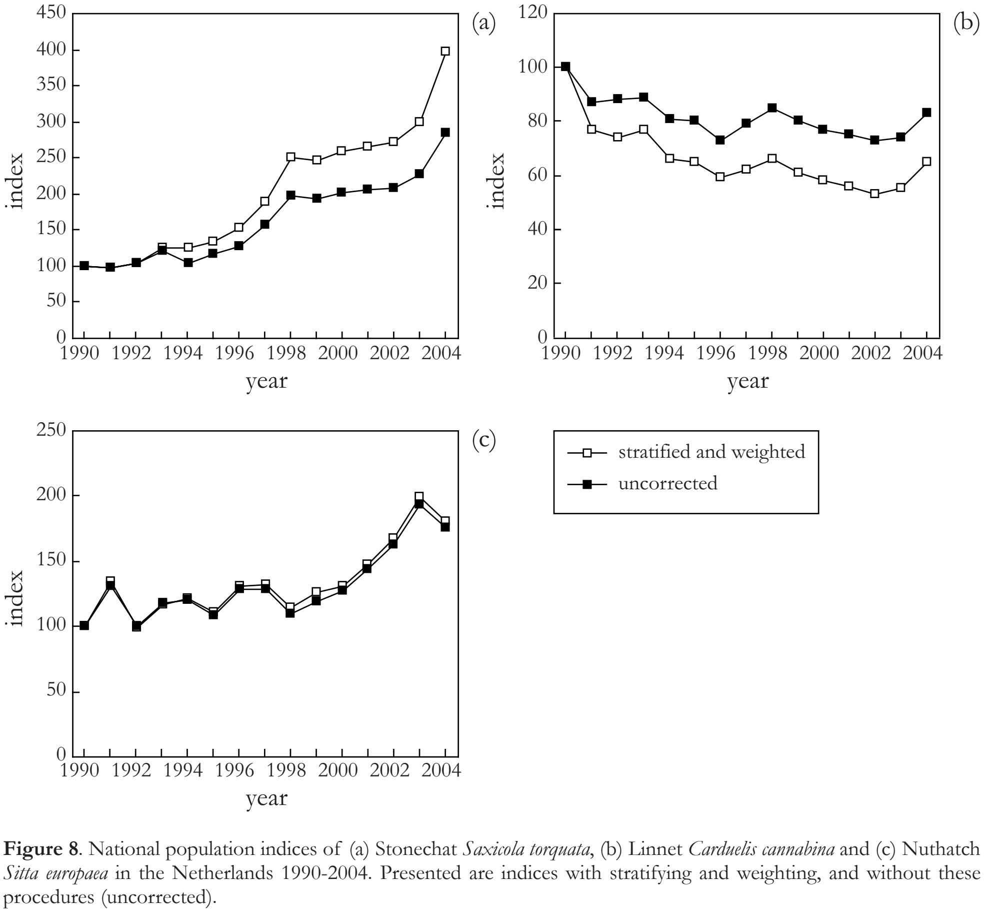


Figure 8. National population indices of (a) Stonechat *Saxicola torquata*, (b) Linnet *Carduelis cannabina* and (c) Nuthatch *Sitta europaea* in the Netherlands 1990-2004. Presented are indices with stratifying and weighting, and without these procedures (uncorrected).

strata are decreasing. For the three remaining species stratified and unstratified trends are identical (Figure 8c), which implies that there is no unequal sampling for these species or that trends in (important) strata are similar.

Standard errors of linear trends have significantly increased by a factor 1.67 after stratification and weighting: 0.60% (*SE* 0.03%) versus 0.36% (*SE* 0.02%) without correction for unequal sampling (paired t-test, $p<0.0001$).

In appendix 1 year indices and linear trends are presented for 102 common and scarce breeding birds in the period 1990-2004, after stratification and weighting. In total 40 species have significantly increased in numbers during the study period, Greylag Goose *Anser anser* and Egyptian Goose *Alopochen aegyptiacus* most strongly. In total 37 species have significantly decreased in numbers, Long-eared Owl *Asio otus* and Wood Warbler *Phylloscopus sibilatrix* the most strongly. The remaining 25 species are stable or show fluctuating numbers.

Discussion

In this chapter we present a method which deals with probably one of the most important problems of the Dutch Breeding Bird Monitoring Program, the unequal sampling that results from the non-random plot selection. This problem also exists in other monitoring schemes in which participants can freely choose their study plots, such as the Dutch Butterfly Monitoring Scheme (Van Swaay *et al.* 2002) and the (former) British Common Bird Census (CBC) (Marchant *et al.* 1990). A solution for this problem is to start a new, randomised or random stratified scheme, as in the United Kingdom where the CBC has been replaced by the Breeding Bird Survey (Gregory 2000, Raven & Noble 2001). However, to guarantee sufficient participation of volunteer observers in a randomised scheme, less labour-intensive field work methods, such as point or line transect counts, would need to be adopted (Gibbons & Gregory 2006). One of the risks of designing and implementing such a new scheme for Dutch breeding birds is the incomparability of old and new data. As a result, BMP-data might be seen as increasingly less relevant and useful, and the long-term perspective might be lost. This potential problem could be handled by running both schemes simultaneously for a few years, as was done in the United Kingdom (Freeman *et al.* 2007). However, we expect that justifying and funding this solution will be a major problem in our situation. More importantly, in a randomised scheme a very large number of points or transects would be necessary to achieve a sufficiently large sample size for scarce breeding birds, which are particularly important in nature policy and conservation. Lastly, randomised point or transect counts might be less useful at local scale, compared to the intensive territory mapping method (which results in more precise estimates of absolute numbers for all sites), for instance to evaluate the effects of local habitat management in nature reserves (Alldredge *et al.* 2008). Given these considerations, we have decided to correct for unequal sampling by implementing a stratification and weighting procedure in the calculation of indices and trends.

Our results show that large differences in species trends exist between regions and between habitats. This means that a stratified imputing of missing values not only results in substantially different, but also improved (less biased) population trends. The results also show that weighting of strata has a further, but less marked, effect on national trends. Further evidence for the improvement of trends comes from the fact that impressions of ornithologists accord better with the corrected than the uncorrected trends (Teunissen *et al.* 2002).

For meadow birds in general, stratification according to bird density appears to have less effect than stratification according to physio-geographical region. This might be due to small differences in trends between high, medium and low density areas, or by large differences in weight factors, as a result of which differences in stratum trends are not expressed at the national scale. Clearly, many other factors may be responsible for differences in meadow bird trends, such as water table level, farming intensity, habitat management, nest protection and predation. However, we expect that most of these are correlated to either region or bird density to some extent. In addition, distinction of bird density areas might be insufficient, due to heterogeneity within the underlying study plots, or due to an inadequate scale of atlas data collection for this purpose. Based on the results for meadow birds, stratification according to bird densities was not implemented for other breeding birds.

We have chosen to use independently collected atlas data to calculate relative population sizes per region (weight factors), instead of using densities in BMP-plots in combination with the surface of regions. The latter corrects for unequal sampling between regions, but assumes equal sampling within regions (and that densities in study plots are representative of the region concerned). A pilot on meadow birds revealed that these alternative weighting procedures yield very different results (Teunissen *et al.* 2002). Unfortunately, we have not been able to use atlas data to calculate relative population sizes for different habitat types within regions. These are therefore based on densities in BMP-plots, which does assume representativeness within habitat strata. In addition, although for 67% of the strata only homogeneous plots are used (consisting for at least 75% of only one habitat type), population sizes in the remaining 33% of the strata are partly based on heterogeneous plots, due to too few homogeneous plots. Also, densities in 12% of the strata are based on less than three plots (especially in urban areas), which might result in unreliable weight factors. However, national trends generally appear not very sensitive to small deviations in weight factors.

For some strata insufficient data are available, especially for farmland and urban areas. Therefore, strata have to be lumped on the basis of expert judgement, which is subjective and difficult to standardize. Moreover, an even more refined stratification might be needed, because of trend differences within main habitat types (e.g. coniferous versus deciduous forest, arable land versus grassland). However, the more detailed the stratification, the more study plots are needed, and coniferous forest and arable land are particularly undersampled.

Standard errors of stratified national trends appear significantly larger than those of uncorrected national trends. This might be caused by the fact that sample sizes become smaller when dividing the total number of study plots over a large number of strata. In particular strata with relatively small sample sizes (5-10 study plots per year) and large weights (holding an important part of the species' population) will result in large standard errors, because a small sample size results in imprecise estimates of both trends and weight factors. An increase in the standard errors of national trends leads to a decrease in the power of the monitoring scheme. This effect will be balanced to some extent by the less conservative trends after stratification. From an earlier study, the BMP appeared to be quite sensitive for most breeding species. In a ten year period a 50% or smaller change would be detectable for 79 out of 89 species, using a probability of detection of 80% (Van Strien *et al.* 1994).

We conclude that for the majority of common and scarce breeding birds in the Netherlands the stratification and weighting procedure results in slightly different trends and indices, which provide a substantially better picture of their population status. Although we realize that a (stratified) random scheme is prone to less bias than a non-randomised scheme, at least for the group of common breeding birds, we plan to continue the BMP in its present form for the time being. In our opinion, the major challenge at the moment is to gather more data in undersampled strata. We will therefore try to set up a well-designed and labour-extensive scheme in habitats that are currently particularly undersampled. In 2007 such a scheme was launched for urban habitats (Van Turnhout & Aarts 2007). Combining trends from very different monitoring schemes has been proven to be a practical and statistically sound method (Gregory *et al.* 2005). We aim at carrying out atlas projects at least once every 15-20 years, which is essential to validate the representativeness of the BMP-sample and to periodically update the weight factors.

Acknowledgements

The BMP is part of the Network Ecological Monitoring, a national governmental scheme for monitoring of Dutch flora and fauna, under the auspices of Ministry of Agriculture, Nature and Food quality, and others. The bird monitoring is largely carried out by a large number of volunteers, to whom we are greatly indebted. Also several provincial monitoring schemes are incorporated, most focusing on meadow birds. Adriaan Gmelig Meyling (Statistics Netherlands) and Dirk Zoetebier (SOVON) co-operated in the technical and statistical part of the analyses. Leo Soldaat and Marco van Veller (both Statistics Netherlands) collaborated in the pilot on meadow bird trends. An anonymous referee gave useful comments on a draft of this chapter.

References

Alldredge M.W., Pacifici K., Simons T.R. & Pollock K.H. 2008. A novel field evaluation of the effectiveness of distance and independent observer sampling to estimate aural avian detection probabilities. *Journal of Applied Ecology* 36: 1349-1356.

Bal D., Beije H.M., Hoogeveen Y.R., Jansen S.R.J. & Van der Reest P.J. 1995. Handboek Natuurdoeltypen in Nederland. IKC-Natuurbeheer, Wageningen.

Bibby C.J., Burgess N.D. & Hill D.A. 1997. Bird Census Techniques. Academic Press, London.

Burrough P.A. & McDonnel R.A. 1998. Principles of geographical information systems. Oxford University Press, Oxford.

Freeman S.N., Noble D.G., Newson S.E. & Baillie S.R. 2007. Modelling bird populations using data from the Common Birds Census and the Breeding Bird Survey. *Bird Study* 54: 61-72.

Furness R.W. & Greenwood J.J.D. 1993. Birds as monitors of environmental change. Chapman & Hall, London.

Gibbons D.W. & Gregory A.J. 2006. Birds. In Sutherland, W.J. (ed): Ecological Census Techniques: A Handbook. Pp. 308-350. 2nd edition. Cambridge: Cambridge University Press.

Gregory R.D. 2000. Development of breeding bird monitoring in the United Kingdom and adopting its principles elsewhere. *Ring* 22: 35-44.

Gregory R.D., Van Strien A., Vorisek P., Gmelig Meyling A.W., Noble D.G., Foppen R.P.B. & Gibbons D.W. 2005. Developing indicators for European birds. *Philosophical Transactions of the Royal Society B* 360: 269-288.

Hustings M.F.H., Kwak R.G.M., Opdam P.F.M. & Reijnen M.J.S.M. (eds.) 1985. Vogelinventarisatie. Natuurbeheer in Nederland, 3. Pudoc, Wageningen and Vogelbescherming, Zeist.

Marchant J.H., Hudson R., Carter S.P. & Whittington P. 1990. Population trends in British breeding birds. NCC/BTO, Tring.

Pannekoek J. & Van Strien A.J. 2005. TRIM 3 Manual (TRends & Indices for Monitoring Data). Statitics Netherlands, Voorburg.

Raven M. & Noble D. 2001. Breeding Bird Survey: 1994-2000. *Bird Populations* 6: 107-113

SOVON 2002. Atlas van de Nederlandse Broedvogels 1998-2000. Nederlandse Fauna 5. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & European Invertebrate Survey-Nederland, Leiden.

Ter Braak C.J.F., Van Strien A.J., Meijer R. & Verstrael T.J. 1994. Analysis of monitoring data with many missing values: which method? In: Hagemeijer W. and Verstrael T. (eds). Bird Numbers 1992. Distribution, Monitoring and Ecological aspects. Proc. 12th Int. Conf. of IBCC and EOAC, 663-673. Statistics Netherlands, Voorburg & Sovon, Beek-Ubbergen.

Teunissen W., Soldaat L., Van Veller M., Willems F. & Van Strien A.J. 2002. Berekening van indexcijfers in het weidevogelmeetnet. SOVON-onderzoeksrapport 2002/09. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Beusekom R., Huigen P., Hustings F., De Pater K. & Thissen J. 2005. Rode Lijst van de Nederlandse broedvogels. Tirion, Baarn.

Van Dijk A.J. 1985. Handleiding Broedvogel Monitoring Project. SOVON, Arnhem.

Van Dijk A.J. 1992. The Breeding bird monitoring program of SOVON in the Netherlands. *Die Vogelwelt* 113: 197-209.

Van Dijk A.J. 2004. Handleiding Broedvogel Monitoring Project. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Strien A., Vos P., Hagemeijer W., Verstrael T. & Gmelig Meyling A. 1994. The sensitivity of two national bird monitoring programmes. *Limosa* 67: 69-75.

Van Swaay C.A.M., Plate C.L. & Van Strien A.J. 2002. Monitoring butterflies in the Netherlands: how to get unbiased indices. In: Bruin, J. (ed.). Proceedings of the 13th annual meeting of entomologists in the Netherlands, 21-27. NEV, Amsterdam.

Van Turnhout C. & Aarts B. 2007. A new monitoring scheme for breeding birds in urban habitats. *Limosa* 80: 40-43.

Appendix 1. National population indices and linear trends of 102 common and scarce breeding birds in the Netherlands 1990-2004. Headings are: scientific name, English name, annual indices 1990-2004 (1990 = 100), total number of positive study plots, slope of linear trend ('overall slope imputed', Pannekoek & Van Strien 2005), standard error of slope, and classification of linear trend : ++ strong increase (>5% per year), + moderate increase (<5% per year), 0 (no significant change), - moderate decline (<5% per year), -- steep decline (>5% per year).

Scientific name	English name	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	plots	slope	error	tr
Tachybaptus ruficollis	Little Grebe	100	50	69	83	94	138	75	75	92	133	153	160	168	167	180	463	1.07	0.008	++
Podiceps cristatus	Great Crested Grebe	100	107	105	103	111	96	86	82	81	80	93	92	91	86	83	806	0.98	0.003	-
Cygnus olor	Mute Swan	100	106	116	103	104	114	112	134	147	164	164	165	166	173	195	828	1.05	0.005	+
Anser anser	Greylag Goose	100	110	114	162	280	398	495	753	792	1083	1378	1745	2338	3158	3702	575	1.32	0.018	++
Alopochen aegyptiacus	Egyptian Goose	100	91	115	125	224	269	289	253	314	399	514	606	730	772	834	986	1.18	0.008	++
Tadorna tadorna	Common Shelduck	100	104	108	100	117	125	110	131	144	120	128	133	139	131	123	896	1.02	0.004	+
Mareca strepera	Gadwall	100	102	113	102	119	138	143	141	171	220	255	267	282	278	321	798	1.10	0.006	++
Anas crecca	Common Teal	100	109	93	93	87	90	59	59	61	68	77	81	87	84	81	486	0.98	0.006	-
Anas platyrhynchos	Mallard	100	93	80	82	91	96	100	87	74	87	93	95	96	95	88	1701	1.00	0.006	0
Anas querquedula	Garganey	100	83	83	88	91	96	63	80	91	102	119	100	85	69	61	630	0.99	0.007	0
Anas clypeata	Northern Shoveler	100	96	105	105	99	83	61	71	97	108	94	88	82	72	69	999	0.98	0.004	-
Aythya ferina	Common Pochard	100	89	94	102	110	100	87	92	105	120	106	109	115	103	107	300	1.01	0.010	0
Aythya fuligula	Tufted Duck	100	103	105	109	107	114	99	120	127	126	136	137	139	131	128	1263	1.02	0.004	+
Accipiter gentilis	Northern Goshawk	100	132	130	117	119	121	138	125	124	131	126	126	128	131	132	646	1.01	0.008	0
Accipiter nisus	Eurasian Sparrowhawk	100	135	118	125	153	131	140	141	142	143	124	118	112	129	125	689	1.00	0.011	0
Buteo buteo	Common Buzzard	100	118	113	138	141	148	152	160	167	174	180	183	186	186	190	1363	1.04	0.006	+
Falco tinnunculus	Common Kestrel	100	108	86	95	74	58	82	60	67	63	61	56	51	49	48	987	0.95	0.006	-
Falco subbuteo	Eurasian Hobby	100	100	78	59	53	47	52	52	68	52	49	49	49	50	40	474	0.95	0.013	-
Perdix perdix	Grey Partridge	100	93	83	88	75	57	58	51	43	39	40	37	35	36	47	685	0.93	0.006	--
Coturnix coturnix	Common Quail	100	41	139	94	132	106	89	257	195	156	137	149	164	95	153	466	1.05	0.010	+
Phasianus colchicus	Common Pheasant	100	103	95	89	80	74	81	71	70	71	67	64	61	64	70	1401	0.97	0.005	-
Rallus aquaticus	Water Rail	100	72	81	98	130	129	86	83	118	151	156	149	142	156	124	578	1.04	0.005	+
Gallinula chloropus	Common Moorhen	100	78	105	110	108	114	78	62	71	87	98	94	91	76	84	1095	0.99	0.007	0
Fulica atra	Common Coot	100	97	101	103	108	104	93	82	91	108	108	107	107	103	100	1190	1.00	0.004	0
Haematopus ostralegus	Eurasian Oystercatcher	100	116	101	89	83	87	78	71	66	64	62	60	58	57	50	1467	0.95	0.002	-
Vanellus vanellus	Northern Lapwing	100	99	88	94	99	98	107	101	94	97	93	90	88	90	84	1479	0.99	0.002	-
Gallinago gallinago	Common Snipe	100	87	64	56	66	56	54	57	59	57	56	56	57	57	59	381	0.98	0.006	-
Scolopax rusticola	Eurasian Woodcock	100	59	55	46	79	105	53	57	62	57	64	61	58	66	56	360	0.99	0.011	0
Limosa limosa	Black-tailed Godwit	100	101	89	94	102	86	81	83	79	79	77	74	71	67	65	936	0.97	0.002	-
Numenius arquata	Eurasian Curlew	100	93	104	80	76	78	82	84	82	76	77	75	73	72	78	663	0.98	0.005	-
Tringa totanus	Common Redshank	100	90	94	94	96	93	97	100	108	102	108	107	107	99	100	1046	1.01	0.002	+
Columba oenas	Stock Dove	100	115	101	117	115	123	150	144	132	121	128	122	117	126	132	1119	1.01	0.006	+
Columba palumbus	Common Wood Pigeon	100	111	100	106	104	96	98	95	93	93	89	85	82	80	89	1652	0.98	0.003	-
Streptopelia decaocto	Eurasian Collared Dove	100	87	82	81	80	69	84	101	103	97	99	105	110	109	101	641	1.02	0.006	+
Streptopelia turtur	European Turtle Dove	100	83	88	78	69	76	72	68	59	53	46	39	36	35	36	1042	0.93	0.011	--

Scientific name	English name	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	plots	slope	error	tr
Cuculus canorus	Common Cuckoo	100	89	98	110	101	106	99	105	91	89	82	80	80	77	83	1299	0.98	0.004	-
Strix aluco	Tawny Owl	100	91	86	95	91	84	100	83	80	111	77	85	94	91	95	617	1.00	0.007	0
Asio otus	Long-eared Owl	100	75	63	67	51	54	62	41	43	47	36	33	30	24	30	690	0.92	0.007	--
Picus viridis	European Green Woodpecker	100	99	127	144	145	157	152	147	139	160	161	176	195	268	229	929	1.06	0.012	+
Dryocopus martius	Black Woodpecker	100	87	79	90	98	104	111	106	99	99	106	105	105	94	91	470	1.01	0.006	0
Dendrocopos major	Great Spotted Woodpecker	100	102	95	108	118	117	126	139	124	137	125	132	143	137	128	1168	1.03	0.005	+
Dendrocopos minor	Lesser Spotted Woodpecker	100	92	93	116	137	124	150	184	198	172	166	187	211	255	248	661	1.07	0.008	++
Lullula arborea	Wood Lark	100	121	157	214	336	294	313	330	339	297	318	312	307	274	269	414	1.06	0.010	+
Alauda arvensis	Eurasian Skylark	100	85	88	84	82	72	65	66	64	58	57	52	48	38	41	1350	0.94	0.003	--
Hirundo rustica	Barn Swallow	100	81	85	72	55	49	55	60	60	70	73	68	67	84	97	393	1.00	0.007	0
Anthus trivialis	Tree Pipit	100	85	86	85	85	77	100	93	96	108	107	101	95	97	107	964	1.01	0.004	+
Anthus pratensis	Meadow Pipit	100	86	86	88	87	89	79	71	83	81	84	82	80	75	78	1534	0.99	0.003	-
Motacilla flava	Blue-headed Wagtail	100	72	72	66	71	84	98	93	100	89	98	82	70	61	70	966	0.99	0.004	0
Motacilla alba	White Wagtail	100	97	87	91	74	79	78	76	81	73	65	62	59	66	70	1201	0.97	0.005	-
Troglodytes troglodytes	Winter Wren	100	78	84	98	101	121	64	57	68	87	94	100	107	100	99	1655	1.01	0.005	0
Prunella modularis	Dunnock	100	112	104	111	103	94	111	96	92	89	84	88	94	109	101	1483	0.99	0.005	0
Erithacus rubecula	European Robin	100	101	104	124	117	120	102	88	107	125	128	125	123	115	117	1347	1.01	0.003	+
Luscinia megarhynchos	Common Nightingale	100	108	77	100	122	121	107	113	108	112	99	95	91	85	100	748	1.00	0.006	0
Luscinia svecica	Bluethroat	100	113	130	134	151	184	161	179	200	197	201	209	218	237	256	845	1.06	0.006	+
Phoenicurus ochruros	Black Redstart	100	103	80	71	63	54	90	109	116	96	94	85	80	83	99	518	1.01	0.009	0
Phoenicurus phoenicurus	Common Redstart	100	103	78	95	105	102	102	107	104	101	101	91	82	82	82	1002	0.99	0.004	-
Saxicola torquata	European Stonechat	100	98	104	125	125	134	152	188	250	247	260	265	272	300	396	791	1.11	0.005	++
Turdus merula	Common Blackbird	100	98	96	105	108	99	107	110	111	114	118	117	118	119	118	1660	1.02	0.004	+
Turdus philomelos	Song Thrush	100	96	90	103	111	111	117	118	123	131	143	147	155	172	153	1368	1.04	0.005	+
Turdus viscivorus	Mistle Thrush	100	93	98	102	95	99	91	90	85	82	82	81	81	84	87	1147	0.98	0.005	-
Locustella naevia	Common Grasshopper Warbler	100	90	89	87	89	113	122	134	152	150	165	152	143	147	187	906	1.05	0.006	+
Locustella luscinioides	Savi's Warbler	100	82	72	78	80	87	91	86	88	102	114	113	112	106	90	237	1.02	0.007	+
Acrocephalus palustris	Marsh Warbler	100	76	68	70	67	73	87	84	80	73	72	68	65	69	82	1023	0.99	0.005	0
Acrocephalus scirpaceus	European Reed Warbler	100	77	92	100	122	132	113	107	95	104	110	102	97	96	109	959	1.01	0.005	0
A. schoenobaenus	Sedge Warbler	100	79	100	114	122	178	193	175	189	183	226	225	225	189	222	720	1.07	0.004	++
Hippolais icterina	Icterine Warbler	100	86	87	73	66	61	61	53	49	53	45	44	45	47	62	758	0.95	0.007	-
Sylvia curruca	Lesser Whitethroat	100	80	93	91	111	113	117	87	84	89	94	82	73	86	99	952	0.99	0.004	-
Sylvia communis	Common Whitethroat	100	89	87	93	95	101	116	124	127	126	134	125	117	116	134	1821	1.03	0.003	+
Sylvia borin	Garden Warbler	100	96	99	103	98	98	109	99	95	93	81	82	83	78	80	1418	0.98	0.004	-
Sylvia atricapilla	Blackcap	100	91	103	114	124	120	102	122	133	137	135	141	147	144	153	1448	1.03	0.004	+

Scientific name	English name	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	plots	slope	error	tr
Phylloscopus sibilatrix	Wood Warbler	100	61	57	116	67	66	60	42	40	36	33	34	37	35	27	485	0.92	0.007	--
Phylloscopus collybita	Northern Chiffchaff	100	82	102	107	101	112	99	121	134	98	89	95	102	113	117	1581	1.01	0.003	+
Phylloscopus trochilus	Willow Warbler	100	86	79	79	78	88	85	80	74	79	73	67	61	62	69	1609	0.98	0.004	-
Regulus regulus	Goldcrest	100	43	50	43	46	55	58	49	62	87	113	110	108	138	119	511	1.07	0.006	++
Muscicapa striata	Spotted Flycatcher	100	83	80	78	83	71	67	73	59	64	64	58	54	65	86	730	0.98	0.010	-
Ficedula hypoleuca	European Pied Flycatcher	100	90	82	88	80	88	81	101	98	89	85	81	77	96	98	530	1.00	0.006	0
Aegithalos caudatus	Long-tailed Tit	100	113	97	112	104	79	97	94	61	68	71	71	73	79	66	1139	0.96	0.011	-
Parus palustris	Marsh Tit	100	114	92	95	95	84	108	95	94	84	89	94	100	106	101	542	1.00	0.004	0
Parus montanus	Willow Tit	100	103	90	76	81	65	66	77	69	69	65	64	62	65	53	856	0.96	0.005	-
Parus cristatus	Crested Tit	100	97	101	96	99	71	91	86	90	93	93	93	94	103	90	436	1.00	0.006	0
Parus ater	Coal Tit	100	93	82	89	93	72	91	83	71	63	77	83	94	91	87	433	0.99	0.005	0
Parus caeruleus	Blue Tit	100	118	111	114	118	107	139	138	117	121	120	125	129	137	132	1494	1.02	0.004	+
Parus major	Great Tit	100	102	100	99	105	94	117	121	106	105	101	103	105	112	110	1607	1.01	0.003	+
Sitta europaea	Eurasian Nuthatch	100	135	99	117	122	111	131	132	114	126	131	147	167	199	181	675	1.04	0.004	+
Certhia brachydactyla	Short-toed Treecreeper	100	94	88	96	102	91	97	102	91	94	104	105	107	125	123	1057	1.02	0.005	+
Oriolus oriolus	Eurasian Golden Oriole	100	106	105	130	121	103	112	98	94	80	80	78	76	81	72	853	0.97	0.008	-
Garrulus glandarius	Eurasian Jay	100	117	113	110	108	117	114	133	116	127	119	123	128	138	129	1246	1.02	0.005	+
Pica pica	Common Magpie	100	88	82	77	83	81	76	70	64	70	70	71	71	78	71	1033	0.98	0.006	-
Corvus monedula	Western Jackdaw	100	97	70	84	80	76	76	71	84	88	80	82	85	92	106	744	1.01	0.006	0
Corvus corone	Carrion Crow	100	108	103	103	113	123	112	120	108	123	127	130	135	124	126	1537	1.02	0.005	+
Sturnus vulgaris	Common Starling	100	99	92	101	99	93	79	95	73	71	78	78	78	65	73	1020	0.97	0.008	-
Passer domesticus	House Sparrow	100	99	87	86	75	85	81	70	62	63	53	54	55	52	51	493	0.95	0.007	-
Passer montanus	Eurasian Tree Sparrow	100	83	66	64	68	79	84	88	76	74	56	56	57	78	62	569	0.98	0.008	-
Fringilla coelebs	Common Chaffinch	100	113	112	129	136	130	149	150	139	143	133	136	142	155	147	1411	1.02	0.004	+
Chloris chloris	European Greenfinch	100	98	91	101	95	86	88	93	88	90	85	91	99	110	124	965	1.01	0.006	0
Carduelis carduelis	European Goldfinch	100	101	133	142	128	127	129	204	200	194	205	233	266	243	244	769	1.07	0.009	++
Carduelis cannabina	Common Linnet	100	77	74	77	66	65	59	62	66	61	58	56	53	55	65	1421	0.97	0.004	-
Carduelis cabaret	Lesser Redpoll	100	113	78	66	36	46	45	103	55	49	37	45	55	24	70	125	0.95	0.018	-
Pyrrhula pyrrhula	Eurasian Bullfinch	100	90	79	90	102	93	100	98	96	93	92	89	87	103	100	600	1.00	0.006	0
Coccothraustes coccot.	Hawfinch	100	113	118	119	120	135	134	164	113	95	103	96	90	101	90	564	0.98	0.007	-
Emberiza citrinella	Yellowhammer	100	104	108	106	120	112	124	124	124	125	118	120	123	125	131	710	1.02	0.005	+
Emberiza schoeniclus	Common Reed Bunting	100	93	106	113	122	111	118	120	118	126	128	131	134	151	180	1019	1.03	0.004	+

Chapter 3

Long-term population developments in typical marshland birds in the Netherlands

Chris van Turnhout, Ward Hagemeijer and Ruud Foppen

Published in 2010 in Ardea 98: 283-299

Abstract

In this chapter long-term developments in the breeding populations of 23 typical marshland bird species in the Netherlands are reconstructed, using data of several monitoring schemes and atlas studies, as well as published sources. Twelve species increased in numbers since the 1950s: Great Cormorant *Phalacrocorax carbo*, Great Egret *Casmerodius alba*, Little Egret *Egretta garzetta*, Eurasian Spoonbill *Platelea leucorodia*, Greylag Goose *Anser anser*, Red-crested Pochard *Netta rufina*, Western Marsh Harrier *Circus aeruginosus*, Bluethroat *Luscinia svecica*, Common Grasshopper Warbler *Locustella naevia*, European Reed Warbler *Acrocephalus scirpaceus*, Penduline Tit *Remiz pendulinus* and Common Reed Bunting *Emberiza schoeniclus*. Nine species declined: Great Bittern *Botaurus stellaris*, Little Bittern *Ixobrychus minutus*, Black-crowned Night Heron *Nycticorax nycticorax*, Purple Heron *Ardea purpurea*, Black Tern *Chlidonias niger*, Savi's Warbler *Locustella luscinioides*, Sedge Warbler *Acrocephalus schoenobaenus*, Great Reed Warbler *Acrocephalus arundinaceus* and Bearded Reedling *Panurus biarmicus*. For Water Rail *Rallus aquaticus* and Spotted Crake *Porzana porzana* numbers fluctuated without a clear trend. Species typical of uncut reedbeds over standing water declined most strongly, whereas the majority of species preferring drier marshlands with shrubs and bushes, and species with a rather broad habitat choice, on average increased. Possible causes of long-term population developments are discussed. At present, changes in water table management, falling water tables, terrestrialization and eutrophication have the highest impact on trends of marshland birds in the Netherlands.

Introduction

The Netherlands are situated at the estuaries of the rivers Rhine, Meuse and Scheldt. Large parts of the country are flat lowlands, and the presence of marshes and wetlands is a typical feature of the Dutch landscape. Several bird species completely depend on these wetlands for completing their life cycle. They breed, forage and sometimes overwinter in open freshwater bodies with submerged and floating vegetation, reedbeds and riverine forests.

In the past few centuries, and particularly during the 19th and 20th centuries, the area covered with wetlands has seriously contracted, while remaining wetlands suffered ecological deterioration (Van Eerden *et al.* 1998). Floodplains have been embanked and drained, and rivers have been more or less rebuilt into artificial channels, leaving less space for original ecosystems to exist (Admiraal *et al.* 1993). Marshlands have been drained and converted into farmland or urban areas (together accounting for 86% of the Dutch land surface; www.statline.cbs), a process which has only recently been halted (Haartsen *et al.* 1989). In the past decades the remaining wetlands suffered from eutrophication, contamination, falling water tables and human disturbance. This resulted in the predominantly agricultural landscape of today in which large marshes have disappeared and remaining wetlands have become patchy and fragmented. Despite this, the Netherlands still hold a large number of wetlands that are of international importance for breeding birds (SOVON & CBS 2005).

The long-term deterioration and decrease in the surface area of wetlands in the Netherlands was only temporarily interrupted by side-effects of large-scale land reclamations in the 1940s, 1950s and 1960s. These projects resulted successively in the temporary creation of huge marshlands with extensive reedbeds (Cavé 1961, Van Dobben 1995), not a goal in itself but a step towards cultivation. Consequently, conversion of these marshes into farmland normally started within a few years after reclamation, leaving less than 5% of the original surface as protected marshlands.

Changes in population sizes of marshland bird species have been deeply influenced by the processes outlined above. Furthermore, factors determining the suitability of wintering grounds and stopover sites played an important role (Zwarts *et al.* 2009). The main aim of this chapter is to reconstruct the long-term developments in the breeding populations of typical marshland bird species in the Netherlands since the 1950s, using data of several monitoring schemes and atlas studies, and published sources. Possible causes of population trends, as described in the literature, are discussed.

Materials and methods

Species selection

We arbitrary selected 23 species of which the majority of the population in the Netherlands annually breeds in good numbers in marshlands (Table 1). Rare species with less than ten breeding pairs in most years are not included (Baillon's Crake *Porzana pusilla*, Little Crake *Porzana parva*, Cetti's Warbler *Cettia cetti*, River Warbler *Locustella fluviatilis*), as are species of which the largest part of the population breeds in other habitats, such as farmland (Northern Shoveler *Anas clypeata*, Garganey *Anas querquedula*).

Table 1. Selection of breeding bird species in marshlands in the Netherlands for which population estimates (E) or population indices (I) are presented. Start year refers to start of the trend. For species with population indices the average number of study plots and territories per year is given (*SD*) for two separate periods, i.e. before and after 1990. The number of plots includes all plots where the species was recorded in at least one year.

Species *Scientific name*	Est./Ind.	Start year	No. plots		No. territories	
			<1990	*>=1990*	*<1990*	*>=1990*
Great Cormorant *Phalacrocorax carbo*	E	1952				
Great Bittern *Botaurus stellaris*	I	1968	25 (4)	96 (23)	32 (20)	74 (34)
Little Bittern *Ixobrychus minutus*	E	1965				
Night Heron *Nycticorax nycticorax*	-	1950				
Little Egret *Egretta garzetta*	E	1950				
Great Egret *Casmerodius alba*	E	1950				
Purple Heron *Ardea purpurea*	E	1970				
Eurasian Spoonbill *Platelea leucorodia*	E	1961				
Greylag Goose *Anser anser*	I	1984	79 (36)	319 (103)	77 (124)	2046 (1571)
Red-crested Pochard *Netta rufina*	E	1954				
Western Marsh Harrier *Circus aeruginosus*	E	1950				
Water Rail *Rallus aquaticus*	-					
Spotted Crake *Porzana porzana*	-					
Black Tern *Chlidonias niger*	E	1955				
Bluethroat *Luscinia svecica*	I	1963	45 (41)	423 (114)	272 (342)	1738 (533)
Common Grasshopper Warbler *Locustella naevia*	I	1977	29 (15)	121 (28)	83 (48)	371 (101)
Savi's Warbler *Locustella luscinioides*	I	1966	32 (13)	123 (32)	79 (43)	281 (95)
Sedge Warbler *Acrocephalus schoenobaenus*	I	1965	98 (40)	325 (76)	986 (337)	3430 (1666)
European Reed Warbler *Acrocephalus scirpaceus*	I	1965	132 (67)	435 (84)	1490 (1355)	5590 (1127)
Great Reed Warbler *Acrocephalus arundinaceus*	I	1968	35 (6)	53 (11)	86 (45)	53 (20)
Bearded Reedling *Panurus biarmicus*	-					
Penduline Tit *Remiz pendulinus*	E	1950				
Common Reed Bunting *Emberiza schoeniclus*	I	1965	30 (15)	99 (20)	480 (327)	1533 (333)

Monitoring data

Monitoring of breeding birds in the Netherlands, organized by SOVON and Statistics Netherlands, is based on the method of territory mapping in fixed study plots (Bibby *et al.* 1997, Hustings *et al.* 1985). Currently, two schemes are employed, focussed on common and scarce breeding birds (BMP, since 1984) and on rare and colonial breeding birds (LSB, since 1990). Fieldwork and interpretation methods are highly standardized and are described in detail in manuals (Van Dijk 2004, Van Dijk *et al.* 2004). Territory mapping uses 5-10 field visits between March and July. Size of study plots, as well as number, timing and duration of visits, depend on habitat type and species selection. All birds with behaviour indicative of a territory (e.g. song, pair bond, display, alarm, nests) are recorded on field maps. Species-specific interpretation criteria are used to determine the number of territories at the end of the season (Van Dijk 2004). Interpretation criteria focus on the type of behaviour observed, the number of observations required (depending on species-specific observation probabilities), and the period of observations (to exclude non-breeding migrants). Between 1984 and 2004 in total 3,374 different BMP-plots were covered, ranging from around 300 per year in 1984 to a maximum of around 1,750 in 1998-2000. LSB-methods are similar, but size of study plots and number and timing of visits are generally focussed on a smaller selection of species. For colonial breeding species generally occupied nests are counted. Some species receive a complete national coverage annually.

Before the start of SOVON's monitoring schemes, annually repeated breeding bird surveys were already carried out in the Netherlands, be it on a smaller scale and using less standardized methods than nowadays. In the past decades SOVON has collected such data in order to reconstruct long-term population trends of as many bird species as possible. To achieve this, national and regional periodicals, reports and archives have been systematically checked for suitable surveys. Furthermore, individual observers and institutes were asked to supply unpublished material using standard forms. Time series of individual study plots were considered useful if fieldwork and interpretation methods were more or less constant between years. The resulting *Old Timeseries* database contains census data for some 2,000 study sites.

For ten rare or colonial breeding species complete population surveys or estimates are available for the period 1950-2008 (Table 1). They vary from complete counts annually (Great Cormorant *Phalacrocorax carbo*, Eurasian Spoonbill *Platalea leucorodia*, Purple Heron *Ardea purpurea*) to estimates based on incomplete counts (Little Bittern *Ixobrychus minutus*, Black Tern *Chlidonias niger*). The most important sources are mentioned in the species texts, using Bijlsma *et al.* (2001) as a general source. For four species only few population estimates are available, and these are presented in the text only (Table 1).

Atlas data

Information on changes in distribution of species was derived from two breeding bird atlases. Data were collected in the periods of 1973-77 period (Teixeira 1979) and 1998-2000 period (SOVON 2002). Fieldwork for both atlases was based on the Dutch national grid consisting of 1,674 5×5 km squares (referred to as atlas squares). For both atlases observers were requested to compile a list of all breeding bird species present in their atlas square, including a classification of breeding status using international atlas codes (possible, probable or confirmed breeding) (Hagemeijer & Blair 1997). All atlas squares were surveyed during one breeding season in both census periods, but additional records from other years within the census period were included. Also, estimates of national breeding populations were derived from these atlases, using SOVON (1988) as an additional source. The estimates were obtained using various methods, ranging from complete counts of the national population to extrapolation of estimates per atlas square or regional and habitat-specific densities. For further details, including sources of bias and dealing with differences in completeness of coverage, we refer to SOVON (2002) and Van Turnhout *et al.* (2007).

Calculation of population indices

For nine common and scarce species yearly changes in numbers of species are presented as indices (Table 1). Indices are calculated using TRIM-software (Pannekoek & Van Strien 2005). TRIM is specifically developed for the analysis of time series of counts with missing data (Ter Braak *et al.* 1994), and is based on loglinear Poisson regression. The regression model estimates a year and site factor using the observed counts. Subsequently the model is used to predict the missing counts. Indices are calculated on the basis of a completed data set with the predicted counts replacing the missing counts. Overdispersion is taken into account by TRIM, to adjust for deviations from Poisson distribution, and so is serial correlation. Separate analyses are run for two periods. Indices after 1990 are calculated by using a post-hoc stratification and weighting procedure, to correct for the unequal distribution of study plots over Dutch regions and habitat types. Indices are first calculated for each stratum separately (stratified imputing of missing values). Thereafter, the indices per stratum are combined to a national index, weighted by population sizes and sampling efforts per stratum. If all strata are equally sampled according to the number of territories present, all weights would be similar. If a stratum is undersampled, the stratum index is given a higher weight in compiling the national index. For further details we refer to Van Turnhout *et al.* (2008). Because of the smaller number of plots the indices before 1990 are not calculated using a stratification procedure, and are therefore less reliable. This is visualized in Figure 1 by using dashed lines before 1990 and solid lines after 1990. For Common Grasshopper Warbler *Locustella naevia* and Common Reed Bunting *Emberiza schoeniclus*, of which substantial numbers breed outside marshland habitats, only plots in marshland are included. Indices are presented using 1990 as a base year (index=100). Indices are based on at least 14 study plots per year. Mean number of plots and territories per species per year are given in Table 1.

Results

Population indices and total population numbers of marshland birds in the Netherlands in the period 1950-2008 are presented in Figures 1 and 2, and described below. Also, possible causes of year-to-year fluctuations in numbers as described in the literature are mentioned briefly below, whereas causes of long-term trends are described in the discussion section.

All major **Great Cormorant** colonies in the Netherlands are located within 15-20 km of large water bodies and are situated in or near wetlands below sea level. The breeding population was low in the first half of the 20th century. Numbers decreased even further in the early 1960s, to some 1,100 breeding pairs in two colonies (Coomans de Ruiter 1966). After legal protection in 1965 the population initially recovered slowly. In 1978 4,470 breeding pairs were present in five colonies, whereas in 1993 almost 21,000 pairs bred in 27 colonies (Van Eerden & Gregersen 1995). In 1994 the population decreased by almost 30% to less than 15,000. Breeding success in the largest colony Oostvaardersplassen was very poor in 1993, mostly because food (Smelt *Osmerus eperlanus*) and foraging conditions (increased visibility of water layer in Lake IJsselmeer) were particularly unfavourable in 1994. Both of these factors are held responsible for the sudden decline (Van Eerden & Zijlstra 1995). Since the mid-1990s the population has fully recovered, reaching a new apex of over 23,000 breeding pairs in 54 colonies in 2004 (in 2008 65 colonies). Coastal colonies in the Delta and Wadden Sea areas, established in the 1980s and 1990s respectively, are largely responsible for the recent increase, whereas numbers in the traditional strongholds around Lake IJsselmeer have been fairly stable in the last two decades.

The breeding distribution of **Great Bittern** *Botaurus stellaris* is largely confined to extensive marshlands. During the second half of the 20th century breeding numbers probably peaked in the 1970s, when large areas of Reed marshes were created in the reclaimed Flevopolders. Since then numbers and distribution have declined. Of the squares occupied in 1973-77, 50% was abandoned in 1998-2000 and numbers dropped from 500-700 to 140-160 booming males in 1996-97. Numbers have been increasing since then, to 275-325 in 2004, but have decreased again in recent years (220-270 in 2007). As a result of low detection probabilities these numbers may be underestimates (Van Turnhout *et al.* 2006), but the trends are considered to be realistic. Core areas are Oostvaardersplassen and De Wieden, together holding over a quarter of the Dutch population. Severe winters resulted in strong population declines, as was the case in 1979 (reduction to approximately one third of the population), 1985, 1986, 1991 and 1996. Great Bitterns are unable to catch fish when water bodies are frozen and will succumb if alternative food sources (voles and Moles *Talpa europaea*) are not available (Day & Wilson 1978). This was, for instance, the case in the winter of 1985/86, when especially the population cycle of Common Voles *Microtus arvalis* reached a trough (Bijlsma 1993). Since 1997 severe winters did not occur, which is probably the main reason for the modest recovery.

Little Bittern has shown the largest decline of all marshland bird species in the Netherlands. In the 1960s the species was present at 100-150 sites and the population was estimated at 170-260 breeding pairs (Braaksma 1968). However, due to its secretive behaviour this probably is an underestimate, and 400 pairs may have been a more realistic estimate (Heijnen & Van der Winden 2002). In the second half of the 1990s less than ten territories were recorded annually in the Netherlands, a decrease of at least 95%. Between 1973-77 and 1998-2000 80% of the atlas squares occupied in the first period were abandoned. Although numbers were a little higher in recent years (20-40 pairs in 2008, distributed over more than twelve sites), the Little Bittern is still considered critically endangered in the Netherlands.

The secretive nature of **Black-crowned Night Heron** *Nycticorax nycticorax* and the absence of large colonies make it difficult to determine the number of breeding pairs. However, in the second half of the 20th century numbers have never been high in the Netherlands. In earlier centuries the species was more numerous. In the period 1946-83 Night Herons annually bred in the Biesbosch (maximum of 18 nests in 1946). In the 1960s the species probably also bred in a number of other sites, together holding a few tens of breeding pairs at most. Despite the growth of the number of observers, the number of records decreased: 12-15 pairs in 1973-77, 0-3 in 1983-91 and 1-6 in 1998-2004. These figures exclude around 30 free-flying pairs in zoos, which relate to (offspring of) released birds.

First breeding of **Little Egret** *Egretta garzetta* in the Netherlands took place in 1979 (leaving aside the presence of large colonies in the 14th century), and the second successful attempt was recorded in 1994. Since then numbers have grown rapidly, reaching a total of 160-180 pairs in 2008, with strongholds in the Delta (at least 132 pairs in five breeding sites) and Wadden Sea area (27 pairs on four islands).

Great Egret *Casmerodius alba* successfully bred for the first time in the Netherlands in 1978. Until 1999 numbers remained low, but since then the population has grown to 59 pairs in 2003 and 147-155 pairs in 2006. In 2007 the population

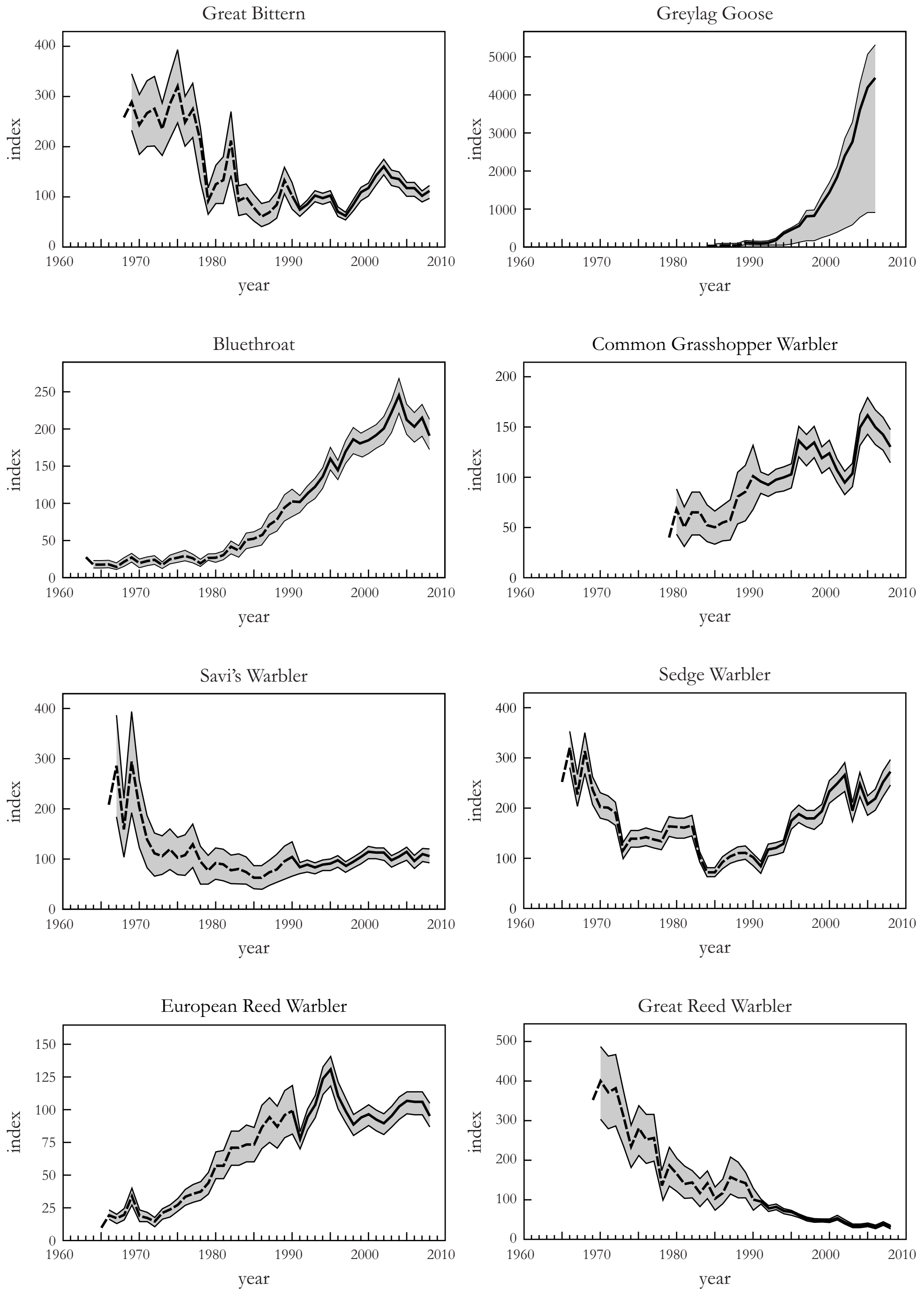


Figure 1. Population indices (± *SE*) for nine breeding birds of marshland in the Netherlands between 1960 and 2008.

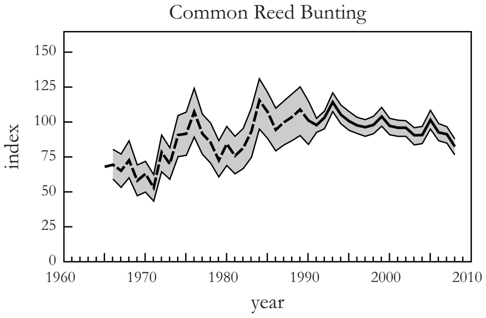


Figure 1. (continued).

dropped to 46 pairs, as a result of drought in the main breeding site, Oostvaardersplassen (>90% of Dutch population). In 2008, the national population recovered to 86-90 breeding pairs, distributed over five sites.

Major colonies of **Purple Heron** are situated in marshlands, surrounded by polders with a dense network of ditches, in the low-lying regions of the country. The breeding population increased steadily since the 1940s, and fluctuated to a maximum of around 900 breeding pairs in the 1970s. From 1980 onwards, when more than 800 pairs were present in 23 colonies, the population declined, first steeply until 1984, then more slowly until the nadir was reached in 1991, with only 221 pairs left in 17 colonies. Since then, numbers have shown an increase up to 700-720 pairs in 2008 (distributed across 25 colonies), thus reaching the population level of 1979-80 (Van der Kooij 2005). However, only eleven sites hold more than four breeding pairs at the moment, two thirds of the population residing in four large colonies.

Breeding numbers of **Eurasian Spoonbill** were low until the early 1930s. Then numbers started to increase to a maximum of 400-500 pairs in the 1940s and 1950s. In the 1960s the population declined to a minimum of 151 breeding pairs in 1968. Only five colonies were left at the time. The population has been growing ever since, to 1,900-2,000 pairs scattered over more than 30 colonies in 2008 (Voslamber 1994, Overdijk 1999, Overdijk & Horn 2005), the largest number since the mid-19th century. The increase accelerated in the mid-1980s, when the species started to colonize all major Wadden Sea islands. These now hold two thirds of the total population, followed by the Delta area. The importance of the traditional strongholds around Lake IJsselmeer has decreased in recent years.

Greylag Goose *Anser anser* breeds in large and small marshlands, preferably surrounded by intensively managed farmland. The population has shown one of the largest increases of all marshland birds. The species is a native breeding bird in the Netherlands, but became extinct in the first half of the 20th century (Van den Bergh 1991a, 1991b). In the 1970s it was successfully reintroduced in a number of sites, whereas other sites (Flevopolders, River district) were spontaneously recolonized. Since the first breeding in 1961 the annual population growth has been around 20%. In the early 1970s 50-100 pairs bred, while the population already numbered 8,000-9,000 pairs in 1998-2000. The number of occupied atlas squares has increased with 1200% in the same period. Presently, more than one third of all squares in the Netherlands have been colonized. In 2005 the Dutch breeding population was estimated at 25,000 pairs and 100,000 individuals (including non-breeding birds). At the moment numbers in the traditional strongholds seem to stabilize or decrease, whereas strong population growth continues in recently colonized areas (Voslamber *et al.* 2007).

The first confirmed breeding of **Red-crested Pochard** *Netta rufina* in the Netherlands dates back to 1942. Numbers increased to 5-15 pairs in 1942-55, 15-25 in 1956-65, 30-50 in 1967-70, and 40-60 in 1973-77. In the 1980s the population declined, reaching a minimum of 6-15 pairs in 1989-90 (Van der Winden *et al.* 1994). Since then, numbers have been increasing, especially since 2000, up to 370-420 pairs in 2008. The traditional stronghold at Vinkeveense Plassen (still 30% of the Dutch population, numbers stable since 2002) has recently been outnumbered by the Lake Veluwemeer population (129 territories in 2008). The breeding distribution is strongly correlated with the occurrence of stoneworts and other submerged macrophytes. The Dutch population is most likely of wild origin (Van der Winden & Dirksen 2005).

More than 95% of the Dutch breeding population of **Western Marsh Harrier** *Circus aeruginosus* occurs in the lower half of the country, mostly in marshland but also in crops in arable land. The population expanded to some 400 pairs in 1950, then declined to a low of 50-90 in the late 1960s. Embankment of Zuidelijk Flevoland and Lauwersmeer initiated a renewed increase in the 1970s. These areas probably functioned as a source for other parts of the country (Ouweneel 1978, Meininger 1984). In 1977 725-850 pairs bred in the Netherlands, 900-1,250 in 1980 and 1,370-1,410 in 1991-92 (Bijlsma 1993, Vogt 1994). Numbers stabilized in the 1990s (1,300-1,450 pairs in 1998-2000). Although the populations in the reclaimed polders gradually decreased after cultivation, large parts of western and northern Netherlands were colonized. Between 1973-77 and 1998-2000 the number of occupied atlas squares increased with 84%. Since 2000, however, numbers have decreased by 10-15% (Bijlsma 2006).

Two species of rails in the Netherlands are largely confined to marshlands. However, due to their secretive behaviour, nocturnal activity, erratic occurrence and large annual fluctuations in numbers long-term trends are largely unknown. For **Water Rail** *Rallus aquaticus* national population estimates of 2,000-3,600 pairs in 1973-85 and 2,500-3,200 pairs in 1998-2000 are available. Monitoring data since 1990 indicate increasing numbers, but annual fluctuations are large (mainly as a response to spring water levels and winter conditions). However, the species disappeared as a breeding bird in 6% of the atlas squares between 1973-77 and 1998-2000.

For **Spotted Crake** *Porzana porzana* national population estimates are 150-300 pairs in both 1979-85 and 1998-2000. Remarkably, the number of occupied atlas squares increased with 79% in the same period. Influxes in the river forelands as a response to spring inundations were recorded in 1970, 1978, 1983 and 1987. In such years numbers may rise to 800-1,100 breeding pairs. In other areas fluctuations rarely occur synchronously. Since 2000 local populations seem to have declined in 16 out of 23 relatively well-studied sites, whereas increases or stable numbers were recorded in only four and three sites, respectively.

Most **Black Tern** colonies are located in marshes and grasslands on peat soils in the lower parts of the country. In the 1950s the Dutch population numbered 15,000-20,000 breeding pairs. Numbers declined strongly in the 1960s and 1970s, to 2,200-3,000 in 1976-80. Since the 1990s the population has stabilized around 1,000-1,400 breeding pairs (Van der Winden *et al.* 1996). The most recent estimate is 1,200-1,300 pairs in 2008. Between 1973-77 and 1998-2000 the number of occupied atlas squares decreased with 65%. In peat districts this decline has continued until recently, but Black Terns in riverine landscapes have shown a recovery. This correlates with differences in breeding success. Relatively high breeding success was found in fluviatile landscapes, intermediate success in lowland peat marshes and low success in grasslands and moors (Van der Winden *et al.* 2004). In 1999-2003 only 15 sites held on average more than 12 pairs, and three sites on average more than 100 pairs. At least 80% of the Dutch population now breeds on artificial nest platforms.

A large proportion of the Dutch **Bluethroat** *Luscinia svecica* population is confined to large wetlands in the lower parts of the country. The species also breeds in arable land, mainly along ditches. Decreasing trends until at least the 1970s (800 breeding pairs, when the species was concentrated in the east and south of the country in fens and raised bogs) were followed by a strong recovery of numbers and a (re)colonization of many breeding sites in recent decades. This was initiated by strong increases in reclaimed Zuidelijk Flevoland and in the Biesbosch; in the latter area tidal fluctuations disappeared as a result of damming (Meijer & Van der Nat 1989, Hustings *et al.* 1995). The Dutch population increased to 3,000 pairs in 1980, 6,500 in 1990 (the two strongholds containing half of the population at that time) and 9,000-11,000 pairs in 1998-2000. The population has stabilized since 2000, although declining numbers have been reported locally in marshlands in recent years. The number of occupied atlas squares increased with 318% between 1973-77 and 1998-2000.

The largest populations of **Common Grasshopper Warbler** *Locustella naevia* are present in extensive marshlands in the lower parts of the country, but the species is also present in different types of drier vegetations (dunes, heathlands, fallow land). The marshland population strongly increased since the late 1970s, although annual fluctuations may be large in response to water level dynamics and vegetation succession. The Dutch population increased from an estimated 3,000-5,000 pairs in 1979-85 to 4,000-6,000 in 1998-2000. Simultaneously, the number of occupied atlas squares increased with 27%. Distribution expanded in marshland habitats in the lower parts of the country, and in the River district.

Savi's Warbler *Locustella luscinioides* is patchily distributed in the Netherlands, with strongholds in extensive marshlands in the lower parts of the country. Although trends derived from the sparse monitoring data are not very reliable, the observed long-term decrease, which mainly took place in the 1960s and 1970s, is realistic. National population estimates (around 3,500 breeding pairs in 1973-77, 1,350-2,050 in 1989-91 and 1,700-2,100 in 1998-2000) also indicate a decrease in the long run. The species' distribution has contracted at the end of the 20th century, and Savi's Warblers disappeared from 42% of the atlas squares which were occupied in 1973-77. Breeding in marshlands above sea level, in the south and east of the country, has become very scarce. About one third of the Dutch population breeds in one site, Oostvaardersplassen. Here, numbers have been fairly stable since the mid-1980s. In other sites, stable numbers or modest increases (peat marshes) have been reported since 1990.

Sedge Warbler *Acrocephalus schoenobaenus* mainly breeds in lowland marshes, but also occurs along ditches in farmland. The national trend is characterized by periods of strong decline, especially in the early 1970s and early 1980s, followed by partial

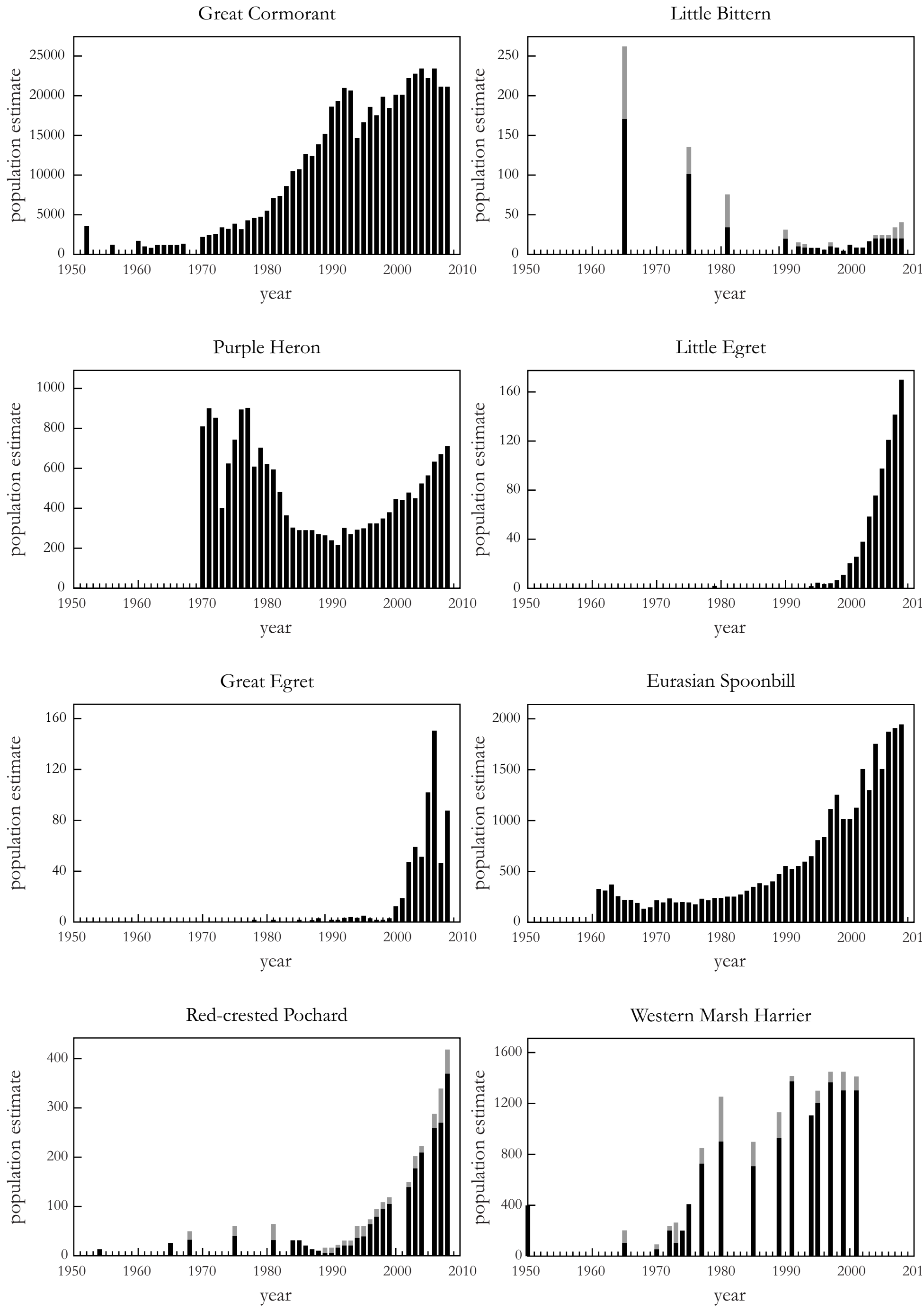


Figure 2. Total population estimates for ten breeding bird species of marshland in the Netherlands between 1950 and 2008. Estimates reflect number of breeding pairs, territories or occupied nests, and are given per year or for periods of years (Little Bittern, Red-crested Pochard, Western Marsh Harrier, Black Tern), including or excluding minimum and maximum estimates.

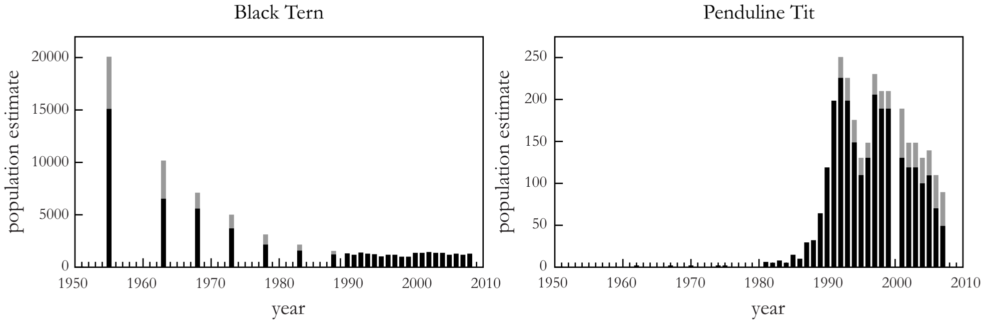


Figure 2. (continued).

recoveries. Decreases were most steep in the eastern and southern parts of the country, and recolonizations failed to occur here. This resulted in a decrease of 27% of occupied atlas squares between 1973-77 and 1998-2000. In some parts of the low-lying Netherlands present numbers are similar to those in the late 1960s, but the overall Dutch population must have decreased. In 1998-2000 the population was estimated at 20,000-25,000 breeding pairs.

Although highest densities of **European Reed Warbler** *Acrocephalus scirpaceus* occur in extensive marshlands in the lower parts of the country, the species is widely distributed and breeds in 84% of all atlas squares. The long-term trend shows an increase, especially in the 1970s and early 1980s, and numbers seem to have grown five- to tenfold between the 1960s and 1990s. Since then, the population has stabilized. The scale of the increase may be prone to some overestimation caused by more thorough fieldwork in recent decades. The number of occupied atlas squares also increased with 12% between 1973-77 and 1998-2000. The population is estimated at 150,000-250,000 breeding pairs, making the European Reed Warbler the most numerous marshland bird in the Netherlands.

The breeding distribution of **Great Reed Warbler** *Acrocephalus arundinaceus* is concentrated in a few core areas. Over three quarters of the population breeds in the north-western part of the province of Overijssel. Since the 1950s numbers have been more than decimated, from an estimated 10,000 pairs to 400 pairs in the early 1990s (Graveland 1996), and around 250 in 1998-2000. Simultaneously, the distribution has contracted and the number of occupied atlas squares decreased with 78% between 1973-77 and 1998-2000. The decrease has not yet halted, given the only 170-200 pairs in 2008.

Few reliable estimates are available for the Dutch population of **Bearded Reedling** *Panurus biarmicus*. Due to its lack of territorial behaviour and the inaccessibility of large marshes where the majority of the population breeds (less than ten sites hold over 25 breeding pairs), the species is difficult to census. Furthermore, numbers and distribution show large annual fluctuations, caused by winter weather (Campbell *et al.* 1996) and, especially, habitat management (Beemster 1997). High numbers of Bearded Reedlings occurred initially in the recently reclaimed Flevopolders in the 1960s and 1970s, leading to a (inter)national increase in numbers (Bibby 1983, Campbell *et al.* 1996). In 1975 the population was estimated at 7,000 breeding pairs in Zuidelijk Flevoland, and 7,500-8,000 in the whole country. The population decreased steeply in the past decades, mainly as a result of the cultivation of Zuidelijk Flevoland, where numbers dropped to 300-800 in 1998-2000. At the same time, however, some expansion to other sites was recorded. The Dutch population was estimated at 750-1,350 pairs in 1989-91, 1,800-2,000 in 1995-97 and 1,200-2,000 in 1998-2000.

The first breeding attempts of **Penduline Tit** *Remiz pendulinus* in the Netherlands occurred in the 1960s, but it was not until 1981 that breeding became regular. From 1986 onwards the population strongly increased to a maximum of 225-250 territories in 1992 (Bekhuis *et al.* 1993). The core breeding areas shifted from the northern part of the country to marshlands and riverine wetlands in the central part of the country. In the 1990s marked fluctuations were observed, but since 1997 numbers have been declining. In 2008 the remaining population was estimated at only 50-90 territories. Many regular breeding sites have now been abandoned.

Highest densities of **Common Reed Bunting** *Emberiza schoeniclus* occur in marshlands in the lower parts of the country, but the species exploits a wide array of habitats and breeds in 81% of all atlas squares. The Dutch population is estimated at 70,000-100,000 breeding pairs. The marshland population shows large annual fluctuations, but seems to have increased in the long run, especially in the 1960s and 1970s. However, since the mid-1990s population monitoring data indicate a modest decline, especially in marshes on peat soils. Between 1973-77 and 1998-2000 Common Reed Buntings disappeared from 8% of the previously occupied atlas squares, especially in the higher parts of the country outside marshland habitats.

Discussion

Reliability of trends

Several problems may arise when old and recent census results are compared. The number of birders in the Netherlands has increased significantly during the 20th century, especially from 1970 onwards. Their mobility, amount of spare time, optical equipment and determination skills have grown simultaneously. Furthermore, interest in systematic censusing of breeding birds has grown rapidly in the 1970s and 1980s. Finally, birders are better organized nowadays, using systematic and standardized census techniques (Zijlstra & Hustings 1992). These developments have led to improved coverage of breeding areas, better knowledge of distribution patterns and increased reliability of censuses. This applies especially for nocturnal and crepuscular species, such as Great Bittern and Little Bittern. Another source of bias is to be expected from differences in the interpretation of observations. Numbers given for some species in old census reports often indicate (successful) nests, not territories based on standardized species-specific criteria, as is the case since 1984 (Hustings 1991). These problems imply an underestimate of historical numbers in relation to recent numbers. Therefore, declines generally will be more extensive than calculated, whereas increases may be slightly exaggerated. This is particularly evident for non-passerine species for which we present indices, such as Great Bittern and Greylag Goose. For species for which total population estimates are presented, it was tried to take these problems into account. However, comparing population estimates for different periods is hazardous as well, because the underlying effort and methods are usually different (SOVON 2002, Van Turnhout *et al.* 2007).

Monitoring plots are not distributed randomly over the country, especially in the period before 1980. For marshlands, the western part of the country is overrepresented, whereas the north and the river district are underrepresented. Indices after 1990 are generally more reliable because of the larger number of plots and the use of a correction procedure for over- and undersampling of regions (see Methods). Furthermore, the land reclamation projects in the 1960s and 1970s are not incorporated in the samples, because bird data from these areas were not available. These events had a major impact on the populations of at least some of the marshland bird species involved. The first large reclamation projects were carried out in 1930 (Wieringermeer) and 1942 (Noordoostpolder in Lake IJsselmeer) respectively. Large marshlands, especially with reedbeds, were created, offering suitable habitat for a variety of marshland birds (e.g. Western Marsh Harrier, Vogt 1994). However, almost the entire polder was cultivated during the 1940s, and the effect on bird populations is probably not recognizable in the period described in this chapter. This probably also (partly) applies for the reclamation of Oostelijk Flevoland in 1957 (Cavé 1961). On the other hand, the reclamation of Zuidelijk Flevoland in 1968 and Lauwerszee in 1969 had a major impact on the population levels of marshland birds described in this chapter. Immediately after reclamation, large-scale sowing of Reed *Phragmites australis* was started, in order to accelerate the maturation of the soil. This resulted in extensive reedbeds in the years following reclamation (Van Dobben 1995). Although quantitative information is largely lacking, the numbers of marshland birds must have increased tremendously. For some species the impact was visible on a national and even international scale, as described for Bearded Reedling (Mead & Pearson 1974), Western Marsh Harrier (Altenburg *et al.* 1987, Bijlsma 1993, Vogt 1994) and Greylag Goose (Van den Bergh 1991a), not only because numbers in the reclaimed areas itself were relatively important, but probably also because of high reproductive rates, improved survival and the subsequent increase of numbers in 'surrounding' marshlands following an influx of individuals originating from the reclaimed areas. Then, within a few years after reclamation, cultivation was started. This resulted in a drop in numbers of marshland birds, as was the case for Western Marsh Harrier from 1977 onwards (Zijlstra 1983). When interpreting the indices, one should keep in mind that the core areas for which the above processes are described are not taken into account. 'Overspill effects' in the surrounding areas may have had a buffering – or even contrary – effect on the trends in our sampled regions: collapsing populations in the core areas may have resulted in temporary invasion of surrounding areas by 'refugees'. This was described for Savi's Warbler in the northwest of the country in the late 1960s, as a response to the cultivation of Oostelijk Flevoland (Van der Hut 1983). These are expected to be short-term effects.

Driving forces

The long-term trends described are a result of various processes influencing survival and reproduction. These processes are complex and not acting simultaneously on all species in the same way. Birds migrating to and wintering in southern Europe and Africa will encounter several additional problems which impact their survival. This applies for the greater part of the Dutch breeding population of Great Cormorant, Eurasian Spoonbill, Purple Heron, Little Bittern, Western Marsh Harrier, Spotted Crake, Black Tern, Bluethroat, Common Grasshopper Warbler, Savi's Warbler, Sedge Warbler, European Reed Warbler, Great Reed Warbler and Penduline Tit (SOVON 1987, Zwarts *et al.* 2009). Here, we give a brief overview of the factors that have been demonstrated to influence population trends.

Cultivation and periodical droughts

Cultivation of marshlands has played an important role in the Netherlands, especially up to the second half of the 20th century when extensive areas of marshlands were drained and converted into farmland. During the second half of the 20th century, the remaining marshes gradually received protection and thus preservation initially was guaranteed. However, small and isolated patches of marshlands in farmland and near urban areas are still being cultivated at present. In addition, such fragmented patches are most vulnerable to factors influencing habitat quality, like falling water tables. On the other hand, new marshland habitats have been (re)created locally in the recent decade, especially in river floodplains and around existing core marshland areas. Some of these rehabilitated sites have been colonized by marshland birds, including rarer species, such as Great Bittern (Van Turnhout *et al.* 2006). Large-scale cultivation of marshlands and, particularly, damming of rivers still is a major problem in southern Europe and Africa (Zwarts *et al.* 2009). It may negatively impact foraging grounds of, for instance, Little Bittern (Bekhuis 1990). On the other hand, the creation of large-scale rice fields in Mediterranean Europe and Western Africa has resulted in an important foraging habitat for both local breeding populations of herons (Fasola *et al.* 1996) and migrating and wintering populations of a large number of wader, waterfowl and marshland species (Czech & Parsons 2002, Lourenço & Piersma 2009). However, creation of irrigated rice fields in the Sahel only partly compensates for losses of natural floodplains (Zwarts *et al.* 2009), and rice plantations in Southern France attract fewer species and lower numbers than natural marshes (Tourenq *et al.* 2001).

An additional problem in parts of Africa is periodical drought due to a lack of precipitation. In the early 1980s this was proven to be a major cause of decline of breeding populations of some marshland birds in western Europe. In the 1960s, 1970s (Den Held 1981, Cavé 1983) and 1980s (Van der Kooij 1991) the number of breeding Purple Herons in the Netherlands was largely determined by the discharge of the rivers Niger and Senegal. Drought in the Sahel was also responsible for the decline of British and Dutch Sedge Warbler populations, especially in the mid-1980s (Peach *et al.* 1991, Foppen *et al.* 1991). The population recoveries of these species since the 1990s coincide with a period of improved rainfall (Zwarts *et al.* 2009). Also, for Western Marsh Harrier a correlation between the size of the floodplains in the Sahel and breeding numbers in the Netherlands was found, but only after the population had fully recovered from pesticide- and persecution-related crashes in 1960s and 1970s (Zwarts *et al.* 2009). Held *et al.* (2005) predict that rainfall in the Sahel will remain rather stable until 2020-2040, but will gradually decrease by about 20% in the next 50-100 years as a result of climate change. If correct, that would spell renewed crashes among marshland birds wintering in this region.

Water table management and eutrophication

Several factors have caused a further loss in quality of marshlands in the Netherlands in recent decades. Especially the surface area of early successional stages, such as Reed growing in standing water, has declined. Although the magnitude of the decrease is unknown (Graveland & Coops 1997), information from a small number of sites is available, and is thought to be representative for large parts of the country. In 1928 and 1967, respectively 65% and 32% of the shores of Reeuwijkse Plassen were covered with reedbeds in water; in 1995 only 13% was left (Graveland & Coops 1997). At Loosdrechtse Plassen the surface area of water Reed declined with 85% between 1960 and 1990 (Barendrecht *et al.* 1990). Two factors are held responsible for the die-back of Reed stands. Changes in water table management for agricultural and recreational purposes have resulted in a reduction of natural water level oscillations, while Reed growth and regeneration need a high water level in winter and a low level in summer (Graveland & Coops 1997). Stabilized water levels result in a slow and incomplete decomposition of litter. In combination with eutrophication, especially through the inlet of alkaline and nutrient-rich river water (resulting in an increased accumulation of organic compounds), toxic elements are released under anaerobic conditions, which are detrimental for plant growth (Graveland & Coops 1997). Furthermore, a decreased carbon/nitrogen-ratio leads to a decrease of sclerenchyma formation, Reed shoots thus becoming more vulnerable to physical damage by wind, strong wave action, recreation and probably fungal diseases (Den Hartog *et al.* 1989). Additionally, direct destruction (recreation, intensified and mechanized Reed harvesting, wash of filamentous algae), grazing by cattle, falling water tables and terrestrialization have also caused Reed die-back (Ostendorp 1989, Graveland & Coops 1997). This is considered the major cause of the decline of Reed inhabiting species, such as Great Reed Warbler (Graveland 1996, 1998), Great Bittern (Van Turnhout *et al.* 2006), Little Bittern (Bekhuis 1990) and Purple Heron (Van der Kooij 1991). The presence of a sufficient amount of uncut Reed is also important for Sedge Warbler and European Reed Warbler. In many marshlands, reed management includes a high proportion (>50%) of all reed to be harvested every year. In harvested reedlands, the risk of predation is higher and the nesting season starts later, which may hamper the production of multiple broods (Graveland 1997).

Eutrophication, in combination with other pollutants, caused a change in water quality, which in its turn has negatively affected diversity and number of invertebrate prey , impacting reproductive success and condition of chicks. This is believed to have further accelerated the decline of Great Reed Warbler and Black Tern (Graveland 1996, Beintema 1997) and possibly Great Bittern (Smith & Tyler 1993), Little Bittern (Bekhuis 1990) and Purple Heron (Tucker & Evans 1997). Eutrophication also resulted in the decline of floating vegetation in marshlands (especially Water Soldier *Stratiotes aloides*), and therefore in a significant loss of suitable breeding places for Black Tern, an important cause of the decline in this species (Van der Winden *et al.* 1996). Furthermore, eutrophication led to a decline of stoneworts (especially *Nitellopsis obtusa*), being the dominant component in the diet of Red-crested Pochard (Ruiters *et al.* 1994). This likely caused the decrease of the breeding population in the 1980s (Van der Winden *et al.* 1994). Since the 1990s water quality has improved again, the transparancy of the water has increased and stoneworts have returned at many sites (Ruiters *et al.*

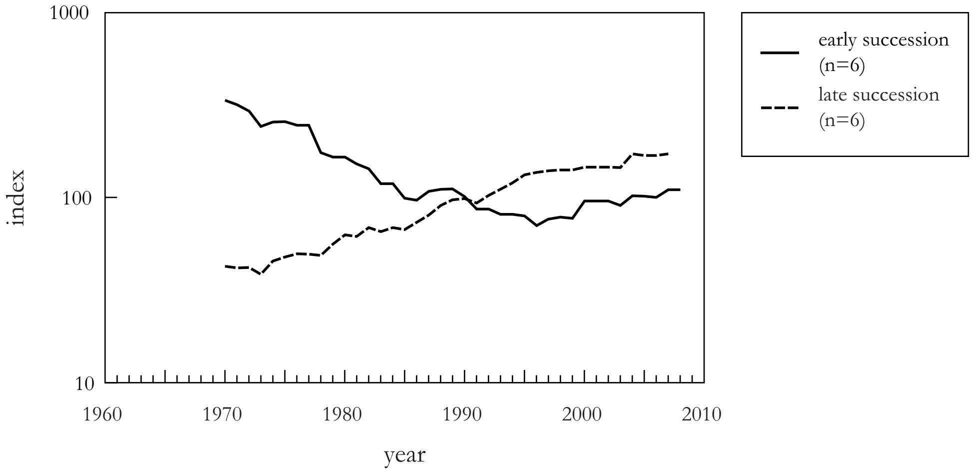


Figure 3. Aggregated population trends in 1970-2008 for six marshland birds typical for early succession stages (particularly reed beds standing in water: Great Bittern, Little Bittern, Purple Heron, Black Tern, Savi's Warbler, Great Reed Warbler), and for six marshland birds typical for late succession stages (drier marshland with shrubs and bushes, including species with a broad habitat choice: Eurasian Spoonbill, Bluethroat, Common Grasshopper Warbler, European Reed Warbler, Sedge Warbler, Common Reed Bunting). Shown are geometrical means of annual population indices per species.

1994). Simultaneously, the population of Red-crested Pochard strongly increased (Dirksen & Van der Winden 1996). However, the effects of eutrophication are not univocal. It has, for example, led to an increase of inland populations of several fish species, responsible for the large increase of Great Cormorant numbers all over Europe (De Nie 1995). Also, eutrophication indirectly resulted in intrusion of marshlands by bushes, initially favouring species such as Bluethroat (Hustings *et al.* 1995) and Penduline Tit (Bekhuis *et al.* 1993), especially in combination with falling water tables.

Of the 23 species of marshland birds described in this chapter, twelve showed an increase in numbers since the 1950s. Nine species declined, and two species fluctuated in numbers without a clear trend (Spotted Crake, Water Rail). Particularly species typical for early successional stages, such as reedbeds in standing water, have declined (Figure 3): Great Bittern, Little Bittern, Purple Heron, Savi's Warbler and Great Reed Warbler (Van der Hut 1986, Graveland 1998, Barbraud *et al.* 2002, Poulin *et al.* 2002, Gilbert *et al.* 2005, Grujbarova 2005, Neto 2006). Most species preferring drier marshland habitats with shrubs and bushes, and species with a broad habitat choice, have increased, such as Great Cormorant, Eurasian Spoonbill, Western Marsh Harrier, Bluethroat, Common Grasshopper Warbler, European Reed Warbler, Penduline Tit and Common Reed Bunting (Van der Hut 1986, Baldi & Kisbedenek 1999, Poulin *et al.* 2002). It may therefore be concluded that particularly changes in water table management, falling water tables, terrestrialization and eutrophication have been the dominant processes population for trends in marshland birds in the Netherlands in the past decades.

Persecution and pollution

However, there are several additional problems that have affected population numbers of marshland bird species, both at present and in the past. Persecution on the breeding grounds will have played an important role in population developments in some of the larger species involved, especially up to and including the first half of the century (Great Bittern, Braaksma & Mörzer Bruijns 1954; Little Bittern, Braaksma 1968; Night Heron, Bijlsma *et al.* 2001; Eurasian Spoonbill, Van der Hut 1992; Greylag Goose, Van den Bergh 1991a). Great Cormorants were (and still are; Van Eerden *et al.* 1995) thought to be a threat to fishery and consequently the population was controlled by shooting, cutting of nesting trees and harvesting of chicks (Veldkamp 1986). Numbers increased rapidly once the species received legal protection in 1965 (Van Eerden & Gregersen 1995). The Western Marsh Harrier has suffered from persecution too (Zwarts *et al.* 2009). For instance, in the early 1950s hundreds were shot in the newly reclaimed Noordoostpolder (Bijlsma 1993). Hunting at stopover sites and wintering grounds may have a negative impact on population sizes of some of the larger species, such as Purple Heron (Hagemeijer *et al.* 1998) and Eurasian Spoonbill (Van der Hut 1992). Legal protection and improved law enforcement may have contributed to a decrease in mortality caused by shooting, and hence to the increase of the Dutch Eurasian Spoonbill population after 1968 (Voslamber 1994).

The use of chlorinated carbons like PCBs and DDT was a major cause of the decline of some top predators in the 1960s, when biocides were massively used in agriculture, as recorded for Great Cormorant (Van Eerden & Gregersen 1995), Western Marsh Harrier (Bijlsma 1993), Eurasian Spoonbill (Voslamber 1994) and Great Bittern (Newton *et al.* 1994). Van den Berg *et al.* (1995) and Boudewijn & Dirksen (1995) found that the relatively high levels of chlorinated carbons in eggs of Great Cormorants breeding in polluted sedimentation areas probably were responsible for their reduced reproductive success at least until the 1990s. Other sources also mention the negative impact of biocides and heavy metals on the populations of Eurasian Spoonbill (Van der Hut 1992), Western Marsh Harrier (effects of lead poisoning in South-France, Fisher *et al.* 2006) and Black Tern (Glutz von Blotzheim & Bauer 1982). Although a ban on part of the persistent pesticides improved the situation on the breeding grounds, enabling populations to recover in several species, biocides are still massively used in southern European agriculture, which may severely decrease the food resources available to waterbirds (Tourenq *et al.* 2003).

Intensification, fragmentation and disturbance

Agricultural intensification (including reallotment, changes in water table management, soil fertilization, crop changes) has caused a substantial loss of suitable foraging habitat through decreasing food availability for Purple Heron and Eurasian Spoonbill (loss of many shallow waters needed for foraging, intensive maintenance of ditches, obstruction of fish migration; Wintermans & Wymenga 1996, Van der Winden *et al.* 2004), Black Tern (Van der Winden *et al.* 1996), Great Reed Warbler (Graveland 1996) and possibly Common Reed Bunting (decrease of overwinter stubble; Peach *et al.* 1999). However, for herbivores, such as Greylag Goose, the increased food quality and availability in farmland led to a steep population growth (Voslamber *et al.* 2007).

Effects of habitat fragmentation on population numbers were demonstrated for Sedge Warbler. In marshlands the decline in number of breeding birds as a response to droughts in the wintering grounds was steeper in fragmented than in unfragmented habitats. Besides, the rate of recovery in the following years was much slower in fragmented landscapes (Foppen *et al.* 1999). There are also indications of negative effects of habitat fragmentation on Great Bittern (Foppen 2001), and possibly Purple Heron (Van der Kooij 1996) and Great Reed Warbler (Foppen 2001, Hansson *et al.* 2002). An increase in recreational disturbance may have a negative impact on several species, although effects on population level are largely unknown. However, disturbance of Black Tern colonies resulted in a reduced survival of chicks (Van der Winden 2002). Bone fractures occurring in chicks of Black Terns breeding on sandy soils are attributed to acidification, which probably has caused the disappearance of fish in fens and peatbogs, an important component of the species' diet in these areas (Beintema 1997). It seems unlikely, however, that acidification is an important cause of population changes in breeding haunts of Black Terns with well buffered soils, as found in the rest of the country. In some Dutch Eurasian Spoonbill colonies, predation by Red Foxes *Vulpes vulpes* has had a big impact, resulting in colonies moving elsewhere (Voslamber 1994). Eurasian Spoonbills have switched their stronghold to the Wadden Sea islands, where no Foxes occur; meanwhile their number has reached the highest level since centuries (Overdijk 1999, Overdijk & Horn 2005). Purple Herons are able to adapt to the presence of Foxes to a certain extent, in that breeding became more dispersed and in wetter vegetations once Foxes showed up. In colonies in shrubs, average nest height increased and higher shrub or tree species were preferred, probably an antipredator strategy (Van der Kooij 1995).

Biogeographical processes and climate change

Large-scale biogeographical processes, some possibly connected with climate change, may be responsible for population changes in species reaching their distribution limit in the Netherlands. The recent colonization of Little Egret in the Netherlands coincides with a northward expansion of the species in France and the United Kingdom (Musgrove 2002, Voisin *et al.* 2005). Also, the colonization of Great Egret (Van der Kooij & Voslamber 1997, Voslamber, this issue of Ardea) and Penduline Tit (Flade *et al.* 1986, Bekhuis *et al.* 1993) follow the European trend of range expansion, and, for the latter, the subsequent range contraction. The recent recovery of the Great Bittern population may be attributed to a decreasing frequency of severe winters since the early 1990s (Van Turnhout *et al.* 2006). Climate change is expected to become a major factor in determining population changes of marshland birds in the near future. European Reed Warblers have already advanced their laying date between 1990 and 2006, enabling a larger proportion of pairs to produce a second clutch and hence improve their breeding success (Halupka *et al.* 2008). In general, long-distance migrants breeding in marshes seem able to adapt to the advanced phenology of their habitat, probably because of the extended period of insect abundance during the breeding season, compared to migratory birds in seasonal forests, which are increasingly confronted with trophic mismatches (Both *et al.* 2010). However, it is hard to predict the combined and species-specific impact of different aspects of climate change: increasing temperatures, increasing precipitation, increasing evaporation, increased frequency of extreme weather events, and differences in these variables between breeding and wintering grounds and stopover sites. Continued monitoring of distribution and numbers is needed to keep track of population developments. Because the Netherlands hold an important part of the north-west European population of a number of marshland species (e.g. Eurasian Spoonbill, Purple Heron, Great Bittern, Bluethroat, Bearded Reedling; BirdLife International 2004), this is also essential from an international point of view.

Acknowledgements

First of all we would like to thank the thousands of observers, both professionals and volunteers, who gathered breeding bird data in the past decennia. Without their praiseworthy efforts the preparation of this chapter would never have been possible. Fred Hustings, Arend-Jan van Dijk, Henk Sierdsema, Arjan Boele and Berend Voslamber (all SOVON) gave useful advice during the preparation. Dirk Zoetebier and Calijn Plate (Statistics Netherlands) assisted in calculating population indices. Fred Hustings, Rob Vogel (SOVON), Maarten Platteeuw (RIZA), Rob Bijlsma and an anonymus referee commented on earlier drafts, which clearly improved this chapter.

References

Admiraal W. Van der Velde G., Smit H. & Cazemier W.G. 1993. The rivers Rhine and Meuse in the Netherlands: present state and signs of ecological recovery. *Hydrobiologia* 265: 97-128.

Altenburg W., Bruinenberg-Rinsma J., Wildschut P. & Zijlstra M. 1987. Colonization of a new area by the Marsh Harrier. *Ardea* 75: 213-220.

Baldi A. & Kisbenedek T. 1999. Species-specific distribution of reed-nesting passerine birds across reed-bed edges: Effects of spatial scale and edge type. *Acta Zoologica Academiae Scientiarum Hungaricae* 45: 97-114.

Barbraud C., Lepley M., Mathevet R. & Mauchamp A. 2002. Reedbed selection and colony size of breeding Purple Herons *Ardea purpurea* in southern France. *Ibis* 144: 227-235.

Barendrecht A., Wassen M.J. & Van Leerdam A. 1990. Nivellering van de verlanding. *Landschap* 7: 17-23.

Beemster N. 1997. Dynamisch waterpeil in de Oostvaardersplassen, effecten op broedvogels in relatie tot vegetatieontwikkeling. Flevobericht nr. 400. Directoraat-Generaal Rijkswaterstaat, Lelystad.

Beintema A.J. 1997. European Black Terns (*Chlidonias niger*) in trouble: Examples of dietary problems. *Colonial Waterbirds* 20: 558-565.

Bekhuis J. 1990. Hoe lang nog broedende Woudaapjes *Ixobrychus minutus* in Nederland? *Limosa* 63: 47-50.

Bekhuis J., Nienhuis J., Wymenga E., Beemster N. & Van Beusekom R. 1993. Opmars van de Buidelmees *Remiz pendulinus* in Nederland in de periode 1988-92. *Limosa* 66: 97-106.

Bibby C.J. 1983. Studies of west Palearctic birds 186. Bearded Tit. *British Birds* 76: 549-563.

Bibby C.J., Burgess N.D. & Hill D.A. 1997. Bird Census Techniques. Academic Press, London.

Bijlsma R.G. 1993. Ecologische atlas van de Nederlandse roofvogels. Schuyt & Co., Haarlem.

Bijlsma R.G. 2006. Trends en broedresultaten van roofvogels in Nederland in 2005. *De Takkeling* 14: 6-53.

Bijlsma R.G., Hustings F. & Camphuysen C.J. 2001. Algemene en schaarse vogels van Nederland (Avifauna van Nederland 2). GMB Uitgeverij/KNNV Uitgeverij, Haarlem/Utrecht.

BirdLife International 2004. Birds in Europe: population estimates, trends and conservation status. BirdLife International, Cambridge.

Both C., Van Turnhout C.A.M., Bijlsma R.G., Siepel H., Van Strien A.J. & Foppen R.P.B. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B* 277: 1259-1266.

Boudewijn T.J. & Dirksen S. 1995. Impact of contaminants on the breeding succes of the Cormorant *Phalacrocorax carbo sinensis* in the Netherlands. *Ardea* 83: 325-338.

Braaksma S. 1968. De verspreiding van het Woudaapje (*Ixobrychus minutus*) als broedvogel. *Limosa* 41: 41-61.

Braaksma S. & Mörzer Bruijns M.F. 1954. De stand van de Roerdomp *Botaurus stellaris* L., als broedvogel in Nederland tot 1953. *Ardea* 42: 151-162.

Campbell L., Cayford J. & Pearson D. 1996. Bearded Tits in Britain and Ireland. *British Birds* 89: 335-346.

Cavé A.J. 1961. De Broedvogels van Oostelijk Flevoland in 1958-60. *Limosa* 34: 231-251.

Coomans de Ruiter L. 1966. De Aalscholver, *Phalacrocorax carbo sinensis* (Shaw & Nodder) als broedvogel in Nederland, in vergelijking met andere Westeuropese landen. Rivon-mededeling nr. 244.

Czech H.A. & Parsons K.C. 2002. Agricultural wetlands and waterbirds: A review. *Waterbirds* 25: 56-65.

Day J.C.U. & Wilson J. 1978. Breeding Bitterns in Britain. *British Birds* 71: 285-300.

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

Den Held J.J. 1981. Population changes in the Purple Heron in relation to drought in the wintering area. *Ardea* 69: 185-191.

De Nie H.W. 1995. Changes in the inland fish populations in Europe and its consequences for the increase in the Cormorant *Phalacrocorax carbo*. *Ardea* 83: 115-122.

Dirksen S. & Van der Winden J. 1996. Aantallen Krooneenden *Netta rufina* in nazomer en herfst op de Gouwzee fluctueren met broedsucces Nederlandse populatie. *Limosa* 69: 131-133.

Fasola M., Canova L. & Saino N. 1996. Rice fields support a large portion of herons breeding in the Mediterranean region. *Colonial Waterbirds* 19: 129-134.

Fasola M., Hafner H., Prosper J., Van der Kooij H. & Von Schogolev I. 2000. Population changes in European herons in relation to African climate. *Ostrich* 71: 52-55.

Fisher I.J., Pain D.J. & Thomas V.G. 2006. A review of lead poisoning from ammunition sources in terrestrial birds. *Biological Conservation* 131: 421-432.

Flade M., Franz D. & Helbig A. 1986. Die Ausbreitung der Beutelmeise (*Remiz pendulinus*) an ihrer nordwestlichen Verbreitungsgrenze bis 1985. *Journal of Ornithology* 127: 261-283.

Foppen R., Ter Braak C.J.F., Verboom J. & Reijnen R. 1999. Dutch Sedge Warblers *Acrocephalus schoenobaenus* and west-african rainfall: empirical data and simulation modelling show low population resilience in fragmented marshlands. *Ardea* 87: 113-127.

Foppen R.P.B. 2001. Bridging gaps in fragmented marshland. Applying landscape ecology for bird conservation. Thesis University of Wageningen, Wageningen.

Gilbert G., Tyler G.A., Dunn C.J. & Smith K.W. 2005. Nesting habitat selection by bitterns *Botaurus stellaris* in Britain and implications for wetland management. *Biological Conservation* 124: 547-553.

Glutz von Blotzheim U.M. & Bauer K.M. 1982 (eds). Handbuch der Vögel Mitteleuropas, Band 8/II. Akademische Verlagsgesellschaft, Wiesbaden.

Graveland J.J. 1996. Watervogel en zangvogel: de achteruitgang van de Grote Karekiet *Acrocephalus arundinaceus* in Nederland. *Limosa* 69: 85-96.

Graveland J. 1997. Dichtheid en nestsucces van Kleine Karekiet *Acrocephalus scirpaceus* en Rietzanger *A. schoenobaenus* in overjarig riet. *Limosa* 70: 151-162.

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

Graveland J. & Coops H. 1997. Verdwijnen van rietgordels in Nederland. Oorzaken, gevolgen en een strategie voor herstel. *Landschap* 14: 67-86.

Grujbarova Z., Kocian L. & Nemethova D. 2005. Habitat selection in the sedge warbler (*Acrocephalus schoenobaenus*) and the reed bunting (*Emberiza schoeniclus*). *Biologia* 60: 571-577.

Haartsen A.J., De Klerk A.P., Vervloet J.A.J. & Borger G.J. 1989. Levend verleden. Een verkenning van de cultuurhistorische betekenis van het Nederlandse landschap. SDU uitgeverij, 's-Gravenhage.

Hagemeijer, E.J.M. & Blair, M.J. (eds) 1997. The EBCC Atlas of European breeding birds: their distribution and abundance. Poyser, London.

Hagemeijer E.J.M., Poot M.J.M., Adjakpa J.B. & Coubeou P.T. 1998. Waterbird survey in the wetlands of South Benin, 1996 and 1997. SOVON-onderzoeksrapport 1997/09. SOVON Vogelonderzoek Nederland, Beek-Ubbergen

Halupka L., Dyrcz A. & Borowiec M. 2008. Climate change affects breeding of reed warblers *Acrocephalus scirpaceus*. *Journal of Avian Biology* 39: 95-100.

Hansson B., Bensch S., Hasselquist D. & Nielsen B. 2002. Restricted dispersal in a long-distance migrant bird with patchy distribution, the great reed warbler. *Oecologia* 130: 536-542.

Heijnen T. & Van der Winden J. 2002. Woudaap. In: SOVON 2002. Atlas van de Nederlandse Broedvogels 1998-2000: 72-73. (Nederlandse Fauna 5). Nationaal Natuurhistorisch Museum Leiden, KNNV Uitgeverij & European Invertebrate Survey-Nederland, Leiden.

Held I.M., Delworth T.L., Lu J., Findell K.L. & Knutson T.R. 2005. Simulation of Sahel drought in the 20th and 21st centuries. *Proceedings of the National Academy of Sciences* 102: 17891-17896.

Hustings F. 1991. Explosieve toename van broedende Geoorde Futen *Podiceps nigricollis* in 1983-89 in Nederland. *Limosa* 64: 17-24.

Hustings M.F.H., Kwak R.G.M., Opdam P.F.M. & Reijnen M.J.S.M. (eds) 1985. Vogelinventarisatie. Natuurbeheer in Nederland, 3. Pudoc, Wageningen/Vogelbescherming, Zeist.

Hustings F., Foppen R., Beemster N., Castelijns H., Groot H., Meijer R. & Strucker R. 1995. Spectaculaire opleving van Blauwborst *Luscinia svecica cyanecula* als broedvogel in Nederland. *Limosa* 68: 147-158.

Lourenço P.M. & Piersma T. 2009. Waterbird densities in South European rice fields as a function of rice management. *Ibis* 151: 196-199.

Mead C.J. & Pearson D.J. 1974. Bearded Reedling populations in England and Holland. *Bird Study* 21: 211-214.

Meininger P.L. 1984. Bruine Kiekendief *Circus aeruginosus* als broedvogel in het Deltagebied in 1979-82. *Limosa* 57: 81-86.

Meijer R. & Van der Nat J. 1989. De Witgesterde Blauwborst *Luscinia svecica cyanecula* gered door de Biesbosch? *Limosa* 62: 67-74.

Musgrove A.J. 2002. The non-breeding status of the Little Egret in Britain. *British Birds* 95: 62-80.

Neto J.M. 2006. Nest-site selection and predation in Savi's Warblers *Locustella luscinioides*. *Bird Study* 53: 171-176.

Newton I., Wyllie I. & Asher A. 1994. Pollutants in Great Britain. *British Birds* 87: 22-25.

Ouweneel G.L. 1978. Het voorkomen van de Bruine Kiekendief *Circus aeruginosus* in het Hollandsch Diep-Haringvlietgebied. *Limosa* 51: 81-87.

Overdijk O. 1999. De ontwikkeling van het aantal broedparen van de Lepelaar *Platalea leucorodia* in Nederland in de periode 1994-1998. *Limosa* 72: 41-48.

Overdijk O. & Horn H. 2005. Broedende Lepelaars in Nederland in 1999-2004. *Limosa* 78: 97-102.

Pannekoek J. & Van Strien A.J. 2005. TRIM 3 Manual (TRends & Indices for Monitoring Data). Statitics Netherlands, Voorburg.

Peach W., Baillie S. & Underhill L. 1991. Survival of British Sedge Warblers *Acrocephalus schoenobaenus* in relation to west African rainfall. *Ibis* 133: 300-305.

Peach W.J., Siriwardena G.M. & Gregory R.D. 1999. Long-term changes in over-winter survival rates explain the decline of Reed Bunting *Emberiza schoeniclus* in Britain. *Journal of Applied Ecology* 36: 798-811.

Poulin B., Lefebvre G. & Mauchamp A. 2002. Habitat requirements of passerines and reedbed management in southern France. *Biological Conservation* 107: 315-325.

Ruiters P.S., Noordhuis R. & Van de Berg M.S. 1994. Kranswieren verklaren aantalsfluctuaties van Krooneenden *Netta rufina* in Nederland. *Limosa* 67: 147-158.

Smith K.W. & Tyler G.A. 1993. Trends in the numbers of breeding Bitterns in the UK. In: Andrews J. & Carter S. (eds.) Britain's Birds in 1990-91: the conservation and monitoring review: 139-140. BTO & JNCC, Thetford & Peterborough.

SOVON 1987. Atlas van de Nederlandse Vogels. SOVON, Arnhem.

SOVON 1988. Nieuwe aantalsschattingen van Nederlandse broedvogels. *Limosa* 61: 151-162.

SOVON 2002. Atlas van de Nederlandse Broedvogels 1998-2000. (Nederlandse Fauna 5). Nationaal Natuurhistorisch Museum Leiden, KNNV Uitgeverij & European Invertebrate Survey-Nederland, Leiden.

SOVON & CBS 2005. Trends van vogels in het Nederlandse Natura 2000 netwerk. SOVON-informatierapport 2005/09. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Teixeira R.M. 1979. Atlas van de Nederlandse broedvogels. Natuurmonumenten, 's-Graveland.

Ter Braak C.J.F., Van Strien A.J., Meijer R. & Verstrael T.J. 1994. Analysis of monitoring data with many missing values: which method? In: Hagemeijer W. and Verstrael T. (eds). Bird Numbers 1992. Distribution, Monitoring and Ecological aspects: 663-673. Proc. 12th Int. Conf. of IBCC and EOAC . Statistics Netherlands, Voorburg & SOVON, Beek-Ubbergen.

Tourenq C., Bennetts R.E., Kowalski H., Vialet E., Lucchesi J.L., Kayser Y. & Isenmann P. 2001. Are ricefields a good alternative to natural marshes for waterbird communities in the Camargue, southern France? *Biological Conservation* 100: 335-343.

Tourenq C., Sadoul N., Beck N., Mesleard F. & Martin J.L. 2003. Effects of cropping practices on the use of rice fields by waterbirds in the Camargue, France. *Agriculture, Ecosystems & Environment* 95: 543-549.

Tucker G.M. & Evans M.I. 1997. Habitats for birds in Europe: a conservation strategy for the wider environment. BirdLife Conservation Series no. 6. BirdLife International, Cambridge.

Van den Berg M., Craane L.H.J., Van Mourik S. & Brouwer A. 1995. The (possible) impact of chlorinated dioxins (pcdds), dibenzofurans (pcdfs) and biphenyls (pcbs) on the reproduction of the Cormorant *Phalacrocorax carbo* – an ecotoxicological approach. *Ardea* 83: 299-314.

Van den Bergh L.M.J. 1991a. De Grauwe Gans als broedvogel in Nederland. RIN-rapport 91/1. Arnhem.

Van den Bergh L.M.J. 1991b. Hoeveel Grauwe Ganzen broeden er in Nederland? *Vogeljaar* 39: 117-120.

Van der Hut R.M.G. 1983. De Snor *Locustella luscinioides*. In: Zaanse Vogels. Vogelbeschermingswacht Zaanstreek.

Van der Hut R. 1986. Habitat choice and temporal differentiation in reed passerines of a Dutch marsh. *Ardea* 74: 159-176.

Van der Hut R.M.G. 1992. Biologie en bescherming van de Lepelaar *Platalea leucorodia*. Aanzet tot het beschermingsplan. Technisch rapport 6. Vogelbescherming, Zeist.

Van der Jeugd H.P., Voslamber B, Van Turnhout C., Sierdsema H., Feige N. & Koffijberg K. 2006. Overzomerende ganzen in Nederland: grenzen aan de groei? SOVON-onderzoeksrapport 2006/02. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van der Kooij H. 1991. Het broedseizoen 1990 van de Purperreiger in Nederland: een dieptepunt! *Vogeljaar* 39: 251-255.

Van der Kooij H. 1995. Werkt de vos *Vulpes vulpes* de Purperreiger *Ardea purpurea* in de nesten? *Limosa* 68: 137-142.

Van der Kooij H. 1996. Het broedseizoen 1995 van de Purperreiger in Nederland. *Vogeljaar* 44: 179-181.

Van der Kooij H. 2005. De broedseizoenen 2003 en 2004 van de Purperreiger in Nederland. *Vogeljaar* 53: 151-156.

Van der Kooij H. & Voslamber B. 1997. Aantalsontwikkeling van de Grote Zilverreiger *Egretta alba* in Nederland sinds 1970 in een Europees perspectief. *Limosa* 70: 119-125.

Van der Winden J. 2002. Disturbance as an important factor in the decline of Black Terns *Chlidonias niger* in the Netherlands. *Vogelwelt* 123: 33-40.

Van der Winden J., Hagemeijer W., Hustings F. & Noordhuis R. 1994. Hoe vergaat het de Krooneend *Netta rufina* in Nederland? *Limosa* 67: 137-145.

Van der Winden J., Hagemeijer W. & Terlouw R. 1996. Heeft de Zwarte Stern *Chlidonias niger* een toekomst als broedvogel in Nederland? *Limosa* 69: 149-164.

Van der Winden J., Bonhof G., Bak A. & van Horssen P.W. 2001. Leefgebieden van moerasvogels in agrarisch gebied. Ligging en kwaliteit van foerageergebieden van Lepelaar, Purperreiger en Zwarte Stern. Bureau Waardenburg rapport 03-055, Culemborg.

Van der Winden J., Beintema A.J. & Heemskerk L. 2004. Habitat-related Black Tern *Chlidonias niger* breeding success in the Netherlands. *Ardea* 92: 53-61.

Van der Winden J. & Dirksen S. 2005. De Krooneend: exoot of gewoon exotisch mooi? *Limosa* 78: 139-144.

Van Dobben W.H. 1995. De Oostvaardersplassen: de voorgeschiedenis van een vogelparadijs. *Limosa* 68: 169-172.

Van Dijk A.J. 2004. Handleiding Broedvogel Monitoring Project. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Dijk A.J., Hustings F. & Van der Weide M. 2004. Handleiding Landelijk Soortonderzoek Broedvogels. SOVON Vogelonderzoek Nederland,, Beek-Ubbergen.

Van Eerden M.R. & Gregersen J. 1995. Long-term changes in the Northwest European population of Cormorants *Phalacrocorax carbo sinensis*. *Ardea* 83: 61-79.

Van Eerden M.R. & Zijlstra M. 1995. Recent crash of the IJsselmeer population of Great Cormorants *Phalacrocorax carbo sinensis* in the Netherlands. *Cormorant Research Group Bulletin* 1: 27-32.

Van Eerden M.R., Koffijberg K. & Platteeuw M. 1995. Riding on the crest of the wave: possibilities and limitations for a thriving population of migratory Cormorants *Phalacrocorax carbo* in man-dominated wetlands. *Ardea* 83: 1-10.

Van Eerden M.R., Lenselink G. & Zijlstra M. 1998. Long-term changes in wetland area and composition in the Netherlands affecting the carrying capacity for wintering water birds. In: Van Eerden M.R. 1998. Patchwork. Patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands: 31-56. Dissertation, Rijksuniversiteit Groningen, Groningen.

Van Turnhout C., Van Dijk A., Van der Weide M. & Van Beusekom R. 2006. Roepende Roerdompen in Nederland: trefkansen, trends en aantallen. *Limosa* 79: 1-12.

Van Turnhout C.A.M., Foppen R.P.B., Leuven R.S.E.W., Siepel H. & Esselink H. 2007. Scale-dependent homogenization: Changes in breeding bird diversity in the Netherlands over a 25-year period. *Biological Conservation* 134: 505-516.

Van Turnhout C., Willems F., Plate C., Van Strien A., Teunissen W., Van Dijk A. & Foppen R. 2008. Monitoring common and scarce breeding birds in the Netherlands: applying a post-hoc stratification and weighting procedure to obtain less biased population trends. *Revista Catalana d'Ornitologia* 24: 15-29.

Veldkamp R. 1986. Neergang en herstel van de Aalscholver *Phalacrocorax carbo* in NW-Overijssel. *Limosa* 59: 163-168.

Vogt D. 1994. Roofvogels in de Nederlandse wetlands: II. De bruine kiekendief; demografie en terreingebruik. Intern rapport. Directoraat-Generaal Rijkswaterstaat, Directie Flevoland. Lelystad.

Voisin C., Godin J. & Fleury A. 2005. Status and behaviour of Little Egrets wintering in western France. *British Birds* 98: 468-475.

Voslamber B. 1994. De ontwikkeling van de broedvogelaantallen van de Lepelaar *Platalea leucorodia* in Nederland in de periode 1961-93. *Limosa* 67: 89-94.

Voslamber B., Van der Jeugd H. & Koffijberg K. 2007. Aantallen, trends en verspreiding van overzomerende ganzen in Nederland. *Limosa* 80: 1-17.

Wintermans G. & Wymenga E. 1996. Voedsel voor Lepelaars. Knelpunten, oplossingsrichtingen en aanbevelingen voor de inrichting en het beheer van voedselgebieden voor Lepelaars. A&W-rapport 124. Veenwouden.

Zijlstra M. 1983. Kiekendieven in Flevoland: oecologische beschouwingen rond roofvogels in een veranderende habitat. *Limosa* 56: 70-71.

Zijlstra M. & Hustings F. 1992. Teloorgang van de Grauwe Kiekendief *Circus pygargus* als broedvogel in Nederland. *Limosa* 65: 7-18.

Zwarts L., Bijlsma R.G., Van der Kamp J. & Wymenga E. 2009. Living on the edge: Wetlands and birds in a changing Sahel. KNNV Publishing, Zeist.

Chapter 4

Scale-dependent homogenization: changes in breeding bird diversity in the Netherlands over a 25-year period

Chris van Turnhout, Ruud Foppen, Rob Leuven, Henk Siepel and Hans Esselink

Published in 2007 in Biological Conservation 134: 505-516

Abstract

Changes in breeding bird diversity in the Netherlands between 1973-1977 and 1998-2000 were evaluated by testing three hypotheses related to the loss of biodiversity: (1) species diversity is declining, (2) biotic homogenization is increasing and (3) rare species are declining more severely than abundant species. Using data collected for two successive national breeding bird atlases, changes in diversity were assessed at different spatial scales (local, regional and national) and among species characteristic for different landscapes (farmland, woodland, heathland, wetland, coastal habitats and urban habitats). National species richness, diversity and equitability had increased between the two atlas periods, with more species increasing than decreasing in range and abundance. Most species in the large groups of woodland and wetland birds showed positive trends, whereas most in the smaller groups of heathland, reed-breeding and meadow birds showed negative trends. However, findings varied between regions and localities. Increases in species richness occurred mainly in regions in the low-lying, western part of the country which were previously relatively poor in species. By contrast, species richness decreased in some previously species-rich regions in the eastern part of the country. This has resulted in a homogenization of breeding bird communities between regions. We advocate the conservation and restoration of regional identity as a priority for landscape planning in the Netherlands. We did not find a clear relation between species abundance and trends, although both rare and very abundant species tended to decrease on average.

Introduction

There is broad consensus that global biodiversity is declining more rapidly now than at any time in human history (Millennium Ecosystem Assessment 2005). Large, diverse, well-known, easily identified and easily censused groups such as birds show these trends particularly clearly. Deteriorations have occurred in all major biogeographic regions and ecosystems (Butchart *et al.* 2004). In Europe, farmland birds have declined particularly strongly over the last two decades (Siriwardena *et al.* 1998, Gregory *et al.* 2005). The Netherlands, being one of the most densely populated countries in the world and with 24% of its surface area below sea level, has a highly anthropogenic landscape. Heywood (1995) used the Netherlands as an example to illustrate his claim that the smaller the area and the more radical the environmental change, the higher the rate of local loss of populations of species. Human pressure on Dutch ecosystems is indeed high, and habitat loss, eutrophication, acidification, drainage, habitat fragmentation and disturbance have probably combined to impact substantially on plant and animal species in recent decades (Schekkerman *et al.* 1994, Graveland & Van der Wal 1996, Reijnen *et al.* 1997, Graveland 1998, Van Tol *et al.* 1998, Foppen *et al.* 1999).

Against this background, we describe the changes in the Dutch breeding bird community between the 1973-1977 and 1998-2000 periods. Data were collected for the first and second editions of the Atlas of Breeding Birds in the Netherlands (Teixeira 1979, SOVON 2002). These atlases are among the few European data sets that provide information at national scale about trends in abundance and distribution of all coexisting breeding bird species in the medium term. We evaluated the changes in Dutch avian diversity by testing three hypotheses related to the loss of biodiversity world-wide.

(1) Species richness and diversity are declining (e.g. Millennium Ecosystem Assessment 2005). Because species diversity seems to be changing in fundamentally different ways at different spatial scales (Sax & Gaines 2003), we assessed the changes in breeding bird richness and diversity in a largely anthropogenic country at national, regional and local scales. We also differentiated between landscape types. Since habitat loss and degradation are important factors causing loss of biodiversity, the magnitude of population changes may differ between species characteristic for different landscapes (Gibbons *et al.* 1993, Bohning-Gaese & Bauer 1996, Gregory *et al.* 2005).

(2) Biotic homogenization is increasing (e.g. Lockwood *et al.* 2000, Olden & Poff 2003). Although usually referred to as the replacement of local taxa with non-native species, often introduced by humans, biotic homogenization need not involve either species invasion or extinction (Olden & Poff 2004, Olden *et al.* 2006). It generally occurs when an environmental change promotes the geographic expansion of some species and the geographic reduction of others (McKinney & Lockwood 1999). It results in ecosystems being simplified and similarity between regions being increased (Fisher & Owens 2004, Schwartz *et al.* 2006). The magnitude and spatial extent of biotic homogenization for different taxonomic groups remain largely unknown, however, due to a lack of attempts at empirical quantification (Olden *et al.* 2006). We assessed changes in similarity between regional breeding bird communities, excluding introduced non-native species.

Although this has been studied at relatively small spatial scales, such studies have involved mainly urban areas (Clergeau *et al.* 2006, Kühn & Klotz 2006, McKinney 2006, Pauchard *et al.* 2006).

(3) Species that occur at low abundance are more negatively affected by environmental change than abundant species (e.g. McKinney & Lockwood 1999, Gaston & Blackburn 2002, Fisher & Owens 2004). Metapopulation ecology principles imply that small populations are particularly prone to chance extinction from demographic accidents and localized threats (Brown 1995). We examined the relation between population size and population trend for all Dutch breeding birds.

Materials and methods

Distribution data

The breeding bird atlas data were collected in the 1973-1977 period (Teixeira 1979) and the 1998-2000 period (SOVON 2002). More than 4,000 volunteer observers were involved, organized at regional level by local coordinators and supervised by a national coordinator and professional staff at the SOVON Dutch Centre for Field Ornithology. Fieldwork for both atlases was based on the Dutch national grid consisting of 1,674 5×5 km squares (referred to as atlas squares), covering an area of 41,500 km^2 and an altitudinal range from –7 m below to 321 m above sea level. The Netherlands is situated in the deltas of the large rivers Rhine, Meuse, Scheldt and Ems, and has been almost completely cultivated: 70% of the country consists of farmland, 16% of urban environments, leaving only 14% for semi-natural habitats such as woodland and heathland (both mainly in the eastern part of the country), marshland and coastal dunes (both mainly in the western part) (statline.cbs.nl).

Fieldwork guidelines were similar for the two census periods. Observers were requested to compile a list of all breeding bird species present in their atlas square, including a classification of breeding status according to international atlas codes (possible, probable or confirmed breeding) (Hagemeijer & Blair 1997). All atlas squares were surveyed during one breeding season in both census periods, but additional records from other years within the census period were included. All habitat types present within each atlas square had to be visited at least four times at regular intervals between March and June, in the early morning and during favourable weather conditions. Additional visits in February and July were carried out for some early and late breeding species. Additional evening and night visits were carried out to record species active at night, such as owls and rails. No further standardization of field work effort was attempted, mainly because the time needed to compile complete species lists for a given atlas square depends strongly on the type and number of habitats present and the quality of the observer. Instead, we assessed the completeness of coverage for all atlas squares afterwards, using a multiple loglinear Poisson regression model (McCullagh & Nelder 1989). The number of breeding bird species expected to be present per atlas square was assumed to depend on the total area of each atlas square (which is not always 25 km^2 in squares along the borders and coast), the region (using the 18 breeding bird districts distinguished by Kwak *et al.* 1988) and the area of each of the following habitat types per atlas square: deciduous woodland, coniferous woodland, arable land, grassland, coastal dune, heathland, saltmarsh, marshland and built-up areas, and the length of shorelines. All these explanatory factors and variables proved significant in the regression model ($p<0.05$). In addition, five significant interaction terms were included in the model. All atlas squares for which the standardized residuals of the regression were smaller than –2 were regarded as outliers with insufficient coverage (Oude Voshaar 1995), unless the expected number of breeding species was unrealistic due to atypical habitat. Four atlas squares were covered insufficiently in both census periods, 32 in the 1998-2000 period and 160 in the 1973-1977 period. These atlas squares were omitted from all further analyses (SOVON 2002).

Abundance data

Data from the atlas fieldwork were combined with data from the national monitoring scheme for breeding birds (Van Dijk *et al.* 2005) to allow estimates of the national breeding populations of all breeding bird species. Population estimates for the 1973-1977 period have been given by Teixeira (1979), 61 of which were corrected by SOVON (1988). The estimates were obtained using various methods, ranging from complete counts of the national population to extrapolation of regional and habitat-specific density data. Population estimates for the 1998-2000 period have been provided by SOVON (2002). These were also based on different methods, depending on the rarity of individual species. For 115 rare and colonial breeding species, estimates could be directly derived from the national monitoring scheme, as their populations are counted (almost) completely each year. For 65 scarce breeding birds, observers estimated the number of breeding pairs for each atlas square, using six categories (1-3; 4-10; 11-25; 26-100; 101-500; >500). The geometrical mean of each category was multiplied by the number of atlas squares within each category, using only atlas squares with probable or confirmed breeding records. The population was then estimated by adding up these totals. For 56 common and abundant breeding birds, density data from the national monitoring scheme were extrapolated, using atlas data as a correction factor for oversampling and undersampling of certain habitats and regions (SOVON 2002).

Classification of regions and species

Changes in regional species richness and similarity were assessed using the classification of *physio-geographic regions*, which is based on main soil type, main landscape characteristics and location (adapted from Bal *et al.* 1995). This classification, consisting of 18 regions, is independent of bird distribution. Eleven regions are situated in the low-lying, western part of the country. Apart from the two coastal dune regions, they all consist of flat open landscapes (farmland, marshland or saltmarsh) on clay or peat soils. Seven regions are situated in the higher, eastern part of the country. They consist of enclosed landscapes (mainly farmland or wood- and heathland) on sand or loess soils. See Table 1 for further details of the 18 regions.

Changes in the abundance and distribution of groups of species according to breeding habitat were assessed by means of the classification developed by Van Dijk *et al.* (2005). Using bird data, literature data and expert judgement, they categorized bird species into one of six landscape types: farmland (arable land, grassland, hedgerows;

Table 1. Characteristics of the 18 physio-geographic regions in the Netherlands.

Region code	Main soil type	Location	Main landscape features
Low-lying, western part of the Netherlands (Holocene)			
A	non-calcareous sand	north	coastal dunes
B	calcareous sand	southwest	coastal dunes
C	sea clay	north	(salt)marsh (outside dikes)
D	sea clay	southwest	(salt)marsh (outside dikes)
E	peat	north	marshland and grassland (open)
F	peat	west	marshland and grassland (open)
G	river clay	central	grassland and marshland
H	sea clay	north	arable land (open)
I	sea clay	northwest	arable land (open)
J	sea clay	central	arable land (open) and marshland
K	sea clay	southwest	arable land (open)
Higher, eastern part of the Netherlands (Pleistocene)			
L	sand	north	grassland and arable land (enclosed)
M	sand	east/central	grassland and arable land (enclosed)
N	sand	south	grassland and arable land (enclosed)
O	sand	north	forest and heathland
P	sand	east/central	forest and heathland
R	sand	south	forest and heathland
S	loess	southeast	arable land and forest

32 species), woodland (deciduous, coniferous and mixed forest; 33 species), heathland (dry and wet heathland, bog and inland drift sands; 10 species), wetland (open water, freshwater marsh; 37 species), coastal habitats (dune, beach, saltmarsh; 19 species) and urban habitats (city, suburbs, industrial zones, parks, farm houses; 8 species). We added meadow birds as a separate subgroup of farmland birds (11 species) and reed-breeding species as a separate subgroup of wetland birds (8 species), because both of these groups contain many species for which the Netherlands houses important populations in the Northwest-European context (BirdLife International 2004). Species were assigned only if the national population at the end of the 20th century was confined (exclusively or to a large extent) to only one of these landscape types. Consequently, generalist species were not assigned.

Assessing community attributes and trends

Species richness was computed by adding up the total number of breeding bird species with probable or confirmed breeding records. Introduced species (non-native species that were transported outside their native range by humans and subsequently released or escaped; Sol *et al.* 2005) were excluded from all analyses; the number of species introduced in the Netherlands is presented separately. Species richness was assessed at national and regional scales, and per atlas square (local scale). At local scale, atlas squares smaller than 250 hectares (i.e. squares largely lying on Belgian or German territory or consisting largely of sea) were excluded. Species diversity and community evenness were calculated at national scale only. As a measure of community evenness, we used the Shannon equitability index $J = -[\text{sum } p_i \times \ln(p_i)] / \ln S$, where p_i is the proportional abundance of species i and S is the number of species with probable or confirmed breeding records. This index describes the relative abundance of species within a community. As a measure of species diversity we used the Shannon diversity index $H = J \times \ln S$, which combines species richness and community evenness measures (Ludwig & Reynolds 1988).

To calculate changes in the number of species and in distribution and abundance for groups of species according to breeding habitat or rarity, we defined change as [status in 1998-2000 – status in 1973-1977] / [(status in 1973-1977 + status in 1998-2000) / 2], in which status is either number of species, range size (fraction of atlas squares occupied) or population estimate. This formula makes increases and decreases symmetrical, the maximum decline, i.e. extinction, being –2, and the maximum increase, i.e. colonization, being +2 (Bohning-Gaese & Bauer 1996). Four species for which population estimates were insufficiently accurate due to counting problems were omitted from the analyses.

To assess changes in the similarity of regional breeding bird communities we used the Bray-Curtis similarity index (Pielou 1984), using the fraction of occupied atlas squares per species per region as input for the calculations. For all pairs of regions (n=153) we computed separate similarity indexes for the 1973-1977 and 1998-2000 periods, and then computed the percentage change in similarity between the census periods. To assess the sensitivity of the method to the occurrence of rare species, we repeated the analysis omitting all 92 species with a national range size <10% in either 1973-1977 or 1998-2000. This yielded no significantly different results. Using the same data, we performed a Principal Components Analysis to visualize similarities or changes in similarities between regional breeding bird communities (Pielou 1984).

Results

Species richness and diversity

At national scale, the number of breeding bird species increased by 31 between the 1973-1977 and 1998-2000 periods, 17 of which were introduced (Table 2). Twenty-seven introduced species now breed in the Netherlands, of which at least six have spread beyond their release area and have succeeded in establishing viable populations. Egyptian Goose *Alopochen aegyptiacus* and Greater Canada Goose *Branta canadensis* are

Table 2. Species richness, diversity and equitability of breeding birds in the Netherlands (at national scale) in the periods 1973-1977 and 1998-2000. Diversity and equitability indices were calculated excluding introduced species.

	1973-1977	1998-2000
Number of breeding species, excluding introduced species		
Probably breeding	10	13
Confirmed as breeding	183	194
Total	193	207
Number of introduced species		
Probably breeding	2	6
Confirmed as breeding	8	21
Total	10	27
Shannon diversity index (H)	1.52	1.61
Shannon equitability index (J)	0.68	0.71

the most numerous of the introduced species, with 4,500-5,000 and 1,000-1,400 breeding pairs, respectively, in 1998-2000. Excluding introduced species, species richness increased by 14. Species richness also increased if we leave out a selection of very rare species (less than five breeding pairs), whose occurrence may be influenced by coincidence. Apart from species richness, species equitability and diversity at national scale also increased between the 1973-1977 and 1998-2000 periods (Table 2).

Six species disappeared as probable or confirmed breeding birds between the first and second atlas surveys. However, viable populations of these species had already vanished long before 1973 and/or were only accidental breeding birds in 1973-1977 (e.g. European Golden Plover *Pluvialis apricaria* and Stone-curlew *Burhinus oedicnemus*). Populations of another three species had decreased to less than five breeding pairs in 1998-2000: Cetti's Warbler *Cettia cetti*, Great Grey Shrike *Lanius excubitor* and Ortolan Bunting *Emberiza hortulana*. Other species on the verge of extinction are Little Bittern *Ixobrychus minutus*, Black Grouse *Tetrao tetrix* and Tawny Pipit *Anthus campestris*. Twenty species had appeared or reappeared as new breeding birds in the Netherlands since the first census period, five of which were only accidental breeders in 1998-2000. The other 15 species had expanded their range, without direct human intervention (e.g. Little Egret *Egretta garzetta*, Great Egret *Casmerodius albus* and Common Rosefinch *Carpodacus erythrinus*). Another nine species had expanded their population from less than five breeding pairs in 1973-1977.

Since the 1973-1977 census, more species had increased than decreased in terms of abundance (53% and 40%, respectively; Figure 1a) and distribution (40% and 31%, respectively; Figure 1b). Only 6% of the species showed stable population numbers (change <10%), whereas 30% of the species had remained stable in terms of range size. Sky Lark *Alauda arvensis*, House Sparrow *Passer domesticus*, Tree Sparrow *Passer montanus* and Linnet *Carduelis cannabina* are examples of species showing severe or very severe population declines, but stable range sizes at atlas square scale.

Species richness also increased at regional scale: the mean number of species per region was significantly higher in 1998-2000 (147.0, *SE* 1.98) than in 1973-1977 (141.2, *SE* 2.70) (paired t-test: p<0.001). The total number of species had increased in 15 regions and decreased in three regions (Figure 2). The latter are all situated in eastern part of the country. Regions that were relatively species-poor in 1973-1977 showed a

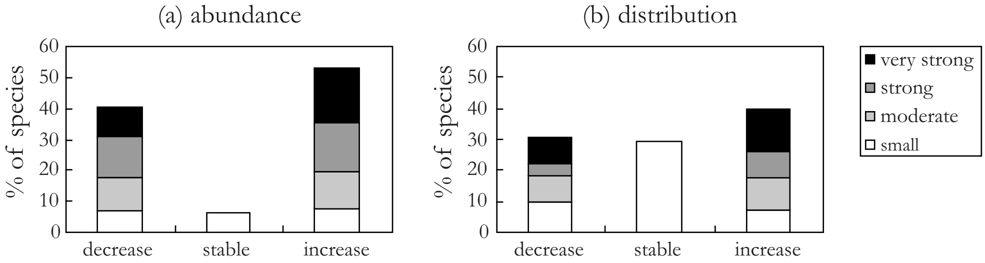


Figure 1. Changes in (a) abundance (population estimates) and (b) distribution (fraction of atlas squares occupied) of breeding birds in the Netherlands between the 1973-1977 and 1998-2000 censuses. The figure shows the percentage of species with decreasing, stable or increasing trends, using the following classes: stable (change <10%), small increase (10-33%) or decrease (10-25%), moderate increase (33-100%) or decrease (25-50%), strong increase (100-400%) or decrease (50-75%) and very strong increase (>400%) or decrease (>75%). Introduced species have been excluded.

greater increase in the total number of species than relatively species-rich regions (linear regression, $R^2=0.19$, $p=0.04$).

At local scale, too, species richness had generally increased over time, the mean number of species per atlas square being significantly higher in 1998-2000 (79.8, *SE* 0.39) than in 1973-1977 (77.2, *SE* 0.41) (paired t-test: $p<0.0001$). However, in comparison with changes at regional scale, the fraction of units with a decrease in species richness tended to be higher: 3 out of 18 regions versus 516 out of 1302 atlas squares (Fisher's Exact test: $p=0.053$). Again, the findings show that the lower the species richness in 1973-1977, the greater its increase since 1973-1977 (Figure 3a; linear regression, $R^2=0.02$, $p<0.001$).

Grouping atlas squares according to region results in the mean number of species per atlas square having significantly increased in eleven regions and significantly decreased in two regions (paired t-tests; $p<0.05$; Figure 3b). In regions that were relatively species-poor in 1973-1977, the increase in mean number of species per atlas square was greater than in relatively species-rich regions (linear regression, $R^2=0.37$, $p<0.01$). Local species richness had increased in all but one of the regions in the western part of the country, whereas it had remained stable or even decreased in all but one of the regions in the eastern part of the country.

Breeding birds that are characteristic of woodland habitats showed a significant average increase in both abundance and distribution between the 1973-1977 and 1998-2000 censuses (Wilcoxon test: $p=0.02$ and $p=0.01$, respectively), whereas heathland species had significantly declined in terms of distribution (Wilcoxon test: $p=0.05$) (Figure 4). Mean changes in other landscape types were not significant, although wetland species tended, on average, to have increased their abundance

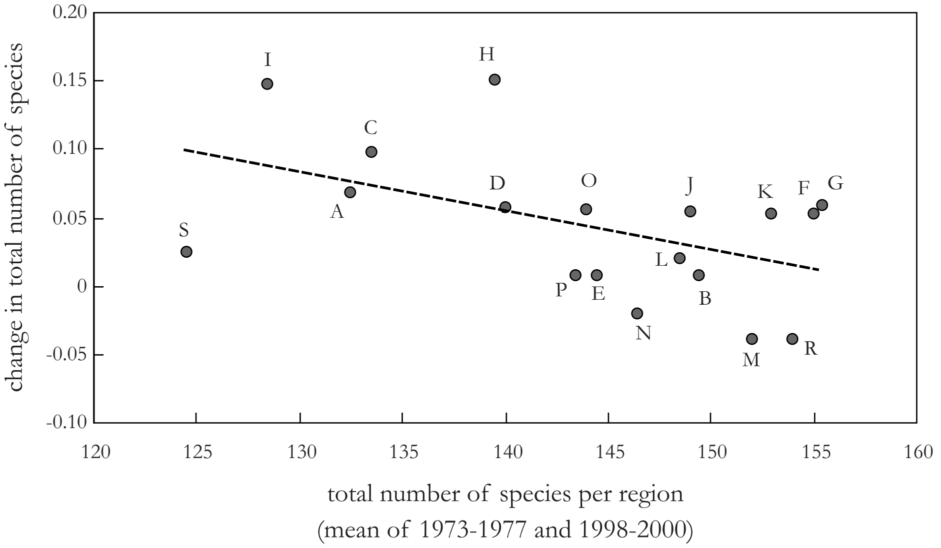


Figure 2. Changes in regional species richness of breeding birds in 18 regions of the Netherlands between the 1973-1977 and 1998-2000 censuses. The figure shows the relative change in the total number of breeding bird species per region, relative to the mean of the number of breeding bird species in 1973-1977 and in 1998-2000. Maximum decline, i.e. extinction of all species, is –2, and maximum increase, i.e. colonization by all species, is +2. Introduced species have been excluded. For an explanation of the region codes, see Table 1. Linear regression, $R^2=0.19$, $p=0.04$.

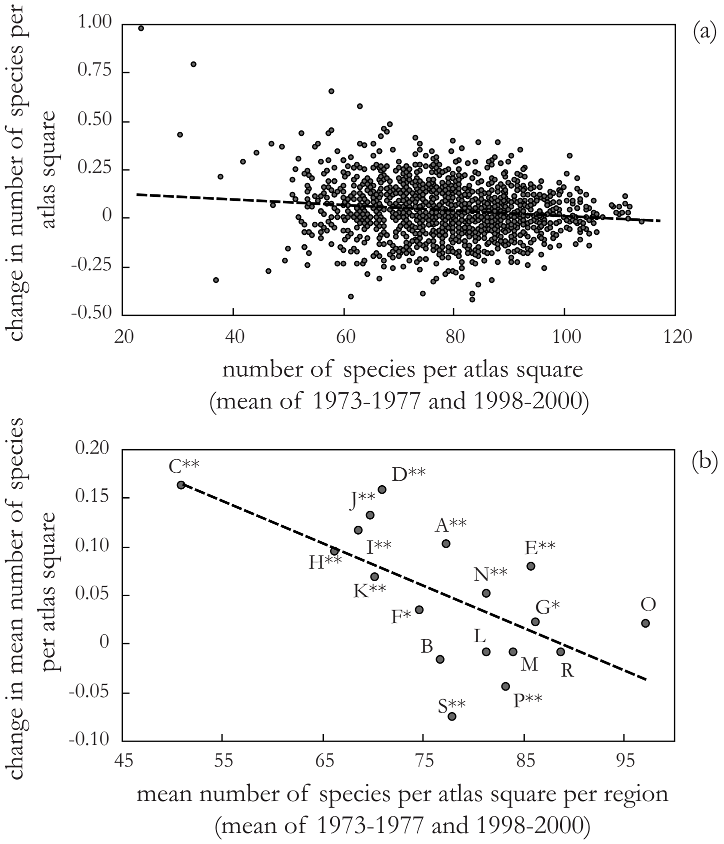


Figure 3. Changes in local species richness of breeding birds in the Netherlands between the 1973-1977 and 1998-2000 censuses. The figure shows the relative change in (a) the number of breeding bird species per atlas square (n=1366) and (b) the mean number of breeding bird species per atlas square per region (n=18), relative to the mean number of breeding bird species in 1973-1977 and in 1998-2000. Maximum decline, i.e. extinction of all species, is –2, and maximum increase, i.e. colonization by all species, is +2. Introduced species have been excluded. For an explanation of the region codes, see Table 1. Asterisks in region codes in (b) refer to significant changes (paired t-test: * is $p<0.05$; ** is $p<0.01$). Linear regression in (a) $R^2=0.02$, $p<0.001$ and (b) $R^2=0.37$, $p<0.01$.

(Wilcoxon test: p=0.13), whereas farmland species tended to have decreased in terms of distribution (Wilcoxon test: p=0.12). Reed-breeding species as a subgroup of wetland birds showed a significant decrease in both abundance and distribution (Wilcoxon test: p=0.05 and p=0.04, respectively), whereas meadow birds as a subgroup of farmland birds showed a significant decline in distribution (Wilcoxon test: p=0.03).

The regions in the eastern part of the Netherlands showed a greater decline in the distribution of meadow birds than regions in the western part (paired Wilcoxon test: p=0.05), whereas the increase in woodland birds was much greater in the west than in the east (paired Wilcoxon test: $p<0.01$). Changes in the distribution of other groups did not significantly differ between the western and eastern parts of the country, although the decline in the distribution of farmland birds tended to be less severe in western regions (paired Wilcoxon test: p=0.13).

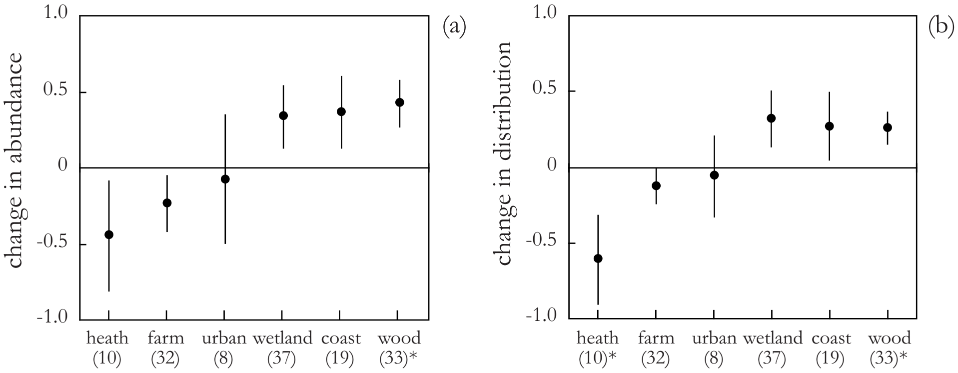


Figure 4. Mean changes (± 1 *SE*) in (a) abundance and (b) distribution between the 1973-1977 and 1998-2000 censuses for groups of breeding bird species that are characteristic of different breeding habitats (heathland, farmland, urban environments, coastal dunes, woodland and wetlands). Maximum decline, i.e. extinction of all species within a group, is –2, and maximum increase, i.e. colonization by all species, is +2. The number of species per habitat is shown in brackets. Asterisks refer to significant changes (Wilcoxon test: p<0.05).

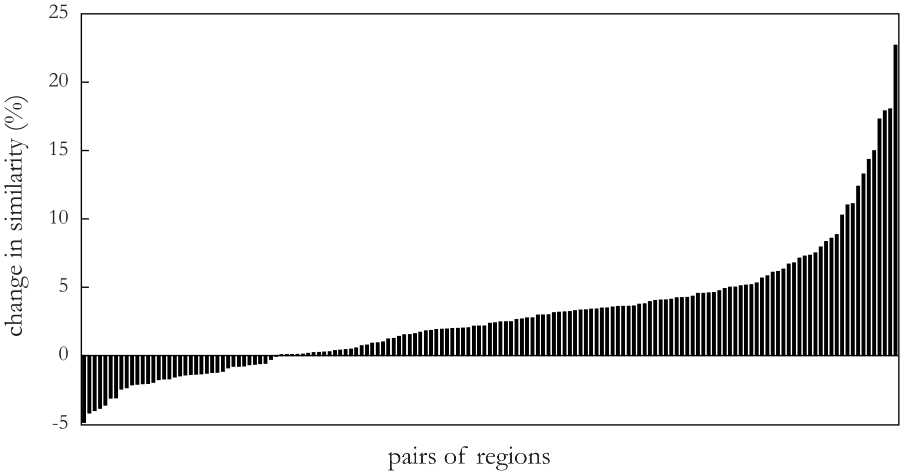


Figure 5. Changes in similarity of breeding bird communities in 18 regions in the Netherlands between the 1973-1977 and 1998-2000 censuses. The figure shows the relative change in similarities between all pairs of regions, ranked by increasing similarity. Negative values indicate a decrease in similarity, positive values an increase. Introduced species have been excluded.

Biotic homogenization

Similarities in breeding bird composition between pairs of regions had generally increased (paired Wilcoxon test: p<0.0001), indicating that breeding bird communities became homogenized between regions between the 1973-1977 and 1998-2000 census periods (Figure 5). The mean change in similarity was 2.84%. Regions in the western part of the country showed an increasing resemblance to those in the east (Figure 6). Furthermore, some regions in the western part of the Netherlands showed an increasing resemblance to other regions in this part of the country, especially D, A and J.

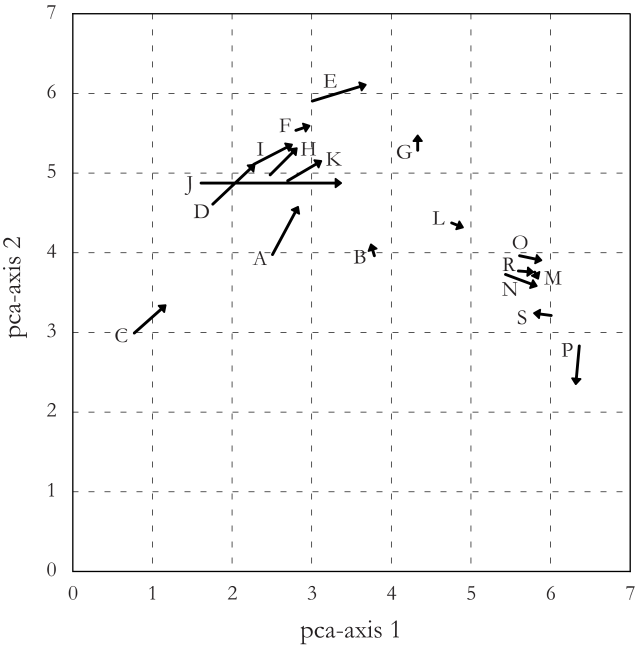


Figure 6. Principal Components Analysis of 18 regional breeding bird communities in the Netherlands. For an explanation of the region codes, see Table 1. Regions in the low-lying, western part of the country are situated in the left part of the figure (pca-axis1 < 4.5), regions in the higher, eastern part of the country in the right part (pca-axis1 > 4.5). Arrows indicate the direction and extent of relative change in breeding bird composition between the 1973-1977 and 1998-2000 censuses. Eigenvalues of PCA axes 1 and 2 are 54.1 and 29.5, respectively. Introduced species have been excluded.

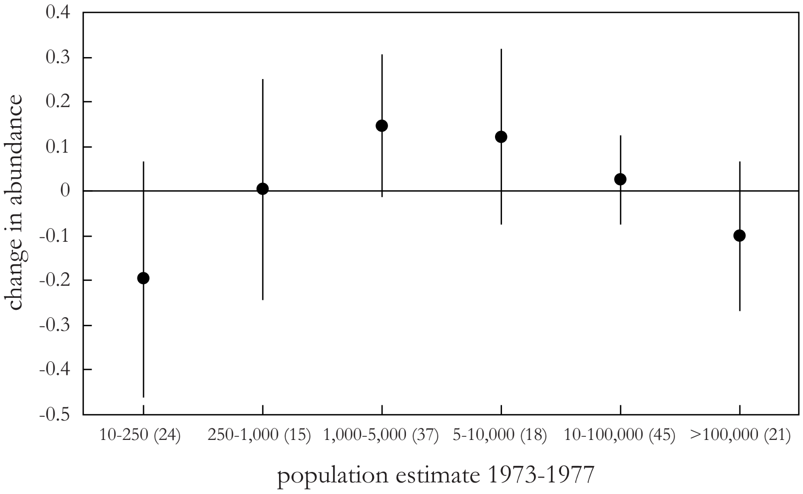


Figure 7. Mean changes (± 1 *SE*) in abundance between the 1973-1977 and 1998-2000 censuses for groups of breeding bird species that differ in rarity (based on population estimates in 1973-1977). Maximum decline, i.e. extinction of all species within a group, is –2, and maximum increase, i.e. colonization by all species, is +2. The number of species per class is shown in brackets.

Differences in trends between rare and abundant species

Both the very rare (<250 breeding pairs) and the very abundant species (>100,000 breeding pairs) tended, on average, to decrease in abundance between the 1973-1977 and 1998-2000 censuses, while the moderately abundant species tended to increase (Figure 7). However, there were large variations in species trends within each class. Consequently, none of the group trends differed significantly from zero (Wilcoxon test: $p>0.05$), and group trends did not differ significantly from each other (ANOVA, $p>0.05$).

Discussion

Sources of bias

Semi-quantitative breeding bird atlases based on the efforts of volunteer observers, such as those used in this study, are a compromise between large spatial scale and data quality. The main factors affecting data quality are variations in the duration of census periods, intensity of coverage and observer quality. The first factor will only be important for a small group of species with large annual fluctuations in distribution at atlas square scale level, such as Common Crossbill *Loxia curvirostra*. The second factor was discussed by Greenwood *et al.* (1997) in relation to the second British breeding bird atlas. They concluded that it is possible to assess changes in distribution on the basis of atlas data, but that this has to be done with care. We expect to have achieved this by removing atlas squares with insufficient coverage from the analyses, and by presenting changes in classes or calculating mean changes for groups of species. The relative imprecision of the method is thus balanced by the ability to calculate average values over a large number of independent samples (both species and atlas squares) for a comparatively extensive area. Furthermore, we assume that differences in intensity of coverage were less important in our study than in the British one, because both observer effort and terrain accessibility are greater in the Dutch situation. Observer quality has been discussed by Bohning-Gaese & Bauer (1996). Although they found a significant effect of observer quality on species richness, it explained only a very small fraction of the variation (3.7%). They found no influence of observer quality on community evenness.

We used different methods to derive national population estimates, which obviously hampers comparability, especially for common species. Again, we converted changes into classes or calculated mean changes for groups of species in order to minimize the effect of methodological differences. More importantly, we validated the changes in abundance using independent data from the national monitoring scheme (Van Dijk *et al.* 2005). For common species, this is based on territory mapping in a sample of an average of 657 study plots per year (*SE* 42.1), which has been done since 1984. For rare and colonial breeding species, the total population is censused almost completely each year. This validation can also evaluate the extent to which only year-to-year population fluctuations were analyzed, because we had only two census periods to establish trends (although they consisted of five and three years, respectively). For 80% of the 157 species with reliable monitoring data, our trend directions (increase, decrease or stable) were identical to the monitoring trends. For the remaining species, most of the differences between trends were probably caused by trend reversals over the 25-year study period, as has been described for Sedge Warbler *Acrocephalus schoenobaenus* (Foppen *et al.* 1999). Populations of a number of forest passerines in particular have recently declined or stabilized, after a period of steady increase. This was also observed in the United Kingdom (Fuller *et al.* 2005).

Increases in species richness and diversity

Even within the relatively short period of 25 years, the Dutch breeding bird community appears highly dynamic, and there is only a very small fraction of populations that did not show clear trends in abundance between the 1973-1977 and 1998-2000 censuses. The results also show that overall richness, diversity and equitability of breeding bird species in the Netherlands have increased since the mid seventies. More species have increased than decreased in terms of range and abundance. This trend is not specific for the study period, but also holds for the longer term. In an evaluation of a large number of historical sources, Parlevliet (2003) concluded that the number of breeding birds in the Netherlands was larger at the end of the 20th century than at the beginning of that century, and that the number of species that had increased in abundance since 1900 was larger than the number of species that had decreased. At global scale, most studies of birds and other taxa have shown a decrease in species diversity in recent decades (e.g. McKinney & Lockwood 1999, Butchart *et al.* 2004, Millennium Ecosystem Assessment 2005). At regional scale (i.e. areas that are intermediate in size between the entire globe and small study plots of less than a few dozen hectares), however, diversity appears to be increasing for many taxonomic groups, though remaining relatively unchanged for others, such as birds in most studies (Sax & Gaines 2003). Julliard *et al.* (2004) even found that populations of common breeding birds had tended to decrease in France between 1989 and 2001. These observations on avian diversity contradict our results, which demonstrate that bird diversity may also increase at regional scales.

Starting from the dynamic equilibrium model, which states that species diversity will respond unimodally to both energy availability and disturbance rate (Huston 1994, Kondoh 2001), and given the highly anthropogenic Dutch landscape where ecosystems have long been experiencing very strong human pressure, we expected that breeding bird diversity in the Netherlands would be declining. Apparently, this is not (or at least not yet) the case at national level, although it may be true for some of the eastern regions of the country.

Differences between landscapes

A variety of causes could underlie the observed net increase in avian diversity, including changes in the area and quality of habitats (Bohning-Gaese & Bauer 1996, Butchart *et al.* 2004). Positive trends in woodland and, to a lesser extent, wetland species suggest beneficial changes in these landscapes since the mid 1970s. Indeed, the total forest area in the Netherlands expanded by 29% between 1964-1968 and 2000 (www.natuurcompendium.nl). Simultaneously, existing forests have matured, especially in the eastern part of the country, where most plantations originated in the first part of the 20th century. As a result, forests became more attractive for hole-nesting breeding birds and raptors. This was probably enhanced by changes in forest management, such as less intensive exploitation, conversion of coniferous into deciduous forest, selective cutting of introduced tree species and greater tolerance of dead timber (Van Beusekom *et al.* 2005). Furthermore, reductions in the use of DDT and other organochlorine pesticides from around 1970 have allowed the recovery and resettlement of raptor species and other top-predators (Lensink 1997). By contrast, populations of forest birds around Lake Constance in Central Europe remained stable between 1980-81 and 1990-92 (Bohning-Gaese & Bauer 1996) and those in France even decreased between 1989 and 2001 (Julliard *et al.* 2004). A number of wetland species probably benefited from legal protection, reduction of water pollution, larger fish populations, increased plant food quality and vegetation succession (Van Eerden & Gregersen 1995, Van Eerden 1997, Van Turnhout & Hagemeijer 1999). Furthermore, ecological rehabilitation of wet habitats had positive effects on wetland species, especially in the floodplains of the Dutch river district (Leuven *et al.* 2004).

Average positive trends in the relatively large groups of woodland and wetland species are apparently not balanced by average negative trends for typical species of other breeding habitats and more generalist species. Only the small groups of typical heathland species, reed-breeding species and meadow birds had significantly declined. For heathland species, this is probably caused by the detrimental effects of eutrophication, acidification and desiccation, such as encroachment by nitrophilic grasses (Roelofs *et al.* 1996). This may have led to a decrease in arthropod abundance and thus in food availability for insectivorous heathland species (Van Turnhout 2005). Heathland management seems not yet to have succeeded in halting the decline of these species. For meadow birds and a number of other farmland species, the causes of decline are thought to be related to a multitude of changes, all linked to the intensification of agricultural practice across Europe (Newton 2004, Gregory *et al.* 2005). Conversion of pastures into arable land, drainage, earlier and more frequent mowing, increased cattle density and larger input of inorganic fertilizers have reduced nesting and feeding opportunities and breeding success in meadow birds, whereas agri-environment schemes have not yet resulted in favourable effects for these species (Kleijn *et al.* 2001). Reed-breeding species have suffered major declines, which are thought to be mainly caused by the cultivation of embankments, eutrophication, loss of water table dynamics, heavy exploitation of reed beds and habitat fragmentation (Foppen *et al.* 1999, Van Turnhout & Hagemeijer 1999).

Conservation efforts should therefore, more than ever, focus on farmland, reed-breeding and heathland birds. That this may be successful is demonstrated by the large population increases in some farmland species (e.g. White Stork *Ciconia ciconia*, Barn Owl *Tyto alba* and Rook *Corvus frugilegus*), which have benefited from species-specific conservation measures (SOVON 2002). However, a conservation approach focused on improvement of habitat quality will be successful for a much broader set of species (Tucker & Evans 1997). Further research should clarify and assess the relative importance of each of the possible causes underlying the decline of the species involved. We will focus our future research on the relation between species trends and ecological and life-history traits, thereby evaluating to what extent changes in taxonomic diversity correspond to changes in functional diversity (Davies *et al.* 2000, Ballard *et al.* 2003, Julliard *et al.* 2004).

Biotic homogenization

Our results show that within the Netherlands, there is a large variation in regional and especially local species richness that underlies the general pattern of increase. This suggests that using simple national measures of diversity could conceal differentiated environmental processes at smaller spatial scales, which may be important from a conservation point of view. In this study we found that increases in species richness occurred mainly in regions that were relatively species-poor in 1973-1977, and are concentrated in the low-lying, western part of the country. Species richness even decreased in some previously species-rich regions in the eastern part of the country. This is not caused by random behaviour of changes (large numbers tend to become smaller while small numbers tend to become larger), because the set of species is not fixed over time (due to colonization and extinction at different spatial scales). More importantly, the species composition in an atlas square is not a result of random sampling, but is largely dependent on atlas square characteristics, such as landscape type, or changes in these characteristics. A homogenization of breeding bird communities between regions has therefore occurred, with regions losing their distinctive character.

Biotic homogenization has also been demonstrated for other taxa, but generally in relation to the invasion of non-native species and for larger spatial scales (McKinney & Lockwood 1999, Rahel 2000, Fisher & Owens 2004, Marchetti *et al.* 2006). We calculated a mean change in similarity between pairs of regions of 2.84%, which is of the same order of magnitude as the long-term increase in similarity of fish faunas between pairs of provinces in Canada and pairs of states in the US (1.3% and 7.2%, respectively, Olden *et al.* 2006). It is difficult, however, to compare quantitative estimates of biotic homogenization, because of differences in the nature of the underlying data and the inclusion or exclusion of non-native species. Efforts to collect and analyse comparable sets of empirical data for different taxonomic groups in different parts of the world and for different spatial scales need to be stepped up to elucidate the ecological mechanisms that best describe patterns of homogenization.

Regionally differentiated trends in especially woodland and farmland species suggest that regions have become more similar in their landscape features. Indeed, the openness of the unique Dutch polder landscape in the western part of the country has decreased as a result of the establishment of roadside plantations, young forestry plantations, parks and urban expansion (www.natuurcompendium.nl). Furthermore, the area of woodland has increased in recently reclaimed areas, marshland habitats and coastal dunes, as a result of natural vegetation succession enhanced by the effects of desiccation and eutrophication (Kooijman *et al.* 1998, SOVON 2002). The total area of woodland in the western part of the country increased by 132% between 1964-1968 and 2000, whereas that in the eastern part only increased by 17% in the same period (www.natuurcompendium.nl). Finally, almost all large estuaries in the Delta region in the south-west of the country have been closed off from the sea by barriers and have lost most of their original tidal dynamics (Schekkerman *et al.* 1994). These processes have been beneficial to birds of scrubs and woodland, but detrimental to the relatively species-poor but very distinctive communities of reed-breeding birds and meadow birds.

Simultaneously, the formerly enclosed farmland landscape in the eastern part of the country has become more open, as a result of the removal of hedgerows and small woodlots. The total length of hedgerows declined by 27% between 1950 and 1990 (www.natuurcompendium.nl). Typical heathland species, which occur only in the eastern part of the Netherlands, have also declined. As a result, regional breeding bird communities have become more similar. Several authors regard urbanization as a major cause of biotic homogenization, for both birds and other taxa (McKinney 2006, Clergeau *et al.* 2006). Nevertheless, Olden *et al.* (2006) were unable to explain between two-thirds and three-quarters of the variation in estimates of faunal and floral homogenization from human population size and urbanization. We argue that afforestation and degradation of several semi-natural habitats are the main factors responsible for regional homogenization of breeding bird communities in the Netherlands. Furthermore, we argue that the conservation and restoration of regional identity should be given greater priority in landscape planning in the Netherlands, because homogenization can be regarded as a major exponent of biodiversity loss (Olden *et al.* 2004). Homogenization of breeding bird composition may also be occurring at Northwest-European scale, given the fact that the declining groups of meadow and reed-breeding birds include many species for which the Netherlands houses disproportionate large populations (BirdLife International 2004).

Trends in relation to species rarity

Finally, we did not find a clear relation between species abundance and trends. By contrast, other studies did conclude that rarity is a trait that promotes extinction, both at global (McKinney & Lockwood 1999, Fisher & Owens 2004) and local scale (Davies *et al.* 2000, Gaston & Blackburn 2002). Although the very rare birds in our study did indeed show an average decrease in the Netherlands between 1973-1977 and 1998-2000, the same was true for the very abundant species, such as House Sparrow *Passer domesticus*, Tree Sparrow *Passer montanus* and Skylark *Alauda arvensis*. Bohning-Gaese & Bauer (1996) also found disproportionate declines in abundant species. This might be explained by the phenomenon that species that have achieved high abundance have an increased chance of subsequently declining when environmental conditions change, because there is an upper limit to their abundance. Consequently, other species may increase and fill the gap left by the formerly highly abundant species. Indeed, the moderately abundant bird species tended to have increased in our study. However, none of the group trends reached statistical significance.

Acknowledgements

This work would not have been possible without the unpaid efforts of thousands of skilled and enthusiastic volunteer bird-watchers, who gathered the field data. Several local co-ordinators and SOVON colleagues were responsible for processing and analysing the data and preparing the publication of two national breeding bird atlases. The preparation of this chapter was a project of the Netherlands Centre for Nature research (NCN), and was financially supported by a WeWi-pool grant by Radboud University. The Faculty of Science (Radboud University) and SOVON co-financed this project. Prof. A.J. Hendriks (Radboud University), Prof. S.J. Ormerod (Cardiff University) and Dr. H.P. van der Jeugd (SOVON / University of Groningen) commented on a draft of this chapter. J. Klerkx gave linguistic comments.

References

Bal D., Beije H.M. Hoogeveen Y.R. Jansen S.R.J. & Van der Reest P.J. 1995. Handboek Natuurdoeltypen in Nederland. IKC-Natuurbeheer, Wageningen.

Ballard G., Geupel G.R., Nur N. & Gandali T. 2003. Long-term declines and decadal patterns in population trends of songbirds in western North America 1979-1999. *Condor* 105: 737-755.

BirdLife International 2004. Birds in Europe: population estimates, trends and conservation status. Cambridge, UK: BirdLife International. (BirdLife Conservation Series No. 12).

Bohning-Gaese K. & Bauer H.G. 1996. Changes in species abundance, distribution, and diversity in a central European bird community. *Conservation Biology* 10: 175-187.

Brown J.H. 1995. Macroecology. The University of Chicago Press.

Butchart S.H.M., Stattersfield A.J., Bennun L.A., Shutes S.M., Akcakaya H.R., Baillie J.E.M., Stuart S.N., Hilton-Taylor C. & Mace G.M. 2004. Measuring global trends in the status of biodiversity: Red list indices for birds. *PLoS Biology* 2: 2294-2304.

Clergeau P., Croci S., Jokimäki J., Kaisanlahti-Jokimäki M.J. & Dinetti M. 2006. Avifauna homogenisation by urbanisation: Analysis at different European latitudes. *Biological Conservation* 127: 336-344.

Davies K.F., Margules C.R. & Lawrence K.F. 2000. Which traits of species predict population declines in experimental forest fragments? *Ecology* 81: 1450-1461.

Fisher D.O. & Owens I.P.F. 2004. The comparative method in conservation biology. *Trends in Ecology and Evolution* 19: 391-398.

Foppen R., Ter Braak C.J.F., Verboom J. & Reijnen R. 1999. Dutch sedge warblers *Acrocephalus schoenobaenus* and West-African rainfall: empirical data and simulation modelling show low population resilience in fragmented marshlands. *Ardea* 87: 113-127.

Fuller R.J., Noble D.G., Smith K.W. & Vanhinsbergh D. 2005. Recent declines in populations of woodland birds in Britain: a review of possible causes. *British Bird*s 98: 116-143.

Gaston K.J. & Blackburn T.M. 2002. Large-scale dynamics in colonization and extinction for breeding birds in Britain. *Journal of Animal Ecology* 71: 390-399.

Gibbons D.W., Reid J.B., Chapman R.A. 1993. The new atlas of breeding birds in Britain and Ireland: 1988-1991. T & AD Poyser, London.

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

Graveland J. & Van de Wal R. 1996. Decline in snail abundance due to soil acidification causes eggshell defects in forest passerines. *Oecologia* 105: 351-360.

Greenwood J.J.D., Fuller R.J. & Gibbons D.W. 1997. Assessing changes in distribution from atlas data: reply to Bircham and Jordan. *Ibis* 139: 186-188.

Gregory R.D., Van Strien A., Vorisek P., Meyling A.W.G., Noble D.G., Foppen R.P.B. & Gibbons D.W. 2005. Developing indicators for European birds. *Philosophical Transactions of the Royal Society of London B* 360: 269-288.

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

Heywood V.H. 1995. Global Biodiversity Assessment. United Nations Environment Programme. Cambridge University Press, Cambridge.

Huston M.A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge.

Julliard R., Jiguet F. & Couvet D. 2004. Common birds facing global changes: what makes a species at risk? *Global Change Biology* 10: 148-154.

Kleijn D., Berendse F., Smit R. & Gilissen N. 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature* 413: 723-725.

Kondoh M. 2001. Unifying the relationships of species richness to productivity and disturbance. *Proceedings of the Royal Society of London B* 268: 269-271.

Kooijman A.M., Dopheide J., Sevink J., Takken I. & Verstraten J.M. 1998. Nutrient limitation and their implications on the effects of atmospheric deposition in coastal dunes: lime-poor and lime-rich sites in The Netherlands. *Journal of Ecology* 86: 511-526.

Kühn I. & Klotz S. 2006. Urbanization and homogenization – Comparing the floras of urban and rural areas in Germany. *Biological Conservation* 127: 292-300.

Kwak R.G.M., Reyrink L.A.F., Opdam P.F.M. & Vos W. 1988. Broedvogeldistricten van Nederland. Een ruimtelijke visie op de Nederlandse avifauna. Pudoc Wageningen.

Lensink R. 1997. Range expansion of raptors in Britain and The Netherlands since the 1960s: testing an individual-based diffusion model. *Journal of Animal Ecology* 66: 811-826.

Leuven R.S.E.W., Foppen R.B.P., Houlliere A.M.G.R., Lenders H.J.R. & De Nooij R.J.W. 2004. Impact of land use changes on breeding birds in floodplains along the rivers Rhine and Meuse in The Netherlands. In: Douben N., Van Os A.G. (eds.). Dealing with floods within constraints. Proceedings NCR-days 2003. NCR-publication 24-2004, Netherlands Centre for River Studies, Delft, pp. 43-45.

Lockwood J.L., Brooks T.M. & McKinney M.L. 2000. Taxonomic homogenization of the global avifauna. *Animal Conservation* 3: 27-35.

Ludwig J.A. & Reynolds J.F. 1988. Statistical ecology: a primer on methods and computing. John Wiley and Sons, New York.

Marchetti M.P., Lockwood J.L. & Light T. 2006. Effects of urbanization on California's fish diversity: differentiation, homogenization and the influence of spatial scale. *Biological Conservatation* 127: 310-318.

McCullagh P. & Nelder J.A. 1989. Generalized Linear Models 2nd edition. Chapman and Hall, London.

McKinney M.L. & Lockwood J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* 14: 450-453.

McKinney M.L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127: 247-260.

Millennium Ecosystem Assessment 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

Newton I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* 146: 579-600.

Olden J.D. & Poff N.L. 2003. Toward a mechanistic understanding and prediction of biotic homogenization. *American Naturalist* 162: 442-460.

Olden J.D., Poff N.L., Douglas M.R., Douglas M.E. & Fausch K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* 19: 18-24.

Olden J.D. & Poff N.L. 2004. Clarifying biotic homogenization. *Trends in Ecology and Evolution* 19: 283-284.

Olden J.D., Poff N.L. & McKinney M.L. 2006. Forecasting faunal and floral homogenization associated with human population geography in North America. *Biological Conservation* 127: 261-271.

Oude Voshaar J.H. 1995. Statistiek voor onderzoekers. Wageningen Pers, Wageningen.

Parlevliet J. 2003. Breeding birds in The Netherlands in the 20th century. *Limosa* 76: 141-156.

Pauchard A., Aguayo M., Peña E. & Urrutia R. 2006. Multiple effects of urbanization on the biodiversity of developing countries: The case of a fast-growing metropolitan area (Concepción, Chile). *Biological Conservation* 127: 272-281.

Pielou E.C. 1984. The interpretation of ecological data. Wiley, New York.

Rahel F.J. 2000. Homogenization of fish faunas across the United States. *Science* 288: 854-856.

Reijnen R., Foppen R. & Veenbaas G. 1997. Disturbance by traffic of breeding birds: Evaluation of the effect and considerations in planning and managing road corridors. *Biodiversity and Conservation* 6: 567-581.

Roelofs J.G.M., Bobbink R., Brouwer E. & De Graaf M.C.C. 1996. Restoration ecology of aquatic and terrestrial vegetation on non-calcareous sandy soils in The Netherlands. *Acta Botanica Neerlandica* 45: 517-541.

Sax D.F. & Gaines S.D. 2003. Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution* 18: 561-566.

Schekkerman H., Meininger P.L. & Meire P.M. 1994. Changes in the waterbird populations of the Oosterschelde (SW Netherlands) as a result of large-scale coastal engineering works. *Hydrobiologia* 283: 509-524.

Schwartz M.W., Thorne J.H. & Viers J.H. 2006. Biotic homogenization of the California flora in urban and urbanizing regions. *Biological Conservation* 127: 282-291.

Siriwardena G.M., Baillie S.R., Buckland S.T., Fewster R.M., Marchant J.H. & Wilson J.D. 1998. Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *Journal of Applied Ecology* 35: 24-43.

Sol D., Blackburn T.M., Cassey P., Duncan R.P. & Clavell J. 2005. The ecology and impact of non-indigenous birds. In: Del Hoyo J., Elliott A. & Christie D.A. (eds.), Handbook of the birds of the world. Vol. 10. Cuckoo-shrikes to Thrushes. Lynx Edicions, Barcelona, pp. 13-35.

SOVON 1988. New estimates of breeding bird numbers in The Netherlands. *Limosa* 61: 151-162.

SOVON 2002. Atlas van de Nederlandse Broedvogels 1998-2000. Nederlandse Fauna 5. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij and European Invertebrate Survey-Nederland, Leiden.

Teixeira R.M. (ed.) 1979. Atlas van de Nederlandse broedvogels. Natuurmonumenten, 's-Graveland.

Tucker G.M. & Davies G. 1997. Habitats for birds in Europe: a conservation strategy for the wider environment. Cambridge, U.K.: BirdLife International (BirdLife Conservation Series no. 6).

Van Beusekom R., Huigen P., Hustings F., De Pater K. & Thissen J. 2005. Rode Lijst van de Nederlandse broedvogels. Tirion, Baarn.

Van Dijk A.J., Dijksen L., Hustings F., Koffijberg K., Schoppers J., Teunissen W., Van Turnhout C., Van der Weide M.J.T., Zoetebier D. & Plate C. 2005. Broedvogels in Nederland in 2003. SOVON-monitoringrapport 2005/01. SOVON, Beek-Ubbergen.

Van Eerden M.R. 1997. Patchwork: patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands. Van Zee tot Land 65. Rijkswaterstaat, Lelystad.

Van Eerden M.R. & Gregersen J. 1995. Long-term changes in the northwest European population of Cormorants *Phalacrocorax carbo sinensis*. *Ardea* 83: 61-79.

Van Tol G., Van Dobben H.F., Schmidt P. & Klap J.M. 1998. Biodiversity of Dutch forest ecosystems as affected by receding groundwater levels and atmospheric deposition. *Biodiversity and Conservation* 7: 221-228.

Van Turnhout. C. & Hagemeijer W. 1999. Marshland birds in The Netherlands: causes of long-term population trends in 1965-95. *Vogelwelt* 120: 185-191.

Van Turnhout C. 2005. The disappearance of the Tawny Pipit *Anthus campestris* as a breeding bird from The Netherlands and Northwest-Europe. *Limosa* 78: 1-14.

Chapter 5

Life-history and ecological correlates of population change in Dutch breeding birds

Chris van Turnhout, Ruud Foppen, Rob Leuven, Arco van Strien and Henk Siepel

Published in 2010 in Biological Conservation 143: 173-181

Abstract

Predicting relative extinction risks of animals has become a major challenge in conservation biology. Identifying life-history and ecological traits related to the decline of species helps understand what causes population decreases and sets priorities for conservation action. Here, we use Dutch breeding bird data to correlate species characteristics with national population changes. We modelled population changes between 1990 and 2005 of all 170 breeding bird species using 25 life-history, ecological and behavioural traits as explanatory variables. We used multiple regression and multi-model inference to account for intercorrelated variables, to assess the relative importance of traits that best explain interspecific differences in population trend, and to identify the environmental changes most likely responsible. We found that more breeding birds have increased than decreased in number. The most parsimonious models suggest that ground-nesting and late arrival at the breeding grounds in migratory birds are most strongly correlated with decline. Increasing populations are mainly found among herbivores, sedentary and short-distance migrants, herb- and shrub-nesting birds and large species with a small European range. Declines in ground-nesting and late arriving migrant birds suggest that agricultural intensification, eutrophication and climate change are most likely responsible for changes in Dutch breeding bird diversity. We illustrate that management strategies should primarily focus on the traits and causes responsible for the population changes, in order to be effective and sustainable.

Introduction

Large-scale population declines have been documented for many animals across the world (Loh *et al.* 2005), including birds (Butchart *et al.* 2004). However, there is much variation in the direction and magnitude of population trends of individual species, and few indications of which species' characteristics are associated with such trends (Shultz *et al.* 2005). Nevertheless, the current pattern of threat appears often non-random and is clustered amongst groups of species that share similar traits (Bennett & Owens 2002). Predicting relative extinction risks of species has therefore become of interest for conservation (Reed 1999), and comparative methods have appeared to be a valuable tool in achieving this (Fisher & Owens 2004). Identifying life-history, ecological and behavioural traits related to the decline and extinction of species helps understand underlying mechanisms, prediction of species that will face problems, prioritizing conservation research, and developing management strategies (Kotiaho *et al.* 2005). Therefore, species traits have been correlated with extinction risks for a variety of taxa, ranging from higher plants (Smart *et al.* 2005) to primates (Purvis *et al.* 2000).

Birds, being relatively well-known, are well represented in these studies. However, most studies have focused on a subset of the total bird community, such as common species (Julliard *et al.* 2004, Jiguet *et al.* 2007, Seoane & Carrascal 2008), endangered species (Collen *et al.* 2006), certain taxa (Keane *et al.* 2005), or species restricted to a certain habitat (Shultz *et al.* 2005). All of these potentially are biased (Davies *et al.* 2004). Another potential problem is that generally only a small number of traits has been considered, whereas the total number of traits that has been identified as influencing population changes or extinction is quite large (Reed 1999). We checked 19 peer-reviewed publications (including two reviews) on the relation between bird species characteristics and either extinction risk or population trend. In these, at least 33 different traits were considered, but on average only 4.7 per study (range 2-12). This limits the potential to disentangle and prioritize traits in a world which is affected by multiple environmental changes.

Here, we use data on breeding birds in the Netherlands to investigate correlations between species characteristics and medium-term population changes, thereby examining which traits appear associated with successful and unsuccessful species in a rapidly changing and highly modified environment. Our goal is to make a global ranking of traits, or logical combinations of these as shown in trade-offs, to select the most relevant ones with respect to population changes. Combining bird monitoring data with life-history traits of species offer possibilities to quantify which traits are most affected and, indirectly, which environmental changes are most likely responsible for these effects. These rankings of meaningful environmentally based traits, or trait-combinations, for a large group of species are particularly of interest for identification of priorities in conservation and management (Kotiaho *et al.* 2005). To illustrate this, if habitat isolation would be a major problem for Dutch breeding birds at the national scale, we expect that especially species with relatively low dispersal capacities would show population declines. Increasing habitat connectivity might then be identified as the key management strategy for the conservation of declining breeding birds.

Breeding birds in the Netherlands have appeared highly dynamic in recent decades. Although species richness has increased, there is much spatial variation underlying this general pattern, resulting in a homogenization of the species compositions (Van Turnhout *et al.* 2007). In this study we consider all breeding birds in the Netherlands, including common, scarce and rare species. In contrast to most other countries, the latter two groups are well surveyed annually in the Netherlands, as a result of different monitoring programs and an extensive network of volunteer birdwatchers (Van Dijk 2004, Van Dijk *et al.* 2004). Furthermore, we consider a relatively large number of species traits for which relationships with population trends have been demonstrated in literature, more than in any other study on birds that we know of. Finally, we adopt a multiple regression approach to account for intercorrelated variables and to assess the relative importance of traits; other studies have not often attempted to discriminate between traits (Purvis *et al.* 2000). To attempt ecological generalizations and models, we need 'regional' studies as an intermediate between multi-species global studies and more targeted local studies (Fisher & Owens 2004, Collen *et al.* 2006). The former are often limited by the heterogeneity of threats, whereas the latter often lack multi-species data and may be confined to very specific threats. This study helps fill this gap in conservation knowledge.

Materials and methods

Study area and data collection

The Netherlands are situated in Northwest-Europe, in the deltas of the large rivers Rhine, Meuse, Scheldt and Ems. They cover an area of 41,500 km^2 and an altitudinal range from 7 m below to 321 m above sea level. The landscape is almost completely cultivated, 70% of the country consists of farmland, 16% of urban environments, leaving only 14% for semi-natural habitats such as woodland and heath land (both mainly in the eastern part of the country), marshland and coastal dunes (both mainly in the western part) (statline.cbs.nl).

The Dutch Breeding Bird Monitoring Program (BMP) has been running since 1984. It is based on intensive territory mapping in fixed study plots (Bibby *et al.* 1997). All common and scarce breeding birds in the Netherlands are covered. Fieldwork and interpretation methods are highly standardized and are described in detail in a manual (Van Dijk 2004). Territory mapping uses a high, and yearly constant, number of field visits (5-10 between March and July). Size of study plots, as well as exact number, timing and duration of visits, depend on habitat type and species selection. All birds with territory-indicative behaviour (e.g. song, pair bond, display, alarm, nests) are noted down on field maps. Species-specific interpretation criteria are used to determine the number of 'territories' per species at the end of the season. Interpretation criteria focus on the type of behaviour observed, the number of observations required (taking into account the varying detection probability between species and within the breeding season), and the period of observations (to exclude non-breeding migrants). We consider the number of 'territories' to be a proxy of true abundance and expect approximate linear relationships between the surveyed samples and the total population sizes of each species. The number of study plots grew from around 300 per year in the mid 1980s to 1,900 at the end of the study period. On average these plots have been surveyed 8.1 years. A total of over 8 million bird territories were counted during an estimated 700,000 hours of field work.

The national monitoring program for colonial and rare breeding bird species (LSB) has been running since 1990. It is based on territory mapping (78 rare species), or nest counting where territory mapping is inappropriate (17 colonial birds). As in the BMP, fieldwork and interpretation methods are standardized and are described in detail in a manual (Van Dijk *et al.* 2004). For most colonial birds and many rare species, over 90% of the entire Dutch breeding population is covered annually. For the remaining species, census efforts are primarily directed towards core areas, resulting in a large and representative annual sample of the total population (Van Dijk *et al.* 2007). The program is coordinated by regional and national supervisors, and carried out by volunteers and professionals.

Deriving population trends

Linear trends are calculated using TRIM-software (Pannekoek & Van Strien 2005). TRIM is specifically developed for the analysis of time series of counts with missing data (Ter Braak *et al.* 1994), and is based on Poisson regression. The regression model for each species estimates a year and plot factor per stratum (i.e. a combination of habitat and region) using the observed counts. The year estimates per stratum are combined in a national population trend, weighted by population sizes and sampling efforts per stratum. With this procedure, we improve the estimation models and correct for the unequal distribution of study plots over Dutch regions and habitat types (Van Turnhout *et al.* 2008). Serial correlation and overdispersion are taken into account. The national population trend of a species is represented by a single estimate, the average annual growth rate in the period 1990-2005, and its standard error. Deviations from linearity of population trends within the study period appear limited. Linear trends for the period 1990-2005 strongly correlate with those for the period 1996-2005 (r=0.86, p<0.001, n=170).

National population trends are available for 170 breeding bird species. These include all regular breeding birds of the Netherlands, except for two species for which monitoring data are unreliable because of unsuitable methods (Swift *Apus apus* and Honey Buzzard *Pernis apivorus*). Recently introduced species are not included, because populations are still largely depending on active releases of feral birds into the wild. Species that have spread naturally into the Netherlands, and succeeded in establishing viable populations, were included. Support for the reliability of our trend estimates is provided by a comparison with changes in national population estimates derived from independent sets of atlas data (Van Turnhout *et al.* 2007). Furthermore, Dutch trend estimates are similar to those from surveys in France and various other European countries (Julliard *et al.* 2004, Jiguet *et al.* 2007). These monitoring programs are widely used to assess trends in biodiversity (Donald *et al.*, 2007), and the Dutch data contribute to pan-European biodiversity indicators (Gregory *et al.* 2005).

Defining traits

We gathered data on 25 life-history, ecological and behavioural traits of Dutch breeding birds. Most of these have been demonstrated to correlate with population trend or extinction risk in other studies (key references are given below). We added a few traits which, in theory, may affect populations arising from the main environmental changes that birds are facing in the Netherlands (Van Turnhout *et al.* 2007), such as agricultural intensification (e.g. duration of breeding: species with relatively long incubation periods may suffer more from an increase in agricultural activities), afforestation (e.g. foraging location: species which forage in high vegetation may be favoured) and climate change (timing of arrival: late-arriving migrants may be less able to adjust to climate change than residents and early arriving migrants). All trait data are derived from Cramp & Simmons, 1977-1994 (data from studies in the Netherlands or Northwest-Europe were selected when available), unless stated otherwise below. Some traits are expressed in different ways.

For each species, we used the following continuous traits: (1) average body mass (Bennett & Owens 2002), discriminating between males and females, (2) average brain size (data from Sol *et al.* 2007), (3) generation time (Collen *et al.* 2006), as the average age of first breeding, (4) average egg mass, (5) duration of breeding, time needed for hatching of eggs and fledging of young, (6) average clutch size (Siriwardena *et al.* 1998) (data from the Dutch Nest Record Scheme for 87 species, on average 830 nests per species (range 25-14,300 nests); data for remaining species from Cramp & Simmons), (7) clutch size flexibility, the difference between maximum and minimum number of eggs, divided by the average, (8) average number of broods per year (Jiguet *et al.* 2007), (9) annual fecundity (Fisher & Owens 2004), as the product of average clutch size and average number of broods per year, (10) dispersal capacity (Martensen *et al.* 2008), discriminating between breeding and natal dispersal distance (modal values from Paradis *et al.* 1998 and Wernham *et al.* 2002), (11) timing of arrival of migrant species, as the average date of annual first observations in the southern part of the country in 1970-2000 (data from Hustings *et al.* 2007), (12) timing of territorial activity (Collen *et al.* 2006), discriminating between observed start, end and length of breeding season in ten-day periods (data from Van Dijk 2004), (13) timing of breeding, as the average start of egg-laying (data from the Dutch Nest Record Scheme), (14) rarity (Gaston & Blackburn 2002), as the number of occupied 50×50 km UTM-squares in Europe (data from Hagemeijer & Blair 1997), as the number of occupied 5×5 km squares in the Netherlands (data from SOVON 2002) and as the population estimate in the Netherlands in 1998-2000 (data from SOVON 2002), (15) latitudinal distribution (Jiguet *et al.* 2007), discriminating between minimum (most southerly) and maximum latitude (most northerly) of breeding in Europe, and latitudinal range (difference between maximum and minimum) (data from Hagemeijer & Blair 1997), (16) thermal maximum, as the mean of local average monthly temperatures in spring and summer for the hottest 50 breeding grid cells in Europe according to Hagemeijer & Blair (1997) (data from Jiguet *et al.* 2007) and (17) habitat specialization (Fisher & Owens 2004), as the coefficient of variation in abundance of a species (standard deviation/mean) in 12 different habitats in the Netherlands, using abundance data from BMP study plots in 2001-2005 (Species Specialization Index; after Julliard *et al.* 2006). Habitats were classified using aerial photography, calibrated in the field by our bird-watchers.

For each species, we used the following categorical traits: (18) parental care (Siriwardena *et al.* 1998), discriminating between eggs and young: female only or both parents, (19) offspring development: precocial or altricial (Sol *et al.* 2007), (20) sociality during breeding season (Reed 1999): colonial, semi-colonial or territorial, (21) sociality during non-breeding season: solitary/pairs, groups or both, (22) migration behaviour (Sanderson *et al.* 2006), as migration strategy (sedentary, partial migrant/short-distance migrant or long-distance migrant (trans-Sahara)), and as main wintering area (West-African Sahel zone, West-African Guinean zone, East- or Southern-Africa, Mediterranean, Western-Europe or Netherlands only) (data from Speek & Speek 1984, Wernham *et al.* 2002), (23) main diet of adults during the breeding season (Jiguet *et al.* 2007): vegetative parts of plants, generative parts of plants (seeds, nuts), invertebrates, fish, vertebrates or omnivorous, (24) foraging location: water, ground, low vegetation (herb and shrub layer), high vegetation (tree layer) or air, and (25) nest location (Seoane & Carrascal 2008): water(side), ground (terrestrial), low vegetation (herb and shrub layer), high vegetation (tree layer) or hole-nesting.

Of course, the available information on these traits for the 170 species is unequal. Reliable data on particularly brain size, dispersal capacity and main wintering area are scarce and scattered (see next paragraph). A classification of main diet does not account for all food items present in a species' menu (except for omnivorous species). Finally, we do not account for within-species variability in some of the life-history traits, such as body mass and clutch size. However, we do not expect that this seriously affects the results of our global, interspecific analysis.

Statistical analyses

Within the 25 selected traits we consider a number of 'clusters', traits that are biologically strongly related. Cluster (1) consists of body mass, brain size, egg mass, duration of breeding and generation time (Pearson-r of all pairs >0.9; $p<0.001$). In order to check for effects on population trends of the latter four traits in addition to the effect of body mass (effects which have been demonstrated in literature, see previous paragraph for references), we used the residuals of loglinear regressions with body mass for further analyses. The other clusters we consider are (2) average clutch size and annual fecundity, (3) minimum latitude of breeding in Europe and thermal maximum, and (4) European range size and latitudinal range (Pearson-r of all pairs >0.7; $p<0.01$). We regard the traits within these clusters as biologically exchangeable with respect to explaining population trends, and use only one trait per cluster in models with multiple predictors (see below). We chose the one for which most data were available (cluster 1) or with the highest correlation in the univariate analysis (other clusters). The same procedure was followed for traits that were expressed in different ways (amongst others male and female body weight, maximum latitude and latitudinal range, migration strategy and main wintering area; Pearson-r of all pairs >0.7; $p<0.01$), again choosing the one with the highest correlation in the univariate analysis.

All traits were first tested alone in Generalized Linear Models (univariate analysis). To reduce the effect of outliers, continuous traits were log-transformed and additionally the robustness of significant results was tested by excluding the remaining outliers (standardized residuals $>–2$; Oude Voshaar 1995) from the dataset and rerunning the analysis.

Then, to select subsets of traits predicting most parsimoniously the variance in population trends, we used GLM to test multivariate models. After dealing with clusters, as described above, the remaining 22 traits were entered into the modelling. For this, we performed the RSEARCH procedure in GenStat 9 (Payne & Lane 2006). In this all possible models are fitted and evaluated according to a criterion. The advantage of this method compared to the forward selection and backward elimination procedure is that the latter results in only one final model, whereas alternative models with an equivalent or even better fit maybe overlooked. Particularly in observational studies with many non-orthogonal predictors, such as ours, selection of just one well-fitting model is unsatisfactory and possibly misleading (Payne & Lane 2006). Models were ranked using Akaikes Information Criterion (AIC) metric. The differences in AIC of each model compared with minimum AIC were assessed and converted into AIC weights (Burnham & Anderson 2002, MacKenzie *et al.* 2006). Parameter estimates and their variances were then averaged across models by using the AIC weights. Because the sample sizes (165-168 species in each model) were quite large compared to the number of parameters (4-5 per model), correction of AIC for small sample sizes (AICc) produced similar results. We did not check for non-linear relationships, to avoid further methodological complexities of our global analysis and because this might have a biological meaning for at most a few of the traits involved.

To test if the effects of certain traits depend on the effects of other traits (belonging to a different cluster), we selected 18 two-way interactions for which an effect on population trends has been demonstrated in literature or can be hypothesized (e.g. the effect of dispersal depends on migration strategy; Paradis *et al.* 1998). These were first added to models containing only both traits separately, and then to the ten best-fitting multivariate models also including both variables.

Finally, some variables contain many missing values: brain size (38 out of 170 missing), thermal maximum (106), timing of arrival (128), timing of breeding (81) and natal (94) and breeding dispersal distance (108). These were added to the ten best-fitting multivariate models in a complementary analysis, to examine the potential effect of these traits on population trends for the reduced subset of species with available data (following Jiguet *et al.* 2007).

Due to the large number of sample sites and the long time span of the monitoring schemes, standard errors of estimated population trends are generally small (mean *SE* 0.010, range 0.001-0.091). Incorporating standard errors of trends as weighting factors in the analysis did not change any result and for simplicity's sake we do not present these.

It has been argued that bird species should not be treated as independent sample units, because they are evolutionarily related through a phylogenetic tree. Therefore, in comparative analyses 'independent contrasts' are often used to correct for this (Felsenstein 1985, Fisher & Owens 2004). In some studies results of phylogenetic and non-phylogenetic analyses were similar (Gregory & Gaston 2000, Shultz *et al.* 2005), whereas another non-phylogenetic analysis gave more significant relationships than phylogenetic analyses (Purvis *et al.* 2000). In phylogenetic tests with our data using the PDAP module (Midford *et al.* 2005) we found only minor differences in significance of correlations between selected traits and population trends. Phylogenetic analyses are subjected to controversy and debate (Westoby *et al.* 1995, Julliard *et al.* 2004, Collen *et al.* 2006), and taxonomic classifications are continuously challenged (Hackett *et al.* 2008). In this study we are not primarily interested in patterns of diversification across evolutionary time, but in correlations between traits and species trends in the highly anthropogenic environment of today. Therefore, following Seoane & Carrascal (2008) we have simplified data analyses avoiding the complexities and drawbacks of correcting for phylogenetic relatedness.

Results

Population trends of Dutch breeding birds differ markedly in the 1990-2005 period, ranging from a mean annual decrease of 21% in Crested Lark *Galerida cristata* to a mean annual increase of 52% in Little Egret *Egretta garzetta*. The geometric mean of population change for all 170 species is +1.6% per year, with more species increasing than decreasing in abundance.

In the univariate analysis, 12 out of the 25 traits explained a (nearly) significant amount of variation in national population trends. However, two of these were not robust when outliers were excluded, and another three only explained a very small part of the variation (less than 5%) (Table 1). In addition, four two-way interactions added significantly to the separate effects of these variables.

Table 1. All significant ($p<0.05$) and nearly significant effects ($0.05<p<0.1$) of life-history and ecological traits on national population trends of 170 breeding birds in the Netherlands in 1990-2005 (univariate analysis), including interactions. First, traits that are strongly intercorrelated (Pearson-r >0.7) are indicated using the same symbol (see Materials and methods section). Then the % variance accounted for, the slope of regression line and its standard error (for continuous variables only), p-value and sample size are presented. Trend estimates of categorical variables are presented in Table 3.

Univariate models	Corr	R^2	Slope	Slope error	p	n
Continuous traits						
Body mass						
male	a	9.2	0.016	0.004	<0.001	168
female	a	9.9	0.015	0.003	<0.001	156
Dispersal capacity						
natal		2.8	0.012	0.007	0.080[1]	76
Timing of arrival of migrants		11.9	–0.083	0.032	0.015	42
Timing of breeding		13.9	–0.126	0.032	<0.001[2]	89
Rarity						
European range size	c	23.3	–0.059	0.008	<0.001	169
Dutch range size	b	4.3	–0.013	0.004	0.004	169
Dutch population size	b	2.9	–0.005	0.002	0.015	169
Latitudinal distribution						
maximum	c	3.4	–0.214	0.079	0.009	169
range	c	11.1	–0.153	0.032	<0.001	169
Categorical traits						
Parental care						
eggs		1.8			0.045	169
Sociality						
breeding season		8.2			<0.001	170
Migration behaviour						
migration strategy	d	2.4			0.071	170
main wintering area	d	2.0			0.100	170
Main diet		12.9			<0.001	169
Foraging location		8.5			<0.001	170
Nest location		4.7			0.018	169
Interactions						
Main diet × Body mass		2.9			0.050	167
Main diet × Foraging location		4.5			0.030	169
Rarity × Body mass		7.5			<0.001	167
Nest location × Body mass		7.0			0.001	167

[1] effect not robust to the exclusion of outliers: excluding outliers $p=0.13$
[2] effect not robust to the exclusion of outliers: excluding outliers $p=0.75$

Table 2. The ten best-fitting models predicting national population trends of 170 breeding birds in the Netherlands in 1990-2005 from life-history and ecological traits (multivariate analysis). For all models, sorted by AIC, the slopes of the regression lines of the variables are presented (for continuous variables only). These estimates account for the effects of other variables in the model. Significant effects ($p<0.05$) of continuous variables are indicated with an asterisk. Trend estimates of categorical variables (indicated with 'x') are presented in Table 3. Also, the % variance explained by the ten best models is given (R^2_{adj}). In the last three columns the number of times that every variable is included in one of the ten best-fitting models is presented, as well as the average slope and its standard error (calculated by model averaging, see Materials and methods section). All traits that were significant or nearly significant in the univariate analysis are included in the table. Results of the complementary analysis of two-way interactions and variables containing many missing values are presented separately.

Multivariate models	1	2	3	4	5	6	7	8	9	10	Top10	Slope	*SE*
Body mass													
male					0.007	0.006	0.008		0.003	0.001	5	0.005	0.005
Rarity													
European range	–0.061*	–0.063*	–0.065*	–0.068*	–0.063*	–0.059*	–0.057*	–0.064*	–0.059*	–0.060*	10	–0.062	0.009
Parental care													
eggs											0		
Sociality													
breeding season											0		
Migration behaviour													
migration strategy	x		x	x	x	x		x		x	7		
Main diet	x	x						x	x	x	5		
Foraging location				x	x						2		
Nest location	x	x	x	x	x	x	x	x	x	x	10		
AIC	177.4	177.8	177.9	178.1	178.4	178.8	178.9	179.3	179.3	179.4			
R^2_{adj}	34.5	33.4	32.0	33.6	32.7	31.0	30.3	34.1	31.9	32.8			
Complementary analysis													
Main diet × Body mass											0		
Main diet × Foraging loc.											0		
Rarity × Body mass					–0.017*	–0.018*	–0.018*		–0.017*	–0.017*	5	–0.017	0.005
Nest location × Body mass									x	x	2		
Dispersal capacity													
natal				0.024							1	0.024	0.012
Timing of arrival of migr.		–0.094*		–0.091*	–0.094*		–0.084*		–0.107*	–0.115*	6	–0.096	0.041
Timing of breeding											0		

In the multivariate analysis the data fitted a large number of candidate models more or less equally, with the ten best-fitting models all explaining 30-35% of the variance in population trends (Table 2). Nest location, European range size, migration strategy, main diet and body mass featured most often in the ten best models (Table 1), although the latter was only significant in interaction with range size. The first four variables also were in the best-fitting model ($R^2_{adj}=34.5\%$, $p<0.001$). Foraging location was less often incorporated in the ten best models, whereas parental care and sociality during the breeding season were not selected at all. No other variable entered into the top ten models.

In addition, the interaction between European range size and male body mass added significantly in five of the final models, resulting in an extra 4-5% of the variation explained (Table 2). Finally, timing of arrival of migrants showed a significant correlation with population trend when added to seven of the final models in the analysis with a reduced subset of species (Table 2).

On average the numbers of ground-nesting bird species declined. Populations of species using other nest locations generally increased, although only significant for herb and shrub nesting birds (Figure 1 and Table 3). Increasing species had relatively small European range sizes, but this correlation holds for larger species only (Figure 2).

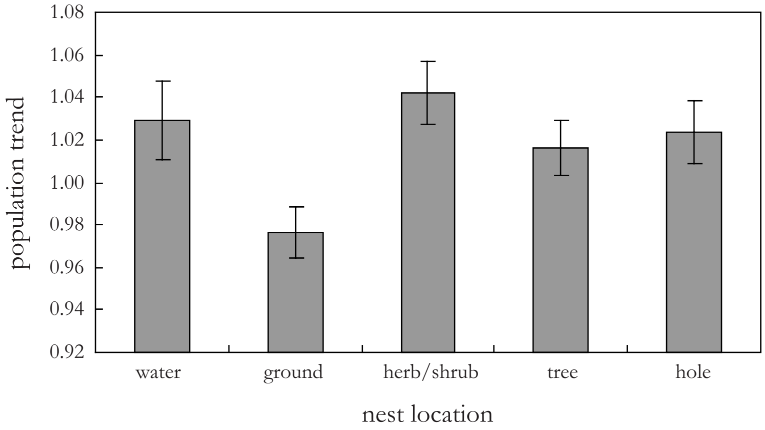


Figure 1. Relationship between Dutch population trends of breeding birds 1990-2005 and nest location. Trend estimates (± *SE*) are weighted averages and account for the effects of other variables in the models (see Materials and methods section). The trend is presented as a multiplicative parameter: a value of 1.1 represents an annual increase of 10%, a value of 0.9 an annual decrease of 10%.

Table 3. Trend estimates of categorical traits that are significant in the multivariate analyses, and sample sizes. Multivariate estimates are calculated by model averaging (see Materials and methods section) , and account for the effects of other variables in the model. Trend estimates represent multiplicative parameters: a value of 1.1 represents an annual population increase of 10%, a value of 0.9 an annual decrease of 10%. Significant deviations from 1 ($p<0.05$) are indicated with an asterisk.

		Multivariate		Univariate		*n*
		Mean estimate	*SE*	*Estimate*	*SE*	
Migration strategy	short-distance	1.026*	0.010	1.026*	0.011	59
	sedentary	1.019	0.011	1.026*	0.012	57
	long-distance	0.993	0.011	0.993	0.012	54
Main diet	herbivorous	1.067*	0.036	1.126*	0.026	10
	carnivorous	1.032	0.020	1.031	0.018	21
	piscivorous	1.016	0.022	1.062*	0.021	16
	granivorous	1.001	0.017	0.986	0.019	20
	insectivorous	1.006	0.008	1.001	0.008	102
Foraging location	air	1.068*	0.023	1.020	0.022	15
	tree	1.023	0.018	1.008	0.018	23
	herb/shrub	1.015	0.010	1.006	0.011	63
	water	1.004	0.014	1.061*	0.013	41
	ground	0.992	0.015	0.974	0.016	28
Nest location	herb/shrub	1.042*	0.015	1.034*	0.016	29
	water	1.029	0.018	1.068*	0.019	22
	hole	1.024	0.015	1.006	0.016	31
	tree	1.016	0.013	1.006	0.014	40
	ground	0.976*	0.012	0.996	0.013	47
Wintering area	Mediterr.	1.057*	0.028	1.025	0.024	10
	Netherlands	1.026*	0.012	1.020*	0.010	58
	SW-Europe	1.020	0.013	1.029*	0.011	48
	Sahel zone	1.012	0.020	1.002	0.017	20
	E/S-Africa	0.990	0.018	0.999	0.016	24
	Guinea zone	0.961	0.028	0.976	0.025	10

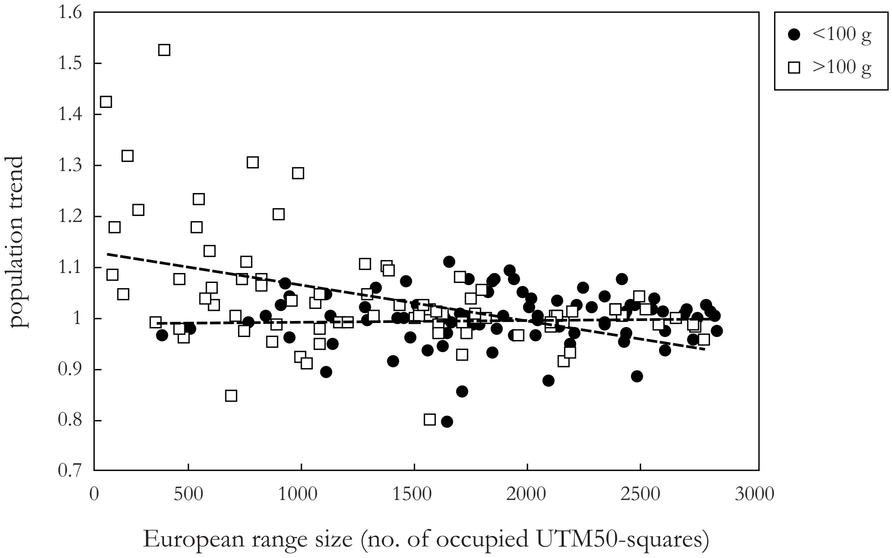


Figure 2. Relationship between Dutch population trends of breeding birds 1990-2005 and European range size (number of occupied 50×50 km UTM-squares), for species with a body mass smaller than 100 grams (closed symbols), and larger than 100 grams (open symbols) respectively (*n*=168).

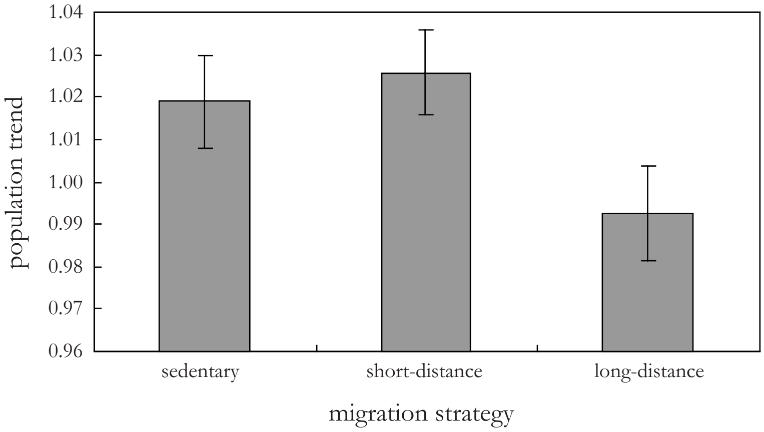


Figure 3. Relationship between Dutch population trends of breeding birds 1990-2005 and migration strategy.

Sedentary species and short-distance migrants generally increased, as shown by both migration strategy (Figure 3) and wintering area (Table 3). Long-distance migrants on average declined, especially migrants that arrive relatively late at the breeding grounds in spring, compared to early-arriving migratory birds (Figure 4). From the univariate analyses it appears that, within Africa, species that winter in the Guinean zone tended to decrease, whereas birds that winter in the Sahel zone or other parts did not decline on average in the 1990-2005 period (Table 3). Herbivorous species show on average strong positive trends, whereas other food guilds are generally rather stable (Table 3).

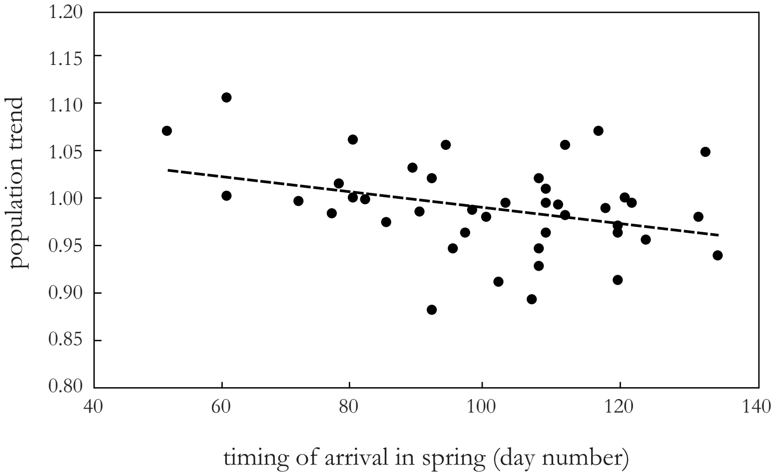


Figure 4. Relationship between Dutch population trends of migratory breeding birds 1990-2005 and timing of arrival at the breeding grounds in spring (day number; January 1 = day 1) (*n*=42).

Discussion

Changes in taxonomic and functional diversity

We found that more breeding birds have increased than decreased in number in the Netherlands between 1990 and 2005. This trend is not specific just for the study period, but also holds earlier. Van Turnhout *et al.* (2007) showed that bird species richness and diversity have increased since the mid seventies, and that most species have increased their range and abundance. After evaluating a large number of historical sources, Parlevliet (2003) reached the same conclusion for population changes since 1900. However, findings differ between habitats and regions (Van Turnhout *et al.* 2007). Regions have become more similar in their landscape features. This has resulted in a homogenization of breeding bird communities, contributing to a loss of avian diversity in the Netherlands and abroad (Devictor *et al.* 2008). In similar time periods as our study half of the species in both Spain and the United Kingdom increased (Seoane & Carrascal 2008), whereas breeding birds in France tended to decrease (Julliard *et al.* 2004). Whereas our study was of all breeding bird species, the latter studies were on a selection of common terrestrial passerines. This may explain some of the differences, because working with subsets of species may give biased results, as population trends depend on rarity and differ between terrestrial and water birds (Gaston & Blackburn 2002, Fisher & Owens 2004, Van Turnhout *et al.* 2007).

Associating population change with life-histories of species requires good analytical techniques and ecological understanding. In this chapter we have attempted such an analysis based on large-scale bird monitoring data and many life-history and ecological variables, so as to identify and rank traits and sets of traits that are correlated with population trend in Dutch breeding birds. Starting with traits for which a correlation with population trend has been demonstrated, or can be hypothesised, our statistical methods help to disentangle and cluster those most associated with trend. Ecological interpretation links them to the environmental changes most likely to be responsible. This clarifies which sets of traits are primarily associated with successful and unsuccessful species, suggests priorities for further research on processes, and directs conservation action (Kotiaho *et al.* 2005).

Our most parsimonious models suggest that recent population decline was associated with ground-nesting and late arrival at the breeding grounds in migratory species. Increasing populations are mainly found among sedentary species and short-distance migrants, herbivores, herb- and shrub-nesting birds and species with a small European range in combination with a large body-mass.

Nest location and diet as correlates of population change

Population declines in ground-nesters are found for species that inhabit a variety of habitats. Indeed, opportunities for species that nest (and forage) on the ground have deteriorated in all terrestrial habitats, both agricultural and semi-natural. In farmland, an increase in agricultural activities during the breeding season, such as earlier and more frequent mowing, has increased nest disturbance and greatly reduced nesting success and chick survival of meadow birds (Schekkerman *et al.* 2008). Increased predation rates may have contributed to the decline, as a result of growing raptor and Red Fox *Vulpes vulpes* populations (Newton 2004, Schekkerman *et al.* 2008). Also in most other habitats ground-nesters are disproportionately susceptible to predation (Martin 1993, Isaksson *et al.* 2007). In many semi-natural habitats however, the effects of terrestrial eutrophication are probably most important (Verstrael & Van Dijk 1997). This has resulted in encroachment by nitrophilic grasses and shrubs, which have replaced the original low vegetation with a large fraction of bare ground, particularly in heathlands and coastal habitats (Roelofs *et al.* 1996, Kooijman *et al.* 1998). Loss of natural ecosystem dynamics and decrease of rabbit populations have also contributed to these vegetation changes (Verstrael & Van Dijk 1997). This has led to a deterioration in nesting and foraging conditions for birds in early successional habitats (Van Turnhout 2005). Simultaneously, herb- and shrub-nesting species will have benefited from these vegetation changes (Verstrael & Van Dijk 1997), and partly also from the establishment of roadside and young forestry plantations and parks, mainly in the formerly open western part of the country (Van Turnhout *et al.* 2007). Apart from its probable effects on breeding birds, eutrophication is also regarded as the most important cause of plant biodiversity changes in the Netherlands during the 20th century (Tamis *et al.* 2005).

Herbivores, to a large extent birds that nest in or near water, have generally been very successful in the Netherlands. Reduction of water pollution and ecological rehabilitation of wetlands may have contributed to this increase (Van Turnhout *et al.* 2007). In addition, some herbivores forage in farmland near water bodies, such as Mute Swan *Cygnus olor* and Greylag Goose *Anser anser*. These species have benefited from the ongoing improvement of grassland quality (protein content, digestibility and length of growing season) since the 1950s (Voslamber *et al.* 2007). Agricultural intensification (drainage and use of fertilizers) has made Dutch farmland among the most productive in the world, and the yields per hectare are almost five times larger than the West-European average (RIVM 2003). Not only breeding birds, but also wintering waterfowl have benefited from this development (Van Eerden *et al.* 2005).

Rarity and body mass as correlates of population change

Based on population theory and empirical evidence, other studies have concluded that rarity (small range and low abundance) is a trait that promotes extinction (Gaston & Blackburn 2002, Fisher & Owens 2004, Julliard *et al.* 2004). Therefore, we had expected to find that larger ranges would correlate with population increases. Instead we found that the smaller the range, the greater the population increase. However, this correlation only exists for larger species. The true relationship might be curvilinear or including a threshold effect, given the generally positive deviations from linearity for heavy species with small ranges. Large birds with small European distribution ranges that have exhibited strong population increases in the Netherlands in recent years include non-passerine wetland species, such as Barnacle Goose *Branta leucopsis*, Spoonbill *Platalea leucorodia*, Cormorant *Phalacrocorax carbo*, Mediterranean Gull *Larus melanocephalus*, Red-crested Pochard *Netta rufina*, Little Egret *Egretta garzetta* and Great Egret *E. albus*. Some of these have autonomously expanded their range over other parts of Europe too. Interestingly, most of these relatively rare species are listed on Annex 1 of EU's Birds Directive. This international policy has benefited bird populations in the European Union in 1990-2000 (Donald *et al.* 2007). Because rare species with small ranges may have benefited disproportionately, this might explain the correlation we found. Additionally, body size has been found to correlate with extinction risk from human persecution (Bennett & Owens 2002). International legal protection could thus be beneficial for especially larger, often long-lived, species. Alternatively, many of these larger species are colonial breeders. Indeed, sociality during breeding season did show up as a significant correlate of population increase in the univariate analysis. This variable was not incorporated in the multivariate models because it correlates with body mass, which is a stronger predictor. This does not rule out that sociality may be a successful trait in itself (Reed 1999).

Migration strategy as correlate of population change

Migration strategy appears to influence Dutch population trends. Increases in populations of sedentary species and especially partial migrants may be the result of near-absence of severe winter weather in Western Europe in the study period. In the Netherlands 12 of out 16 winters are characterized as mild or very mild according to the classification of IJnsen (1991). This has probably enhanced winter survival, and suggests that further increases can be expected from climate warming (Robinson *et al.* 2007).

Results of other European studies do not concur. Jiguet *et al.* (2007) and Seoane & Carrascal (2008) did not find a relation between migration behaviour and trends of common passerines in France (between 1989 and 2005) and Spain (between 1996 and 2004), respectively. Lemoine *et al.* (2007) however, found a spatial relationship between climatic factors and the proportion of migratory and resident bird species in 21 European bird communities. Sanderson *et al.* (2006), examining more species, also found that populations of Afro-Palearctic migrants declined over large parts of Europe between 1970 and 2000. This was particularly the case for species wintering in arid open habitats in Africa. Although the exact wintering areas of long-distance migrants remain far from clear, we did not find a tendency to decline for species wintering in the

Sahel during the shorter time period we studied. Some of these, such as Whitethroat *Sylvia communis* and Sedge Warbler *Acrocephalus schoenabaenus*, are still recovering from population minima after large-scale droughts in the Sahel in the 1970s and 1980s (Foppen *et al.* 1999). Non-linearity of long-term population trends suggests that traits related to population change may be specific to certain time periods. We found declines for a number of woodland species wintering in the tropical and dry forests of the West-African Guinean zone, although this trend was not statistical significant.

Our data also show that, among migrants, late-arriving species declined more strongly than birds that arrive earlier at the breeding grounds. Further research is needed to assess whether these declines are caused by factors operating on the wintering grounds or breeding grounds. On wintering grounds there may have been habitat loss, in that human pressure on Guinean ecosystems is extremely high and forests are being cleared at a very high rate. However, this would affect both early and late departing migrants. Sahel wintering birds arrive on average seven days earlier than birds wintering in the Guinea zone, but the difference is not statistically significant (*t*-test, p=0.23). Breeding ground changes may be related to climate change. Long-distance migrants may be less able to adjust to climate change than residents, because migrants cannot foresee at their wintering grounds when spring starts at their breeding grounds. This might be most pronounced for species that arrive and breed relatively late in the season (Coppack & Both 2002), and in habitats with short peaks in food availability, such as forests, compared with habitats that are less seasonal (Both *et al.* 2006).

Need for additional habitat-specific analyses

We did not consider habitat explicitly in our analyses, but we believe it may be an important explanatory variable in studies such as ours. For example, within generalist species, population trends may differ between habitats (Gregory *et al.* 2005), suggesting that species are affected by habitat-specific environmental changes. These may affect different traits, or the same traits in a different way. This may partly explain the 65-70% of variation in population trends that was not captured in our analyses of national trends. It may also explain why some traits that were found to correlate strongly to decline by others, were not in our analyses. Several authors have identified habitat specialization or niche breadth as a predictor of population declines in birds (Reed 1999, Seoane & Carrascal 2008). Jiguet *et al.* (2007) even suggested that, although the causes of habitat deterioration may differ between habitats, specialization itself is a better predictor of population decline than living in a particular habitat. Since we did not find an effect of the Species Specialization Index on national population trends, our results indicate otherwise. In addition, we carried out a complementary regression analysis in which we correlated habitat-specific trends in heathland and woodland (by assigning BMP study plots to the prevailing habitat type) with SSI. We found that SSI had a negative effect on population trends in heathland (p=0.020, n=58), but a positive effect on trends in woodland (p=0.031, n=63). This suggests that forest specialists are thriving, whereas heathland specialists are declining at a faster rate than generalists. This agrees with known changes in area and quality of these habitats (Van Turnhout *et al.* 2007). Future comparative studies should focus on the relation between habitat-specific population trends and habitat-specific environmental changes.

Conservation applications

Whether or not there are habitat specific effects, population declines at the national scale were found mainly among ground-nesting birds and late-arriving migrants, suggesting that agricultural intensification, eutrophication and climate change are key drivers. These species are apparently in urgent need of conservation action. The Tawny Pipit *Anthus campestris*, combining both characteristics, is perhaps the most striking representative of this pattern: after a long period of steady decline, the species disappeared as a breeding bird from the Netherlands in 2004 (Van Turnhout 2005). Management will only be effective if focused on the sets of traits that are most seriously affected. Although probably too late for Tawny Pipit, for other ground-breeding birds of coastal and inland dunes large-scale reactivation of natural ecosystem dynamics (erosion activity) might be the key strategy to set back grass encroachment and ensure sufficient nesting and foraging possibilities at the landscape scale ('process management'). Although this approach is only possible in large nature reserves, it is more promising than the restoration of vegetation mosaics in small habitat patches by actively removing the vegetation, which has been the main management strategy in these habitats up to now ('pattern management') (Riksen *et al.* 2006). In farmland large-scale process management is even harder to accomplish. However, ground-breeding meadow birds might profit from rehabilitation of high water levels, to ensure temporal and spatial variation in vegetation structures during the breeding season. Pattern management strategies seem inadequate: delayed and staggered mowing of fields, in combination with active nest protection, is only successful when carried out over large areas of farmland with very favourable pre-conditions (Schekkerman *et al.* 2008). If not targeted on the traits responsible for a species' population change, management will not be effective. This can be illustrated by means of the recently very successful herbivore water birds, such as greylag goose. These are increasingly considered as pest species in the Netherlands, because of conflicts with agriculture (geese damage crops) and nature management goals (eutrophication). Population regulation (mainly by shooting, culling and egg removal) has generally appeared ineffective up to now (Voslamber *et al.* 2007). Instead, a management strategy that will primarily focus on the trait (herbivory) and causes (agricultural intensification, use of fertilizers) responsible for the population increase will be more rewarding and sustainable. Changing the management of grasslands adjacent to breeding sites, such as reducing the vegetation quality, stimulating natural vegetation succession or fencing, to prevent the geese from reaching protein-rich chick-rearing habitat, results in a decrease of the condition and survival of both goslings and adult birds (Voslamber & Van Turnhout 2008).

Acknowledgements

This work would not have been possible without the efforts of many thousands of skilled volunteer bird-watchers, to whom we are greatly indebted. Several SOVON-colleagues, in particular A.J. van Dijk, were responsible for processing the data. P. van Dijk put a great effort in gathering the trait data. We thank the European Bird Census Council for providing the data on European range size, D. Sol for data on brain size and F. Jiguet for data on thermal maximum. Prof. A.J. Hendriks, Dr. W. Verberk, Dr. B. Ens and M. Roodbergen commented on drafts of this chapter. Two anonymous referees and David Dawson gave valuable and constructive comments to improve the chapter. This study is a project of the Netherlands Centre for Nature research (NCN), and was financially supported by a WeWi-pool grant by Radboud University. The Faculty of Science (Radboud University) and SOVON co-financed this project. This chapter is dedicated to the late Hans Esselink, who played a major role in the initiation of this study.

References

Bennett P.M. & Owens I.P.F. 2002. Evolutionary ecology of birds. Life histories, mating systems and extinction. Oxford University Press, Oxford.

Bibby C.J., Burgess N.D. & Hill D.A. 1997. Bird Census Techniques. Academic Press, London.

Both C., Bouwhuis S., Lessells C.M. & Visser M.E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441: 81-83.

Burnham K.P. & Anderson D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach (2nd edition). Springer-Verlag, New York.

Butchart S.H.M., Stattersfield A.J. & Bennun L.A. 2004. Measuring global trends in the status of biodiversity: Red list indices for birds. *PLoS Biology* 2: 2294-2304.

Collen B., Bykova E., Ling S., Milner-Gulland E.J. & Purvis A. 2006. Extinction risk: A comparative analysis of central Asian vertebrates. *Biodiversity and Conservation* 15: 1859-1871.

Coppack T. & Both C. 2002. Predicting life-cycle adaptation of migratory birds to global climate change. *Ardea* 90: 369-378.

Cramp S. & Simmons K.E.L. 1977-1994. Handbook of the Birds of Europe, the Middle East and North Africa: the birds of the Western Paleartic. Volume 1-9. Oxford University press, Oxford.

Davies K.F., Margules C.R. & Lawrence J.F. 2004. A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology* 85: 265-271.

Devictor V., Julliard R., Clavel J., Jiguet F., Lee A. & Couvet D. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography* 17: 252-261.

Donald P.F., Sanderson F.J., Burfield I.J., Bierman S.M., Gregory R.D. & Waliczky Z. 2007. International conservation policy delivers benefits for birds in Europe. *Science* 317: 810-813.

Felsenstein J. 1985. Phylogenies and the Comparative Method. *American Naturalist* 125: 1-15.

Fisher D.O. & Owens I.P.F. 2004. The comparative method in conservation biology. *Trends in Ecology and Evolution* 19: 391-398.

Foppen R., Ter Braak C.J.F., Verboom J. & Reijnen R. 1999. Dutch sedge warblers *Acrocephalus schoenobaenus* and West-African rainfall: empirical data and simulation modelling show low population resilience in fragmented marshlands. *Ardea* 87: 113-127.

Gaston K.J. & Blackburn T.M. 2002. Large-scale dynamics in colonization and extinction for breeding birds in Britain. *Journal of Animal Ecology* 71: 390-399.

Gregory R.D. & Gaston K.J. 2000. Explanations of commonness and rarity in British breeding birds: separating resource use and resource availability. *Oikos* 88: 515-526.

Gregory R.D., Van Strien A., Vorisek P., Meyling A.W.G., Noble D.G., Foppen R.P.B. & Gibbons D.W. 2005. Developing indicators for European birds. *Philosophical Transactions of the Royal Society of London Series B* 360: 269-288.

Hackett S.J., Kimball R.T., Reddy S., Bowie R.C.K., Braun E.L., Braun M.J., Chojnowski J.L., Cox W.A., Han K.L., Harshman J., Huddleston C.J., Marks B.D., Miglia K.J., Moore W.S., Sheldon F.H., Steadman D.W., Witt C.C. & Yuri T. 2008. A phylogenomic study of birds reveals their evolutionary history. *Science* 321: 417-421.

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

Hustings F., Van der Coelen J., Van Noorden B., Schols R. & Voskamp P. 2007. Avifauna van Limburg. Stichting Natuurpublicatie Limburg, Maastricht.

IJnsen F. 1991. Karaktergetallen van de winters vanaf 1707. *Zenit* 18: 65-73.

Isaksson D., Wallander J. & Larsson M. 2007. Managing predation on ground-nesting birds: The effectiveness of nest exclosures. *Biological Conservation* 136: 136-142.

Jiguet F., Gadot A.S., Julliard R., Newson S.E. & Couvet D. 2007. Climate envelope, life history traits and the resilience of birds facing global change. *Global Change Biology* 13: 1672-1684.

Julliard R., Jiguet F. & Couvet D. 2004. Common birds facing global changes: what makes a species at risk? *Global Change Biology* 10: 148-154.

Julliard R., Clavel J., Devictor V., Jiguet F. & Couvet D. 2006. Spatial segregation of specialists and generalists in bird communities. *Ecology Letters* 9: 1237-1244.

Keane A., Brooke M.D. & McGowan P.J.K. 2005. Correlates of extinction risk and hunting pressure in gamebirds, Galliformes. *Biological Conservation* 126: 216-233.

Kooijman A.M., Dopheide J., Sevink J., Takken I. & Verstraten J.M. 1998. Nutrient limitation and their implications on the effects of atmospheric deposition in coastal dunes: lime-poor and lime-rich sites in The Netherlands. *Journal of Ecology* 86: 511-526.

Kotiaho J.S., Kaitala V., Komonen A. & Paivinen J. 2005. Predicting the risk of extinction from shared ecological characteristics. *Proceedings of the National Academy of Sciences* 102: 1963-1967.

Lemoine N., Schaefer H.C. & Böhning-Gaese K. 2007. Species richness of migratory birds is influenced by global climate change. *Global Ecology and Biogeography* 16: 55-64.

Loh J., Green R.E. & Ricketts T. 2005. The Living Planet Index: using species population time series to track trends in biodiversity. *Philosophical Transactions of the Royal Society of London Series B* 360: 289-295.

MacKenzie D.I., Nichols J.D., Royle J.A., Pollock K.H., Bailey L.L. & Hines J.E. 2006. Occupancy estimation and modelling. Academic Press, London.

Martensen A.C., Pimentel R.G. & Metzger J.P. 2008. Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: Implications for conservation. *Biological Conservation* 141: 2184-2192.

Martin T.E. 1993. Nest predation among vegetation layers and habitat types – revising the dogmas. *American Naturalist* 11: 897-913.

Midford P.E., Garland Jr. T. & Maddison W.P. 2005. PDAP Package of Mesquite. Version 1.06.

Newton I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* 146: 579-600.

Oude Voshaar J.H. 1995. Statistiek voor Onderzoekers. Wageningen Pers, Wageningen.

Pannekoek J. & Van Strien A.J. 2005. TRIM 3 Manual , Trends & Indices for Monitoring Data.. Statitics Netherlands, Voorburg.

Paradis E., Baillie S.R., Sutherland W.J. & Gregory R.D. 1998. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* 67: 518-536.

Parlevliet J 2003. Breeding birds in The Netherlands in the 20th century. *Limosa* 76: 141-156.

Payne R.W. & Lane P.W. (eds.) 2006. GenStat Release 9 Reference Manual. Part 3. Lawes Agricultural Trust, Rothamsted, United Kingdom.

Purvis A., Gittleman J.L., Cowlishaw G. & Mace G.M. 2000. Predicting extinction risk in declining species. *Philosophical Transactions of the Royal Society of London Series B* 267: 1947-1952.

Reed J.M. 1999. The role of behavior in recent avian extinctions and endangerments. *Conservation Biology* 13: 232-241.

Riksen M., Ketner-Oostra R., Van Turnhout C., Nijssen M., Goossens D., Jungerius P.D. & Spaan W. 2006. Will we lose the last active inland drift sands of Western Europe? The origin and development of the inland drift-sand ecotype in the Netherlands. *Landscape Ecology* 21: 431-447.

RIVM 2003. Natuurcompendium 2003. RIVM, CBS, DLO, Bilthoven, Netherlands.

Robinson R.A., Baillie S.R. & Crick H.Q.P. 2007. Weather-dependent survival: implications of climate change for passerine population processes. *Ibis* 149 : 357-364.

Roelofs J.G.M., Bobbink R., Brouwer E. & De Graaf M.C.C. 1996. Restoration ecology of aquatic and terrestrial vegetation on non-calcareous sandy soils in The Netherlands. *Acta Botanica Neerlandica* 45: 517-541.

Sanderson F.J., Donald P.F., Pain D.J., Burfield I.J. & Van Bommel F.P.J. 2006. Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation* 131: 93-105.

Schekkerman H., Teunissen W. & Oosterveld E. 2008. The effect of 'mosaic management' on the demography of black-tailed godwit *Limosa limosa* on farmland. *Journal of Applied Ecology* 45: 1067-1075.

Seoane J. & Carrascal L.M. 2008. Interspecific differences in population trends of Spanish birds are related to habitat and climatic preferences. *Journal of Global Ecology and Biogeography* 17: 111-121.

Shultz S., Bradbury R.B., Evans K.L., Gregory R.D. & Blackburn T.M. 2005. Brain size and resource specialization predict long-term population trends in British birds. *Philosophical Transactions of the Royal Society of London Series B* 272: 2305-2311.

Siriwardena G.M., Baillie S.R., Buckland S.T., Fewster R.M., Marchant J.H. & Wilson J.D. 1998. Trends in abundance of farmland birds: a quantitative comparison of smoothed Common Bird Census Indices. *Journal of Applied Ecology* 35: 24-43.

Smart S.M., Bunce R.G.H. & Marrs R. 2005. Large-scale changes in the abundance of common higher plant species across Britain between 1978 1990 and 1998 as a consequence of human activity: Tests of hypothesised changes in trait representation. *Biological Conservation* 124: 355-371.

Sol D., Szekely T., Liker A. & Lefebvre L. 2007. Big-brained birds survive better in nature. *Philosophical Transactions of the Royal Society of London Series B* 274: 763-769.

SOVON Vogelonderzoek Nederland 2002. Atlas van de Nederlandse Broedvogels 1998-2000. Nederlandse Fauna 5. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij and European Invertebrate Survey-Nederland, Leiden.

Speek B.J. & Speek G. 1984. Thieme's vogeltrekatlas. Thieme, Zutphen.

Tamis W.L.M., Van't Zelfde M., Van der Meijden R. & De Haes H.A.U. 2005. Changes in vascular plant biodiversity in the Netherlands in the 20th century explained by their climatic and other environmental characteristics. *Climate Change* 72: 37-56.

Ter Braak C.J.F., Van Strien A.J., Meijer R. & Verstrael T.J. 1994. Analysis of monitoring data with many missing values: which method? Bird Numbers 1992. Distribution, Monitoring and Ecological aspects. Proc. 12th Int. Conf. of IBCC and EOAC. Statistics Netherlands, Voorburg & Sovon, Beek-Ubbergen.

Van Dijk A.J. 2004. Handleiding Broedvogel Monitoring Project. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Dijk A.J., Hustings F. & Van der Weide M. 2004. Handleiding Landelijk Soortonderzoek Broedvogels. SOVON Vogelonderzoek Nederland,, Beek-Ubbergen.

Van Dijk A., Hustings F., Koffijberg K., Van Turnhout C., Van der Weide M., Zoetebier D. & Plate C. 2007. Rare and colonial breeding birds in The Netherlands in 2003-2005. *Limosa* 80, 49-67.

Van Eerden M.R., Drent R.H., Stahl J. & Bakker J.P. 2005. Connecting seas: western Palaearctic continental flyway for water birds in the perspective of changing land use and climate. *Global Change Biology* 11: 894-908.

Van Turnhout C. 2005. The disappearance of the Tawny Pipit *Anthus campestris* as a breeding bird from The Netherlands and Northwest-Europe. *Limosa* 78: 1-14.

Van Turnhout C.A.M., Foppen R.P.B., Leuven R.S.E.W., Siepel H. & Esselink H. 2007. Scale-dependent homogenization: Changes in breeding bird diversity in the Netherlands over a 25-year period. *Biological Conservation* 134: 505-516.

Van Turnhout C.A.M., Willems F., Plate C., Van Strien A., Teunissen W., Van Dijk A.& Foppen R. 2008. Monitoring common and scarce breeding birds in the Netherlands: applying a post-hoc stratification and weighting procedure to obtain less biased population trends. *Journal of Catalan Ornithology* 24: 15-29.

Verstrael T. & Van Dijk A.J. 1997. Foxes or grasses? Breeding Birds of Dutch coastal dunes since 1984. *Limosa* 70: 163-178.

Voslamber B., Van der Jeugd H. & Koffijberg K. 2007. Numbers, trends and distribution of breeding goose populations in the Netherlands. *Limosa* 80: 1-17.

Voslamber B. & Van Turnhout C. 2008. Effects of site management on the Greylag Goose *Anser anser* population of a Dutch river foreland. *Limosa* 81: 74-76.

Wernham C.V., Toms M.P., Marchant J.H., Clark J.A., Siriwardena G.M. & Baillie S.R. (eds.) 2002. The Migration Atlas : movements of the birds of Britain and Ireland. T & AD Poyser, London.

Westoby M., Leishman M.R. & Lord J.M. 1995. On misinterpreting the phylogenetic correction. *Journal of Ecology* 83: 531-534.

Chapter 6

Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats

Christiaan Both, Chris van Turnhout, Rob Bijlsma, Henk Siepel,
Arco van Strien and Ruud Foppen

Published in 2010 in Proceedings of the Royal Society B 277: 1259-1266

Abstract

One consequence of climate change is an increasing mismatch between timing of food requirements and food availability. Such a mismatch is primarily expected in avian long-distance migrants because of their complex annual cycle, and in habitats with a seasonal food peak. Here we show that insectivorous long-distance migrant species in the Netherlands declined strongly (1984-2004) in forests, a habitat characterised by a short spring food peak, but that they did not decline in less seasonal marshes. Also, within generalist long-distance migrant species, populations declined more strongly in forests than in marshes. Forest inhabiting migrant species arriving latest in spring declined most sharply, probably because their mismatch with the peak in food supply is greatest. Residents and short-distance migrants had non-declining populations in both habitats, suggesting that habitat quality did not deteriorate. Habitat-related differences in trends were most likely caused by climate change, because at a European scale long-distance migrants in forests declined more severely in western Europe, where springs have become considerably warmer, as compared to northern Europe, where temperatures during spring arrival and breeding have increased less. Our results suggest that trophic mismatches may have become a major cause for population declines in long-distance migrants in highly seasonal habitats.

Introduction

Climate change has led to general advances in the timing of organismal life-history events (called phenology), but responses at different trophic levels are often dissimilar, leading to a mismatch between the timing of predators and their prey (Stenseth *et al.* 2002, Parmesan & Yohe 2003, Visser & Both 2005, Both *et al.* 2009). This mismatch has resulted in population consequences in a long-distance migratory bird, the Pied Flycatcher *Ficedula hypoleuca*; populations declined strongest in forests with an early and narrow food peak (Both *et al.* 2006). These declines were due to a limited reaction of breeding date to increased spring temperatures, possibly because arrival from the African wintering grounds has not advanced (Both & Visser 2001, Hüppop & Winkel 2006). Recently it was shown that across Europe, migrant species with the least temporal advance in spring arrival date declined most during the last two decades (Møller *et al.* 2008), suggesting that the problem of insufficient adjustment of arrival phenology to climate change has recently become a more general cause of population declines in long-distance migrants. However, we do not expect the problem of a mismatch to be prevalent in all habitats, because habitats are likely to differ in the penalties of being late depending on the seasonality of food availability. Furthermore, not all areas in Europe have experienced the same amount of spring warming during the pre-laying period of migrant birds (Both *et al.* 2004, Both & Te Marvelde 2007), and consequently the detrimental effect of an increased mismatch is only expected in areas with an advanced phenology. Here, we aim to address the generality of an increased trophic mismatch between food availability and requirements as a consequence of climate change, and examine whether this could be one of the causes of the widespread population declines of long-distance migrants in Europe (Sanderson *et al.* 2006, Heldbjerg & Fox 2008).

We predict that long-distance migrants are more vulnerable to climate change than residents and short-distance migrants, because long-distance migrants – while on their distant wintering grounds – cannot predict when spring starts on their breeding grounds (Gwinner 1996). Long-distance migrants have changed their spring arrival times to a lesser extent than short-distance migrants (Strode 2003, Lehikoinen *et al.* 2004, Rubolini *et al.* 2007, Miller-Rushing *et al.* 2008), probably because their departure from the wintering grounds is less plastic. Furthermore, we predict that a trophic mismatch will lead to the largest population declines in habitats with relatively narrow peaks in food availability as compared with less seasonal habitats, because in seasonal habitats fitness consequences of missing the food peak will be more severe (Both *et al.* 2006).

As seasonal habitats we chose temperate forests, because these have a short burst of mainly herbivorous insects that forage on young leaves of deciduous trees before the production of secondary plant compounds starts (Feeny 1970, Buse & Good 1996, Southwood *et al.* 2004, see also Appendix 1). Breeding of forest birds has been shown to be highly synchronised with this food peak (Perrins & McCleery 1989, Charmantier *et al.* 2008, Both *et al.* 2009), and failure to adjust to directional changes in the food peak date can lead to population declines (Both *et al.* 2006). We chose *Phragmites*-dominated marshlands as less seasonal habitats, because these are known to have more extended periods of food abundance, as reflected in the long breeding season of marsh-inhabiting passerines (see e.g. Schaefer *et al.* 2006, Halupka *et al.* 2008, Dyrcz & Halupka

2009). The reason for the longer period of insect abundance is probably because Reed *Phragmites australis* continues growing during spring and summer (Dykyjova *et al.* 1970) and the biomass of herbivorous insects is consequently less peaked (Halupka *et al.* 2008, see Appendix 1 for seasonal changes in insect abundance in Dutch marshes and forests). Additionally, insects emerge from the water over an extended period in spring and summer (Ward 2005). In conclusion, (deciduous) forests have a stronger seasonality in insect availability than marshes (Ostendorf 1993, Schaefer *et al.* 2006), and because the forest insect peak has advanced due to climate change (Buse *et al.* 1999, Visser *et al.* 2006) we expect that forest birds suffer more from climate change than marshland birds if they fail to adapt to the advanced phenology of their habitat.

We have a clear functional hypothesis of how climate change would affect population trends in different habitats, but we also aim to specifically address the question whether climate change is the likely cause of part of the population declines by comparing regions within Europe with a stronger and weaker degree of spring warming. In contrast to western and central Europe, spring temperatures in northern Europe have increased not or only mildly at the time long-distance migrants arrive and lay their eggs (Both & Te Marvelde 2007), and as a result laying dates of resident tit species *Paridae* (Visser *et al.* 2003) and migratory *Ficedula* flycatchers (Both *et al.* 2004) have not advanced in northern Europe. Moreover, arrival dates of many migrant species, including Pied Flycatchers, on their northern European breeding grounds have advanced (Ahola *et al.* 2004, Jonzen *et al.* 2006, Rubolini *et al.* 2007), possibly due to milder conditions during migration (Ahola *et al.* 2004, Both & Te Marvelde 2007), which may allow them to anticipate earlier food phenology. Furthermore, northern forest habitats are characterised by a greater proportion of coniferous trees compared to more southern forests, and conifers have later and less peaked caterpillar abundance than decidous trees (Gibb & Betts 1963, Van Balen 1973, Eeva *et al.* 2000), making northern habitats less seasonal in this aspect of food availability. If the increased mismatch hypothesis due to spring temperature increases were true, we thus expect that forest-breeding long-distance migrants would decline less severely in northern than in western Europe.

Population trends of individual species are likely caused by multiple factors, which could act during the breeding and/or the non-breeding season, and for each species a different set of factors could be responsible depending on their specific ecology (Newton 1998). We do not aim to explain all variance in population trends due to species-specific factors, but aim to study whether there is support for the hypothesis that increased mismatches with food availability as a result of climate change are a more general cause of population decline in highly seasonal habitats and in long-distance migrants. If trophic mismatches increase as a consequence of climate change and hence contribute to population declines, we expect that (1) the effect is stronger in habitats with a stronger seasonality in food availability, (2) the effect is stronger in species that are less able to advance their breeding, i.e. long-distance migrants, and (3) the effect to be stronger in areas with more warming during the laying period of long-distance migrants. We realise that the presented evidence for a trophic mismatch as general cause of the declines is indirect. We therefore will consider two alternative hypotheses to explain the stronger declines of long-distance migrants. The first is that the declines are due to changes at the wintering grounds or during migration, and for this we compare population trends within species for two habitats within the same geographic region, and for two geographic regions. If the decline is driven by factors on the wintering grounds or during migration we do not expect that the decline is stronger in the seasonal compared to the less seasonal environment, nor in the area with more than with less spring warming. The alternative hypothesis is that residents benefit from milder winters, and outcompete the migrants (Berthold *et al.* 1998, Lemoine & Bohning-Gaese 2003, Ahola *et al.* 2007). Under this hypothesis we expect that long-distance migrants decline stronger in areas with a larger increase in numbers of resident species.

Materials and methods

Breeding bird surveys

We compared population trends of birds species between different habitats and regions to test the different hypotheses, using different data sets and methodologies. (1) We analysed differences in trends between two habitats in the Netherlands (marshes and forests) in relation to the migratory strategy of bird species. In this country, spring temperature has increased considerably during the sampling period, the food peak in forests (herbivorous caterpillars) has advanced (Visser *et al.* 2006) and, for some bird species, a clear advance in laying date has been demonstrated (Both *et al.* 2009). (2) We used the fact that trends in spring temperatures differ across Europe to address why forest species have declined more in geographic regions where spring temperatures increased during the period of arrival and laying of long-distance migrants, than in regions where temperatures increased less (Both & Te Marvelde 2007).

For the analysis of differences in trends between marshes and forests in the Netherlands we used data from the Dutch Breeding Bird Monitoring Program (BMP), which has been running since 1984. The data are collected mainly by volunteers and the project is coordinated by SOVON Dutch Centre for Field Ornithology. It is based on territory mapping in fixed study plots (Bibby *et al.* 1997). All common and scarce breeding bird species in the Netherlands are covered. Fieldwork and interpretation methods are highly standardized (Van Dijk 2004). Between March and July all plots (10-500 hectares each) are visited 5-10 times. Size of study plots, as well as number, timing and duration of visits, depend on habitat type and species selection. All birds showing breeding behaviour (e.g. song, display, alarm-calling, food transportations, fledglings) are mapped. Species-specific interpretation criteria are used to determine the number of territories per species at the end of the season (Van Dijk 2004). Interpretation criteria focus on the type of behaviour observed, the number of observations required (depending on species-specific detection probabilities), and the period of observations (to exclude non-breeding migrants). Observers interpret their own field data and submit the results on standard forms. After a first check by SOVON, Statistics Netherlands performs standardized checks by computer routines to detect possible errors. Observers check and if necessary correct these errors. Between 1984 and 2005 a total of 3,671 different study plots were covered in at least two years, ranging from around 300 per year in 1984 to a maximum of almost 1,900 in 2002 (on average 158 (*SE* 6.5) forest, and 84 (*SE* 6.1) marshland plots per year). These data thus give an estimate of the number of breeding pairs per species per plot per year.

Yearly abundance indices were calculated using Poisson regression (log-linear models; McCullagh & Nelder 1989), as implemented in TRIM-software (TRends and Indices for Monitoring data; Gregory *et al.* 2005, Pannekoek & Van Strien 2005). TRIM is a widely used freeware program with an efficient implementation of Poisson regression to analyze time-series counts (log-linear models) (Gregory *et al.* 2005, Van Dyck *et al.* 2009). Poisson regression is also available in the generalized linear model modules of many statistical packages. The estimation method in TRIM is based on generalized estimating equations (GEE; see Liang & Zeger 1986, McCullagh & Nelder 1989), thereby taking into account serial correlation and over-dispersion from Poisson distribution. The models are run for each species, and the estimated number of breeding pairs per plot are used as the dependent variable. Time-series within the same plots rarely covered the entire study period. Before calculating population trends, data from the missing counts were estimated, based on a GEE model with plot identity, year, and the interactions between year and habitat and year and geographic regions within the Netherlands. We thus estimated the population numbers for the missing counts on the basis of the average numbers within the plot when it was counted, and on the trends over the years observed in other plots with similar habitat and within the same region. On the basis of this dataset with both the observed and estimated counts, habitat specific trends were calculated. These trends were calculated based on the yearly indices computed, taking into account their uncertainty, and expressed as ratios of the population present in 2004 compared to 1984. The estimates of the trends are expected to be normally distributed and were treated as dependent variables in a further GLM with identity link and normal errors. The population trends mostly reflect changes in density within plots, rather than changes in the amount of habitat available within the Netherlands, and are thus hardly influenced by habitat destruction or regeneration.

European trends were analysed for two regions that differ in the extent of spring warming and its subsequent effect on the phenology of the species' breeding seasons (Both & Te Marvelde 2007). We consider the temperature during the period when long-distance migrants arrive on their breeding grounds as the most relevant measure of temperature change. This period differs markedly between latitudes, being relatively late in the north. Temperatures in this time window have changed differently between western/central Europe (hereafter called western Europe) and northern Europe, which is strongly reflected in trends in laying date of at least one migratory bird: the Pied Flycatcher (Both *et al.* 2004). Interestingly, bud burst phenology of some tree species has advanced in northern Europe (Nordli *et al.* 2008), which is most likely caused by increasing temperatures in early spring. Since temperatures during arrival and laying have not strongly increased (Both & Te Marvelde 2007), it is likely that insect food peaks have not advanced greatly. Western Europe (clear spring warming) comprises the countries Austria, Belgium, Denmark, former West Germany, Ireland, the Netherlands, Switzerland, United Kingdom and France. Northern Europe (less spring warming, although some variation exists within this large area) compromises Finland, Norway and Sweden. Information on trends of bird species comes from annual breeding bird monitoring schemes in European countries, collated by the Pan-European Common Bird Monitoring scheme (PECBM: http://www.ebcc.info/pecbm.html). National trend data, obtained via spot mapping, territory mapping, line transects or point counts (Gregory *et al.* 2005), are used to produce yearly indices and scheme totals (with standard errors and covariances between years) for each species for each country, using

TRIM (see above). Species-specific trends for western and northern Europe were produced by combining national results for the selected species, weighted for national population size (Van Strien *et al.* 2001, Gregory *et al.* 2005). A problem is that the time-series per country differ in length and, again, that not all study sites are covered in all years within the study periods. TRIM was used in a similar way to cope with missing values as described for the Dutch trends (Van Strien *et al.* 2001).

Species selection

For the analysis of Dutch data we selected all insectivorous passerine species for which we could calculate a population trend for either one habitat or both habitats separately (see Appendix 2). Species were classified as residents, short-distance migrants (not crossing the Sahara) and long-distance migrants, based on data available for the Netherlands (see Appendix 2). Some species are clearly habitat specialists, but other species are more generalist. For the generalist species occurring in both habitats we also compared within-species differences in population trends between the habitats.

For the analyses of European data we selected all species being (1) widespread, (2) forest specialist, (3) small passerine and (4) insectivorous. Furthermore, we selected species occurring both in western and northern Europe (see Appendix 3 for the species selected). This resulted in six long-distance migrants and nine resident/short-distance migrant species for which we have population trends in both regions.

Bird arrival data

One of us (RGB) recorded in every year during the study period the first arriving three males of all migrant species that do not winter in the area, and breed in the forests of Drenthe (northern Netherlands, 6° 17' E, 52° 52' N). The area was visited on an daily basis during spring and summer (from late February onwards). The study area is forested with conifers and interspersed with heaths and deciduous woodland. Arrival dates of males was monitored by observing singing birds, and given the intensity of the observer's presence, are probably accurate. For instance, when birds were seen before any song was heard, singing was almost always recorded later the same day.

Results

Comparing Dutch population trends between marshes and forests

Between 1984-2004 all species of long-distance migrants in forests declined (on average by 38%), whereas no systematic declines were found in marsh-inhabiting long-distance migrants (average 158% increase), nor in short-distance migrants or residents in both habitats (Figure 1a, see Appendix 2 for species specific data). Intraspecific trends for generalist species living in both marshland and forest gave a similar pattern: long-distance migrants showed a larger decline in forests than in marshes, whereas populations increased in residents and short-distance migrants in both habitats, although stronger in marshes than in forests (Figure 1b). Furthermore, population trends correlated with average spring arrival date of migrant species in forests: species with late spring arrival (such as Wood Warbler *Phylloscopus sibilatrix*,

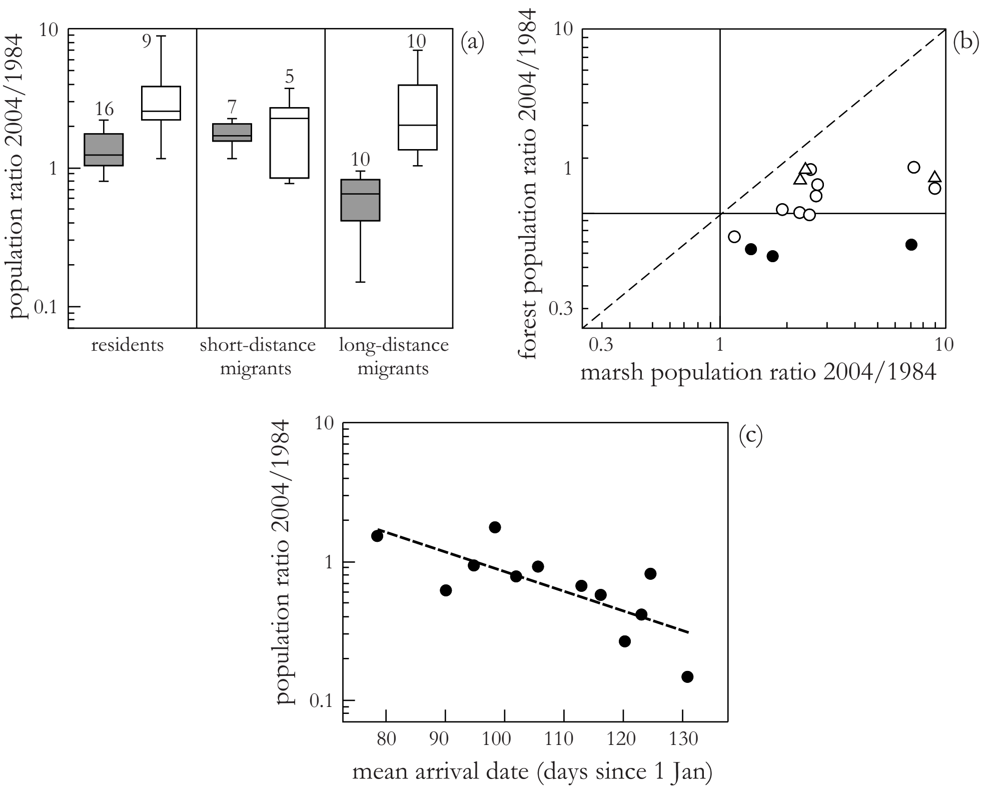


Figure 1. (a) Population trends of passerines in Dutch forests and marshlands between 1984 and 2004 for species with different migration behaviour. Results GLM: interaction habitat×migration status: $F_{2,51}=6.16$, $p=0.004$ (shaded boxes: forest, open boxes: marsh). (b) Within-species comparison of population trends in forests and marshes, showing that within species long-distance migrants decline stronger in forests than in marshes (open triangles: residents, open dots: short-distance migrants, solid dots: long-distance migrants). GLM: dependent: forest growth rate, explanatory variables: marsh growth rate: $F_{1,11}=7.08$, $p=0.022$, migration status: $F_{2,11}=18.49$, $p<0.001$, interaction: $F_{2,9}=0.82$, $p=0.47$. (c) Population trends of migratory passerines living in forests and their spring arrival date on the breeding grounds. Later arriving species declined most (GLM: mean arrival date: $F_{1,10}=12.41$, $p=0.006$). Population trends are expressed as the ratio of the densities present in 2004 relative to 1984, which is based on the annual population growth rates (1=stable, 0.1 is a 90% decline, 10 is a 10-fold increase). Population trends are from the Dutch Breeding Bird Monitoring Program (see Appendix 2 for details). Arrival data are based on the first three males arriving annually in a study site in Drenthe (northern Netherlands).

Icterine Warbler *Hippolais icterina* and Spotted Flycatcher *Muscicapa striata*) showed a stronger decline (up to 85%) than earlier arriving species (Figure 1c). Our data are thus consistent with the hypothesis that long-distance migrants declined as a result of climate change because they have adapted insufficiently to maintain the synchrony with the advanced food peak in a seasonal habitat.

Comparing population trends between western and northern Europe

We found that for five out of six species of forest-breeding long-distance migratory passerines, the decline in numbers was greater in western than in northern Europe (Figure 2, paired t-test: $t_5=3.11$, $p=0.027$). The average decline in western Europe was 35%, in northern Europe 9%. Analysis of trends within species showed significant

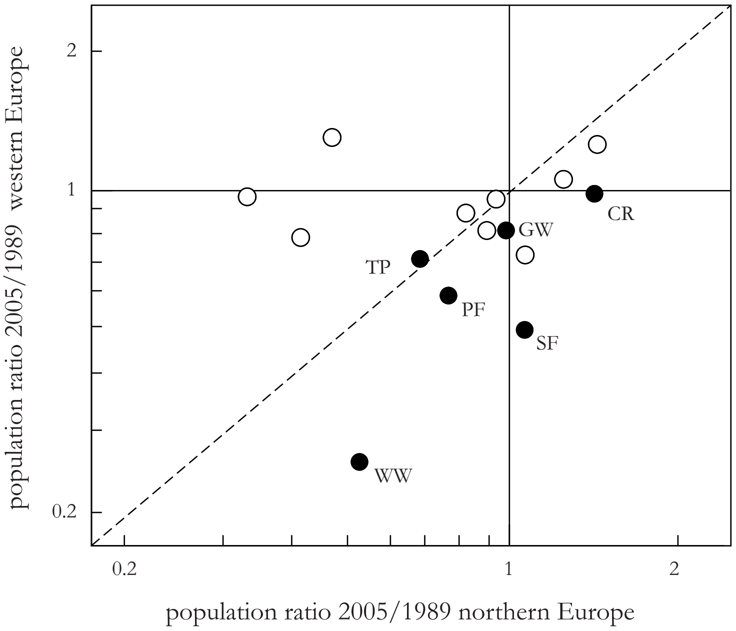


Figure 2. Population trends (1989-2005) of 15 species of forest breeding passerines in northern and western Europe, separated for long-distance migrants (solid dots) and residents and short-distance migrants (open dots). Only species are used for which we had trends in both regions, and each dot is a pair of species' population trends. The x=y line is dotted and species that fall below this line fare worse in western compared to northern Europe. Population trends are from the Pan-European Common Bird Monitoring Scheme (see Appendix 3 for details). For migrants common species names are given in abbreviations: TP: Tree Pipit, CR: Common Redstart, WW: Wood Warbler, GW: Garden Warbler, PF: Pied Flycatcher, SF: Spotted Flycatcher.

interactions of area×year in four out of the six species (see Appendix 3: stronger decline in western Europe: Common Redstart *Phoenicurus phoenicurus*, Wood Warbler, Garden Warbler *Sylvia borin*, Pied Flycatcher, Spotted Flycatcher). The reason is probably not that wintering grounds differ largely between northern and western European breeding populations for these species: recovery positions largely overlap in Africa for Common Redstarts, Garden Warblers and Pied Flycatchers, but less so for Spotted Flycatchers; for Tree Pipit *Anthus trivialis* and Wood Warbler recovery data from sub-Saharan Africa are too few to outline migratory connectivity (Zwarts *et al.* 2009). By contrast, for resident and short-distance migrant species we found no difference in population trends between western and northern Europe (paired-t-test: $t_8=-0.95$, $p=0.37$). The average decline in western Europe was 3%, in northern Europe 15%, suggesting that the forest habitat did not deteriorate to a greater extent in western than in northern Europe over this period of time (see Appendix 3 for individual species trends).

Discussion

Long-distance migrants are relatively inflexible to respond to advances in spring phenology of their breeding habitat (Gwinner 1996). Therefore, climate change is expected to lead to increased trophic mismatches, resulting in declining population sizes (Møller *et al.* 2008). We indeed found that in the Netherlands long-distance migrants in seasonal forests declined much stronger than in less seasonal marshes (both within and between species), whereas no difference in trends between habitats was found for residents and short-distance migrants. Consistent with the mismatch hypothesis, the effect was strongest in species arriving latest in spring. Additional indications that temperature changes in spring are a likely explanation comes from the comparison of population trends between European regions that differ in spring temperature change: long-distance migrants declined stronger in western Europe, where spring warming is prevalent, than in northern Europe, where temperatures around arrival and laying increased only mildly (Visser *et al.* 2003, Both *et al.* 2004). Apart from the weaker advance in the onset of spring in northern compared to western Europe, some northern long-distance migrants have managed to advance their spring arrival to a greater extent than western European birds (Hüppop & Winkel 2006). They may profit from increased temperatures during migration in Europe, whereas birds breeding at more southern latitudes migrate earlier and temperatures during migration for these populations have not increased (Both & Te Marvelde 2007). Furthermore, forest habitats at higher latitudes are likely to have a broader food peak, because they contain higher proportions of coniferous trees, which have lower, but more extended food peaks (Gibb & Betts 1963, Eeva *et al.* 2000). The stronger declines of long-distance migrant populations in the region with more spring warming and more narrow food peaks thus strengthens the conclusion that climate change is the underlying cause.

In contrast to our analyses, Jones & Cresswell (2010) concluded that trophic mismatches on the breeding grounds could explain population declines of long-distance migrants in the nearctic, but not in the palearctic. The apparent contrast between these analyses most likely originates from the fact that these authors did not distinguish between habitats of different seasonality, nor did they acknowledge the spatial variation in the strength of spring warming within continents.

The difference between forests and marshes was partly due to an increase in marsh-inhabiting long-distance migrants, which may be a direct consequence of climate change: Reed Warblers *Acrocephalus scirpaceus* advanced the start, but also extended the length of the breeding season during the last decades, allowing more pairs to raise two successful broods during the season (Halupka *et al.* 2008, see also Dyrcz & Halupka 2009). In contrast, some forest breeding passerines shortened their breeding season in response to climate change, partly due to less birds producing second broods (Visser *et al.* 2003, Husby *et al.* 2009) and also because the laying date distribution of first broods became narrower (Both *et al.* 2009). This may not only be due to a stronger advance of the food peak date relative to the bird breeding dates, but also due to caterpillar peaks becoming narrower at high temperatures (Buse *et al.* 1999). If seasonal habitats therefore become even more seasonal with narrower food peaks, this may seriously negatively affect insectivorous species, and may explain why especially late arriving species suffered most.

Two other, not mutually exclusive, hypotheses have been put forward to explain the vulnerability of long-distance migrants to climate change: (1) migrants face stronger competition from residents because resident populations increase owing to milder winters (Berthold *et al.* 1998, Lemoine & Bohning-Gaese 2003, Ahola *et al.* 2007), (2) climate change leads to a deterioration of wintering habitats (Peach *et al.* 1991, Sillett *et al.* 2000). The data do not support the first hypothesis, because residents increased in both marshes and forests, whereas migrants only declined in forests. Furthermore, at the European scale we did not find that the resident populations increased more in the region with a stronger decline in long-distance migrants. More support exists for the second hypothesis: migrant population sizes are often tightly correlated with climate-related ecological conditions at the wintering sites (Newton 2004). Also in our data we found some support for this, because population trends within the six long-distance migrant species tended to be positively correlated between northern and western Europe (r=0.752, n=6, p=0.085, Figure 2). This suggests that there may be a common cause determining the between-species correlation in population trends, which may well be habitat degradation and/or climate-related habitat change at the shared wintering grounds (Sanderson *et al.* 2006).

That effects in Africa have a large impact on breeding population numbers in Europe has been shown especially for species wintering in the Sahel, of which the numbers plummeted during the severe droughts in the 1970s and 1980s (Baillie & Peach 1992, Foppen *et al.* 1999, Zwarts *et al.* 2009). The start of the monitoring program in the Netherlands coincided with the end of this drought-related population crash, affecting initial population growth rates in several species. The subsequent partial recoveries can be attributed to improvement of rainfall figures in the Sahel, as recorded in Common Whitethroat *Sylvia communis* and Sedge Warbler *Acrocephalus schoenobaenus*. Also, Common Redstart populations crashed as a result of the droughts (Zwarts *et al.* 2009), but interestingly their partial recovery since then in northern Europe is not mirrored by western European populations (see Appendix 3).

Our data support the hypothesis that during the last two decades climate change has contributed to the decline of long-distance migrant bird species inhabiting highly seasonal habitats. Does this mean that these species will continue to suffer while resident species will be unaffected by climate change? Long-distance migrants may adjust their migratory timing, by either phenotypic plasticity and/or an evolutionary response, allowing them to restore the synchrony with their breeding environment (Jonzen *et al.* 2006). Until now there is little evidence for an evolutionary response, but it is likely to happen in the future, although it may still be insufficient to track the advancement of spring. In the past these species have been able to survive drastic climatic fluctuations, but at present habitat loss at the wintering grounds and during migration has put long-distance migrants already under pressure (Sanderson *et al.* 2006), which may reduce their capacity to respond to the ongoing effects of climate change. Insufficient adjustment to the advanced food peak for raising offspring is not restricted to long-distance migrants, but is also observed in one resident Great Tit *Parus major* population (Visser *et al.* 1998), although another great tit population adjusted sufficiently (Charmantier *et al.* 2008). Reduced reproduction in residents is probably compensated by higher survival owing to milder winters and density dependent feedbacks. Therefore, population sizes of these species remain rather stable or even increase. However, a further advance of the food peak may reduce reproduction to such an extent that also resident populations will decline, especially if the food peak narrows further due to climate change (Buse *et al.* 1999). More, in general, we expect that all habitats characterised by a short burst of food availability, such as temperate meadows (Schekkerman & Beintema 2007) and tundras (Tulp & Schekkerman 2008), are probably inhabited by species that require a good temporal match between food requirements and abundance, and hence are susceptible to climate change.

Acknowledgements

This work would not have been possible without the efforts of many thousands of volunteer birdwatchers across Europe, who gathered the trend data. SOVON coordinators were responsible for processing and analysing the Dutch data, of whom we want to mention Arend J. van Dijk in particular. The authors wish to thank the European Bird Census Council for providing the data on European trends: international coordinators Petr Voříšek and Alena Klvaňová and the national coordinators for Austria (Norbert Teufelbauer & Michael Dvorak), Belgium (Jean-Paul Jacob & Anne Weiserbs), Denmark (Henning Heldbjerg & Michael Grell), Finland (Risto Väisänen), France (Frédéric Jiguet), Germany (Martin Flade & Johannes Schwarz), Ireland (Olivia Crowe), Norway (Magne Husby), Sweden (Åke Lindström), Switzerland (Hans Schmid & Verena Keller) and the United Kingdom (David Noble). Adriaan Gmelig Meyling helped computing the trend data. Sandra Bouwhuis collected the forest insect samples.

References

Ahola M., Laaksonen T., Sippola K., Eeva T., Rainio K. & Lehikoinen E. 2004. Variation in climate warming along the migration route uncouples arrival and breeding date. *Global Change Biology* 10: 1-8.

Ahola M. P., Laaksonen T., Eeva T. & Lehikoinen E. 2007. Climate change can alter competitive relationships between resident and migratory birds. *Journal of Animal Ecology* 76: 1045-1052.

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

Berthold P., Fiedler W., Schlenker R. & Querner U. 1998. 25-year study of the population development of Central European songbirds: A general decline, most evident in long-distance migrants. *Naturwissenschaften* 85: 350-353.

Bibby C.J., Burgess N.D. & Hill D.A. 1997. Bird Census Techniques. London: Academic Press.

Bijlsma R.G., Hustings F. & Camphuysen C.J. 2001. Algemene en schaarse vogels van Nederland (Avifauna van Nederland 2). Haarlem/Utrecht: GMB Uitgeverij/KNNV Uitgeverij.

Both C., Artemyev A.A., Blaauw B., Cowie R.J., Dekhuijzen A.J., Eeva T., Enemar A., Gustafsson L., Ivankina E.V., Järvinen A., Metcalfe N.B., Nyholm N.E.I., Potti J., Ravussin P.-A., Sanz J.J., Silverin B., Slater F.M., Sokolov L.V., Winkel W., Wright J., Zang H. & Visser M. E. 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society of London B* 271: 1657-1662.

Both C., Bouwhuis S., Lessells C.M. & Visser M.E. 2006. Climate change and population declines in a long distance migratory bird. *Nature* 441: 81-83.

Both C. & Te Marvelde L. 2007. Climate change and timing of avian breeding and migration throughout Europe. *Climate Research* 35: 93-105.

Both C., Van Asch M., Bijlsma R.G., Van den Burg A.B. & Visser M.E. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations. *Journal of Animal Ecology* 78: 73-83.

Both C. & Visser M.E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411: 296-298.

Buse A., Dury S.J., Woodburn R.J.W., Perrins C.M. & Good J.E.G. 1999. Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Functional Ecology* 13 (Suppl 1), 74-82.

Buse A. & Good J.E.G. 1996. Synchronisation of larval emergence of winter moth (*Operophtera brumata* L) and budburst in pedunculate oak (*Quercus robur* L) under simulated climate change. *Ecological Entomology* 21: 335-343.

Charmantier A., McCleery R.H., Cole L.R., Perrins C., Kruuk L.E.B. & Sheldon B.C. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* 320: 800-803.

Dykyjova D., Ondok J.P. & Priban K. 1970. Seasonal changes in productivity and vertical structure of reed-stands (*Phragmites communis* Trin). *Photosynthetica* 4: 280-287.

Dyrcz A. & Halupka L. 2009. The response of the Great Reed Warbler *Acrocephalus arundinaceus* to climate change. *Journal of Ornithology* 150: 39-44.

Eeva T., Veistola S. & Lehikoinen E. 2000. Timing of breeding in subarctic passerines in relation to food availability. *Canadian Journal of Zoology* 78: 67-78.

Feeny P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565-581.

Foppen R., Ter Braak C.J.F., Verboom J. & Reijnen R. 1999. Dutch sedge warblers *Acrocephalus schoenobaenus* and West-African rainfall: empirical data and simulation modelling show low population resilience in fragmented marshlands. *Ardea* 87: 113-127.

Gibb J.A. & Betts M.M. 1963. Food and Food-Supply of Nestling Tits (*Paridae*) in Breckland Pine. *Journal of Animal Ecology* 32: 489-533.

Gregory R.D., Van Strien A., Vorisek P., Gmelig Meyling A.W., Noble D.G., Foppen R.P.B. & Gibbons D.W. 2005. Developing indicators for European birds. *Philosophical Transactions of the Royal Society London B* 360: 269-288.

Gwinner E. 1996. Circannual clocks in avian reproduction and migration. *Ibis* 138: 47-63.

Halupka L., Dyrcz A. & Borowiec M. 2008. Climate change affects breeding of reed warblers *Acrocephalus scirpaceus*. *Journal of Avian Biology* 39: 95-100.

Heldbjerg H. & Fox T. 2008. Long-term population declines in Danish trans-Saharan migrant birds. *Bird Study* 55: 267-279.

Hüppop O. & Winkel W. 2006. Climate change and timing of spring migration in the long-distance migrant *Ficedula hypoleuca* in central Europe: the role of spatially different temperature changes along migration routes. *Journal of Ornithology* 147: 326-343.

Husby A., Kruuk L.E.B. & Visser M.E. 2009. Decline in the frequency and benefits of multiple brooding in great tits as a consequence of a changing environment. *Proceedings of the Royal Society B* 276: 1845-1854.

Jones T. & Cresswell W. 2010. The phenology mismatch hypothesis: are declines of migrant birds linked to uneven global climate change? *Journal of Animal Ecology* 210: 98-108.

Jonzen N., Lindèn A., Ergon T., Knudsen E., Vik J.O., Rubolini D., Piacentini D., Brinch C., Spina F., Karlsson L., Stervander M., Andersson A., Waldenström J., Lehikoinen A., Edvardsen E., Solvang R. & Stenseth N. C. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312: 1959-1961.

Lehikoinen E., Sparks T.H. & Zalakevicius M. 2004. Arrival and departure dates. *Advances in Ecological Research* 35: 1-31.

Lemoine N. & Bohning-Gaese K. 2003. Potential impact of global climate change on species richness of long-distance migrants. *Conservation Biology* 17: 577-586.

Liang K.Y. & Zeger S.L. 1986. Longitudinal data analysis using generalized linear models. *Biometrika* 73: 13-22.

McCullagh P. & Nelder J.A. 1989. Generalized linear models, 2nd ed. London: Chapman and Hall.

Miller-Rushing A.J., Lloyd-Evans T.L., Primack R.B. & Satzinger P. 2008. Bird migration times, climate change, and changing population sizes. *Global Change Biology* 14: 1959-1972.

Møller A.P., Rubolini D. & Lehikoinen A. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences* 105: 16195-16200.

Newton I. 1998. Population limitation in birds. New York: Academic Press.

Newton I. 2004. Population limitation in migrants. *Ibis* 146: 197-226.

Nordli O., Wielgolaski F.E., Bakken A.K., Hjeltnes S.H., Mage F., Sivle A. & Skre O. 2008. Regional trends for bud burst and flowering of woody plants in Norway as related to climate change. *International Journal of Biometeorology* 52: 625-639.

Ostendorf W. 1993. Schilf als lebensraum. *Beih. Veroff. Naturschutz Landschaftspflege Bad. -Wurtt.* 68: 173-280.

Pannekoek J. & Van Strien A. 2005. TRIM 3 Manual. Trends and indices for monitoring data. Research paper 0102. Voorburg, the Netherlands: Statistics Netherlands, CBS. Available from http://www.ebcc.info/index.php?ID=13.

Parmesan C. & Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.

Peach W. J., Baillie S.R. & Underhill L.G. 1991. Survival of British Sedge warblers *Acrocephalus schoenobaenus* in relation to West African rainfall. *Ibis* 133: 300-305.

Perrins C.M. & McCleery R.H. 1989. Laying dates and clutch size in the Great Tit. *Wilsons Bulletin* 101: 236-253.

Rogers L.E., Hinds W.T. & Buschbom R.L. 1976. A general weight vs. length relationship for insects. *Annals of the Entomological Society of America* 69: 389-395.

Rogers L.E., Buschbom R.L. & Watson C.R. 1977. Length-weight relationships of shrub-steppe invertebrates. *Annals of the Entomological Society of America* 70: 51-53.

Rubolini D., Møller A.P., Rainio K. & Lehikoinen E. 2007. Assessing intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Climate Research* 35: 135-146.

Sanderson F.J., Donald P.F., Pain D.J., Burfield I.J. & Van Bommel F.P.J. 2006. Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation* 131: 93-105.

Schaefer T., Ledebur G., Beier J. & Leisler B. 2006. Reproductive responses of two related coexisting songbird species to environmental changes: global warming, competition, and population sizes. *Journal of Ornithology* 147: 47-56.

Schekkerman H. & Beintema A.J. 2007. Abundance of invertebrates and foraging success of Black-tailed Godwit *Limosa limosa* chicks in relation to agricultural grassland management. *Ardea* 95: 39-54.

Siepel H., Meijer J., Mabelis A.A. & Den Boer M.H. 1989. A tool to assess the influence of management practices on the surface macrofauna of grasslands. *Journal of Applied Entomology* 108: 271-290.

Sillett T.S., Holmes R.T. & Sherry T.W. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288: 2040-2042.

Southwood T.R.E., Wint G.R.W., Kennedy C.E.J. & Greenwood S.R. 2004. Seasonality, abundance, species richness and specificity of the phytophagous guild of insects on oak (*Quercus*) canopies. *European Journal of Entomology* 101: 43-50.

Stenseth N.C., Mysterud A., Ottersen G., Hurrell J.W., Chan K.-S. & Lima M. 2002. Ecological effects of climate fluctuations. *Science* 297: 1292-1296.

Strode P.K. 2003. Implications of climate change for North American wood warblers (*Parulidae*). *Global Change Biology* 9: 1137-1144.

Tulp I. & Schekkerman H. 2008. Has prey availability for arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. *Arctic* 61: 48-60.

Van Balen J.H. 1973. A comparative study of the breeding ecology of the Great tit *Parus major* in different habitats. *Ardea* 61: 1-93.

Van Dijk A.J. 2004. Handleiding Broedvogel Monitoring Project. Beek-Ubbergen: SOVON Vogelonderzoek Nederland.

Van Strien A. J., Pannekoek J. & Gibbons D. W. 2001. Indexing European bird population trends using results of national monitoring schemes: a trial of a new method. *Bird Study* 48: 200-213.

Visser M.E., Van Noordwijk A.J., Tinbergen J.M. & Lessells C.M. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London B* 265: 1867-1870.

Visser M. E., Adriaensen F., Van Balen J.H., Blondel J., Dhondt A.A., Van Dongen S., Du Feau C., Ivankina E.V., Kerimov A.B., De Laet J., Matthysen E., McCleery R.H., Orell M. & Thomson D. L. 2003. Variable responses to large-scale climate change in European *Parus* populations. *Proceedings of the Royal Society of London B* 270: 367-372.

Visser M.E. & Both C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society of London B* 272: 2561-2560.

Visser M.E., Holleman L.J.M. & Gienapp P. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* 147: 167-172.

Ward M.P. 2005. Habitat selection by dispersing yellow-headed blackbirds: evidence of prospecting and the use of public information. *Oecologia* 145: 650-657.

Zwarts L., Bijlsma R.G., Van der Kamp J. & Wymenga E. 2009. Living on the edge: Wetlands and birds in a changing Sahel. Zeist: KNNV Uitgeverij.

Appendix 1. Insect sampling in forests and marshes: methods and data.

The aim of this analysis is to show whether insect availability shows different temporal patterns during the spring-summer period in forests compared to marshland. There is already some evidence for this in literature, but we gathered additional data to confirm this pattern. This strengthens the power of our comparison between a habitat which we consider highly seasonal (forest) and less seasonal (marshland) in temporal insect abundance. We do not make any statements on whether the seasonality may have changed differently in the different habitats, but we can give a general notion of seasonality, because in both habitats data were collected in several replicates.

Data collection

Insect biomass was sampled in reedbeds in 1992 in two peatlands, and in 2003 in nine forests across the Netherlands. Although methods of insect sampling necessarily differed between peatlands and forests, we aim to compare seasonality of insect abundance in these two habitats, rather than comparing absolute abundances.

The lowland peatlands were investigated regarding species composition and abundance of invertebrates. Several vegetation types were incorporated in this research, but here we only present data from reedbeds. In total 50 sites, 18 of those being reedbeds, have been sampled using emergence traps (as described in Siepel *et al.* 1989, but we used larger ones here: surface 1 m^2 , height 1.4 m, in higher vegetations with an extra base element of 1 m). Emergence traps give a good estimate on the abundance of species. Four types of reedbeds (young, dominated by herbs, dominated by *Sphagnum*, and not inundated) were sampled at two sites in the northern Netherlands and two sites in the central part. Inundated reedbeds were only sampled in the northern Netherlands (twice). From May to September traps were operated during four periods of two consecutive weeks each, and samples were collected on a weekly basis. The first two periods covered the main breeding season of marshland birds. Insects were identified to species level if possible. Biomass was measured either directly by dry weight in abundant species, or by interference using length-dry weight ratios in less abundant species (Rogers *et al.* 1976, Rogers *et al.* 1977). We then calculated dry weight per m^2 and vegetation type. As specialist marshland birds mainly forage in reedbeds, we focussed on this vegetation type, but the seasonal pattern of relative insect abundance is very similar for other sampled marshlands (like several types of wet grasslands and carrs). We averaged biomass for each sampling period over all areas. Means are presented with their SD.

In 2003 we sampled forest insects in nine areas by using three methods (see Both *et al.* (2006) for selection of the areas). In each area we sampled caterpillar abundance with frass collectors under two Pendiculate Oaks *Quercus robur*. Frass was collected approximately once every five days during the breeding season of pied flycatchers, from late April until mid-June. In some areas with the highest caterpillar biomass we started sampling at, or just after the caterpillar peak (Both *et al.* 2006), hence the lack of biomass build-up in Figure A1c. We also sampled ground-living insects with five pitfall traps in each of the nine areas, located along a transect with two meters between traps. Pitfall traps were emptied once every five days, and insects were stored in alcohol and later sorted by family and size (<2 mm, 2-5 mm, 5-10 mm, >10 mm). Biomass of all insects was calculated on the basis of length-weight relationships, and values were calculated as mg/day for all five traps. Data from the nine areas were averaged as they produced similar patterns with insect abundance peaking at the end of May and declining afterwards. The third method of sampling was restricted to five areas and involved the use of single malaise traps in the main habitat of Pied Flycatchers. Traps were emptied once every five days, and sorting procedures were similar as for pitfall traps, producing values of insect biomass per trap per 24 hr. Data from the five areas were averaged, but they all give quantitatively similar patterns, showing a rise to a peak in insect abundance at the end of May and a decline afterwards. No samples were collected after mid-June, when all sampling techniques showed declining insect availability. The values for the three different methods cannot be compared quantitatively.

Seasonality of insect availability in two habitats

In this section we show that forests and marshes differ in the seasonality of insect abundance based on data from the Netherlands, backed-up with published data from other study sites. Forests are known to have a short burst of mainly herbivorous insects that forage on young leaves of deciduous trees before the production of secondary plant compounds starts (Feeny 1970, Southwood *et al.* 2004). Our measurements in nine forests in the Netherlands corroborated this pattern: insect availability peaked during a couple of weeks in May and June, and declined thereafter (Figure A1a-c) (Buse *et al.* 1999). Caterpillars were most numerous among the insects, but caterpillar peaks differed between sampling areas, and areas with the earliest peak also had the highest peak (Both *et al.* 2006). The peak of ground-living and flying insects occurred two to three weeks later than the caterpillar peak (Figure A1a-b).

We chose marshlands as the less seasonal habitat. Marshland is known to have a more extended period of food abundance, reflected in the long breeding season of marsh-inhabiting passerines (see e.g. Halupka *et al.* 2008). Indeed, our samples from 50 sites in Dutch marshes showed a gradual increase in insect abundance from May until early August (Figure A1d). The reason for this longer period of insect abundance is probably because Reed *Phragmites australis* continues growing during spring and summer (Dykyjova *et al.* 1970), and the biomass of herbivorous insects is consequently less peaked (Halupka *et al.* 2008). Additionally, insects emerge from the water over an extended period in spring and summer (Ward 2005). In conclusion, forests have a stronger seasonality in insect availability than marshes (Ostendorf 1993, Schaefer *et al.* 2006).

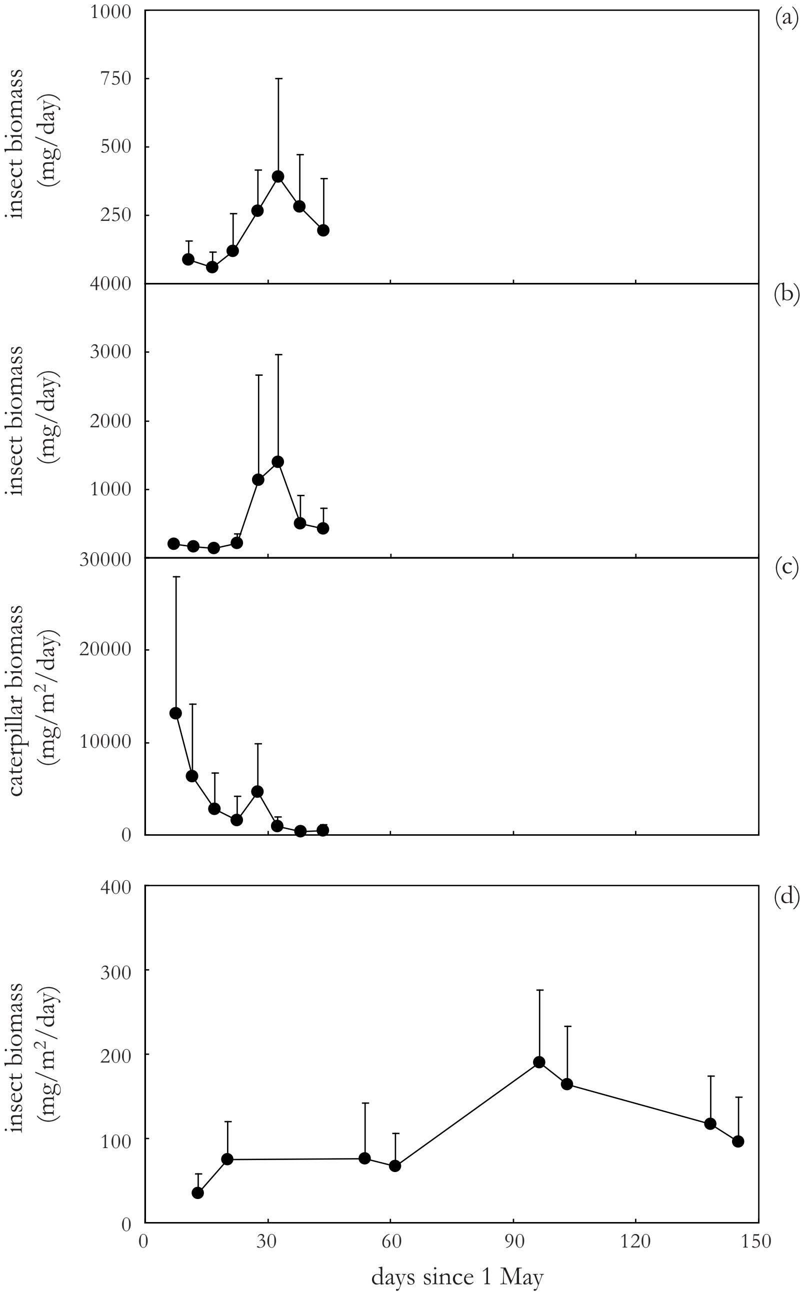


Figure A1. Insect biomass in Dutch forests (a-c) and marshlands (d) during spring and summer. In forests three methods of insect sampling were used: (a) pitfall traps for capturing ground-living insects, (b) malaise traps for capturing flying insects, and (c) frass collectors to measure caterpillar abundance. In the marshes emergence traps were used (d), which sample insects that are present in the vegetation at the moment of placing the trap, as well as insects emerging from the soil or water covered by the trap. The different methods corrupt quantitative comparisons within and across habitats, and we mainly aim to show seasonal variations in insect biomass between habitats. Forests were sampled from late April to mid-June, and marshes between mid-May to mid-September.

Appendix 2. Species population trends in Dutch marshes and forests. Data on population trends between 1984-2004 in Dutch passerines inhabiting forest and marshland, based on the Dutch Breeding Bird Monitoring Program (SOVON/CBS, NEM). Migratory status: RES: resident, SDM: short-distance migrant, LDM: long-distance migrant (Bijlsma *et al.* 2001). Arrival: mean spring arrival of first three observations over 1984-2004, for species not wintering in the Netherlands and breeding in forests. Growth: annual population growth rate, based on the Dutch Breeding Bird Monitoring Program. 2004/1984: ratio of estimated population densities between 1984-2004, which is the annual growth rate to the power 21.

Species	Migratory status	Arrival mean	Forest			Marsh		
			Growth	*SE*	*2004/1984*	*Growth*	*SE*	*2004/1984*
Tree Pipit *Anthus trivialis*	LDM	94.8	0.997	0.004	0.94			
Winter Wren *Troglodytes troglodytes*	RES	.	1.027	0.002	1.72	1.047	0.003	2.52
Hedge Accentor *Prunella modularis*	RES	.	1.000	0.003	1.00	1.042	0.005	2.26
European Robin *Erithacus rubecula*	SDM	.	1.023	0.002	1.59	1.042	0.006	2.26
Common Nightingale *Luscinia megarhynchos*	LDM		0.980	0.006	0.67	1.102	0.012	7.00
Bluethroat *Luscinia svecica*	LDM					1.031	0.004	1.83
Common Redstart *Phoenicurus phoenicurus*	LDM	101.9	0.988	0.004	0.79			
Eurasian Blackbird *Turdus merula*	RES	.	1.017	0.002	1.40	1.051	0.004	2.71
Song Thrush *Turdus philomelos*	SDM	.	1.026	0.003	1.68			
Mistle Thrush *Turdus viscivorus*	SDM	.	1.007	0.004	1.16			
Comm Grasshopper-Warbler *Locustella naevia*	LDM					1.046	0.005	2.46
Savi's Warbler *Locustella luscinioides*	LDM					1.014	0.005	1.32
Sedge Warbler *Acrocephalus schoenobaenus*	LDM					1.071	0.005	3.92
Marsh Warbler *Acrocephalus palustris*	LDM					1.001	0.004	1.03
Eurasian Reed-Warbler *Acrocephalus scirpaceus*	LDM					1.003	0.003	1.06
Icterine Warbler *Hippolais icterina*	LDM	131.0	0.910	0.009	0.15			
Common Whitethroat *Sylvia communis*	LDM					1.073	0.005	4.10
Garden Warbler *Sylvia borin*	LDM	116.2	0.973	0.003	0.58	1.027	0.003	1.71
Blackcap *Sylvia atricapilla*	SDM	98.4	1.029	0.002	1.76	1.067	0.005	3.67
Wood Warbler *Phylloscopus sibilatrix*	LDM	120.3	0.937	0.005	0.27			
Common Chiffchaff *Phylloscopus collybita*	SDM	78.4	1.022	0.002	1.54	1.044	0.003	2.37
Willow Warbler *Phylloscopus trochilus*	LDM	90.0	0.977	0.002	0.63	1.016	0.003	1.38
Goldcrest *Regulus regulus*	RES	.	1.044	0.004	2.35			
Firecrest *Regulus ignicapillus*	SDM	.	1.039	0.007	2.14			
Spotted Flycatcher *Muscicapa striata*	LDM	123.1	0.957	0.004	0.42			
Pied Flycatcher *Ficedula hypoleuca*	LDM	105.6	0.996	0.005	0.92			
Long-tailed Tit *Aegithalos caudatus*	RES	.	1.029	0.004	1.76	1.103	0.009	7.13
Marsh Tit *Poecile palustris*	RES	.	1.010	0.004	1.21			
Willow Tit *Poecile montana*	RES	.	0.984	0.004	0.73	1.008	0.005	1.17
Crested Tit *Lophophanes cristatus*	RES	.	1.011	0.004	1.25			
Coal Tit *Periparus ater*	RES	.	1.002	0.004	1.03			
Blue Tit *Cyanistes caeruleus*	RES	.	1.010	0.002	1.23	1.050	0.004	2.65
Eurasian Great Tit *Parus major*	RES	.	1.002	0.002	1.03	1.032	0.004	1.89
Wood Nuthatch *Sitta europaea*	RES	.	1.030	0.003	1.79			
Short-toed Treecreeper *Certhia brachydactyla*	RES	.	1.027	0.002	1.71			
Eurasian Golden-Oriole *Oriolus oriolus*	LDM	124.6	0.990	0.005	0.82			
Eurasian Jay *Garrulus glandarius*	RES	.	0.999	0.002	0.97	1.047	0.007	2.49
Chaffinch *Fringilla coelebs*	RES	.	1.015	0.002	1.35	1.115	0.008	8.80
Eurasian Linnet *Carduelis cannabina*	SDM	.				0.987	0.005	0.77
Eurasian Bullfinch *Pyrrhula pyrrhula*	RES	.	1.009	0.005	1.19			
Hawfinch *Coccothraustes coccothraustes*	SDM	.	1.042	0.005	2.27			
Reed Bunting *Emberiza schoeniclus*	SDM	.				0.993	0.003	0.87

Appendix 3. Species population trends for northern and western Europe. Population trends in species of European passerines for which we have data in both northern (Norway, Sweden, Finland) and western Europe (Austria, Belgium, Denmark, former West-Germany, Ireland, the Netherlands, Switzerland, United Kingdom, France) in 1989-2005. The analysis is performed on $\log^{10}$-transformed population estimates, in a GLM with year as a covariate and area as factor. If the interaction was significant the *F*-values and *p*-values for the main effects are given in the model including the interaction term (degrees of freedom for the interaction term are always 1,30). If the interaction term is non-significant the *p*-values refer to a back-wards elimination procedure.

Species		Northern Europe			Western Europe			Year		Area		Area×Year	
		Growth	*SE*	*Ratio 2005/1989*	*Growth*	*SE*	*Ratio 2005/1989*	*F*	*p*	*F*	*p*	*F*	*p*
Tree Pipit *Anthus trivialis*	LDM	0.978	0.002	0.685	0.979	0.009	0.708	23.6	0.000	30.7	0.000	0.048	0.83
Common Redstart *Phoenicurus phoenicurus*	LDM	1.021	0.002	1.420	0.999	0.016	0.978	0.06	0.80	0.41	0.53	8.53	**0.007**
Wood Warbler *Phylloscopus sibilatrix*	LDM	0.964	0.003	0.531	0.923	0.017	0.258	398	0.000	15.8	0.001	56.6	**0.000**
Garden Warbler *Sylvia borin*	LDM	0.999	0.002	0.975	0.989	0.006	0.821	4.37	0.044	0.59	0.45	2.69	0.111
Spotted Flycatcher *Muscicapa striata*	LDM	1.003	0.003	1.051	0.960	0.026	0.498	38.7	0.000	4.12	0.051	22.2	**0.001**
Pied Flycatcher *Ficedula hypoleuca*	LDM	0.985	0.002	0.774	0.969	0.005	0.589	42.9	0.000	8.7	0.006	5.71	**0.024**
Long-tailed Tit *Aegithalos caudatus*	RES	1.013	0.016	1.242	1.001	0.013	1.052	0.5	0.48	50.3	0.000	0.18	0.67
Marsh Tit *Poecile palustris*	RES	0.950	0.007	0.417	0.984	0.017	0.788	2.31	0.14	0.79	0.38	8.12	**0.008**
Willow Tit *Poecile montana*	RES	0.957	0.004	0.474	1.030	0.030	1.301	1.37	0.25	7.9	0.009	10.11	**0.003**
Crested Tit *Lophophanes cristatus*	RES	0.989	0.008	0.826	0.985	0.013	0.891	4.58	0.040	0.52	0.48	0.27	0.61
Coal Tit *Periparus ater*	RES	0.938	0.005	0.334	0.989	0.027	0.962	0.08	0.77	2.02	0.16	32.72	**0.000**
Blue Tit *Cyanistes caeruleus*	RES	1.021	0.003	1.423	1.015	0.005	1.254	34.5	0.000	32.6	0.000	1.69	0.20
Wood Nuthatch *Sitta europaea*	RES	0.994	0.004	0.905	0.983	0.015	0.817	4.49	0.040	6	0.02	0.5	0.48
Eurasian Treecreeper *Certhia familiaris*	RES	0.996	0.005	0.936	0.998	0.004	0.958	0.48	0.50	38.9	0.000	0.02	0.89
Bullfinch *Pyrrhula pyrrhula*	RES	1.003	0.004	1.055	0.973	0.014	0.723	1.06	0.31	73.6	0.000	2.13	0.15

Chapter 7

Ecological strategies successfully predict the effects of river floodplain rehabilitation on breeding birds

Chris van Turnhout, Rob Leuven, Jan Hendriks, Gijs Kurstjens, Arco van Strien, Ruud Foppen and Henk Siepel

Published online in 2010 in River Research and Applications, DOI 10.1002/rra.1455

Abstract

To improve the ecological functioning of riverine ecosystems, large-scale floodplain rehabilitation has been carried out in the Rhine-Meuse Delta since the 1990s. This chapter evaluates changes in abundance of 93 breeding bird species over a period of ten years in response to rehabilitation, by comparing population changes in 75 rehabilitated sites with 124 non-rehabilitated reference sites. Such quantitative, multi-species, large-scale and long-term evaluations of floodplain rehabilitation on biodiversity are still scarce, particularly studies that focus on the terrestrial component. We try to understand the effects by relating population trends to ecological and life-history traits and strategies of breeding birds. More specifically, we try to answer the question whether rehabilitation of vegetation succession or hydro-geomorphological river processes is the key driver behind recent population changes in rehabilitated sites. Populations of 35 species have significantly performed better in rehabilitated sites compared to non-rehabilitated floodplains, whereas only 8 have responded negatively to rehabilitation. Differences in effects between species are best explained by the trait selection of nest location. Reproductive investment and migratory behaviour were less strong predictors. Based on these three traits we defined eight life-history strategies that successfully captured a substantial amount of variation in rehabilitation effects. We conclude that spontaneous vegetation succession and initial excavations are currently more important drivers of population changes than rehabilitation of hydrodynamics. The latter are strongly constrained by river regulation. If rehabilitation of hydro-geomorphological processes remains incomplete in future, artificial cyclic floodplain rejuvenation will be necessary for sustainable conservation of characteristic river birds.

Introduction

Pristine river floodplains are very rich in terrestrial and aquatic flora and fauna as a result of a high level of spatio-temporal heterogeneity in abiotic conditions and vegetation structures (Ward *et al.* 1999). However, river floodplains are considered to be among the most degraded ecosystems in the world. This holds particularly in densely populated regions, such as the Rhine and Meuse in north-western Europe (Tockner & Standford 2002). These rivers and their floodplains fulfill a variety of services: agriculture, drainage, navigation, water supply for drinking, cooling and irrigation, excavation of clay and sand, and recreation (Bij de Vaate 2003). To facilitate these services and to protect settlements against flooding, river branches have been dammed off, main streams have been canalized and normalized, dikes have been constructed and floodplains have been disconnected from the river. Agricultural activities rather than fluvial processes have become the main driving forces (Poudevigne *et al.* 2002). In addition, physical deterioration of natural gradients (e.g. between dry and wet, high and low hydrodynamics) and declining water and soil quality have led to a strong decrease in geomorphologic and biological diversity of Rhine and Meuse floodplains, together with desiccation and levelling of floodplains (Admiraal *et al.* 1993, Van Dijk *et al.* 1995, Leuven & Poudevigne 2002, Lenders 2003). Nevertheless, species composition and abundance are still very distinct from those in other areas in the Netherlands, with respect to several taxonomic groups (Lenders *et al.* 2001, De Nooij *et al.* 2004), including breeding birds (Kwak *et al.* 1988).

Around 1990 a number of visions and plans were published that promoted floodplain rehabilitation in the Netherlands by introducing riverine nature reserves and improving river-floodplain interaction (De Bruin *et al.* 1987, WWF 1992, Buijse *et al.* 2002). The core message was that outer dike floodplains ought to have a primary ecological function again, whereas in the hinterland agriculture may prevail. Floodplain restoration in the Netherlands has been carried out since the early 1990s in an area of over 8,000 hectares. Generally, it implies the rehabilitation of ecological and hydro-geomorphological river processes at the landscape scale, such as erosion, sedimentation, flooding and vegetation succession, including low-intensity grazing by free roaming semi-wild herbivores (Smits *et al.* 2000). Consequently, in rehabilitated sites all regular agricultural activities, such as mowing of grasslands, are terminated and large herbivores are introduced. Often secondary channels are excavated, summer levees removed or lowered, and primary dikes reallocated (together referred to as ‘rehabilitation’ in this chapter). Floodplain rehabilitation aims at creating a diverse and (semi-)natural river landscape, consisting of marshes, pioneer habitats (such as eolian dunes), natural grasslands, shrubs and riverine forests (Lenders 2003). In the past decade positive effects of Dutch floodplain rehabilitation on biodiversity have been described (Grift 2001, Raat 2001, Nienhuis *et al.* 2002, Lenders 2003, De Nooij *et al.* 2006, Peters & Kurstjens 2008). However, quantitative evaluations are still scarce and studies are often based on short-term responses in populations of a small selection of species (e.g. Red List species) in individual sites. Besides, studies that focus on the terrestrial component of the river-floodplain system are underrepresented.

Breeding birds are useful and sensitive indicators of food web integrity and landscape quality (Poudevigne *et al.* 2002, Vaughan *et al.* 2007). They use the landscape at different spatial scales, make use of both terrestrial and aquatic components of the floodplain ecosystem, cover a large diversity in habitats and traits, and a number of species are at the top of the food chain (Furness & Greenwood 1993). Birds are therefore particularly useful for incorporating spatial scale and system heterogeneity into river management (Miller *et al.* 2004), an existing gap in our conservation knowledge (Thoms 2006). Moreover, they are relatively easy to identify and to census, and their ecology is relatively well known. Finally, breeding birds are frequently used as indicators for the evaluation of national and international nature policies, such as the European Union Natura 2000 network (De Nooij *et al.* 2004). They may therefore help bridge the gap in the exchange of knowledge that exists between river scientists and water managers (Thoms 2006).

In this chapter we evaluate changes in abundance of the entire breeding bird community in response to large-scale floodplain rehabilitation along the rivers Rhine and Meuse, over periods of five and ten years. We describe and try to understand the effects by relating bird population changes to ecological and life-history traits of species. According to the Flood Pulse Concept, periodic inundation and drought are the driving forces in a natural river-floodplain system. Flooding can be considered as the main disturbance factor that leads to a regular setback of community development and maintains the system in an immature, but highly productive stage (Junk & Wantzen 2004, Thorp *et al.* 2006). We try to answer the question whether rehabilitation of hydrodynamics is indeed the key driver behind recent breeding bird changes in response to floodplain restoration, or if rehabilitation of vegetation succession is more important. Southwood (1977) hypothesized that the habitat acts as a templet onto which evolution has forged biological traits. Because species traits determine the ability of a species to deal with environmental pressures and opportunities, traits are particularly useful for understanding ecological effects (McGill *et al.* 2006, Van Turnhout *et al.* 2010). The habitat templet concept has been frequently tested in river systems, but mainly for aquatic fauna and to understand the distribution of species throughout the river catchment (Juget & Lafont 1994, Tachet *et al.* 1994). Recently, Kyle & Leishman (2009) used a functional trait approach to provide insight into the changes in riparian ecosystem function that have occurred with the loss of native plant species and their replacement by exotics.

Combining separate traits into suites of traits (referred to as strategies), thereby accounting for trade-offs, may be even more successful in unraveling the causal mechanisms underlying species-effect relationships (Stearns 1976). The use of strategies has an additional value in predicting effects on other species assemblages, having comparable traits and strategies, elsewhere (Verberk *et al.* 2008). By adopting this functional approach we provide a tool to predict the effects of future floodplain rehabilitation, and to adapt the rehabilitation strategy, if necessary. By linking ecological strategies to natural river processes, we contribute to dissecting the complex matrix of interactions at different spatial and temporal scales (Thoms 2006), e.g. by differentiating between rehabilitation of vegetation succession or hydrodynamics as key driver of breeding bird changes.

Materials and methods

Study area

Rhine and Meuse are large lowland rivers receiving most of their discharge from mountainous areas: the Rhine from the Alps in Switzerland, Austria and Germany; the Meuse from the Ardennes in France, Belgium and Luxembourg. In the Netherlands, both rivers show a similar pattern of discharge throughout the year, with highest discharges in late autumn and winter. However, discharge fluctuations are larger in the Meuse (depending completely on precipitation) than in the Rhine (constant supply of melting water). Particularly in the lower parts of their trajectories, where they become interconnected and form the Rhine-Meuse Delta, both rivers share many characteristics (Lenders 2003). The upper part of the Meuse in the Netherlands shows characteristics of a submontane gravel river, although braided and meandering sections are largely absent. Total area of floodplains along Rhine and Meuse is 67,925 hectares (Postma *et al.* 1996). For further details on hydrological and morphological characteristics we refer to Simons *et al.* (2001).

Bird data

Changes in breeding bird populations in floodplains were assessed with the national Breeding Bird Monitoring Program, which has been running since 1984. Data are collected mainly by skilled volunteers. The field method is based on intensive territory mapping in fixed study plots (Bibby *et al.* 1997). All common and scarce breeding birds in the Netherlands are covered. Fieldwork and interpretation methods are highly standardized (Van Dijk 2004). Territory mapping uses a high, and yearly constant, number of field visits (5-10 between March and July). Size of study plots, as well as the exact number, timing and duration of visits, depend on habitat type and species selection. All birds with territory-indicative behaviour (e.g. song, pair bond, display, alarm, nests) are noted down on field maps. Species-specific interpretation criteria are used to determine the number of territories per species at the end of the season. Interpretation criteria focus on the type of behaviour observed, the number of observations required (taking into account differences in detection probability between species and within the breeding season), and the period of observations (to exclude non-breeding migrants). We consider the number of territories to be a proxy of true abundance and expect approximate linear relationships between the surveyed samples and the total population sizes of each species (Van Turnhout *et al.* 2010). For the colonial breeding species Grey Heron *Ardea cinerea* and Sand Martin *Riparia riparia* territory mapping is inappropriate. For these species the number of occupied nests is counted annually in nearly all floodplain colonies. Breeding bird monitoring programs such as the one lined out here are widely used to assess trends in biodiversity (Donald *et al.* 2007, Van Turnhout *et al.* 2010), and our data also contribute to pan-European biodiversity indicators (Gregory *et al.* 2005).

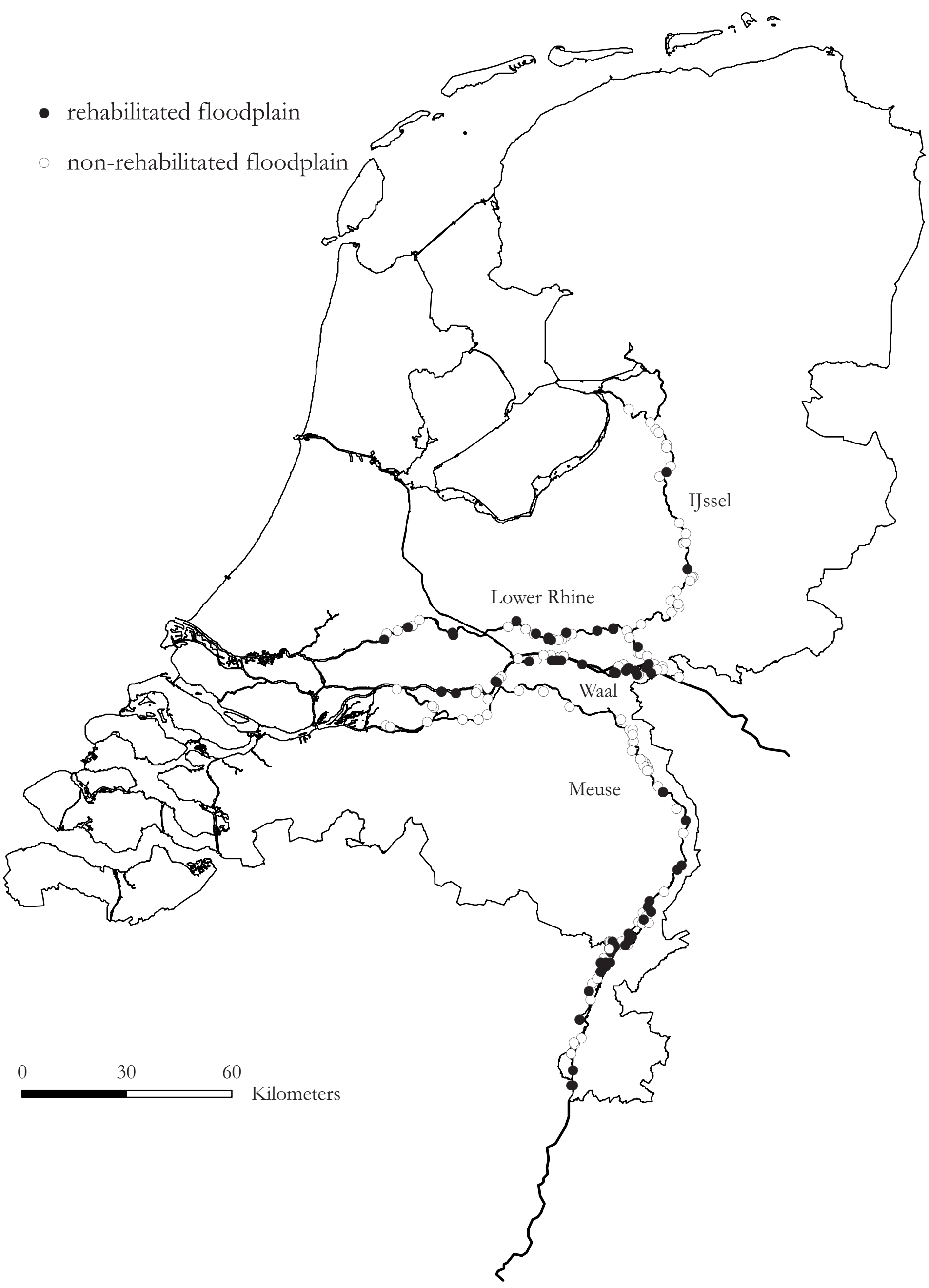


Figure 1. Location of rehabilitated study sites (*n*=75) and non-rehabilitated reference sites (*n*=124) in the floodplains of river Rhine (Lower Rhine, Waal and IJssel) and Meuse in the Netherlands.

Analysis of rehabilitation effects per species

We compared time series of bird counts from 75 rehabilitated sites (in total 10,217 hectares) with those from 124 non-rehabilitated reference sites (15,586 hectares) in the period 1989-2007 (Figure 1). Both rehabilitated and reference sites are located in the floodplains of river Rhine (85) and Meuse (114). They reflect the actual distribution of rehabilitated floodplains: most rehabilitated sites are located along the Rhine distributaries Waal and Lower Rhine, and along the upper part of the Meuse. Rehabilitated floodplains are underrepresented along IJssel and lower Meuse. Rehabilitated sites were surveyed before and after rehabilitation started, similar to a BACI-design (Green 1979). Counting data were available for 93 species, including all common and scarce breeding birds of Rhine-Meuse Delta floodplains (Appendix 1). Time series within the same sites rarely covered the entire study period. Study plots were counted in on average 8.9 years (*SE* 0.34); 32 sites were counted during at least 15 years within the study period (17 rehabilitated and 15 non-rehabilitated).

Effects of floodplain rehabilitation were analysed using Poisson regression (log-linear models; McCullagh & Nelder 1989), as implemented in GenStat 9 (Payne & Lane 2006). This type of generalized linear modelling is especially suitable for the analysis of time series of counts with missing data (Ter Braak *et al.* 1994, Gregory *et al.* 2005). Models were run for each species, and included both non-rehabilitated and rehabilitated sites. The numbers of territories per study plot were used as the dependent variable. To control for differences between study plots and years which are not related to floodplain rehabilitation (e.g. weather conditions), we used plot identity and year as the first and second independent variable. Rehabilitation projects were started in different years throughout the entire study period. Therefore, we added the number of years that had passed since the start of the rehabilitation in a site ('start year') as the third independent variable to the models. For non-rehabilitated sites, and for rehabilitated sites in years prior to the start of rehabilitation, we used a zero value for start year (reference situations). Rehabilitation effects per species are represented by a single estimate and its standard error, reflecting the linear trend in abundance in rehabilitated sites relative to the trend in non-rehabilitated sites. Positive values thus indicate a larger increase, or a smaller decrease, in bird numbers in rehabilitated sites compared to non-rehabilitated sites. We calculated rehabilitation effects for two periods: the first five years and the first ten years after the start of the activities. These periods are based on Geerling *et al.* (2008), who found that pioneer habitats were being replaced by tall herbaceous vegetations after approximately five years in one of the first rehabilitated sites in the Netherlands (i.e. floodplain area Ewijkse Plaat). In addition to linear effects of rehabilitation we calculated effects per start year, by modelling start year as a discrete instead of a continuous variable.

Selection of traits

We selected a limited number of ecological and life-history traits of birds that we regard as particularly relevant in overcoming the environmental constraints related to the main processes associated with large-scale floodplain rehabilitation (Junk & Wantzen 2004, Thorp *et al.* 2006). Through the combination of ceased agricultural activities, stimulation of spontaneous vegetation succession and excavation, floodplain rehabilitation will primarily lead to a decrease in the area of short grasslands and to an increase in the area of pioneer habitats, marshes, tall herbaceous vegetations, shrubs and alluvial woodland. Therefore, we chose selection of nest location as the first trait. Furthermore, floodplain rehabilitation is expected to increase hydrodynamics. This will result in more frequent, prolonged and deeper inundations. We hypothesize that spring and early summer inundations force birds to cope with the risks of losing their feeding territories, nests and young. They can adapt in this dynamic environment by mitigating or compensating the effects of inundation by means of maximizing their per capita reproductive investment (e.g. multiple clutches), which we selected as the second trait. Winter and early spring inundations will strongly reduce habitat availability for terrestrial birds and result in reduced survival. However, this holds for sedentary species only, since migratory species leave their breeding grounds in winter. Therefore, we selected migratory behaviour as the third trait.

Evidence that hydrodynamics and vegetation succession have indeed increased in response to floodplain restoration again comes from Ewijkse Plaat (Geerling *et al.* 2008). Here, sedimentation rates increased strongly and became much higher than the range of mean rates in non-rehabilitated Rhine floodplains. Also, the grassland-based landscape changed towards a landscape mainly consisting of tall herbaceous vegetation (increase in area of 71%), bush (+290%) and softwood forest (+530%) between 1986 (reference situation) and 2005.

Description of traits

We described selection of nest location using the following five classes: 1) in or near water (banks), 2) in or on bare ground, 3) on ground within vegetation, 4) herb- or shrub-layer (below 2 m), and 5) tree-layer (above 2 m), including holes. We quantified relative reproductive investment (*RRI*) by multiplying average clutch size ($\hat{c}$), the number of clutches per season (N_c) and egg mass (m_{egg}), divided by female body mass (m_{female}):

$$RRI = (\hat{c} \times N_c \times m_{egg}) \; / \; m_{female}$$

Migratory behaviour was described using the following three classes: (1) sedentary, (2) partial or short-distance migrant and (3) long-distance (trans-Sahara) migrant. All trait data are derived from Cramp and Simmons (1977-1994; data from studies in the Netherlands or Northwest-Europe were selected when available). Data from the Dutch Nest Record Scheme (for clutch size), Speek & Speek (1984) and Wernham *et al.* (2002) (both for migration behaviour) were used as additional sources. We refer to Van Turnhout *et al.* (2010) for more information on bird traits and data sources.

Analysis of rehabilitation effects for traits and strategies

We first tested the relevance of the selected traits separately with univariate regression models. Linear rehabilitation effects per species after five and ten years, derived from the analyses described above, were used as dependent variables. Selection of nest location, reproductive investment and migratory behaviour were used as independent variables.

We then combined the three traits in order of their significance into one new variable, the life-history strategy (Verberk *et al.* 2008). For classification on the basis of the continuous trait reproductive investment, we consistently chose an (arbitrary) value of 0.8 to distinguish between high and low investment, aiming at comparable sample sizes in both groups. Theoretically, this procedure would result in 30 strategies (three traits with 5, 2 and 3 classes each). However, the majority of these strategies did not contain any species. Furthermore, the last trait was not able to differentiate much further after the first two traits had been applied. Because of very small sample sizes some strategies were therefore lumped. Cuckoo *Cuculus canorus* was not assigned to one of the strategies, because this nest-parasitic species uses several host species with different nest locations. Differences in effects of floodplain rehabilitation in relation to life-history strategy were then analyzed with a regression model.

Also, we compared rehabilitation effects between characteristic river floodplain species and generalists, and in relation to the species' conservation status. We followed the classification of Kwak *et al.* (1988), who analyzed regional occupancies derived from high resolution, national distribution data (period 1973-77) to distinguish characteristic species (distributions largely restricted to floodplains; 7 species), 'preferential' species (species with a relative high occupancy in floodplains; 22 species), and remaining species not typical for river ecosystems (Appendix 1). We selected species from Annex 1 of the EU Bird Directive and from the Dutch Red List (Van Beusekom *et al.* 2005) as species of high conservation concern (Appendix 1). We expect that rehabilitation is particularly beneficial for these species, since they are important in setting policy and management objectives.

To account for interspecific differences in significance of rehabilitation effects we used the standard errors as weighting factors ($1/SE^2$). Weighting generally had only minor effects on model estimates, but the exceptions are presented in the results section where appropriate.

Results

Populations of 35 out of 93 breeding bird species have responded positively to floodplain rehabilitation: they increased significantly stronger, or decreased significantly less, in rehabilitated sites compared to non-rehabilitated floodplains (Appendix 1). Only 8 species have responded negatively to floodplain rehabilitation, predominantly meadow birds. The remaining 50 species showed no significant response in the first ten years after the start of the activities, and for those the trends in rehabilitated sites did not significantly differ from regular floodplains. Effects of rehabilitation after five years did not differ from effects after ten years (paired t-test: t=0.08; p=0.52).

In rehabilitated floodplains bird numbers have significantly increased with on average +5.1% (SE 1.0) per year during the first ten years after the start of the activities (p<0.001). This differed significantly from average population changes in non-rehabilitated floodplains and from national population trends in the same period (paired ANOVA; F=24.3, p<0.0001) (Figure 2). Furthermore, effects of rehabilitation did not significantly correlate with national population trends (r=0.06; p=0.13) (Figure 3). This indicates that there is no tendency that particularly species either declining or increasing at the national scale benefit more from floodplain restoration. Also, species of high conservation concern did not benefit more that non-protected

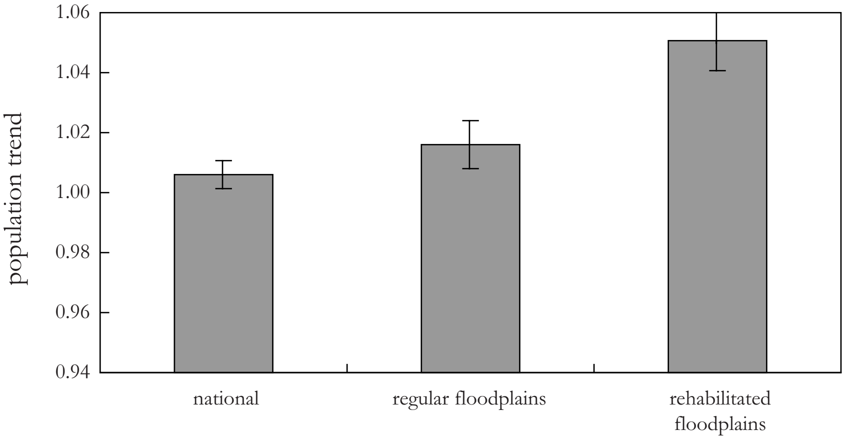


Figure 2. Average population trends (± *SE*) of 93 breeding bird species in the Netherlands in 1989-2007, distinguishing between trends in rehabilitated floodplains, trends in non-rehabilitated floodplains and national population trends. The trend is presented as a multiplicative parameter: a value of 1.05 represents an annual increase of 5%, a value of 0.95 an annual decrease of 5%.

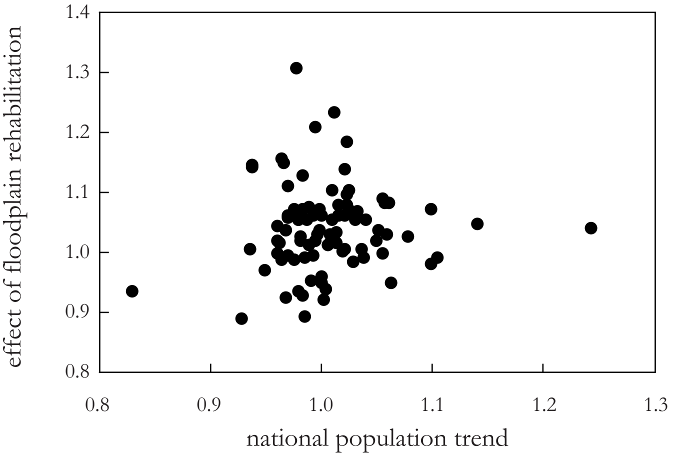


Figure 3. Effect of floodplain rehabilitation in the first ten years after the start, in relation to national population trends of 93 breeding bird species in the Netherlands in 1989-2007. The population trend is presented as a multiplicative parameter: a value of 1.05 represents an annual increase of 5%, a value of 0.95 an annual decrease of 5%. The effect of floodplain rehabilitation is also presented as a multiplicative parameter: a value of 1.05 represents a 5% stronger increase (or smaller decrease) annually in rehabilitated sites compared to non-rehabilitated sites. A value of 1 means no effect of rehabilitation.

species (ANOVA; *p*=0.41 and 0.71, for EU Bird Directive and Red List respectively). However, characteristic and preferential river species have disproportionately benefited from rehabilitation compared to non-typical river species (ANOVA; *p*=0.04) (Figure 4).

The trait selection of nest location best explained differences in effects of

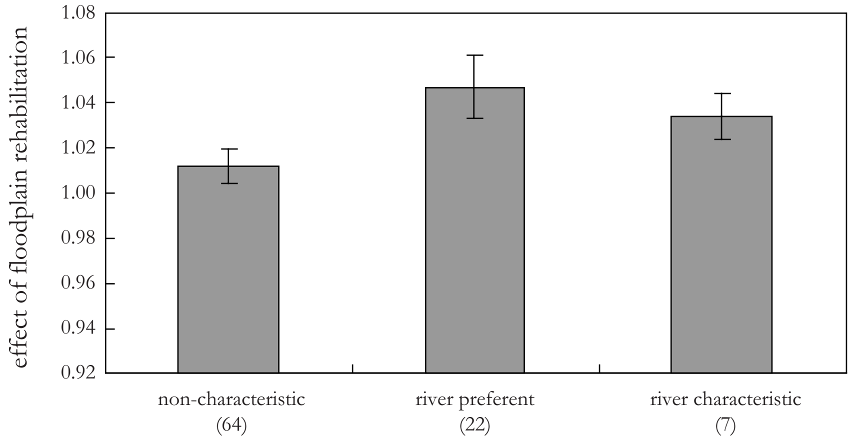


Figure 4. Effect of floodplain rehabilitation in the first ten years after the start for species not typical of river floodplain landscapes, preferential river species and characteristic river species (classification according to Kwak *et al.* 1988). Number of species per category is presented between brackets.

Table 1. Profile of eight life-history strategies for breeding birds in river floodplains, according to the traits selection of nest location, reproductive investment and dominant migratory strategy. For each strategy the number of species is given (# of sp.), as well as the percentage of characteristic and preferential river species (% of sp.), according to Kwak *et al.* (1988). See Appendix 1 for complete species lists.

Abbr.	Nest location	Repr. investm	Migratory behaviour	# of sp.	% of sp.	Species examples
W	in or near water	low[1]	sedentary or short-distance	15	67	grebes, geese, ducks, Coot
P	bare ground	high[2]	migrants	8	75	Avocet, Little Ringed Plover
Gl	vegetated ground	low	sedentary or short-distance	7	14	waders, Grey Partridge
Gh	vegetated ground	high	(partial) migrants	5	40	Corncrake, Yellow Wagtail
Sl	herb- or shrub	low	long-distance migrants	11	27	*Acrocephalus* warblers
Sh	herb- or shrub	high	sedentary or short-distance	11	9	*Phylloscopus* warblers, Wren
Tl	trees or holes	low	sedentary or short-distance	20	15	raptors, woodpeckers, pigeons
Th	trees or holes	high	sedentary or short-distance	15	20	tits, finches, sparrows

[1] except for two species
[2] except for three species

rehabilitation between species, both after five years ($p<0.001$; $R^2=63.2\%$) and after ten years ($p<0.001$; $R^2=23.2\%$). Reproductive investment was a less strong significant predictor of rehabilitation effects after ten years ($r=0.053$; $p<0.001$; $R^2=12.3\%$). Also, migration behaviour significantly explained interspecific variation in effects of rehabilitation after five and ten years ($p<0.001$; $R^2=26.5\%$, and $p=0.008$; $R^2=8.3\%$ respectively).

Based on these three life-history traits we defined eight life-history strategies (Table 1, Appendix 1). Characteristic and preferential river species are not distributed equally over these strategies ($\chi^2=22.8$; $p<0.0001$). Strategies W and P, and to a lesser extent strategy Gh, contain more characteristic species than expected by chance. The strategies explained a considerable amount of the variation in rehabilitation effects after five years ($p<0.001$; $R^2=66.5\%$). Two strategies showed significant positive effects of rehabilitation, and one a negative effect (Figure 5). After ten years the explanatory

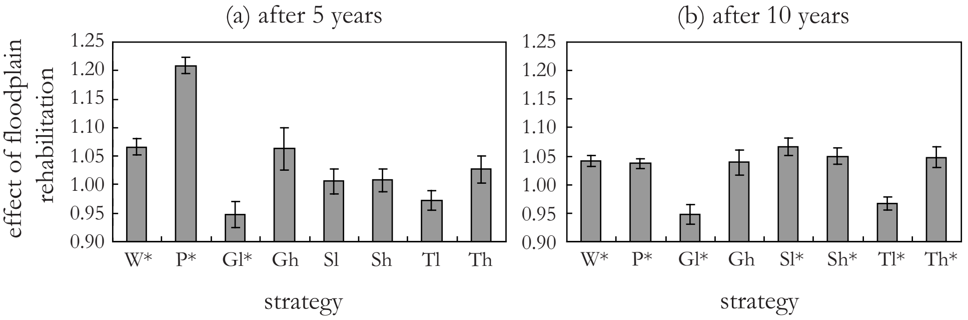


Figure 5. Effect of floodplain rehabilitation in relation to life-history strategy, after (a) five years and (b) ten years. Strategies are briefly described in Table 1. Strategies indicated with an asterisk (*) refer to significant differences from 1 ($p<0.05$).

power of the strategies was lower ($p<0.001$; $R^2=39.7\%$). Five strategies showed on average significant positive effects, whereas two showed a negative effect. For only one strategy effects after five and ten years significantly differed (strategy P; $p<0.05$).

After five years of rehabilitation only birds nesting in or near water (strategy W), and in or on bare ground (strategy P) showed on average positive responses. In contrast to strategy W, rehabilitation effects for species of strategy P were significantly less strong after ten years. This results from trends being stable or even decreasing during the second five year period after rehabilitation (Figure 6).

Three strategies showed positive effects of rehabilitation only after ten years since the start of rehabilitation. Indeed, numbers of the species involved especially increased during the second half of the study period (Figure 6). These are species nesting in the herb- or shrub-layer, irrespective of their reproductive investment and migration behaviour (strategies Sl and Sh), and species nesting in the tree-layer with a high reproductive investment (strategy Th).

Tree-nesting species with a low reproductive investment (strategy Tl) showed a contrasting negative response to rehabilitation after ten years. However, this is strongly influenced by the decrease of Grey Heron in rehabilitated sites (Figure 6). Most other species in this strategy showed neutral or even positive effects, which are generally less significant however. An unweighted analysis resulted in non-significant response to rehabilitation of this strategy.

Only strategy Gl showed an average negative response to rehabilitation both after five and ten years (Figure 6). These species nest on the ground within short vegetation, and have a rather low reproductive investment (e.g. four eggs and no second clutches). Finally, strategy Gh consists of species nesting on the ground within vegetation and with a high reproductive investment, that on average did not show a significant effect of floodplain rehabilitation. In fact, the species within this strategy showed quite contrasting responses, as illustrated by the trends of Skylark *Alauda arvensis* and Yellow Wagtail *Motacilla flava* (Figure 6).

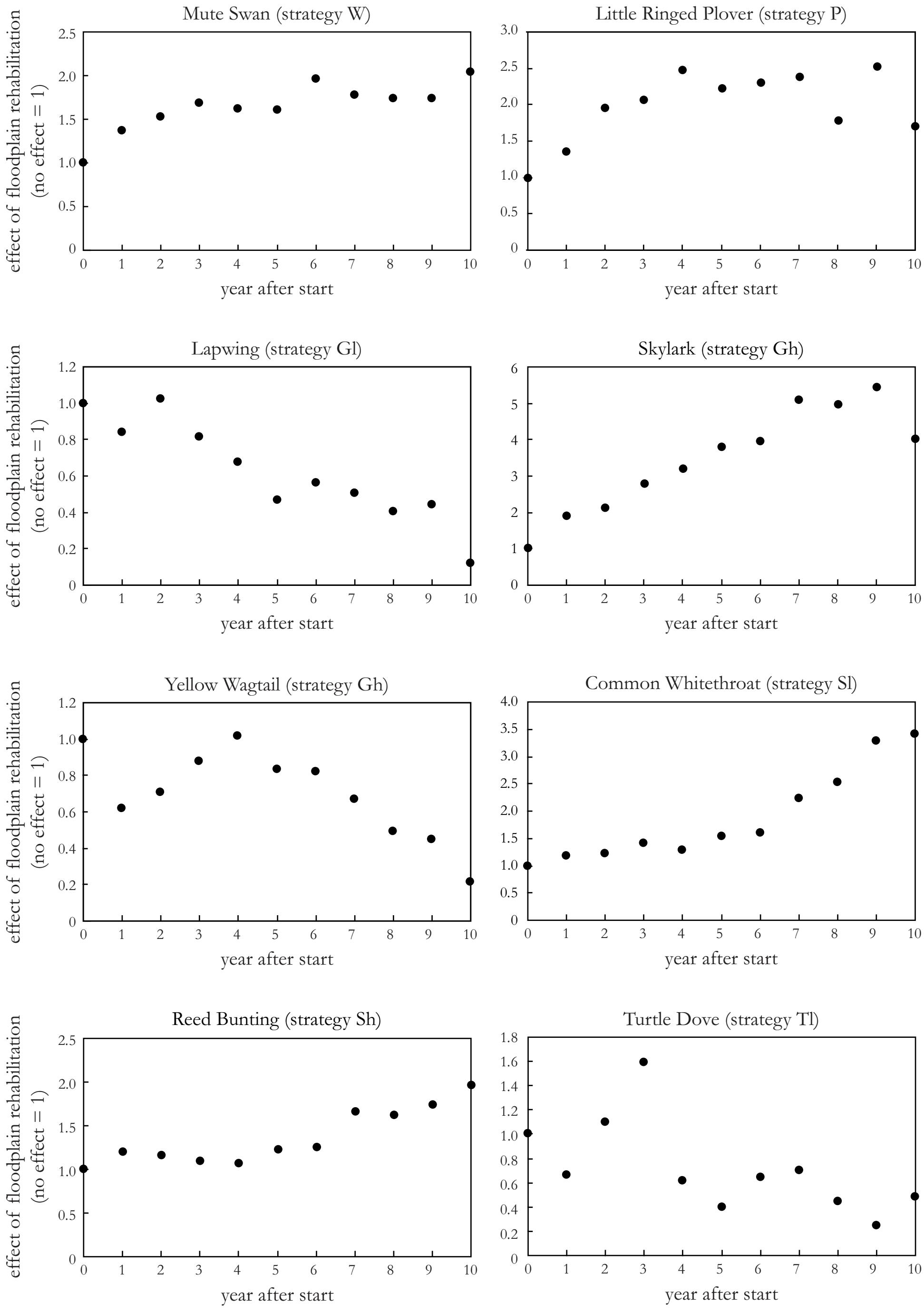


Figure 6. Effect of floodplain rehabilitation in relation to number of years since the start of the activities, for ten breeding bird species of different life-history strategies. Note the different scales of the y-axes.

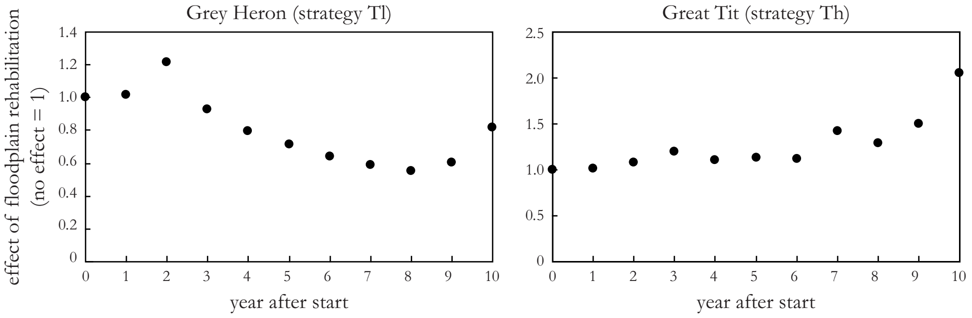


Figure 6. (continued).

Discussion

General effects of floodplain rehabilitation

The effects of floodplain rehabilitation on breeding birds in the Rhine-Meuse Delta have generally been positive in the first ten years after the start of the rehabilitation. Although the majority of analyzed species has not shown a significant response yet, positive effects were dominant among those that have. Since rehabilitation effects did not correlate with national population trends, and trends of species in rehabilitated sites differed from national trends, these at least partly reflect effects of developments restricted to floodplains. Trends of breeding bird populations in floodplains are therefore not only directed by processes operating at higher spatial scales (Van Turnhout *et al.* 2007). Although birds of high conservation concern did not benefit more that non-protected species on average, two strictly protected species listed on Annex 1 of the EU Bird Directive responded positively. Sand Martin increased stronger in rehabilitated sites compared to non-rehabilitated floodplains, whereas Common Snipe *Gallinago gallinago* decreased less in rehabilitated sites. No Annex 1 species responded negatively. Eight species from the Dutch Red List (Van Beusekom *et al.* 2005) significantly benefited from the rehabilitation measures, whereas only two species showed negative effects (Black-Tailed Godwit *Limosa limosa* and Redshank *Tringa totanus*). The majority of flora and fauna species of other taxonomic groups have also benefited from rehabilitation of floodplains in north-western Europe, such as river characteristic plant species, dragonflies, damselflies, butterflies and rheophilic fish (Grift 2001, De Nooij *et al.* 2006, Peters & Kurstjens 2008, Verberk *et al.* 2009).

Selection of traits

To understand the effects of floodplain rehabilitation on breeding bird populations, we selected three ecological and life-history traits that we regarded as particularly relevant in overcoming the environmental constraints related to the main processes associated with rehabilitation (Junk & Wantzen 2004, Thorp *et al.* 2006). Although all selected traits indeed captured a significant amount of variation in interspecific differences in responses to rehabilitation, we realize that alternative traits might be good predictors as well. However, we think that many of the potential candidate traits will be strongly correlated with the traits we selected. For instance, the high reproductive investment of the Corncrake *Crex crex*, a characteristic river species of high conservation concern (Appendix 1), is not only expressed by a relatively large clutch size, but also by a rapid laying of eggs, short hatching and fledging periods, a short period between two broods and limited parental care (Schäffer 1999). Moreover, the species shows other adaptations to its highly dynamic habitat, such as high dispersal capacity, rapid colonization of suitable areas, small site tenacity, short pair bond and polygamy of both male and female (Green *et al.* 1997, Koffijberg 2007). This comes with a trade-off for adult survival, which is remarkably low for a bird of this size (Green 2004). Therefore, the traits we selected might be exchangeable with other traits. Nevertheless, we have clear functional hypotheses of how rehabilitation of floodplains along the Rhine and Meuse river might affect population trends. Furthermore, the selected traits refer to important trade-offs in life-history theory in terms of energy allocation (Siepel 1994, Bennett & Owens 2002), and are among the traits that explain most of the interspecific variation in population changes at the national scale (Van Turnhout *et al.* 2010).

Combining traits into strategies

Traits were combined into eight life-history strategies in an attempt to account for trade-offs and further elucidate the causal mechanisms (Stearns 1976, Verberk *et al.* 2008). Starting with selection of nest location, being the best predictor of rehabilitation effects in the univariate models, as the first variable for classification, and reproductive investment as the second, migratory behaviour was not able to differentiate much further. In our opinion, this is indirect evidence for a tight correlation of traits, including the existence of trade-offs. To illustrate, strategy Sl and Sh are distinguished on the basis of reproductive investment (low and high respectively). However, all species from strategy Sl are also long-distance migrants, whereas most species from strategy Sh are sedentary or short-distance migrants (except for three early arriving long-distance migrants). The distinction between strategies Gl en Gh is comparable. Also, all species nesting in or near water are large, have a relative low reproductive investment and most are sedentary or partial migrants. Species nesting in or on bare ground share a rather high reproductive investment and are mainly (long-distance) migrants. Therefore, the strategies we defined are rather robust, and are not very sensitive to the order in which the traits are used for classification. It might be rewarding to explore more detailed classifications using additional traits, especially when the age of rehabilitated sites increases and also effects on the longer term can be evaluated. This may also help to elucidate why within some strategies species show quite contrasting trends (strategy Gh).

More importantly, the strategies successfully captured a substantial amount of variation in interspecific differences in responses to rehabilitation, both after five and ten years. They were also better predictors of rehabilitation effects than the underlying traits separately. We therefore conclude that our functional approach using strategies provides a useful tool to understand and predict the effects of future floodplain rehabilitation in cultivated lowland river systems within the studied time frame. However, the explanatory power of the strategies was considerably lower after ten years than after five years. This suggests that after ten years additional traits become increasingly important to further differentiate between successful strategies, such as dispersal capacity and territory or home range size (Chardon *et al.* 2000). These traits may determine if the area, connectivity and heterogeneity of rehabilitated habitat patches is sufficient to allow colonization and establishment of viable populations.

Characteristic species are unequally distributed across the strategies. They are over-represented in only three of them. This match between our functional approach, and the independent observational approach that Kwak *et al.* (1988) used to select characteristic river species, gives in our opinion additional credibility to the relevance of the presented life-history strategies. It is however not surprising that in all strategies characteristic species are represented, since floodplains cover a large diversity of habitats (Ward *et al.* 1999). Characteristic river species have disproportionately benefited from rehabilitation compared to non-characteristic river species. This is mainly reflected in the responses of strategies W and P, the only strategies with on average positive effects after both five and ten years. Strategy W compromises mainly waterfowl species, such as grebes, geese and ducks (e.g. Mute Swan *Cygnus olor*, Gadwall *Anas strepera* and Shoveler *A. clypeata*). Strategy P consists of typical 'pioneers', species inhabiting the most dynamic parts of the floodplains and characterized by a high reproductive investment, such as Shellduck *Tadorna tadorna*, Avocet *Recurvirostra avosetta*, Little Ringed Plover *Charadrius dubius* and Sand Martin. These strategies may have benefited from both excavation and increased hydrodynamics, together resulting in a larger area of early successional and inundated habitats (Smits *et al.* 2000, Geerling *et al.* 2008). However, rehabilitation effects on species of strategy P were significantly less strong after ten years, and in some cases populations even decreased during the second five years after the start (e.g. Little Ringed Plover). This indicates that excavations actively carried out in the initial phase of restoration projects are a more important driver of breeding bird population changes than rehabilitation of natural hydro-geomorphological river processes. Indeed, sedimentation, erosion and rejuvenation of vegetation are still strongly constrained by river regulation infrastructure, such as groynes and dikes, in order to facilitate navigation and to protect against flooding (Nienhuis & Leuven 2001, Nienhuis *et al.* 2002, De Nooij *et al.* 2006).

The need for cyclic floodplain rejuvenation

Also, spontaneous vegetation succession seems a more important driver in floodplain rehabilitation than increased hydrodynamics. The trait selection of nest location is a much stronger predictor of variation in rehabilitation effects between species than reproductive investment and migratory behaviour, both after five and ten years. Besides, the strategies with positive responses are all species nesting in higher vegetations (herb-, shrub- and tree-layers), independent of their reproductive investment and migration behaviour. The latter traits, enabling species to avoid or mitigate the effects of inundations, are apparently less important. Finally, positive responses of these strategies generally start after five years, coinciding with the establishment of tall herbaceous vegetations, shrubs and immature softwood forests in rehabilitated sites (Geerling *et al.* 2008). These findings concur with Thorp *et al.* (2006), who in their Riverine Ecosystem Synthesis hypothesized that linkage of life-history characteristics with flooding is relatively weak in temperate seasonal floodplain rivers and depends on the flood pulse occurring in the late spring or summer, which is low in Rhine and Meuse. Nevertheless, creating and maintaining natural variation in hydrogeomorphic processes to develop a dynamic floodplain appear to be the most important elements for successful conservation and restoration concepts in lowland rivers (Poudevigne *et al.* 2002, Junk & Wantzen 2004, De Nooij *et al.* 2006). Also restoration of fish populations is hampered by limited hydrodynamics and a lack of suitable substrates for reproduction in rehabilitated floodplains (Verberk *et al.* 2009, Winter *et al.* 2009).

If rehabilitation of natural hydro-geomorphological river processes remains incomplete in future, river floodplains may lack sufficient rejuvenation and will end up frozen in time as ecological succession continues, despite grazing by introduced large herbivores. Smits *et al.* (2000) therefore proposed a periodic artificial disturbance of such lowland river floodplains, e.g. by the removal of climax vegetation and other mechanical interventions, resulting in the creation of pioneer stages and the restarting of ecological succession. We consider cyclic floodplain rejuvenation a necessary tool for a sustainable conservation of characteristic river birds in floodplains along regulated rivers. Besides, periodic removal of climax vegetations in embanked floodplains safeguards the discharge capacity of our rivers, which is increasingly important considering the expected increase in water supply as a result of climate change (Baptist *et al.* 2004). This approach will not reverse the negative response of species from strategy Gl, the only strategy for which the average effects of floodplain rehabilitation are negative, such as Northern Lapwing *Vanellus vanellus*, Black-Tailed Godwit and Redshank. These typical 'meadow birds' are also declining in non-rehabilitated floodplains and at the national scale (Teunissen & Soldaat 2006). They nest on the ground within short vegetation, and are strongly adapted to extensively managed farmland. Since the area of tall vegetations increases after termination of agricultural activities (grazing, mowing), rehabilitated floodplains will be abandoned by these species as the habitat gradually becomes unsuitable. In Eastern Europe, high densities of these species still occur locally in flooded meadows and pastures in river valleys (Leibak *et al.* 1994, Sikora *et al.* 2007), indicating that these species do belong to the (semi-)natural floodplain ecosystem of lowland rivers.

Optimizing rehabilitation measures

Furthermore, periodic removal of climax vegetations will interfere with the possible recolonization of a number of breeding birds that are still lacking from rehabilitated floodplains in the Rhine-Meuse Delta, such as Black Stork *Ciconia nigra*, Night Heron *Nycticorax nycticorax*, Black Kite *Milvus migrans*, White-tailed Eagle *Haliaeetus albicilla* and Middle Spotted Woodpecker *Dendrocopos medius*. These appealing 'target species' are present in low densities in less degraded lowland river floodplains elsewhere in Europe (Hagemeijer & Blair 1997). Most of them are at the top of the food chain, have large territories comprising a mosaic of different habitats, including mature riverine forests for nesting (Kosinski & Winiecki 2004). Based on species' habitat requirements in floodplains abroad, Foppen & Reijnen (1998) calculated that the development of 10,000 hectares of nature areas in Dutch floodplains, including marshes, softwood and hardwood forests, would still be insufficient to allow viable populations of Black Stork and White-tailed Eagle. However, for Black Kite and Night Heron habitat conditions might be sufficient to support a marginally viable population, depending on habitat quality and configuration. Therefore, optimizing rehabilitation measures is needed to restore habitats for these rare bird species, which are often regarded as prime indicators of ecological integrity of riverine ecosystems and food webs. Reallocation of dikes to create more space, expanding the area of rehabilitated floodplains, improving the spatial cohesion between rehabilitated sites and with nature reserves in the hinterland (Wijnhoven *et al.* 2006), and aiming at complete lateral gradients between high-dynamic aquatic and low-dynamic terrestrial habitats are in our opinion key strategies. Also for other flora and fauna assemblages this may be essential, since many typical plants and butterflies of alluvial grasslands and forests have not yet returned in response to floodplain rehabilitation as well, due to either dispersal limitation or unsuitable soil or habitat conditions (Antheunisse *et al.* 2006, Verberk *et al.* 2009). It requires planning of nature management at the regional or even supranational scale to establish viable ecological networks.

Acknowlegdements

The ongoing field efforts of a few hundred skilled volunteer bird-watchers form the basis of this study: we thank them very much. Several SOVON-colleagues, in particular A.J. van Dijk, A. Boele and A. van Kleunen, were responsible for processing the data. We thank the organisations that participate in the monitoring scheme: Rijkswaterstaat Waterdienst, Ministerie van LNV and the provinces of Limburg, Gelderland and Noord-Brabant. This study is a project of the Netherlands Centre for Nature research (NCN). We thank two anonymous referees for their valuable comments on a draft of this chapter.

References

Admiraal W., Van der Velde G., Smit H. & Cazemier W.G. 1993. The rivers Rhine and Meuse in the Netherlands: present state and signs of ecological recovery. *Hydrobiologia* 265: 97-128.

Antheunisse A.M., Loeb R., Lamers L.P.M. & Verhoeven J.T.A. 2006. Regional differences in nutrient limitation in floodplains of selected European rivers: Implications for rehabilitation of characteristic floodplain vegetation. *River Research and Applications* 22: 1039-1055.

Baptist M.J., Penning W.E., Duel H., Smits A.J.M., Geerling G.W., Van der Lee G.E.M. & Van Alphen J.S.L. 2004. Assessment of the effects of cyclic floodplain rejuvenation on flood levels and biodiversity along the Rhine River. *River Research and Applications* 20: 285-297.

Bennett P.M. & Owens I.P.F. 2002. Evolutionary ecology of birds. Life histories, mating systems and extinction. Oxford University Press, Oxford.

Bibby C.J., Burgess N.D. & Hill D.A. 1997. Bird Census Techniques. Academic Press, London.

Bij de Vaate A. 2003. Degradation and recovery of the freshwater fauna in the lower sections of the rivers Rhine and Meuse. Thesis, Wageningen University, Netherlands.

Buijse A.D., Coops H., Staras M., Jans L.H., Van Geest G.J., Grift R.E., Ibelings B.W., Oosterberg W. & Roozen C.J.M. 2002. Restoration strategies for river floodplains along large lowland rivers in Europe. *Freshwater Biology* 47: 889-907.

Chardon J.P., Foppen R.P.B. & Geilen N. 2000. LARCH-RIVER: a method to assess the functioning of rivers as ecological networks. *European Water Management* 3: 35-43.

Cramp S. & Simmons K.E.L. 1977-1994. Handbook of the Birds of Europe, the Middle East and North Africa: the birds of the Western Paleartic. Volume 1-9. Oxford University press, Oxford.

De Bruin D., Hamhuis D., Van Nieuwenhuijze L., Overmars W., Sijmons D. & Vera F. 1987. Ooievaar. De toekomst van het rivierengebied. Gelderse Milieufederatie, Arnhem.

De Nooij R.J.W., Lenders H.J.R., Leuven R.S.E.W., De Blust G., Geilen N., Goldschmidt B., Muller S., Poudevigne I. & Nienhuis P.H. 2004. Bio-safe: Assessing the impact of physical reconstruction on protected and endangered species. *River Research and Applications* 20: 299-313.

De Nooij R.J.W., Verberk W.C.E.P., Lenders H.J.R. & Nienhuis P.H. 2006. The importance of hydrodynamics for protected and endangered biodiversity of lowland rivers. *Hydrobiologia* 565: 153-162.

Donald P.F., Sanderson F.J., Burfield I.J., Bierman S.M., Gregory R.D. & Waliczky Z. 2007. International conservation policy delivers benefits for birds in Europe. *Science* 317: 810-813.

Foppen R.P.B. & Reijnen R. 1998. Ecological networks in riparian systems: examples for Dutch floodplain rivers. In: Nienhuis P.H., Leuven R.S.E.W. & Ragas A.M.J. New concepts for sustainable management of river basins. Pp. 85-93. Backhuys Publishers, Leiden.

Furness R.W. & Greenwood J.J.D. 1993. Birds as monitors of environmental change. Chapman & Hall, London.

Geerling G.W., Kater E., Van den Brink C., Baptist M.J., Ragas A.M.J. & Smits A.J.M. 2008. Nature rehabilitation by floodplain excavation: the hydraulic effect of 16 years of sedimentation and vegetation succession along the Waal River, NL. *Geomorphology* 99: 317-328.

Green R.H. 1979. Sampling Design and Statistical Methods for Environmental Biologists. John Wiley, New York.

Green R.E. 2004. A new method for estimating the adult survival of the Corncrake *Crex crex* and comparisons with estimates from ring-recovery and ring-recapture-data. *Ibis* 146: 501-508.

Green R.E., Rocamora G. & Schäffer N. 1997. Populations, ecology and threats to the Corncrake *Crex crex* in Europe. *Die Vogelwelt* 118: 117-134.

Gregory R.D., Van Strien A., Vorisek P., Meyling A.W.G., Noble D.G., Foppen R.P.B. & Gibbons D.W. 2005. Developing indicators for European birds. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 360: 269-288.

Grift R.E. 2001. How fish benefit from floodplain restoration along the lower River Rhine. Thesis, University of Wageningen.

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

Juget J, & Lafont M. 1994. Theoretical habitat templets, species traits, and species richness : aquatic oligochaetes in the upper Rhone River and its floodplain. *Freshwater Biology* 31: 327-340.

Junk W.J. & Wantzen K.M. 2004. The flood pulse concept: new aspects, approaches, and applications: an update. In: Welcomme R.L. & Petr T. (eds). Proceedings of the second international symposium on the management of large rivers for fisheries, Volume 2. RAP Publication 2004/16; 117-149.

Koffijberg K. 2007. Conservation of Corn Crakes *Crex crex* in grassland in The Netherlands. *De Levende Natuur* 108: 193-198.

Kosinski Z. & Winiecki A. 2004. Nest-site selection and niche partitioning among the Great Spotted Woodpecker *Dendrocopos major* and Middle Spotted Woodpecker *Dendrocopos medius* in riverine forest of Central Europe. *Ornis Fennica* 81: 145-156.

Kwak R.G.M., Reyrink L.A.F., Opdam P.F.M. & Vos W. 1988. Broedvogeldistricten van Nederland. Een ruimtelijke visie op de Nederlandse avifauna. Pudoc, Wageningen.

Kyle G. & Leishman M.R. 2009. Functional trait differences between extant exotic, native and extinct native plants in the Hunter River, NSW: A potential tool in riparian rehabilitation. *River Research and Management* 25: 892-903.

Leibak E., Lilleleht V. & Veromann H. 1994. Birds of Estonia. Status, distribution and numbers. Estonian Academic Publishers, Tallinn.

Lenders H.J.R., Leuven R.S.E.W., Nienhuis P.H., De Nooij R.J.W. & Van Rooij S.A.M. 2001. BIO-SAFE: A method for evaluation of biodiversity values on the basis of political and legal criteria. *Landscape and Urban Planning* 55: 119-135.

Lenders H.J.R. 2003. Environmental rehabilitation of the river landscape in the Netherlands. A blend of five dimensions. Thesis, University of Nijmegen, Netherlands.

Leuven R.S.E.W. & Poudevigne I. 2002. Riverine landscape dynamics and ecological risk assessment. *Freshwater Biology* 47: 845-865.

McCullagh P. & Nelder J.A. 1989. Generalized linear models. 2nd ed. London, Chapman and Hall.

McGill B.J., Enquist B.J., Weiher E. & Westoby M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 12: 474-478.

Miller J.R., Dixon M.D. & Turner M.G. 2004. Response of avian communities in large-river floodplains to environmental variation at multiple scales. *Ecological Applications* 14: 1394-1410.

Nienhuis P.H. & Leuven R.S.E.W. 2001. River restoration and flood protection: controversy or synergism. *Hydrobiologia* 444: 85-99.

Nienhuis P.H., Buijse A.D., Leuven R.S.E.W., Smits A.J.M., De Nooij R.J.W. & Samborska E.M. 2002. Ecological rehabilitation of the lowland basin of the river Rhine (NW Europe). *Hydrobiologia* 478: 53-72.

Payne R.W. & Lane P.W. (eds.). 2006. GenStat Release 9 Reference Manual. Part 3. Lawes Agricultural Trust, Rothamsted, United Kingdom.

Peters B., & Kurstjens G. 2008. Maas in Beeld: Succesfactoren voor een natuurlijke rivier. Bureau Drift & Kurstjens Ecologisch Adviesbureau, Berg en Dal.

Postma R., Kerkhofs M.J.J., Pedroli G.B.M. & Rademakers J.G.M. 1996. Een Stroom natuur: natuurstreefbeelden voor Rijn en Maas. RIZA report 95060. Ministerie van Verkeer en Waterstaat, Lelystad.

Poudevigne I., Alard D., Leuven R.S.E.W. & Nienhuis P.H. 2002. A systems approach to river restoration: a case study in the lower Seine valley. *River Research and Applications* 18: 239-247.

Raat A.J.P. 2001. Ecological rehabilitation of the Dutch part of the River Rhine with special attention to the fish. *Regulated Rivers: Research and Management* 17: 131-144.

Schäffer N. 1999. Habitatwahl und Partnerschaftssystem von Tupfelralle *Porzana porzana* und Wachtelkönig *Crex crex*. *Ökologie der Vögel* 21: 1-267.

Siepel H. 1994. Life-history strategies of soil micro-arthropods. *Biology and Fertility of Soils* 18: 263-278.

Sikora A., Rohde Z., Gromadzki M., Neubauer G. & Chylarecki P. 2007. The atlas of breeding birds in Poland 1985-2004. Bogucki Wydawnictwo Naukowe, Poznan.

Simons J.H.E.J., Bakker C., Schropp M.H.I., Jans L.H., Kok F.R. & Grift R.E. 2001. Man-made secondary channels along the river Rhine (The Netherlands); Results of post-project monitoring. *Regulated Rivers: Research and Management* 17: 473-491.

Smits A.J.M., Nienhuis P.H. & Leuven R.S.E.W. 2000. New approaches to river management. Backhuys Publishers, Leiden.

Southwood T.R.E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46: 337-365.

Speek B.J. & Speek G. 1984. Thieme's vogeltrekatlas. Thieme, Zutphen.

Stearns S.C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51: 3-47.

Tachet H., Usseglio-Polatera P. & Roux C. 1994. Theoretical habitat templets, species traits, and species richness: Trichoptera in the upper Rhone River and its floodplain. *Freshwater Biology* 31: 397-415.

Ter Braak C.J.F., Van Strien A.J., Meijer R. & Verstrael T.J. 1994. Analysis of monitoring data with many missing values: which method? Bird Numbers 1992. Distribution, Monitoring and Ecological aspects. Proc. 12th Int. Conf. of IBCC and EOAC. Statistics Netherlands, Voorburg & Sovon, Beek-Ubbergen.

Teunissen W. & Soldaat L. 2006. Recent trends of meadow birds in The Netherlands. *De Levende Natuur* 107: 70-74.

Thoms M.C. 2006. Variability in riverine ecosystems. *River Research and Applications* 22: 115-121.

Thorp J.H., Thoms M.C. & Delong M.D. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications* 22: 123-147.

Tockner K. & Stanford J.A. 2002. Riverine floodplains: present state and future trends. *Environmental Conservation* 29: 308-330.

Van Beusekom R., Huigen P., Hustings F., De Pater K. & Thissen J. (eds.). 2005. Rode Lijst van de Nederlandse Broedvogels. Tirion, Baarn.

Van Dijk A.J. 2004. Handleiding Broedvogel Monitoring Project. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Dijk G.M., Marteijn E.C.L. & Schulte-Wulwer-Leidig A. 1995. Ecological rehabilitation of the river Rhine: Plans progress and perspectives. *Regulated rivers: Research and Management* 11: 377-388.

Van Turnhout C.A.M., Foppen R.P.B., Leuven R.S.E.W., Siepel H. & Esselink H. 2007. Scale-dependent homogenization: Changes in breeding bird diversity in the Netherlands over a 25-year period. *Biological Conservation* 134: 505-516.

Van Turnhout C.A.M., Foppen R.P.B., Leuven R.S.E.W., Van Strien A. & Siepel H. 2010. Life-history and ecological correlates of population change in Dutch breeding birds. *Biological Conservation* 143: 173-181.

Vaughan I.P., Noble D.G. & Ormerod S.J. 2007. Combining surveys of river habitats and river birds to appraise riverine hydromorphology. *Freshwater Biology* 52: 2270-2284.

Verberk W.C.E.P., Siepel H. & Esselink H. 2008. Life-history strategies in freshwater macroinvertebrates. *Freshwater Biology* 53: 1722-1738.

Verberk W.C.E.P., Helmer W., Sykora K.V., Leuven R.S.E.W., Saris F.J.A., Wolfert H.P. & Hekhuis H. 2009. Opportunities for further progress in restoring river-floodplain ecosystems. *De Levende Natuur* 110: 148-152.

Ward J.V., Tockner K. & Schiemer F. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regulated rivers: research and management* 15: 125-139.

Wernham C.V., Toms M.P., Marchant J.H., Clark J.A., Siriwardena G.M. & Baillie S.R. (eds.). 2002. The Migration Atlas: movements of the birds of Britain and Ireland. T. & A.D. Poyser, London.

Wijnhoven S., Van der Velde G., Leuven R.S.E.W. & Smits A.J.M. 2006. Modelling recolonization of heterogeneous river floodplains by small mammals. *Hydrobiologia* 565: 135-152.

Winter H.V., Lapinska M. & De Leeuw J.J. 2009. The river Vecht fish community after rehabilitation measures: a comparison to the historical situation by using the river Biebrza as a geographical reference. *River Research and Applications* 25: 16-28.

WWF. 1992. Living Rivers. WWF, Zeist.

Appendix 1. Breeding bird species included in this study. Also presented is species' specialism (after Kwak *et al.* 1988; characteristic, preferential, non-typical for river landscapes), conservation status (EU BD: Annex 1 of EU Bird Directive; RL: Dutch Red List), life-history strategy (see Table 1), and effect of floodplain rehabilitation after five and ten years, including significance (*p*-values). The effect of floodplain rehabilitation is presented as a multiplicative parameter: a value of 1.05 represents a 5% stronger increase (or smaller decrease) annually in rehabilitated sites compared to non-rehabilitated sites.

Species	Scientific name	Specialism	EU BD	RL	Strategy	Effect 5 yr	*p*-value	Effect 10 yr	*p*-value
Little Grebe	*Tachybaptus ruficollis*	pref	+	-	W	1.146	0.10	1.029	0.56
Great Crested Grebe	*Podiceps cristatus*	pref	-	-	W	1.008	0.89	0.993	0.85
Grey Heron	*Ardea cinerea*	non	-	-	Tl	0.948	<.001	0.938	<.001
Mute Swan	*Cygnus olor*	pref	-	-	W	1.100	0.01	1.053	0.00
Greylag Goose	*Anser anser*	spec	-	-	W	1.048	<.001	1.040	<.001
Egyptian Goose	*Alopochen aegyptiacus*	pref	-	-	W	1.068	0.02	1.047	0.00
Shelduck	*Tadorna tadorna*	pref	-	-	P	1.057	0.02	1.059	<.001
Gadwall	*Anas strepera*	pref	-	-	W	1.035	0.17	1.070	<.001
Teal	*Anas crecca*	non	-	+	W	0.774	0.03	0.935	0.20
Mallard	*Anas platyrhynchos*	non	-	-	W	1.087	<.001	1.016	0.20
Garganey	*Anas querquedula*	pref	-	+	W	1.046	0.37	1.010	0.70
Shoveler	*Anas clypeata*	pref	-	+	W	1.075	0.00	1.071	<.001
Pochard	*Aythya ferina*	pref	-	-	W	1.316	<.001	1.207	<.001
Tufted Duck	*Aythya fuligula*	non	-	-	W	1.144	<.001	1.001	0.96
Goshawk	*Accipiter gentilis*	non	-	-	Tl	1.114	0.62	1.029	0.77
Sparrowhawk	*Accipiter nisus*	non	-	-	Tl	1.185	0.10	0.947	0.38
Buzzard	*Buteo buteo*	non	-	-	Tl	0.979	0.71	1.003	0.91
Kestrel	*Falco tinnunculus*	non	-	-	Tl	1.102	0.16	1.016	0.66
Hobby	*Falco subbuteo*	pref	-	+	Tl	0.798	0.23	1.013	0.88
Grey Partridge	*Perdix perdix*	pref	-	+	Gl	1.027	0.36	1.004	0.80
Quail	*Coturnix coturnix*	non	-	-	Gh	1.425	0.06	0.981	0.79
Pheasant	*Phasianus colchicus*	non	-	-	Gl	1.041	0.27	1.056	0.02
Water Rail	*Rallus aquaticus*	pref	-	-	W	1.156	0.15	1.065	0.23
Corncrake	*Crex crex*	spec	+	+	Gh	1.028	0.71	0.948	0.19
Moorhen	*Gallinula chloropus*	non	-	-	W	1.035	0.61	1.072	0.08
Coot	*Fulica atra*	non	-	-	W	1.049	0.01	1.027	0.03
Oystercatcher	*Haematopus ostralegus*	non	-	-	Gl	1.006	0.85	0.969	0.10
Pied Avocet	*Recurvirostra avosetta*	pref	+	-	P	1.003	0.98	1.054	0.34
Little Ringed Plover	*Charadrius dubius*	pref	-	-	P	1.181	<.001	1.078	<.001
Northern Lapwing	*Vanellus vanellus*	non	-	-	Gl	0.896	<.001	0.890	<.001
Common Snipe	*Gallinago gallinago*	non	+	+	Gl	1.073	0.48	1.125	0.02
Black-tailed Godwit	*Limosa limosa*	non	-	+	Gl	0.832	<.001	0.924	0.00
Redshank	*Tringa totanus*	non	-	+	Gl	0.936	0.01	0.919	<.001
Common Sandpiper	*Actitis hypoleucos*	spec	-	+	P	0.895	0.61	1.050	0.69
Common Tern	*Sterna hirundo*	non	+	+	P	1.095	0.01	1.014	0.51
Stock Dove	*Columba oenas*	non	-	-	Tl	1.022	0.67	1.010	0.76
Wood Pigeon	*Columba palumbus*	non	-	-	Tl	1.012	0.60	1.053	<.001
Collared Dove	*Streptopelia decaocto*	non	-	-	Tl	1.045	0.61	1.034	0.47
Turtle Dove	*Streptopelia turtur*	non	-	+	Tl	0.907	0.38	0.888	0.10
Cuckoo	*Cuculus canorus*	non	-	+	-	0.925	0.27	1.017	0.70
Little Owl	*Athene noctua*	pref	-	+	Tl	0.921	0.41	0.988	0.85
Long-eared Owl	*Asio otus*	non	-	+	Tl	1.174	0.32	1.140	0.23
Common Kingfisher	*Alcedo atthis*	spec	+	-	P	1.013	0.90	0.988	0.83
Green Woodpecker	*Picus viridis*	non	-	+	Tl	1.080	0.35	0.998	0.96
Great Spotted Woodpecker	*Picoides major*	non	-	-	Tl	0.985	0.84	1.094	0.06
Lesser Spotted Woodpecker	*Picoides minor*	pref	-	-	Tl	0.989	0.95	1.082	0.30
Skylark	*Alauda arvensis*	non	-	+	Gh	1.278	<.001	1.145	<.001

Species	Scientific name	Specialism	EU BD	RL	Strategy	Effect 5 yr	*p*-value	Effect 10 yr	*p*-value
Sand Martin	*Riparia riparia*	spec	+	-	P	1.243	<.001	1.034	<.001
Meadow Pipit	*Anthus pratensis*	non	-	+	Gh	1.032	0.24	1.060	<.001
Yellow Wagtail	*Motacilla flava*	pref	-	-	Gh	1.005	0.85	0.949	0.00
White Wagtail	*Motacilla alba*	non	-	-	P	0.936	0.10	0.987	0.65
Wren	*Troglodytes troglodytes*	non	-	-	Sh	1.042	0.13	1.061	0.00
Dunnock	*Prunella modularis*	non	-	-	Sh	1.023	0.38	1.065	<.001
Robin	*Erithacus rubecula*	non	-	-	Sh	1.262	0.01	1.230	<.001
Common Nightingale	*Luscinia megarhynchos*	pref	-	+	Sl	0.903	0.16	1.059	0.04
Bluethroat	*Luscinia svecica*	pref	+	-	Sl	0.986	0.75	1.018	0.43
Black Redstart	*Phoenicurus ochruros*	non	-	-	Th	0.923	0.12	0.928	0.01
Stonechat	*Saxicola torquata*	non	+	-	Sh	1.087	0.68	0.981	0.76
Blackbird	*Turdus merula*	non	-	-	Sh	0.986	0.41	1.013	0.26
Song Thrush	*Turdus philomelos*	non	-	-	Th	0.964	0.53	0.988	0.74
Mistle Thrush	*Turdus viscivorus*	non	-	-	Tl	1.168	0.25	1.307	0.01
Grasshopper Warbler	*Locustella naevia*	pref	-	-	Sh	1.135	0.09	1.087	0.02
Sedge Warbler	*Acrocephalus schoenobaenus*	non	+	-	Sl	0.854	0.65	1.079	0.48
Marsh Warbler	*Acrocephalus palustris*	non	-	-	Sl	1.020	0.29	1.067	<.001
Reed Warbler	*Acrocephalus scirpaceus*	non	-	-	Sl	0.904	<.001	0.956	0.02
Icterine Warbler	*Hippolais icterina*	non	-	+	Sl	1.234	0.03	1.154	0.00
Lesser Whitethroat	*Sylvia curruca*	non	-	-	Sl	0.838	0.11	0.992	0.88
Common Whitethroat	*Sylvia communis*	non	-	-	Sl	1.072	0.00	1.137	<.001
Garden Warbler	*Sylvia borin*	non	-	-	Sl	0.982	0.50	1.061	0.00
Blackcap	*Sylvia atricapilla*	non	-	-	Sl	0.985	0.66	1.053	0.01
Chiffchaff	*Phylloscopus collybita*	non	-	-	Sh	1.014	0.57	1.070	<.001
Willow Warbler	*Phylloscopus trochilus*	non	-	-	Sh	0.974	0.49	1.069	0.01
Spotted Flycatcher	*Muscicapa striata*	non	-	+	Th	1.020	0.90	0.986	0.91
Long-tailed Tit	*Aegithalos caudatus*	non	-	-	Sh	1.078	0.45	1.110	0.06
Willow Tit	*Parus montanus*	pref	-	+	Th	1.207	0.02	1.146	0.01
Blue Tit	*Parus caeruleus*	non	-	-	Th	1.117	0.01	1.078	0.00
Great Tit	*Parus major*	non	-	-	Th	1.033	0.24	1.052	0.00
Nuthatch	*Sitta europaea*	non	-	-	Th	*	0.89	*	0.14
Short-toed Treecreeper	*Certhia brachydactyla*	non	-	-	Th	1.153	0.08	1.183	<.001
Penduline Tit	*Remiz pendulinus*	spec	-	-	Th	0.866	0.23	0.803	<.001
Golden Oriole	*Oriolus oriolus*	non	-	+	Tl	1.046	0.67	1.060	0.23
Jay	*Garrulus glandarius*	non	-	-	Tl	1.046	0.70	1.102	0.13
Magpie	*Pica pica*	non	-	-	Tl	0.999	0.99	1.025	0.35
Carrion Crow	*Corvus corone corone*	non	-	-	Tl	0.999	0.97	1.030	0.15
Starling	*Sturnus vulgaris*	non	-	-	Th	0.960	0.34	1.035	0.30
House Sparrow	*Passer domesticus*	non	-	+	Th	1.027	0.37	1.041	0.09
Tree Sparrow	*Passer montanus*	non	-	+	Th	0.938	0.04	1.051	0.01
Chaffinch	*Fringilla coelebs*	non	-	-	Th	1.134	<.001	1.101	<.001
Greenfich	*Carduelis chloris*	non	-	-	Th	1.010	0.91	1.003	0.96
Goldfinch	*Carduelis carduelis*	pref	-	-	Th	0.976	0.57	1.023	0.31
Linnet	*Carduelis cannabina*	non	-	+	Sh	0.973	0.38	0.997	0.90
Reed Bunting	*Emberiza schoeniclus*	non	-	-	Sh	0.997	0.92	1.068	<.001
Corn Bunting	*Miliaria calandra*	spec	-	+	Sl	1.186	0.26	0.932	0.48

Chapter 8

Synthesis

Chris van Turnhout

More species, less diversity: the homogenization paradox

At a global scale, most studies of birds and other taxa have shown a decrease in species diversity in recent decades (e.g. McKinney and Lockwood 1999, Butchart *et al.* 2004, Millennium Ecosystem Assessment 2005, Butchart *et al.* 2010). However, at regional scales (i.e. areas that are intermediate in size between the entire globe and small study plots of a few dozen hectares) diversity appears to be increasing for many taxonomic groups. For some other groups, such as birds, most studies indicate that diversity remains relatively unchanged at regional scales (Sax and Gaines 2003). In the Netherlands the breeding bird community appears highly dynamic. There is only a very small fraction of species of which the national population does not show clear trends in abundance during the different periods studied in this thesis, which are of course all very short from an evolutionary point of view. At national scale, richness, diversity and equitability of breeding birds in the Netherlands have increased. More species have increased than decreased in terms of range and abundance. This trend holds for different time periods: 1900-2000 (Parlevliet 2003, chapter 1), 1975-2000 (chapter 4) and 1990-2005 (chapter 5). The dynamic equilibrium model states that species diversity will respond unimodally to both energy availability and disturbance rate (Huston 1994, Kondoh 2001). Given the highly anthropogenic Dutch landscape where ecosystems have long been experiencing very strong human pressure, the expectation was that breeding bird diversity in the Netherlands would be declining. Apparently, this is at present not the case at the national scale.

However, within the Netherlands there is a large spatial variation in regional and especially local species richness that underlies the general pattern of increase. This suggests that using simple national measures of diversity could conceal differentiated environmental processes at smaller spatial scales. Observed increases in species richness since the mid 1970s occurred mainly in the previously species-poor, low-lying, western part of the country. Species richness decreased in some formerly species-rich regions in the eastern part of the country. Regionally differentiated trends in populations of breeding birds characteristic for woodland and farmland suggest that regions have become more similar in their landscape features. Indeed, the openness of the unique Dutch polder landscape in the western part of the country has decreased as a result of the establishment of roadside plantations, young forestry plantations, parks and urban expansion (chapter 4). Furthermore, the area of shrubs and woodland has increased in recently reclaimed areas, marshland habitats (chapter 3), coastal dunes and river floodplains (chapter 7), as a result of natural vegetation succession, often enhanced by the effects of desiccation, eutrophication and water management (chapter 3). Simultaneously, the formerly enclosed farmland landscape in the eastern part of the country has become more open, as a result of the removal of hedgerows and small woodlots.

These land use changes have been beneficial to the species-rich communities of particularly shrubs and woodlands, but detrimental to the relatively species-poor but very distinctive communities of reed marshland, heathland and meadow birds (chapters 3 and 4). As a result, regional breeding bird communities have become more similar, while simultaneously national species diversity has increased. This process of biotic homogenization, generally referred to as the increase in species similarity in space over time (Olden & Rooney 2006), has also been demonstrated for other taxa.

In the context of global species homogenization, several terms are used, such as 'New Pangaea' and 'Homogocene' (Rosenzweig 2001, McKinney 2005). Generally, it is related to the invasion of non-native species and described for larger spatial scales (McKinney and Lockwood 1999, Fisher and Owens 2004). Several authors regard urbanization as a major cause of biotic homogenization, for both birds and other taxa (McKinney 2006, Clergeau *et al.* 2006). I argue that afforestation and degradation of several semi-natural habitats are the main factors responsible for regional homogenization of breeding bird communities in the Netherlands (chapter 4). The declining groups of meadow and reed marshland birds include many species that have disproportionate large populations in the Netherlands compared to neighbouring countries (BirdLife International 2004). Consequently, homogenization may also be occurring at Northwest-European scale. The conservation and restoration of regional identity should therefore be given greater priority in landscape planning in the Netherlands.

Exploring causes of population change: confronting trends with traits

Biotic homogenization not only has a taxonomic, but also a functional component (Olden *et al.* 2004). By exploring the relationship between population trends of breeding bird species and their ecological and life-history traits, I have evaluated to what extent changes in taxonomic diversity correspond to changes in functional diversity (chapter 5; Julliard *et al.* 2004, Devictor *et al.* 2008a). Traits determine the ability of a species to deal with environmental pressures and opportunities, and are particularly useful for understanding ecological effects (Southwood 1977, McGill *et al.* 2006). Therefore, combining bird monitoring data with traits of species offers possibilities to quantify which traits are most affected and, indirectly, to rank the environmental changes that are most likely responsible for these effects. This helps to understand the mechanisms underlying the observed patterns, to predict which species will face problems in the near future, to prioritize conservation research, and to develop management strategies (Kotiaho *et al.* 2005). I explicitly considered all Dutch breeding birds in this analysis, because working with subsets of species may give biased results, as trends depend on rarity and differ between terrestrial and water birds (Gaston and Blackburn 2002, Fisher and Owens 2004). In contrast to most other countries, scarce and rare species are well surveyed annually in the Netherlands, as a result of different monitoring programs and an extensive network of volunteer birdwatchers (chapter 1). Another potential problem in most studies is that generally only a small number of traits has been considered, whereas the total number of traits that has been identified as influencing population changes or extinction is quite large (Reed 1999). Particularly in analyses at larger spatial scales, such as the ones presented in this thesis, it is important to consider a broad scope of species traits for which relationships with population trends have been demonstrated in literature, or can be hypothesized. Breeding birds are affected by multiple environmental changes simultaneously, even at local scale, and some of the traits for which a mechanistic relation with population trend was previously demonstrated, are intercorrelated. By taking this intercorrelation explicitly into account, alternative explanations are not obscured, but can be properly addressed instead. Furthermore, when all relevant traits are combined in multiple models more accurate parameter estimates are derived, which are corrected for the effects of other relevant traits. To illustrate this, in the univariate analysis presented in chapter 5, 12 out of 25 traits explained a significant amount of variation in national population trends. However, in the multivariate analysis only four remained in the three best-fitting models.

Populations that have increased since the early 1990s are mainly found among sedentary species and short-distance migrants, herbivores, herb- and shrub-nesting birds and species with a small European range in combination with a large body-mass (chapter 5). Recent population decline appeared to be associated with ground-nesting and late arrival at the breeding grounds in migratory species. Selection for nest location and herbivory as important traits in differentiating between successful and unsuccessful species confirm the importance of the land use changes that are related to biotic homogenization, as described above. Afforestation, eutrophication and loss of natural ecosystem dynamics are beneficial for shrub-nesting species. Simultaneously, the same processes are responsible for the decline of ground-nesters, together with agricultural intensification in farmland, including falling water tables (chapters 3, 5 and 7). However, migratory strategy as a dominant trait in explaining national population trends suggests that other environmental processes have become important as well, at least since the 1990s. Increases in populations of sedentary species and partial migrants may be related to recent climate warming, which has enhanced winter survival of these species (Robinson *et al.* 2007). Declines are associated with long-distance migrants, particularly those that arrive relatively late at the breeding grounds and winter in the tropical and dry forests of the West-African Guinean zone. Other studies confirm that trans-Sahara migrants are rapidly declining (Sanderson *et al.* 2006, Heldbjerg & Fox 2008). Since 1990 this concerns particularly species that winter in West-African woodlands (Ewing *et al. in prep.*). On the other hand, nest location, body mass and European range size are not being confirmed as traits strongly associated with pan-European population trends (Ewing *et al. in prep.*). This may imply that the processes related to these latter traits are primarily relevant for Dutch breeding bird populations. However, most international analyses are based on population trends of passerines only, and may therefore be not quite representative for the entire breeding bird community. Of course, other environmental changes, such as habitat fragmentation, might be causing population changes as well (Foppen *et al.* 1999). However, these are considered less important at national scale during this study period, or are restricted to specific habitats and species (chapters 3 and 5).

Expanding the trait approach: the power of comparison

Declines of species migrating to tropical West-Africa may be caused by factors operating on the wintering grounds or the breeding grounds. On the wintering grounds habitat conditions have severely deteriorated. Human pressure on Guinean ecosystems is extremely high and forests are being cleared at a very high rate. Breeding ground changes may be related to climate change, resulting in a mismatch between timing of maximum food availability (advancing more) and food requirements (advancing less; Visser & Both 2005, Both *et al.* 2009). In order to discriminate between these processes and to find additional evidence for climate change as one of the causal drivers of recent population trends, we have expanded the 'trends versus traits' approach. Two comparisons were added: (1) differentiating population trends between habitats, and (2) differentiating population trends between regions in Europe that differ in their extent of spring warming (chapter 6). Within generalist species, population trends often differ between habitats (Gregory *et al.* 2005), which suggests that species are affected by habitat-specific environmental changes. These may affect different traits or the same traits in a different way. This may partly explain why a large part of the total variation in population trends was not captured in my analyses of national trends (chapter 5). The focus on specific processes in specific ecosystems enabled us to further specify hypotheses and research questions and, consequently, restrict the number of species and traits involved in the analyses.

We found that long-distance migrants in Dutch forests declined, whereas residents did not. At the pan-European scale long-distance migrants in forests also declined in other countries with obvious spring warming (western Europe), but not in countries with less spring warming (northern Europe). The reason is probably not a difference in wintering grounds between western and northern breeding populations: recovery positions in Africa largely overlap for most species (chapter 6). This supports the hypothesis that migrants are less able to adapt to changes in timing of food availability due to climate change than residents, because migrants cannot foresee at their wintering grounds when spring starts at their breeding grounds. This hypothesis was first put forward in a species-specific study on the Pied Flycatcher *Ficedula hypoleuca* (Both *et al.* 2001). We were able to refine and upscale this explanation to other species sharing similar traits. Forest inhabiting migrant species arriving late in spring declined most sharply, probably because their mismatch is largest (Coppack and Both 2002). In contrast, long-distance migrants in Dutch marshlands did not decline. Food availability in this habitat shows less seasonal variability than in forest, particularly during spring. Therefore, climate change most likely caused these effects and can be considered as an important driver of population trends since the 1990s, in addition to other factors such as land use changes.

From traits to tactics

Combining separate traits into suites of traits (referred to as strategies or tactics), thereby accounting for trade-offs, may be even more successful in unraveling the causal mechanisms underlying species-effect relationships than dealing with traits separately (Stearns 1976, Siepel 1995, Verberk *et al.* 2008). Recently, Verberk (2008) presented the tactic approach as a strong and useful tool to direct restoration management. It acts as an intermediate between the species approach and the community approach. In the former the causal mechanisms are not prioritized and are difficult to generalize, whereas in the latter causal mechanisms are generally obscured. The tactic approach demands an understanding of the functioning of an ecosystem, which is vital for the effectiveness of habitat management (Hobbs & Norton 1996). I adopted this additional functional approach for a specific habitat management issue: the evaluation and prediction of effects of floodplain rehabilitation on breeding birds (chapter 7). The tactic approach appears particularly strong in explicitly considering the interrelation between species traits, interpreting the function of trait combinations and trade-offs, and realizing that different trait combinations can solve the same environmental problem. This all contributes to formulating solid hypotheses on causal mechanisms for species' survival under particular environmental conditions, directly relating to the core functions of reproduction, development, dispersal, and the synchronization between those (Verberk 2008). Additionally, grouping species according to tactics is an attractive and effective way of communicating results to managers and the general public.

However, other strong points of the tactic approach as identified by Verberk (2008) are also valid for a trait approach: they both generate testable predictions, integrate knowledge on species' ecology and reduce complexity, by assigning many species of many taxonomic groups to a small number of traits, or tactics. One drawback is shared as well: detailed knowledge on species' biology is required. Other weak points identified for the tactic approach may be better dealt with when analysing traits separately. The trait approach (1) does not need criteria for the level of aggregation when grouping species, (2) does not have to deal with strategies consisting of only a few species, (3) does not need criteria on how to classify traits that are expressed using continuous metrics and (4) does not need fixed guidelines for how to assess and interpret the function and (order of) relevance of traits or combination of traits. Furthermore, for practical reasons only a limited number of traits can be considered in the tactic approach. Although many trade-offs exist, the total number of traits that has been quantified and identified as influencing abundance or population changes is very large (Reed 1999), particularly for birds (chapter 5). Therefore, the tactic approach may be prone to more subjectivity during the process of classification, is more difficult to test and does not explicitly consider alternative explanations.

The balance of advantages and disadvantages of the tactic and trait approaches depends on the research questions and the situation studied. If one is interested in specific environmental processes, ecosystems and time periods, the number of potential relevant traits may be limited, and the tactic approach can be particularly strong in underpinning causality (Verberk 2008). In the study on effects of river floodplain restoration, it was concluded that rehabilitation of vegetation succession is the key driver behind breeding bird changes in restored sites in the first ten years, rather than rehabilitation of hydrodynamics (chapter 7). If, on the other hand, one is interested in more complex situations and longer time periods, where species are influenced by several environmental processes simultaneously, possibly affecting a multitude of traits, then the separate trait approach may be more suitable (chapter 5). This is particularly the case when the approach can be expanded with 'smart comparisons' between strata that differ in environmental conditions or changes (chapter 6).

Trends differ between time periods: turn-over of dominant mechanisms

The longest time series that are presented in this thesis date back to the 1950s (chapter 3). However, most population trends cover approximately two decades: 1975-2000 (chapter 4), 1984-2004 (chapter 6) and 1990-2005 (chapter 5). Even within a study period of two decades, for part of the species substantial changes in trend directions were observed: a period of population increase is followed by a period of prolonged

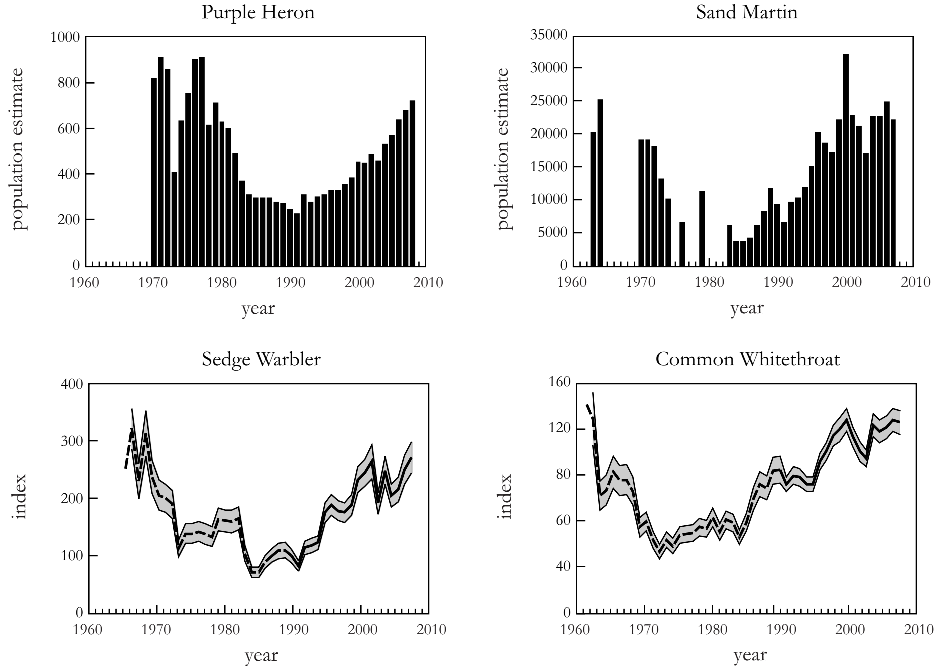


Figure 1. Dutch population trends for four breeding birds wintering in the West-African Sahel zone between 1960 and 2008 (data BMP/OT, see chapter 3): Purple Heron *Ardea purpurea*, Sand Martin *Riparia riparia*, Sedge Warbler *Acrocephalus schoenobaenus* and Common Whitethroat *Sylvia communis*. Presented are either national population estimates (bars; these represent number of occupied nests) or relative population indices (± *SE*) as derived from a sample of study sites. Because of the smaller number of study sites the indices before 1990 are not calculated using a stratification procedure, and are indicated by a dashed line (see chapter 3).

decline, or vice versa. We validated changes in abundance as derived from population estimates using atlas data (1975-2000) with trends derived from monitoring data (1984-2000). For 80% of the species trend directions (either increase, decrease or stable) were identical (chapter 4). For the remaining species, most of the differences between trends were caused by trend reversals within the 25-year study period.

This phenomenon can be well illustrated by population trends of trans-Sahara migrants (Figures 1 and 2). Species wintering in the open habitats of the West-African Sahel generally showed strong declines in the 1970s and 1980s, and recoveries afterwards. Declines appeared to coincide with large-scale droughts in the Sahel, and recoveries were correlated with periods of improved rainfall (chapter 3; Foppen *et al.* 1999, Zwarts *et al.* 2009). An identical pattern was found for pan-European trends of these species (Sanderson *et al.* 2006). For species wintering in the more forested habitats of the West-African Sahel and Guinee zones an opposite pattern was found: Dutch populations generally increased until the 1980s, and declined afterwards (chapters 5 and 6). Ewing *et al.* (*in prep.*) found the same contrasting trends after analyzing pan-European monitoring data: migrants to West-African scrub and grassland habitats declined in the period 1975-1990, whereas migrants to West-African forests declined in the 1991-2005 period. In the Netherlands, breeding populations of these common forest migrants may initially have benefited from an increase in the quantity and quality

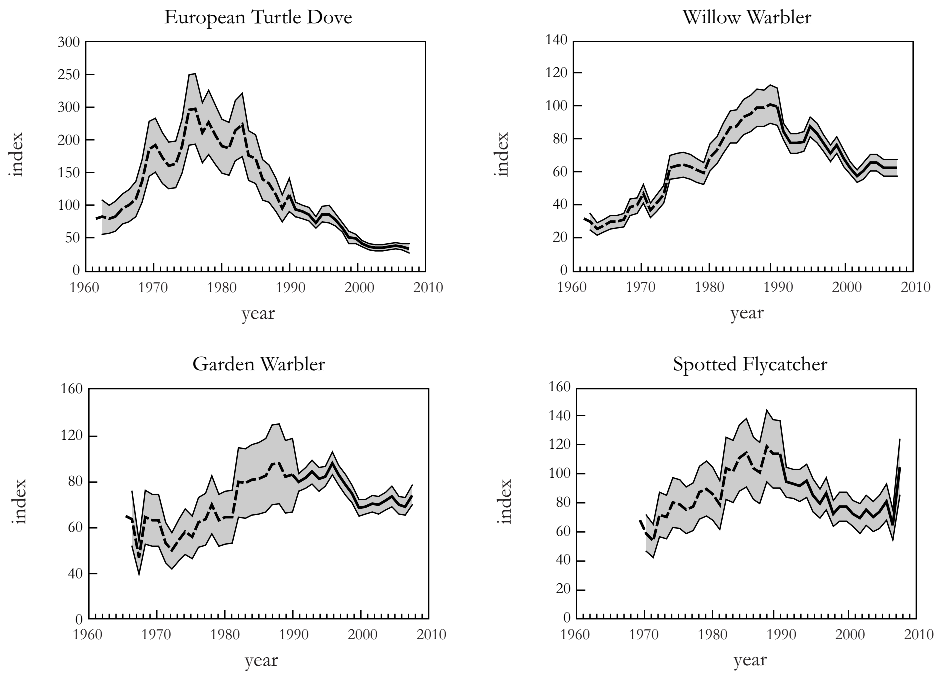


Figure 2. Dutch population indices (± *SE*) for four breeding birds wintering in the West-African Guinee and Sahel zones between 1960 and 2008 (data BMP/OT, see chapter 3): European Turtle Dove *Streptopelia turtur*, Willow Warbler *Phylloscopus trochilus*, Garden Warbler *Sylvia borin* and Spotted Flycatcher *Muscicapa striatia.*

of woodland (chapter 4). However, they are declining since the 1990s, and one of the probable explanatory factors is the occurrence of trophic mismatches due to climate change (chapter 6).

The occurrence of change points in long-term population trends suggests that correlations between traits and trends may be rather specific for certain time periods. Consequently, it is useful to periodically update the analyses presented in this thesis. The species and associated traits that will face problems can be reconsidered, and research and conservation action can be reprioritized. To illustrate this, Lemoine *et al.* (2007) suggested that climate change has recently overtaken land-use modification in determining population trends of Central European birds.

Are rare species and habitat specialists declining?

Many studies have concluded that rarity (small range and low abundance) is a trait that promotes decline and extinction, both at global (McKinney and Lockwood 1999, Fisher & Owens 2004) and local scale (Davies *et al.* 2000, Gaston & Blackburn 2002). The Dutch results were not univocal in this respect. Both the very rare (less than 250 breeding pairs in 1973-77) and the very abundant breeding birds showed an average decline between 1973-1977 and 1998-2000. Simultaneously, the moderately abundant bird species tended to have increased (chapter 4). Regarding the period 1990-2005, I even found that the smaller the species' range at European scale, the greater the population increase in the Netherlands, although this correlation only holds for larger species (chapter 5). Most of these relatively rare and large species are listed on Annex 1 of European Union's Birds Directive, and this international policy has benefited bird populations in the member states (Donald *et al.* 2007). As rare species with small ranges have benefited disproportionately, this might explain the correlation that was found. Additionally, body size has been found to correlate with extinction risk from human persecution (Bennett & Owens 2002). International legal protection could thus be beneficial for especially larger, often long-lived, species.

Many studies have also concluded that specialists are experiencing a higher frequency of decline and extinction relative to more generalist species (Reed 1999, Bennett & Owens 2002, Fisher & Owens 2004, Devictor *et al.* 2008a, Colles *et al.* 2009, Clavel *et al. in press*). However, Devictor *et al.* (2010) have shown that the concept of ecological specialization is highly context-dependent and often inconsistently used in applied ecology. Whereas the Grinnellian specialization of a species reflects the variance in performance or requirements across a range of environmental conditions (what the species *needs*; Grinnell 1917), the Eltonian specialization refers to the functional roles or impacts of a species in its environment (what the species *does*; Elton 1927). The *realized* specialization of a given species measured at a given point in time may only reflect a subsample of the conditions the species is able to cope with during a longer time period, the *fundamental* specialization. Most macroecological bird studies use the realized Grinnellian specialization, generally on the basis of the diversity of habitats that is occupied by a species as observed in the field, which is either qualified (Gregory *et al.* 2005; chapter 4) or quantified (Julliard *et al.* 2004, Seoane & Carrascal 2008). Likewise, I measured habitat specialization in the Netherlands using the Species Specialization Index (SSI), the coefficient of variation in abundance of each species in 12 different habitats (Julliard *et al.* 2006; chapter 5). The advantage of the SSI is that it is a continuous metric based on quantitative field observations, instead of a classification into two modalities (either specialist or generalist) based on expert judgement.

I did not find a significant effect of the SSI on national population trends between 1990-2005, which suggests that at the national scale habitat specialists did not decline more or less than generalist species. This is in contradiction with most other studies. Jiguet *et al.* (2007) even suggested that, although the causes of habitat deterioration may differ between habitats, specialization itself is a better predictor of population decline than living in a particular habitat. Instead, I found that the effect of specialization on population trends differed per habitat. SSI showed a negative correlation with population trends in heathland (p=0.020, n=58) and farmland (p=0.036, n=87), but a positive correlation with trends in woodland (p=0.031, n=63). This suggests that particularly heathland and farmland specialists are declining at a faster rate than generalists, whereas forest specialists are doing better than generalists. This generally concurs with population trends of forest and farmland birds in other European countries (Gregory *et al.* 2005, Gregory *et al.* 2007, Kolecek *et al.* 2010). Many of the long-distance migrants in forests that did show population declines in the Netherlands since 1990 are rather common species, occurring in several types of shrubs and forest (chapter 6).

Although ecological specialization is generally treated as insensitive to differences in temporal and spatial scales (Devictor *et al.* 2010), the realized habitat specialization

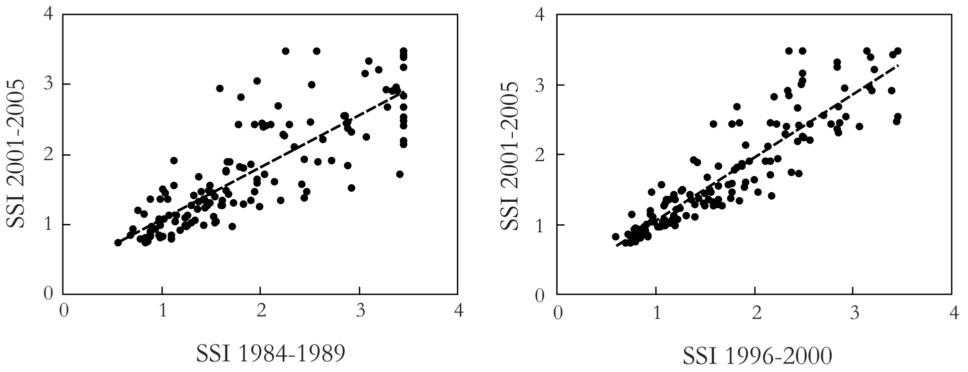


Figure 3. Species Specialization Indices of 142 breeding bird species in the Netherlands in three time periods: 1984-1989, 1996-2000 and 2001-2005. The higher SSI, the higher the degree of realized Grinnellian habitat specialization. For calculation of SSI, see chapter 5.

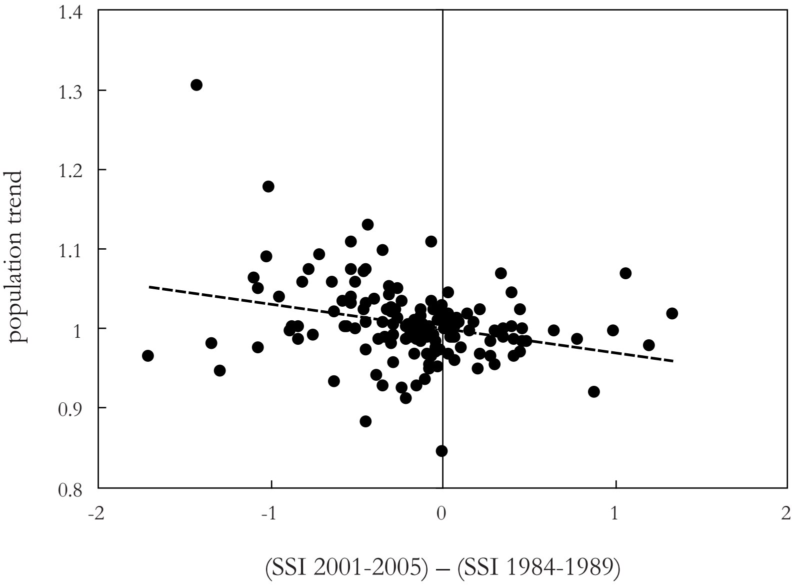


Figure 4. Relationship between Dutch population trends of breeding birds 1990-2005 and change in Species Specialization Indices between 1984-1989 and 2001-2005. The trend is presented as a multiplicative parameter: a value of 1.1 represents an annual increase of 10%. Positive values of change in SSI indicate an increase in realized habitat specialization.

of species appears not to be constant over time. I compared SSI-values as derived from abundance data in monitoring plots in 2001-2005 with those from 1984-1989 and 1996-2000 (Figure 3). SSI's are more similar when calculated for successive time periods than for more distant time periods: the correlation between the SSI's in 2001-2005 and 1996-2000 is stronger (Pearson-$r = 0.89$; $SE=0.038$; $p<0.001$; $n=142$) than between the SSI's in 2001-2005 and 1984-1989 (Pearson-$r = 0.67$; $SE=0.044$; $p<0.001$; $n=142$).

Although additional research is necessary to further elucidate this pattern, this may imply that measured habitat specialization will decrease when a species' population is increasing and gradually new habitats are being occupied (e.g. Blackbird *Turdus merula* expanding from forests into urban and semi-natural habitats; chapter 1). On the other hand, when a species is declining and populations are gradually being confined to a limited number of optimal habitats, then measured habitat specialization will decrease (e.g. Red-backed Shrike *Lanius collurio* disappearing from farmland, heathlands and coastal dunes). Indeed, correlation exists between change in SSI and population trend (Pearson-$r = -0.29$; $p<0.001$; $n=142$). Habitat specialization increases as species decline (Figure 4). This suggests that specialists are vulnerable by definition: they do not decline because they are specialists, but their population declines tend to categorize them as specialists when applying a Grinnellian specialization approach to observational data. Applying the Eltonian approach using species traits to quantify ecological specialization might be a promising, though challenging way to avoid this pitfall (Blüthgen *et al.* 2008, Devictor *et al.* 2010).

The value of citizen ornithology for science and conservation

In this thesis I used large-scale monitoring and distribution data, largely gathered by volunteer birdwatchers, in combination with ecological traits to describe, quantify and understand changes in breeding bird diversity in the Netherlands. The participation of large numbers of volunteers enables scientific research that would otherwise be impossible at the same spatial and temporal scales (Greenwood 2007). Citizen ornithology is essential in describing species' population trends (chapters 2 and 3) and changes in avian diversity patterns more general (chapter 4). Citizen ornithology also contributes to explore causes of changes, such as our understanding of which sets of species traits are primarily associated with successful and not successful species, and to prioritize further research on working mechanisms and to direct conservation action (chapter 5). Finally, it helps unraveling the causal mechanisms underlying specific species-impact relationships, although the level of causality is limited (and to my opinion the maximum level is reached in chapters 6 and 7). The 'comparative approach', by grouping species according to traits (chapter 5), tactics (chapter 7) or habitats (chapter 6), is particularly useful in this respect.

I regard the 'observational' and 'correlative' studies described in this thesis as an essential complement to studies with a more 'experimental' design. Large-scale data on population distribution and trends have often been used to make predictions that are an inspiration for detailed autecological research at the species level (Greenwood 2007). But also vice versa, intensive local research involving one species and few study sites delivers hypotheses that can be evaluated at larger spatial scales (Figure 5). This testing and up-scaling of hypotheses, in order to make generalizations of causal factors to other species (sharing similar traits), areas and time periods, is a surplus value of citizen ornithology that has received much less attention in scientific literature up to now. Also, it offers the possibility to evaluate the importance of one causal factor in relation to other working mechanisms operating in our world, which is affected by multiple environmental changes. This work is most successful where there is a strong

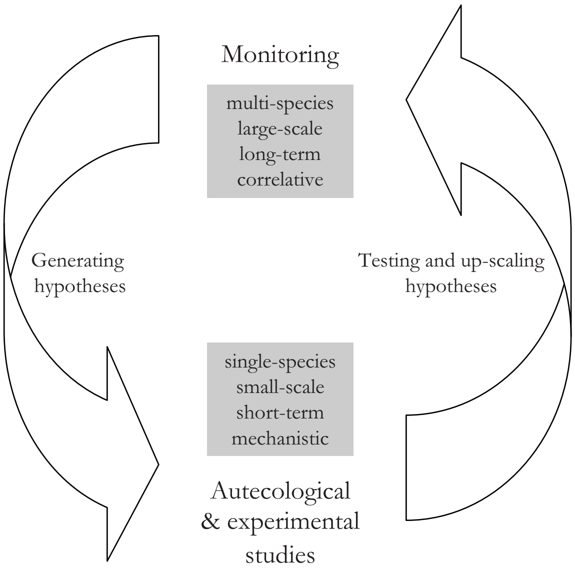


Figure 5. The citizen ornithology cycle: combining a 'top-down' and 'bottom-up' approach between autecological research and large-scale monitoring data.

partnership between the volunteers and professional biologists. Conservation, management and science will therefore benefit from a more intense and well-structured interaction between scientists, who have a thorough understanding of a limited number of species and sites, and volunteer ornithologists, who together have a global understanding of an extended number of species and sites.

Further research and developments

There are many interesting opportunities for applying the approaches presented in this thesis to other research topics and data sets. With respect to breeding birds, the extent of trophic mismatches as a result of climate change (chapter 6) might be explored for other habitats that differ in seasonality, such as inland drift sands and coastal dunes. Differential changes in invertebrate prey availability in the course of the breeding season might partly explain differences in the rates of decline in Northern Wheatears *Oenanthe oenanthe* and populations of other long-distance migrants between inland drift sands and coastal dunes (Nijssen *et al.* 2010). Inference of causal mechanisms will be strongest when population numbers are monitored simultaneously with changes in the composition of the underlying food web, and with changes in productivity and survival of the birds. Such an integrated bird population monitoring enables us to estimate population changes and vital rates independently, thus allowing to draw them together in a population model (Baillie 1990, Freeman & Crick 2003). It is then possible to identify the stage of the life-cycle affected by environmental change, indicate likely causes of population change and distinguish between anthropogenic changes and natural population fluctuations. Volunteers can be very valuable in measuring these demographic variables at the national scale, by supplying nest records and contributing to bird ringing and recapture programs (Greenwood 2007).

Also, the analyses and results presented in this thesis can be up-scaled and tested using pan-European datasets (Jiguet *et al.* 2010, Ewing *et al. in prep.*) or expanded to non-breeding birds. The Netherlands hold internationally important populations of migratory water birds, and many causes have been suggested to explain observed species-specific changes in abundance. These include changes in land use and agricultural practice (Van Eerden *et al.* 2005), climate (Maclean *et al.* 2008), fisheries (Van Gils *et al.* 2006), eutrophication (Philippart *et al.* 2007), hunting (Ebbinge 1991) and habitat restoration (Noordhuis *et al.* 2002). Combining monitoring data with traits of water bird species offer possibilities to quantify which traits are most affected and thereby rank the environmental changes that are responsible (chapter 5). Similarly, this approach may be applied to other taxonomic groups for which reliable trend data and extensive knowledge on species' traits are available, such as butterflies (Van Dyck *et al.* 2008).

Finally, effectiveness of habitat management will increase if the impacts of measures are more often quantitatively assessed. Much of current conservation practice is based upon anecdote and myth rather than upon the systematic appraisal of the evidence (Sutherland *et al.* 2004). Monitoring data should play an important role in these evaluations, e.g. for assessing the impacts of grazing in coastal dunes. Adopting a functional approach can provide a tool to predict the effects of future rehabilitation projects, and to adapt the management strategy, if necessary (Van Kleef *et al.* 2006, Verberk 2008, chapter 7). Of course, a detailed registration of rehabilitation measures per site is vital in this respect, but is unfortunately lacking in most cases. The development of a central database in which key management data can be stored and assessed is crucial in this respect. The potential involvement of volunteers in the registration of detailed habitat and management data deserves further elaboration.

Innovation of monitoring schemes

A sustainable monitoring scheme that keeps continuous track of population trends heavily relies on a representative coverage and continuity for the long term (Greenwood 2007). Simultaneously, information needs of e.g. governmental bodies frequently change, as do the motives, preferences and time budgets of volunteers (chapter 1). Our challenge is to innovate the schemes to fulfil all new demands as much as possible, while maintaining the original main objectives, and to guarantee the high level of participation by volunteer bird watchers. In order to gather more data in hitherto undersampled strata, a labour-extensive monitoring scheme was recently started in the Netherlands in urban habitats, in addition to the Breeding Bird Monitoring Program (chapter 2). It is based on point-counts in a randomised selection of study sites (Van Turnhout & Aarts 2007). A new pool of volunteers is now participating in this program. It will probably be expanded to other habitats in the near future. Combining trends resulting from different schemes has been proven to be a practical and statistically sound method (Gregory *et al.* 2005).

Recently, a broad array of initiatives has started to use the Internet as a tool to gather, archive, validate, analyse and distribute bird information to a wide audience. The Internet has made real-time information exchange possible and thereby broadened the capacity for community outreach (Sullivan *et al.* 2009). Although some registration of effort and a basic sampling protocol (e.g. repeated visits) remain essential for sound analyses of population and distribution trends, the prerequisites are being more relieved as new statistical methodologies become available (Kéry *et al.* 2009). Site-occupancy models appear to be successful in reducing bias in opportunistic data, especially those caused by temporal variation of observation effort and by incomplete reporting of sightings. Occupancy trends of dragonflies in the Netherlands based on comprehensive daily species lists resemble those based on the monitoring scheme, although casual one-species records and short daily lists were too imprecise to be very useful (Van Strien *et al. in press*). Representative sampling and extensive validation of the field data remains necessary under all circumstances, the latter particularly when large numbers of less experienced participants enter the monitoring programs.

Apart from gathering abundance data in the field, also analysis methods need continuous innovation. Changing environments may not only affect population trends of animals, but also their detectability. This might create bias in the observed counts (Kéry & Royle 2010). For instance, climate change results in an earlier arrival of trans-Sahara migrants at their breeding grounds (Jonzen *et al.* 2006), which may affect detection probability if timing of visits is kept constant. Applying a hierarchical modelling framework to estimate abundance trends corrected for detectability using data from the Dutch Breeding Bird Monitoring Program indicates that time trends in detection probabilities of migratory species indeed exist, but that corrected trends do not differ from unadjusted population trends as described in this thesis (*unpublished data*). This suggests that the field method of territory mapping is rather robust, as a result of the high number of visits and the use of species-specific interpretation criteria to determine the number of territories per species at the end of the season (chapter 2). However, this may not hold for more labour-extensive field work methods, such as point counts. These should be properly evaluated regarding this aspect.

Finally, to ensure that research findings on bird population declines will be used for priority setting in conservation policy and are translated into active conservation, monitoring must be embedded in a relevant socio-economic context (Nichols & Williams 2006). Composite ‘state indicators’ can fulfill an essential role in this process. They provide a simple way of measuring progress towards targets of reducing biodiversity loss and have been very successful in influencing policy and communicating to a wider audience (Butchart *et al.* 2004, Gregory *et al.* 2005, Gregory *et al.* 2008; chapter 1). Recently, Devictor *et al.* (2008b) developed a simple framework to measure change in bird community composition in response to climate warming. It would be very interesting to develop such an indicator for the Netherlands, as well as other indicators reflecting changes in ecological integrity at the landscape scale (Van Strien *et al.* 2009).

References

Baillie S.R. 1990. Integrated population monitoring of breeding birds in Britain and Ireland. *Ibis* 132: 151-161.

Bennett P.M. & Owens I.P.F. 2002. Evolutionary ecology of birds. Life histories, mating systems and extinction. Oxford University Press, Oxford.

BirdLife International 2004. Birds in Europe: population estimates, trends and conservation status. Cambridge, UK.

Blüthgen N., Fründ J., Vazquez D.P. & Menzel F. 2008. What do interaction network metrics tell us about specialization and biological traits? *Ecology* 89: 3387-3399.

Both C. & Visser M. E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411: 296-298.

Both C., Van Asch M., Bijlsma R.G., Van den Burg A.B. & Visser M.E. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations. *Journal of Animal Ecology* 78: 73-83.

Butchart S.H.M., Stattersfield A.J., Bennun L.A., Shutes S.M., Akcakaya H.R., Baillie J.E.M., Stuart S.N., Hilton-Taylor C. & Mace G.M. 2004. Measuring global trends in the status of biodiversity: Red list indices for birds. *PLoS Biology* 2: 2294-2304.

Butchart S.H.M., Walpole M., Collen B., *et al.* 2010. Global biodiversity: Indicators of recent declines. *Science* 328: 1164-1168.

Clavel J., Julliard R. & Devictor V. *in press*. Worldwide decline of specialist species: towards a global functional homogenization? *Frontiers in Ecology and Environment.*

Clergeau P., Croci S., Jokimäki J., Kaisanlahti-Jokimäki M.J. & Dinetti M., 2006. Avifauna homogenisation by urbanisation: Analysis at different European latitudes. *Biological Conservation* 127: 336-344.

Colles A., Liow L.H. & Prinzing A. 2009. Are specialists at risk under environmental change? Neoecological, paleoecological and phylogenetic approaches. *Ecology Letters* 12: 849-863,

Coppack T. & Both C. 2002. Predicting life-cycle adaptation of migratory birds to global climate change. *Ardea* 90: 369-378.

Davies K.F., Margules C.R. & Lawrence K.F. 2000. Which traits of species predict population declines in experimental forest fragments? *Ecology* 81: 1450-1461.

Devictor V., Julliard R., Clavel J., Jiguet F., Lee A. & Couvet D. 2008a. Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography* 17: 252-261.

Devictor V., Julliard R., Couvet D. & Jiguet F. 2008b. Birds are tracking climate warming, but not fast enough. *Proceedings Royal Society London B. Biological Sciences* 275: 2743-2748.

Devictor V., Clavel J., Julliard R., Lavergne S., Mouillot D., Thuiller W., Venail P., Villéger S. & Mouquet N. 2010. Defining and measuring ecological specialization. *Journal of Applied Ecology* 47: 15-25.

Donald P.F., Sanderson F.J., Burfield I.J., Bierman S.M., Gregory R.D. & Waliczky Z. 2007. International conservation policy delivers benefits for birds in Europe. *Science* 317: 810-813.

Ebbinge B.S. 1991. The impact of hunting on mortality rates and spatial distribution of geese wintering in the Western Palearctic. *Ardea* 79: 197-209.

Elton C. 1927. Animal Ecology. Sidgwick and Jackson, London.

Ewing S. *et al. in prep*. Correlates of population change in European breeding birds.

Fisher D.O. & Owens I.P.F. 2004. The comparative method in conservation biology. *Trends in Ecology and Evolution* 19: 391-398.

Foppen R., Ter Braak C.J.F., Verboom J. & Reijnen R. 1999. Dutch Sedge Warblers *Acrocephalus schoenobaenus* and west-african rainfall: empirical data and simulation modelling show low population resilience in fragmented marshlands. *Ardea* 87: 113-127.

Freeman S.N. & Crick H.Q.P. 2003. The decline of the spotted flycatcher *Muscicapa striata* in the UK: an integrated population model. *Ibis* 145: 400-412.

Gaston K.J. & Blackburn T.M. 2002. Large-scale dynamics in colonization and extinction for breeding birds in Britain. *Journal of Animal Ecology* 71: 390-399.

Greenwoud J.J.D. 2007. Citizens, science and bird conservation. *Journal of Ornithology* 148: 77-124.

Gregory R.D., Van Strien A., Vorisek P., Meyling A.W.G., Noble D.G., Foppen R.P.B. & Gibbons D.W. 2005. Developing indicators for European birds. *Philosophical Transactions of the Royal Society B*: 269-288.

Gregory R.D., Vorisek P., Van Strien A., Meyling A.W.G., Jiguet F., Fornasari L., Reif J. & Burfield I.J. 2007. Population trends of widespread woodland birds in Europe. *Ibis* 149:78-97.

Gregory R.D., Vorisek P., Noble D.G., Van Strien A., Klvanova A., Eaton M., Meyling A.W.G., Joys A., Foppen R.P.B. & Burfield I. 2008. The generation and use of bird population indicators in Europe. *Bird Conservation International* 18: 233-244.

Grinnell J. 1917. The niche relationship of the California Thrasher. *The Auk* 34: 427-433.

Heldbjerg H. & Fox T. 2008. Long-term population declines in Danish trans-Saharan migrant birds. *Bird Study* 55: 267-279.

Hobbs R.J. & Norton D.A. 1996. Towards a conceptual framework for restoration ecology. *Restoration Ecology* 4: 93-110.

Huston M.A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge.

Jiguet F., Gadot A.S., Julliard R., Newson S.E. & Couvet D. 2007. Climate envelope, life history traits and the resilience of birds facing global change. *Global Change Biology* 13: 1672-1684.

Jiguet F., Devictor V., Ottvall R., Van Turnhout C., Van der Jeugd H. & Lindström A. 2010. Bird population trends are linearly affected by climate change along species thermal ranges. *Proceedings Royal Society London B. Biological Sciences* 277: 3601-3608.

Jonzen N., Lindén A., Ergon T., *et al.* 2006. Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312: 1959-1961.

Julliard R., Jiguet F. & Couvet D. 2004. Common birds facing global changes: what makes a species at risk? *Global Change Biology* 10: 148-154.

Julliard R., Clavel J., Devictor V., Jiguet F. & Couvet D. 2006. Spatial segregation of specialists and generalists in bird communities. *Ecology Letters* 9: 1237-1244.

Kéry M., Dorazio R.M., Soldaat L., van Strien A., Zuiderwijk A. & Royle A.J. 2009. Trend estimation in populations with imperfect detection. *Journal of Applied Ecology* 46: 1163-1172.

Kéry M. & Royle J.A. 2010. Hierarchical modelling and estimation of abundance and population trends in metapopulation designs. *Journal of Animal Ecology* 79: 453-461.

Kolecek J., Reif J., Stastny K. & Bejcek V. 2010. Changes in bird distribution in a Central European country between 1985-1989 and 2001-2003. *Journal of Ornithology* 151: 923-932..

Kondoh M. 2001. Unifying the relationships of species richness to productivity and disturbance. *Proceedings Royal Society London B. Biological Sciences* 268: 269-271.

Kotiaho J.S., Kaitala V., Komonen A. & Paivinen J. 2005. Predicting the risk of extinction from shared ecological characteristics. *Proceedings of the National Academy of Sciences of the United States of America* 102: 1963-1967.

Lemoine N., Schaefer H.C. & Böhning-Gaese K. 2007. Species richness of migratory birds is influenced by global climate change. *Journal of Global Ecology and Biogeography* 16: 55-64.

Maclean I.M.D., Austin G.E., Rehfisch M.M., Blew J., Crowe O., Delany S., Devos K., Deceuninck B., Gunther K., Laursen K., Van Roomen M. & Wahl J. 2008. Climate change causes rapid changes in the distribution and site abundance of birds in winter. *Global Change Biology* 14: 2489-2500.

McGill B.J., Enquist B.J., Weiher E. & Westoby M. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 12: 474-478.

McKinney M.L. 2005. Species introduced from nearby sources have a more homogenizing effect than species from distant sources: evidence from plants and fishes in the USA. *Diversity and Distributions* 11: 367-374

McKinney M.L. 2006. Urbanization as a major cause of biotic homogenization. *Biological Conservation* 127: 247-260.

McKinney M.L. & Lockwood J.L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* 14: 450-453.

Millennium Ecosystem Assessment 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

Nichols J.D. & Williams B.K. 2006. Monitoring for conservation. *Trends in Ecology and Evolution* 21: 668-673.

Noordhuis R., Van der Molen D.T. & Van den Berg M.S. 2002. Response of herbivorous water-birds to the return of *Chara* in Lake Veluwemeer, the Netherlands. *Aquatic Botany* 72: 349-367.

Nijssen M., Riksen M.P.J.M., Sparrius L.B., Bijlsma R.J., De Waal R., Jungerius P.D., Ketner-Oostra R., Kooijman A.M., Kuiters A.L., Van den Burg A., Van Dobben H.F., Van Turnhout C. & Van Swaay C. 2010. Onderzoek naar effectgerichte maatregelen voor het herstel en beheer van stuifzanden. Ministry of Agriculture, Nature and Food Quality, Ede. Report.

Olden J.D. & Rooney T.P. 2006. On defining and quantifying biotic homogenization. *Trends in Ecology and Evolution* 15: 113-120.

Olden J.D., Poff N.L., Douglas M.B., Douglas M.E. & Fausch K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution* 19: 18-24.

Parlevliet J. 2003. Breeding birds in the Netherlands in the 20th century. *Limosa* 76: 141-156.

Philippart C.J.M., Beukema J.J., Cadee G.C., Dekker R., Goedhart P.W., Van Iperen J.M., Leopold M.F. & Herman P.M.J. 2007. Impacts of nutrient reduction on coastal communities. *Ecosystems* 10: 95-118.

Reed J.M. 1999. The role of behavior in recent avian extinctions and endangerments. *Conservation Biology* 13: 232-241.

Robinson R.A., Baillie S.R. & Crick H.Q.P. 2007. Weather-dependent survival: implications of climate change for passerine population processes. *Ibis* 149: 357-364.

Rosenzweig M.L. 2001. The four questions: what does the introduction of exotic species do to diversity? *Evolutionary Ecology Research* 3: 361-367.

Sanderson F.J., Donald P.F., Pain D.J., Burfield I.J. & Van Bommel F.P.J. 2006. Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation* 131: 93-105.

Sax D.F. & Gaines S.D. 2003. Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution* 18: 561-566.

Seoane J. & Carrascal L.M. 2008. Interspecific differences in population trends of Spanish birds are related to habitat and climatic preferences. *Journal of Global Ecology and Biogeography* 17: 111-121.

Siepel H. 1995. Applications of microarthropod life-history tactics in nature management and ecotoxicology. *Biology and Fertility of Soils* 19: 75-83.

Southwood T.R.E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46: 337-365.

Stearns S.C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51: 3-47.

Sullivan B.L., Wood C.L., Iliff M.J., Bonney R.E., Fink D. & Kelling S. 2009. eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation* 142: 2282-2292.

Sutherland W.J., Pullin A.S., Dolman P.M. & Knight T.M. 2004. The need for evidence-based conservation. *Trends in Ecology and Evolution*: 305-308.

Van Dyck H., Van Strien A.J., Maes D. & Van Swaay C.A.M. 2009. Declines in common, widespread Butterflies in a landscape under intense human use. *Conservation Biology* 23: 957-965.

Van Eerden M.R., Drent R.H., Stahl J. & Bakker J.P. 2005. Connecting seas: western Palaearctic continental flyway for water birds in the perspective of changing land use and climate. *Global Change Biology* 11: 894-908.

Van Gils J.A., Piermsa T., Dekinga A., Spaans B. & Kraan C. 2006. Shellfish-dredging pushes a flexible avian toppredator out of a protected marine ecosystem. *PloS Biology* 4: 2399-2404.

Van Kleef H.H., Verberk W.C.E.P., Leuven R.S.E.W., Esselink H., Van der Velde G. & Van Duinen G.A. 2006. Biological traits successfully predict the effects of restoration management on macroinvertebrates in shallow softwater lakes. *Hydrobiologia* 565: 201-216.

Van Strien A.J., Van Duuren L., Foppen R.P.B. & Soldaat L.L. 2009. A typology of indicators of biodiversity change as a tool to make better indicators. *Ecological Indicators* 9: 1041-1048.

Van Strien A.J., Termaat T., Groenendijk D., Mensing V. & Kéry M. *in press*. Site-occupancy models may offer new opportunities for dragonfly monitoring based on daily species lists. *Basic and Applied Ecology*.

Van Turnhout C. & Aarts B. 2007. A new monitoring scheme for breeding birds in urban habitats. *Limosa* 80: 40-43.

Verberk W.C.E.P. 2008. Matching species to a changing landscape. Aquatic macroinvertebrates in a heterogeneous landscape. PhD thesis, Radboud University Nijmegen.

Verberk W.C.E.P., Siepel H. & Esselink H. 2008. Life-history strategies in freshwater macroinvertebrates. *Freshwater Biology* 53: 1722-1738.

Visser M.E. & Both C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings Royal Society London B. Biological Sciences* 272: 2561-2560.

Zwarts L., Bijlsma R.G., Van der Kamp J. & Wymenga E. 2009. Living on the edge: Wetlands and birds in a changing Sahel. KNNV Publishing, Zeist.

Summary

There is broad consensus that global biodiversity is declining more rapidly now than at any time in human history. Large, diverse, well-known, easily identified and easily censused taxonomic groups such as birds show these trends particularly clearly. Deteriorations have occurred in all major biogeographic regions and ecosystems. This thesis describes, quantifies and explains changes in breeding bird diversity in the Netherlands in the past decades (**Chapter 1**). The analyses are based on survey data on distribution and abundance and ecological data on traits of breeding birds. A substantial part of these data is gathered by volunteers, people who go out into the field to count birds merely for the joy of it. Nevertheless, they are generally very skilled and use standard protocols for carrying out the field work, thus enabling scientific sound analyses (**Chapter 2**). An integrated and quantitative analysis of population developments in all co-existing breeding bird species in the Netherlands is not yet available in scientific literature, and international studies based on similar spatial and temporal scales are scarce. The basic idea behind the analyses presented in this thesis is that observed population changes can be explained by life-history and ecological traits of individual species. Confronting trends with species traits may clarify which sets of traits are primarily associated with successful and unsuccessful species in our rapidly changing environment, which is affected by multiple environmental drivers. It may also identify and rank the most important environmental changes responsible, including changes in land use, climate and habitat management.

In the Netherlands the breeding bird community appears to be highly dynamic (**Chapters 3 and 4**). There is only a very small fraction of species of which the national population has not shown clear trends in abundance during the different periods that are studied in this thesis. At national scale, richness, diversity and equitability of breeding birds in the Netherlands have increased. More species have increased than decreased in terms of range and abundance. Both the very rare and the very abundant breeding birds showed an average decline between 1975 and 2000, whereas the moderately abundant bird species tended to have increased (**Chapter 4**). At national scale, habitat specialists did not decline more or less than generalist species since 1990. This is in contradiction with most other studies. The effect of specialization on population trends differs per habitat. Particularly specialists of heathland and farmland habitats are declining at a faster rate than generalists, whereas forest specialists are doing better than generalists (**Chapter 5**).

Within the Netherlands there is a large spatial variation in regional and especially local species richness that underlies the general pattern of increase. This suggests that using simple national measures of diversity could conceal differentiated environmental processes at smaller spatial scales. Observed increases in species richness since the mid 1970s occurred mainly in the previously species-poor, low-lying, western part of the country. Species richness decreased in some formerly species-rich regions in the eastern part of the country. Regionally differentiated trends in populations of breeding birds characteristic for woodland and farmland suggest that regions have become more similar in their landscape features. Indeed, the openness of the unique Dutch polder landscape in the western part of the country has decreased as a result of the establishment of roadside plantations, young forestry plantations, parks and urban expansion. Furthermore, the area of shrubs and woodland has increased in recently reclaimed areas, marshland habitats, coastal dunes and river floodplains. These land use changes have been beneficial to the species-rich communities of particularly shrubs and woodlands, but detrimental to the relatively species-poor but very distinctive communities of meadow birds, heathland and reed marshland (**Chapter 3**). Simultaneously, the formerly enclosed farmland landscape in the eastern part of the country has become more open, as a result of the removal of hedgerows and small woodlots. As a result, regional breeding bird communities have become more similar, while simultaneously national species diversity has increased (**Chapter 4**). This process of biotic homogenization has also been demonstrated for other taxa and study areas abroad, and is generally regarded as a result of global urbanization. However, regional homogenization of breeding bird communities in the Netherlands is primarily caused by afforestation and degradation of several semi-natural habitats. The conservation and restoration of regional identity should be given greater priority in landscape planning in the Netherlands.

Biotic homogenization not only has a taxonomic, but also a functional component. Populations that have increased since the early 1990s are mainly found among sedentary species and short-distance migrants, herbivores, herb- and shrub-nesting birds and species with a small European range in combination with a large body-mass. Recent population decline appeared to be associated with ground-nesting and late arrival at the breeding grounds in migratory species (**Chapter 5**). Selection for nest location and herbivory are important traits that explain the difference between successful and unsuccessful species. This confirms the importance of the land use changes that are related to biotic homogenization. Afforestation, eutrophication and loss of natural ecosystem dynamics are beneficial for shrub-nesting species, whereas the same processes are responsible for the decline of ground-nesters, together with agricultural intensification in farmland. Conservation management will only be effective if focused on the sets of traits that are most seriously affected. Process management, such as the large-scale reactivation of natural ecosystem dynamics in coastal and inland dunes and rehabilitation of high ground water levels in farmland, is the most promising approach to halt the decline of ground-nesting birds. Pattern management strategies, such as the restoration of vegetation mosaics in small habitat patches by actively removing the vegetation in inland drift sands and delayed and staggered mowing in grasslands, in combination with active nest protection, seem inadequate to reverse declining population trends of these species.

Migratory strategy as an important trait in explaining national population trends suggests that other environmental processes are important as well, at least since the 1990s (**Chapter 5**). Increases in populations of sedentary species and partial migrants may be related to recent climate warming, which has enhanced winter survival of these species. Recent declines are associated with long-distance migrants, particularly those that arrive relatively late at the breeding grounds in spring and winter in the tropical and dry forests of the West-African Guinean zone. Declines of these trans-Sahara migrants may be caused by factors operating on the wintering grounds (loss of habitat) or the breeding grounds. The latter may be (partly) related to climate change, resulting in a mismatch between timing of maximum food availability (advancing more) and food requirements (advancing less). In order to discriminate between these processes and to find additional evidence for climate change as one of the causal drivers of recent population trends, trends were compared between two habitats that differ in seasonality, and between regions in Europe that differ in their extent of spring warming (**Chapter 6**). We found that long-distance migrants in Dutch forests declined, whereas residents did not. At the pan-European scale long-distance migrants in forests also declined in other countries with obvious spring warming (western Europe), but not in countries with less spring warming (northern Europe), whereas they most probably share the same wintering areas. This supports the hypothesis that migrants are less able to adapt to changes in timing of food availability due to climate change than residents, because migrants cannot foresee at their wintering grounds when spring starts at their breeding grounds. In contrast, long-distance migrants in Dutch marshlands did not decline. Food availability in this habitat is more constant than in forest during spring. Therefore, climate change most likely caused these effects and can be considered as an important driver of population trends since the 1990s, in addition to other factors such as land use changes.

Combining separate traits into strategies, thereby accounting for trade-offs, may be even more successful in unraveling the causal mechanisms underlying species-effect relationships than dealing with traits separately. This additional functional approach was adopted for a specific habitat management issue: the evaluation of effects of large-scale rehabilitation of Dutch river floodplains on breeding birds (**Chapter 7**). These effects have generally been positive in the first ten years after the start of the rehabilitation. Although the majority of the analyzed species has not shown a significant response yet, positive effects were dominant among those that have. Differences in effects between species are best explained by the trait selection of nest location. Spontaneous vegetation succession and initial excavations are currently more important drivers of population changes than rehabilitation of natural hydrodynamics. The latter are strongly constrained by river regulation. If rehabilitation of hydro-geomorphological processes remains incomplete in future, artificial cyclic floodplain rejuvenation will be necessary for sustainable conservation of characteristic river birds. Furthermore, optimizing rehabilitation measures is needed to enable recolonization of a number of rare target species of river floodplains, which are often regarded as prime indicators of ecological integrity of riverine ecosystems. Reallocation of dikes to create more space, expanding the area of rehabilitated floodplains, improving the spatial cohesion between rehabilitated sites and with nature reserves in the hinterland, and aiming at complete lateral gradients between high-dynamic aquatic and low-dynamic terrestrial habitats are key strategies to achieve this.

This thesis shows that the participation of large numbers of volunteers in large-scale monitoring and distribution studies enables scientific research that would otherwise be impossible at the same spatial and temporal scales (**Chapter 8**). Citizen ornithology is essential in describing species' population trends and changes in avian diversity patterns more general. Citizen ornithology also contributes to exploring causes of changes, and to prioritize further research on working mechanisms and to direct conservation action. Finally, it helps unraveling the causal mechanisms underlying specific species-impact relationships. The 'comparative approach', by grouping species according to traits, tactics or habitats, is particularly useful in this respect. The correlative studies described in this thesis are an essential complement to studies with a more experimental design. Large-scale data on population distribution and trends have often been used to make predictions that are an inspiration for detailed autecological research at the species level. But also vice versa, intensive local research involving one species and few study sites delivers hypotheses that can be evaluated at larger spatial scales. This testing and up-scaling of hypotheses, in order to make generalizations of causal factors to other species (sharing similar traits), areas and time periods, is a surplus value of citizen ornithology that has received much less attention in scientific literature up to now. It also offers the possibility to evaluate the importance of one causal factor in relation to other working mechanisms operating in our world, which is affected by multiple environmental changes simultaneously. Conservation, management and science will therefore benefit from a more intense and well-structured interaction between scientists and volunteer ornithologists.

Samenvatting

De biodiversiteit op aarde neemt momenteel sneller af dan op enig ander moment in de geschiedenis van de mensheid. Deze ontwikkeling is vooral goed zichtbaar bij vogels. Deze diergroep bestaat namelijk uit een grote diversiteit aan soorten, waarover relatief veel bekend is. Bovendien zijn vogels, in vergelijking met de meeste andere diergroepen, eenvoudig te herkennen en te tellen. In dit proefschrift worden de veranderingen in de Nederlandse broedvogeldiversiteit, zoals die gedurende de afgelopen decennia hebben plaatsgevonden, beschreven, gekwantificeerd en verklaard (**Hoofdstuk 1**). De gepresenteerde analyses zijn gebaseerd op gegevens afkomstig van grootschalige vogeltellingen, die zijn gericht op het in beeld brengen van de verspreiding, aantallen en aantalontwikkelingen van broedvogels. Daarnaast is voor de analyses gebruik gemaakt van ecologische gegevens over eigenschappen van vogels. Een substantieel deel van de telgegevens is verzameld door vrijwilligers, 'amateur-ornithologen' die in eerste instantie puur voor hun plezier het veld in gaan om vogels te tellen. Dit laat onverlet dat deze vrijwilligers over het algemeen zeer kundig zijn in het herkennen en tellen van vogels en bovendien de tellingen uitvoeren volgens gestandaardiseerde veldwerkmethoden. Mede door deze standaardisatie is een wetenschappelijke analyse van de telgegevens goed mogelijk (**Hoofdstuk 2**). Een integraal en gekwantificeerd overzicht van de populatieontwikkelingen van alle Nederlandse broedvogels is in de wetenschappelijke literatuur tot op heden niet beschikbaar. Ook buitenlandse studies die betrekking hebben op vergelijkbare tijd- en ruimteschalen zijn schaars. De basisgedachte achter de in dit proefschrift gepresenteerde analyses is dat de vastgestelde populatieveranderingen van vogelsoorten kunnen worden verklaard door hun biologische eigenschappen. Door de trends van soorten te relateren aan hun eigenschappen, krijgen we dus inzicht in welke eigenschappen zijn geassocieerd met succesvolle of juist niet succesvolle soorten in onze snel veranderende omgeving. Dit inzicht draagt bij aan het opsporen van de belangrijkste processen die aan populatietrends ten grondslag liggen, zoals veranderingen in landgebruik, klimaat en natuurbeheer.

De Nederlandse broedvogelbevolking blijkt enorm dynamisch (**Hoofdstukken 2 en 3**). Van slechts een klein deel van de soorten laten de landelijke populaties geen duidelijke toe- of afname zien gedurende de verschillende tijdsperioden die in dit proefschrift aan de orde komen (1900-2000, 1975-2000 and 1990-2005). Op landelijke schaal zijn de soortenrijkdom en -diversiteit van broedvogels toegenomen. Ook zijn er meer soorten waarvan de aantallen en verspreiding zijn toegenomen dan waarvan die zijn afgenomen. De tendens is dat de categorieën van zowel de zeer zeldzame als de zeer talrijke broedvogels gemiddeld in aantal afnamen tussen 1975 en 2000. De tussencategorieën van schaarse en talrijke broedvogels neigen gemiddeld juist naar toename (**Hoofdstuk 4**). Op landelijke schaal namen de populaties van habitatspecialisten sinds 1990 niet sterker af dan die van generalisten, hetgeen in tegenspraak is met de meeste andere studies. De effecten van specialisatie blijken sterk te verschillen tussen habitats. Vooral specialisten van heide en agrarisch gebied doen het slechter dan de generalisten in deze habitats, terwijl specialisten van bos het juist beter doen dan generalisten (**Hoofdstuk 5**).

Binnen Nederland is sprake van een grote regionale en locale variatie op de algemene trend van toename in soortenrijkdom. Dit indiceert dat door het gebruik van vereenvoudigde landelijke biodiversiteitgraadmeters belangrijke milieuveranderingen, die zich op kleinere ruimtelijke schaalniveaus afspelen en een gedifferentieerde uitwerking hebben, verborgen kunnen blijven. De vastgestelde toenames in soortenrijkdom sinds de jaren zeventig hebben met name in het oorspronkelijk relatief soortenarme, laag gelegen westelijke deel van Nederland plaatsgevonden. In een aantal regio's in het voorheen relatief soortenrijke, hoog gelegen oostelijke deel van Nederland is de soortenrijkdom juist afgenomen. Veel bosvogels hebben hun verspreiding in laag Nederland sterk uitgebreid, maar in hoog Nederland niet of nauwelijks. Deze en andere verschillen in populatietrends tussen hoog en laag Nederland suggereren dat de landschappen in deze regio's meer op elkaar zijn gaan lijken (**Hoofdstuk 4**). Het open karakter van het unieke Nederlandse polderlandschap in laag Nederland is inderdaad aan het verdwijnen, als gevolg van de aanplant van bossen, wegbeplanting, aanleg van parken en de uitbreiding van stedelijk gebied. Daarnaast is de oppervlakte bos en struweel toegenomen in moerasgebieden, kustduinen en rivieruiterwaarden, deels door versnelde vegetatiesuccessie als gevolg van de effecten van verdroging en eutrofiëring. Deze ontwikkelingen zijn gunstig geweest voor de relatief soortenrijke en algemeen voorkomende broedvogelgemeenschappen van bos en struweel. Dezelfde ontwikkelingen zijn echter juist negatief geweest voor de relatief soortenarme gemeenschappen van weidevogels, rietvogels (**Hoofdstuk 3**) en heidevogels, die alle in zowel nationale als internationale context zeer bijzonder zijn. Het voorheen besloten landschap in hoog Nederland is juist meer open geworden, als gevolg van het verwijderen van heggen en kleine bospercelen. Als gevolg van deze landschappelijke ontwikkelingen zijn regionale broedvogelgemeenschappen in Nederland steeds meer op elkaar gaan lijken, terwijl de soortenrijkdom op landelijke schaal tegelijkertijd is toegenomen (**Hoofdstuk 4**). Dit proces van 'biotische homogenisering' is ook beschreven voor andere diergroepen en voor gebieden in andere delen van de wereld. Het wordt vaak beschouwd als een gevolg van wereldwijde verstedelijking. De regionale homogenisering van broedvogelgemeenschappen in Nederland wordt daarentegen primair veroorzaakt door bosaanleg en de degradatie van diverse halfnatuurlijke habitats. Het behoud en herstel van de regionale identiteit zou meer prioriteit moeten krijgen bij de landschappelijke inrichting van Nederland.

Homogenisering heeft niet alleen een taxonomisch aspect (diversiteit in soorten), maar ook een functionele component (diversiteit in eigenschappen). Sinds 1990 zijn vooral de populaties toegenomen van standvogels, korte afstandtrekkers, planteneters, struikbroeders en grote vogels met een relatief klein Europees verspreidingsgebied. Populatieafnames komen vooral voor bij grondbroeders en trekvogels die in het voorjaar relatief laat in de broedgebieden aankomen (**Hoofdstuk 5**). Herbivorie en nestplaatsvoorkeur zijn dus belangrijke eigenschappen die maken dat een soort wel of niet succesvol is. Vooral nestplaatsvoorkeur is sterk gerelateerd aan de in de vorige paragraaf genoemde veranderingen in landgebruik, die aan het proces van homogenisering ten grondslag liggen. Bosaanplant, verstruweling en verlies van natuurlijke ecosysteemdynamiek zijn gunstig voor struweelbroeders, maar ongunstig voor grondbroeders. In boerenland hebben grondbroeders daarnaast te lijden van intensivering van agrarisch gebruik. Beschermingsstrategieën kunnen alleen tot succes leiden wanneer ze zich richten op de vogeleigenschappen die het meest onder druk staan. Voor grondbroeders valt het meest te verwachten van 'procesbeheer', zoals de grootschalige reactivering van natuurlijke ecosysteemdynamiek in kustduinen en stuifzanden, of het herstel van hoge grondwaterpeilen in boerenland. 'Patroonbeheer' blijkt tot op heden nauwelijks effectief voor het herstel van bedreigde broedvogelpopulaties. Hierbij valt te denken aan het herstel van kleinschalige vegetatiemozaïeken in stuifzanden door plaggen, en uitgesteld en gefaseerd maaibeheer in combinatie met actieve nestbescherming in graslanden.

Trekgedrag is een andere belangrijke eigenschap die een deel van de variatie in landelijke populatietrends van broedvogels verklaart (**Hoofdstuk 5**). Toegenomen populaties van standvogels en deeltrekkers zijn waarschijnlijk gerelateerd aan de opwarming van het klimaat, waardoor de winteroverleving van deze soorten is toegenomen. Tegelijkertijd staan populaties van veel lange-afstandtrekkers onder druk, vooral van soorten die pas laat in het voorjaar in de broedgebieden arriveren en die overwinteren in de tropische en droge bossen van West-Afrika. Aan de negatieve populatietrends kunnen zowel veranderingen in de Afrikaanse overwinteringsgebieden ten grondslag liggen, zoals habitatverlies door grootschalige boskap, als processen die plaatsvinden in de broedgebieden, zoals klimaatverandering. Een toename van voorjaarstemperaturen kan resulteren in een 'mismatch' in voedselketens. Dit treedt op als de periode waarin de voedselbehoefte voor vogels maximaal is (als er jongen zijn) steeds meer uit de pas gaat lopen met de periode waarin ook het voedselaanbod maximaal is. Vogels beginnen weliswaar steeds eerder in het voorjaar met de eileg, maar deze vervroeging is minder sterk dan de vervroeging van de piek in de beschikbaarheid van insecten. Om te onderzoeken of klimaatverandering inderdaad een belangrijke oorzaak is van populatieafnames bij trekvogels, en mismatch in predator-prooi relaties het onderliggende mechanisme, zijn de trends van een brede selectie van zangvogels nader geanalyseerd. Hierbij hebben we soorten vergeleken op basis van verschillen in hun trekgedrag. Daarnaast hebben we de populatietrends uitgesplitst naar enerzijds habitats die verschillen in voedselbeschikbaarheid en anderzijds regio's binnen Europa die verschillen in de mate waarin het klimaat is opgewarmd (**Hoofdstuk 6**). In Nederlandse loofbossen, waar het voedselaanbod in het voorjaar sterk gepiekt is en het risico op mismatch dus het grootst is, blijken de meeste lange-afstandtrekkers in aantal af te nemen, maar de standvogels niet. Op Europese schaal nemen lange-afstandtrekkers in loofbossen ook af in andere landen waar de voorjaarstemperaturen sterk zijn toegenomen (West-Europa). Ze nemen gemiddeld echter niet af in landen waar niet of nauwelijks van voorjaarsopwarming sprake is (Noord-Europa). Dit ondersteunt de hypothese dat trekvogels minder goed in staat zijn om zich aan te passen aan veranderingen in de timing van voedselbeschikbaarheid als gevolg van klimaatopwarming dan standvogels, omdat trekvogels in hun ver weg gelegen overwinteringsgebieden niet kunnen voorzien wanneer het voorjaar in hun broedgebieden begint. In tegenstelling tot bosvogels, nemen de populaties van lange-afstandtrekkers in Nederlandse moerassen gemiddeld niet af. In deze habitat is de voedselbeschikbaarheid dan ook minder gepiekt en gedurende een langere periode in het voorjaar beschikbaar dan in loofbossen. Hierdoor is het risico op mismatch ook minder groot. De conclusie is derhalve dat klimaatverandering in de broedgebieden een belangrijke oorzaak is van geconstateerde populatieveranderingen van broedvogels sinds 1990, in aanvulling op andere factoren zoals veranderingen in landgebruik.

Het combineren van eigenschappen van broedvogels tot levensstrategieën, waarbij rekening kan worden gehouden met 'trade-offs', kan in potentie ook een effectieve manier zijn om de werkingsmechanismen achter populatieveranderingen te achterhalen. Deze aanvullende functionele benadering is gebruikt ten behoeve van de evaluatie van de effecten van grootschalige natuurontwikkeling in de uiterwaarden van de grote rivieren (**Hoofdstuk 7**). Deze effecten zijn over het geheel genomen positief voor broedvogels in de eerste tien jaren na de start van herinrichting. Hoewel het merendeel van de onderzochte soorten nog geen significante reactie op natuurontwikkeling heeft laten zien, overheersen de positieve effecten bij de soorten die wel hebben gereageerd. Verschillen in de reacties tussen soorten worden vooral veroorzaakt door verschillen in nestplaatsvoorkeur. Dit indiceert dat graafwerkzaamheden, die veelal in de startfase worden uitgevoerd, en spontane vegetatiesuccessie van grotere invloed zijn op broedvogelontwikkelingen dan het beoogde herstel van natuurlijke rivierdynamiek. Dit laatste wordt in de praktijk dan ook sterk beperkt door de randvoorwaarden die vanuit de scheepvaart en veiligheid aan rivierherstel worden gesteld. Als ook in de toekomst het herstel van hydrodynamiek uitblijft, dan zal kunstmatige cyclische verjonging om de successie periodiek terug te zetten noodzakelijk zijn voor het duurzaam voortbestaan van rivierkarakteristieke broedvogels in uiterwaarden. Bovendien is optimalisatie van de maatregelen nodig om herkolonisatie mogelijk te maken van een aantal aansprekende ‘doelsoorten’ van natuurontwikkeling, die van oorsprong thuishoren in het Nederlandse rivierengebied. Verlegging van winterdijken teneinde meer ruimte buitendijks te creëren, vergroting van het areaal uiterwaarden met natuurontwikkeling, verbetering van de ruimtelijke samenhang tussen buitendijkse en binnendijkse natuurgebieden en herstel van volledige laterale gradiënten tussen hoog- en laag-dynamische, en droge en natte delen in uiterwaarden, zijn daarbij essentieel.

Dit proefschrift laat zien dat de grootschalige deelname van vrijwilligers aan landelijke monitoring- en atlasprojecten onderzoek mogelijk maakt dat anderszins onmogelijk zou kunnen worden uitgevoerd op dezelfde tijd- en ruimteschalen (**Hoofdstuk 8**). De bijdrage van vrijwilligers aan ornithologisch onderzoek is daarom essentieel voor het beschrijven van populatietrends van soorten en veranderingen in de landelijke vogeldiversiteit. Vrijwilligers dragen daarnaast bij aan het opsporen en ontrafelen van oorzaken van populatieveranderingen, het prioriteren van onderzoek naar onderliggende mechanismen en het sturen van beschermingsmaatregelen. Vooral het maken van vergelijkingen tussen soorten, waarbij vogels worden gegroepeerd op basis van hun eigenschappen, levensstrategieën of habitats, is een krachtig middel bij de analyse van hun telgegevens. Correlatieve analyses zoals gepresenteerd in dit proefschrift vormen dan ook een belangrijke aanvulling op meer experimenteel onderzoek. Trend- en verspreidingsgegevens zijn in het verleden vaak de aanleiding en inspiratie geweest voor meer diepgravend ecologisch onderzoek aan individuele soorten. Andersom genereert soortgericht onderzoek, noodgedwongen vaak kortdurend en beperkt tot een klein aantal studiegebieden, hypotheses over werkingsmechanismen die op hogere schaalniveaus getest zouden moeten worden. Bij het evalueren en opschalen van deze hypotheses naar andere soorten (met dezelfde eigenschappen), gebieden en tijdsperioden kunnen monitoringgegevens erg waardevol zijn, maar tot op heden wordt deze toepassing in de wetenschappelijke literatuur onvoldoende benut. Het gebruik van grootschalige telgegevens biedt ook de mogelijkheid om het belang van één proces af te zetten tegen andere factoren die vogelpopulaties beïnvloeden en die tegelijkertijd een rol spelen. Daarom zullen natuurbescherming, natuurbeheer en wetenschap profiteren van een intensievere en beter gestructureerde samenwerking tussen professionele biologen en vrijwillige vogeltellers.

Dankwoord

Het dankwoord: voor een deel van jullie het eerste hoofdstuk dat je uit dit proefschrift zult lezen, voor mij daarom een uitgelezen kans om iedereen te bedanken die heeft bijgedragen aan de totstandkoming ervan.

Ik kijk met veel plezier terug op dit promotietraject. Jammer dat het voorbij is! De perioden dat ik aan het proefschrift werkte, voelden als oases van rust. Ik hoefde me dan namelijk maar met één onderwerp tegelijk bezig te houden en kon daarin mooi de verdieping zoeken; zaken die er in de werkdrukte van alledag nog al eens bij inschieten. In sommige opzichten was dit een nogal atypisch promotietraject. Het uitgangspunt was immers niet zozeer een bepaalde onderzoeksvraag, als wel een grote hoeveelheid monitoringdata die behalve voor de reguliere toepassingen ook voor het beantwoorden van specifieke wetenschappelijke vragen bruikbaar zouden moeten zijn, zo was de gedachte. De dataverzameling vond dus grotendeels plaats voor de literatuurstudie en het formuleren van de onderzoeksvragen, een merkwaardige omkering die af en toe wat bevreemdend aanvoelde. Daar stond tegenover dat ik nooit druk heb gevoeld om het proefschrift binnen een bepaalde periode af te moeten ronden. Hierdoor had ik de tijd om de manuscripten aan het tijdrovende *peer-review* proces te onderwerpen. Toegegeven, ik zat niet altijd in blijde verwachting in mijn handen te wrijven als de reactie van de reviewers in mijn emailbox verscheen (ik kan me een *major revision* herinneren die was ingegeven door 14 A4-tjes commentaar), maar de artikelen zijn er ongetwijfeld beter en begrijpelijker door geworden.

Mijn promotietraject begon halverwege 2004, op het moment dat SOVON en de Radboud Universiteit hun contacten intensiveerden. Frank Saris, Rob Leuven, Hans Esselink en Ruud Foppen speelden een cruciale rol bij het werven van fondsen en het opstellen van het onderzoeksplan. De eerste fase van het project werd gefinancierd door de Faculteit der Natuurwetenschappen, Wiskunde en Informatica en de Wetenschapswinkel (WeWi-pool 2003) van de Radboud Universiteit. Bij de Wetenschapswinkel was Paula Haarhuis onze contactpersoon, en ik bedank haar voor het gestelde vertrouwen in de goede afloop van het project. Aanvankelijk werkte ik als gastmedewerker van de afdelingen Milieukunde en Dierecologie periodiek vrij intensief aan het proefschrift, maar al snel werd het meer een kwestie van 'tussen de bedrijven door'. Ik ben blij dat mijn (co)promotoren al die tijd veel geduld hebben getoond, ook in perioden dat het voor geen meter opschoot. Ze hebben daarnaast een belangrijke inhoudelijke inbreng gehad in de totstandkoming, verbetering en publicatie van de manuscripten. Henk, ik heb veel opgestoken van je grote algemene dierecologische kennis en denk inmiddels met plezier terug aan onze terugkerende discussies over *traits* en *tactics* van diersoorten. Rob, ik dank jou vooral voor je niet aflatende vertrouwen en positivisme, en de voortvarendheid en nauwgezetheid waarmee je ruwe manuscripten in gepubliceerde artikelen hebt helpen omzetten. Ruud, jouw aanstekelijke enthousiasme, goede ideeën en pragmatisme hebben er mede voor gezorgd dat het uiteindelijk gelukt is om dit werkje af te maken. Jan, jij trad weliswaar pas later tot het clubje begeleiders toe, maar ik heb veel gehad aan je scherpe vragen en kritische beschouwingen, die mij regelmatig op mijn wat al te rasse schreden deden terugkeren. Helaas heeft Hans door zijn vroegtijdige overlijden de totstandkoming van dit boekje niet meer kunnen meemaken; zonder hem is het Nederlandse ecologenwereldje er beslist minder kleurrijk en bevlogen op geworden.

Mijn grote dank gaat uit naar alle vrijwillige vogeltellers die aan de broedvogelmonitoring en atlasprojecten hebben deelgenomen. Zonder hun enorme inzet zouden we niet weten hoe het met de vogelstand in Nederland gesteld is en zouden de gegevens simpelweg ontbreken om een proefschrift als dit te kunnen schrijven. Alleen al de data gebruikt in hoofdstuk 5 zijn gebaseerd op een geschatte 700.000 uren veldwerk. Tel daar de verzamelde gegevens van voor 1990 (hoofdstuk 3), beide broedvogelatlassen (hoofdstuk 4) en de pan-Europese monitoring (hoofdstuk 6) bij op, en het is duidelijk dat het om een overweldigende inspanning gaat. Ik beschouw het ook na vijftien jaar SOVON nog als een voorrecht om dagelijks met die geweldige datasets te mogen werken.

Bij de verwerking van al die telgegevens hebben de vrijwillige districtscoördinatoren en mijn SOVON-broedvogelcollega's een onmisbare rol gespeeld. In willekeurige volgorde: Arend van Dijk, Arjan Boele, Joost van Bruggen, Michiel van der Weide, Dirk Zoetebier, Lara Marx, Rob Vogel, Lieuwe Dijksen, André van Kleunen, Kees Koffijberg, Jan-Willem Vergeer, Fred Hustings en 'roomie' Wolf Teunissen. Al mijn andere collega's ben ik dankbaar voor de immer prettige werksfeer bij SOVON. De bezieling is nog altijd groot op de werkvloer: iets om zuinig op te zijn! Het management van SOVON, in het bijzonder Frank Saris, bedank ik voor de tijd die ze mij heeft gegeven om dit traject tot een goed einde te brengen. De collega's van Stichting Bargerveen zorgden voor een leuke tijd op de dagen dat ik daar aan het werk was. Veel had ik aan de inhoudelijke discussies met onder andere Hein van Kleef, Marijn Nijssen en Wilco Verberk. Van Wilco's ideeën over habitatspecialisatie heb ik in hoofdstuk 8 gebruik gemaakt; hopelijk vinden we nu de tijd om ze samen verder uit te werken voor een artikel. Ik dank de opdrachtgevers van het Meetnet Broedvogels en de medewerkers van partner Centaal Bureau voor de Statistiek, met name Arco van Strien, Calijn Plate en Leo Soldaat, met wie het altijd prettig en constructief samenwerken is. Een bijdrage uit het Rob Goldbach fonds maakte de druk van dit proefschrift mede mogelijk.

Mijn veertien coauteurs ben ik zeer erkentelijk voor hun goede suggesties en concrete bijdragen. Ik wil hierbij met name Christiaan Both noemen, de trekker van hoofdstuk 6, voor de creativiteit waarmee hij verschillende datasets aan elkaar knoopte. Studenten Philip van Dijk en Dimitri Emond participeerden in het onderzoek, en verzetten bergen werk. Veel dank ook voor het gedegen, maar vaak zo onzichtbare werk van de vele al dan niet anonieme reviewers, die mijn aan tijdschriften aangeboden manuscripten van kritisch commentaar voorzagen. Maar het oog wil ook wat. Martijn Antheunisse voorzag dit proefschrift van zijn mooie opmaak en viste er in zijn gedrevenheid en passant nog de nodige foutjes uit. Peter Eekelder maakte de prachtige kaft. Ik ben blij dat Jos Zwarts graag bereid was om speciaal voor dit werk een aantal pareltjes van tekeningen te maken.

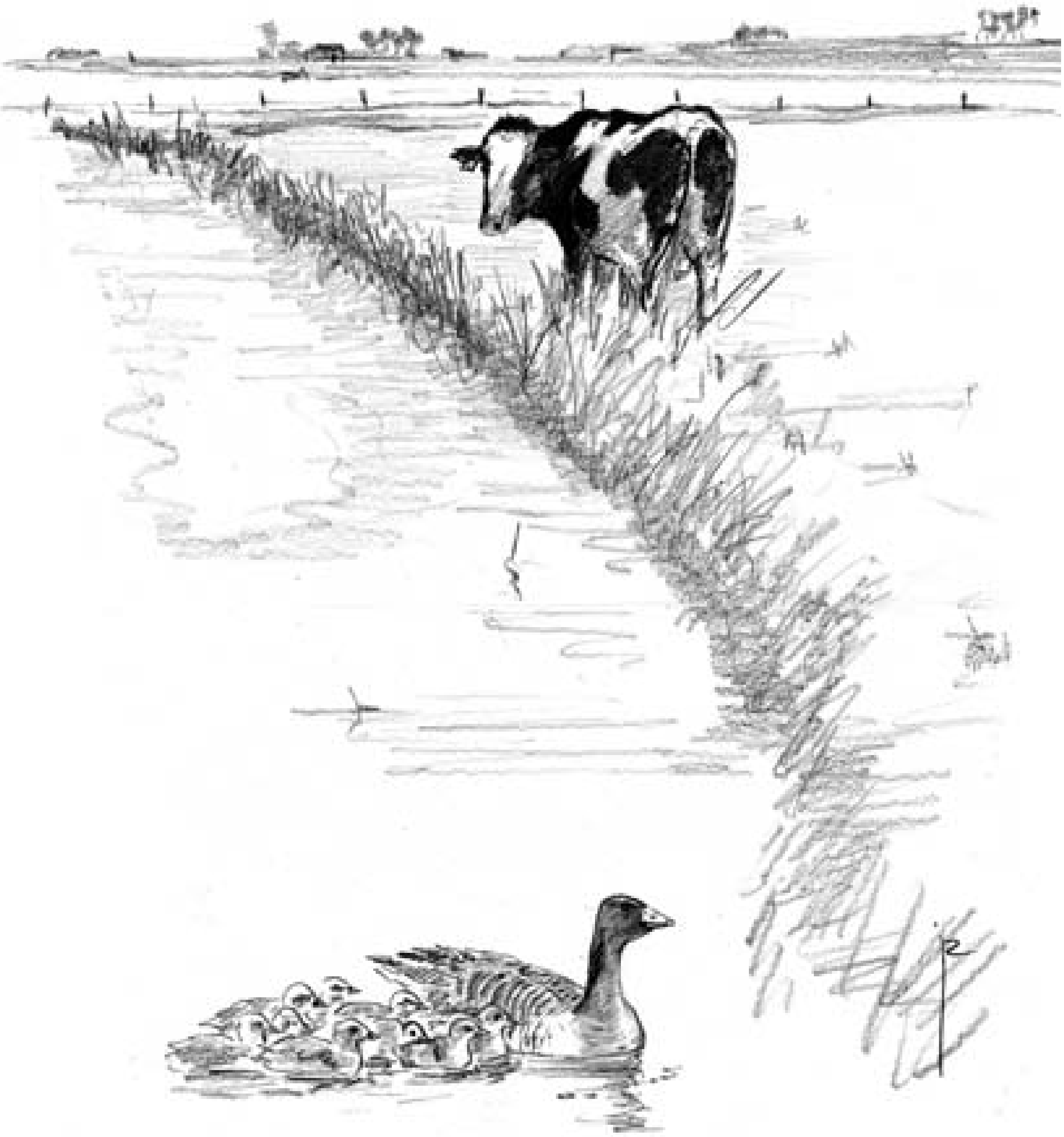
In zekere zin is dit promotietraject voor mij al veel eerder begonnen dan in 2004. Al in mijn kinderjaren bracht ik met vriend Joris hele middagen door met het kopiëren, knippen en plakken van vogelfoto's uit bibliotheekboeken. In mijn opstelschriftje van de vijfde klas lagere school schreef ik 'dat ik later graag een beroep zou willen hebben dat te maken heeft met de natuur, bijvoorbeeld bioloog of ornitholoog'. Volgens mij ben ik nu beide. Op mijn elfde werk ik lid van de ACJN, later Jeugdbond voor Natuur- en Milieustudie. Ik heb daar ontzettend veel opgestoken. Behalve het botvieren van een gedeelde natuurpassie, was het ook in sociaal opzicht een goede leerschool. Sommige van de mensen die ik toen heb leren kennen, behoren nog steeds tot mijn beste vrienden. Ook alle anderen waarmee ik destijds optrok, bedank ik voor het delen van hun kennis en voor hun gezelschap. Het waren mooie tijden!

Mijn ouders hebben er altijd alles aan gedaan om mijn ontluikende interesse voor de natuur te stimuleren en faciliteren. Dat begon met het meegeven van zoonlief aan een zooitje ongeregelde jeugdbonders op zondagen en tijdens schoolvakanties. Ik bewaar daarnaast warme herinneringen aan de buitenlandse zomervakanties, waar altijd werd gezorgd dat ik ruimschoots in mijn vogelbehoeftes kon voorzien. Die Lammergier boven de auto in de uitlopers van Spaanse Pyreneeën behoort nog steeds tot mijn mooiste waarnemingen. Pa en ma, bedankt hiervoor en voor jullie onvoorwaardelijke steun in de keuzes die ik in het leven heb gemaakt! Hierbij mag het geduld (of moet ik zeggen berusting) van mijn zus Alice ook niet onvermeld blijven, die zich mijn uitgebreide verhandelingen over de determinatiekenmerken van Rode en Zwarte Wouw moest laten welgevallen, terwijl haar interesses toch duidelijk elders lagen.

Er is natuurlijk veel meer in het leven dan onderzoek doen, en dan komen vrienden om de hoek kijken. Daarvan heb ik gelukkig een aantal hele leuke. Rob, Frank, Hein, Yves, Tie, Martijn, Martin, René, Eva, Marijn, Gerrit, Harvey, Peter, Job en degenen die ik tegenwoordig wat minder vaak zie: de gezamenlijke veldtripjes, vogelvakanties, potjes badminton en kroegbezoekjes zijn goud waard!

Tristan, mijn zoon, ik hoop iets van mijn interesse voor de natuur aan je mee te kunnen geven. Momenteel vind je Volvo's tellen nog oneindig veel boeiender dan vogels tellen, maar da's ook best.

En dan Maaike, mijn lief, wat fijn dat jij er bent! Bedankt voor al je liefde en openheid, en je steun bij zaken die veel ingewikkelder zijn dan het schrijven van een proefschrift.



Curriculum vitae
and list of publications

Op 17 april 1971 werd ik geboren in Heerlen. Op mijn derde verhuisde ik met mijn ouders naar Brabant, het land waar hun wieg had gestaan. Ik groeide op in Veldhoven en doorliep het VWO aan het Anton van Duinkerkencollege. Van mijn 11^e tot 23^e was ik lid van de Jeugdbond voor Natuur- en Milieustudie (daarvoor ACJN). Ik leerde hier veel beesten en plannen kennen tijdens wekelijkse tochten door de Kempen, en vervulde daarnaast verschillende bestuursfuncties binnen de locale afdeling. In 1989 vertrok ik naar Nijmegen om biologie te gaan studeren aan de Katholieke Universiteit. Tijdens mijn afstudeeronderzoeken bestudeerde ik achtereenvolgens de effecten van verzuring en vermesting op de bodemchemie en vegetatie van heideterreinen (afdeling Milieubiologie), de invloed van versnippering op de populatie Noordse Woelmuizen in de Delta (afdeling Dierecologie) en de effecten van dijkversterking op vegetatie en fauna in het rivierengebied (afdeling Milieukunde). In 1995 studeerde ik af als bioloog en als natuurwetenschappelijk milieukundige.

Meteen daarna kreeg ik een baan als wetenschappelijk medewerker bij SOVON Vogelonderzoek Nederland, bij de zojuist opgestarte afdeling onderzoek. Ik hield me aanvankelijk vooral bezig met het beheren en completeren van de database voor de Europese broedvogelatlas. Vervolgens was ik nauw betrokken bij de methodologische voorbereiding en gegevensanalyse voor de tweede Nederlandse broedvogelatlas. Daarna werkte ik aan een diversiteit aan projecten: van het opzetten en evalueren van meetnetten, het toepassen van monitoring- en verspreidingsgegevens ten behoeve van beheer- en beleidsvraagstukken, tot soortgericht onderzoek voor de onderbouwing van beschermingsmaatregelen. Sinds 2009 ben ik teamleider monitoring bij SOVON.

Van 1999 tot 2002 was ik gedetacheerd bij Stichting Bargerveen. Ik verruimde daar mijn blik van vogels naar andere diergroepen, en deed onderzoek aan de effecten van herstelmaatregelen tegen verdroging, verzuring en vermesting op de fauna van heiden, stuifzanden en kustduinen. Van 2004 tot 2007 was ik gedetacheerd bij de afdelingen Milieukunde en Dierecologie & -ecofysiologie van de Radboud Universiteit Nijmegen. Ik werkte daar aan het project 'Veranderingen in de broedvogelstand in Nederland: implicaties voor natuurbeleid en -beheer'. Dit proefschrift is het resultaat van dat project. Ik heb als gastmedewerker aan de RUN ook studenten begeleid, colleges dierecologie en rivierecologie gegeven en een practicum dierecologie verzorgd. Ik ben lid van het nationale Deskundigenteam Duin- en Kustlandschap van het netwerk Ontwikkeling en Beheer Natuurkwaliteit (O+BN).

In mijn vrije tijd doe ik mee aan verschillende vogeltelprojecten. Zo heb ik sinds 1988 jaarlijks broedvogelinventarisaties uitgevoerd in onder andere de Kempen, Ooijpolder en, wat verder van huis, arctisch Siberië (als onderdeel van een expeditie in 1998 voor Stichting WIWO). Sinds 1995 doe ik mee aan de wadvogeltellingen op Terschelling. Vanaf 1997 heb ik tien jaar lang geparticipeerd in een onderzoek naar broedsucces en overleving van Grauwe Ganzen in de Ooijpolder.

List of publications

Peer-reviewed papers

Lenders H.J.R., Huijbregts M.A.J., Aarts B.G.W. & Van Turnhout C.A.M. 1999. Assessing the degree of preservation of landscape, natural and cultural-historical values in river dike reinforcement planning in the Netherlands. *Regulated Rivers: Research & Management* 15: 325-337.

Atkinson P.W., Austin G.E., Rehfisch M.M., Baker H., Cranswick P., Kershaw M., Robinson J., Langston R.H.W., Stroud D.A., Van Turnhout C. & Maclean I.M.D. 2006. Identifying declines in waterbirds: The effects of missing data, population variability and count period on the interpretation of long-term survey data. *Biological Conservation* 130: 549-559.

Riksen M., Ketner-Oostra R., Van Turnhout C., Nijssen M., Goossens D., Jungerius P.D. & Spaan W. 2006. Will we lose the last active inland drift sands of Western Europe? The origin and development of the inland drift-sand ecotype in the Netherlands. *Landscape Ecology* 21: 431-447.

Van Turnhout C.A.M., Foppen R.P.B., Leuven R.S.E.W., Siepel H. & Esselink H. 2007. Scale-dependent homogenization: Changes in breeding bird diversity in the Netherlands over a 25-year period. *Biological Conservation* 134: 505-516.

Van Turnhout C.A.M., Willems F., Plate C., Van Strien A., Teunissen W., Van Dijk A. & Foppen R. 2008. Monitoring common and scarce breeding birds in the Netherlands: applying a post-hoc stratification and weighting procedure to obtain less biased population trends. *Revista Catalana d'Ornitologia* 24: 15-29.

Van Turnhout C.A.M., Foppen R.P.B., Leuven R.S.E.W., Van Strien A. & Siepel H. 2010. Life-history and ecological correlates of population change in Dutch breeding birds. *Biological Conservation* 143: 173-181.

Both C., Van Turnhout C.A.M., Bijlsma R.G., Siepel H., Van Strien A.J. & Foppen R.P.B. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings Royal Society of London B* 277: 1259-1266.

Jiguet F., Devictor V., Ottvall R., Van Turnhout C., Van der Jeugd H. & Lindström A. 2010. Bird population trends are linearly affected by climate change along species thermal ranges. *Proceedings Royal Society of London B* 277: 3601-3608.

Klok C., Van Turnhout C.A.M., Willems F., Voslamber B., Ebbinge B. & Schekkerman H. 2010. Analysis of population development and effectiveness of management in resident Greylag Geese *Anser anser* in the Netherlands. *Animal Biology* 60: 373-393.

Van Turnhout C.A.M., Hagemeijer E.J.M. & Foppen R.P.B. 2010. Long-term population developments in typical marshland birds in the Netherlands. *Ardea* 98: 283-299.

Van Turnhout C.A.M., Leuven R.S.E.W., Hendriks A.J., Kurstjens G., Van Strien A., Foppen R.P.B. & Siepel H. *in press*. Ecological strategies successfully predict the effects of river floodplain rehabilitation on breeding birds. *River Research and Applications*.

Cormont A., Vos C.C., Van Turnhout C.A.M., Foppen R.P.B. & Ter Braak C.J.F. *submitted*. Using life-history traits to distinguish strategies that explain bird responses to changing weather variability.

Van Turnhout C.A.M., Van Winden E., Troost G., Hustings F. & Koffijberg K. *submitted*. Changes in timing of visible bird migration in The Netherlands in autumn.

Devictor V., Van Swaay C., Brereton T., Brotons L., Chamberlain D., Heliölä J., Herrando S., Julliard R., Kuussaari M., Lindström Å., Reif J., Roy D., Van Strien A., Settele J., Schweiger O., Stefanescu C., Vermouzek Z., Van Turnhout C., Wallis de Vries M. & Jiguet F. *submitted*. Differences in the climate debts of birds and butterflies at continental scale.

Non peer-reviewed papers (Dutch titles include English summary)

Habraken J.M.P.M., Van Turnhout C.A.M. & Crombaghs B. 1996. Huidige status van de Blauwband in Nederland. *Natuurhistorisch Maandblad* 85: 31-33.

Van Turnhout C. & Vogel R. 1997. The New Atlas of Dutch Breeding Birds 1998-2000. *Bird Census News* 10: 26-32.

Van Turnhout C. & Hustings F. 1998. Methodologische achtergronden van het Atlasproject Broedvogels 1998-2000. *Limosa* 71: 130-135.

Van Turnhout C. & Hagemeijer W. 1999. Marshland birds in the Netherlands: causes of long-term population trends in 1965-95. *Vogelwelt* 120: 185-191.

Van Turnhout C. & Verstrael T. 1999. Is het aanbod van beukennootjes van invloed op de aantallen in Nederland overwinterende zaadeters? *Limosa* 72: 162-165.

Van Turnhout C., Stuijfzand S. & Esselink H. 2001. Is het huidige herstelbeheer toereikend voor de heidefauna? *De Levende Natuur* 102: 183-188.

Ebbinge B., Klok C., Schekkerman H., Van Turnhout C., Voslamber B. & Willems F. 2002. Perspectief voor de Grauwe gans als broedvogel in het Deltagebied bij verschillende beheersmaatregelen. *De Levende Natuur* 103: 118-124.

Saris F., Vergeer J.W., Hustings F. & Van Turnhout C. 2002. Volkstelling onder broedvogels biedt gevarieerd beeld. *De Levende Natuur* 103: 196-205.

Van Turnhout C., Voslamber B., Willems F. & Van Houwelingen G. 2003. Trekgedrag en overleving van Grauwe Ganzen *Anser anser* in de Ooijpolder. *Limosa* 76: 117-122.

Van Turnhout C. 2005. Het verdwijnen van de Duinpieper als broedvogel uit Nederland en Noordwest-Europa. *Limosa* 78: 1-14.

Van Roomen M., Van Turnhout C., Van Winden E., Koks B., Goedhart P., Leopold M. & Smit C. 2005. Trends van benthivore watervogels in de Nederlandse Waddenzee 1975-2002: grote verschillen tussen schelpdiereneters en wormeneters. *Limosa* 78: 21-38.

Van Turnhout C., Van Dijk A., Van der Weide M. & Van Beusekom R. 2006. Roepende Roerdompen in Nederland: trefkansen, trends en aantallen. *Limosa* 79: 1-12.

Van Turnhout C.A.M., Van der Weide M.J.T., Kurstjens G. & Leuven R.S.E.W. 2007. Natuurontwikkeling in uiterwaarden: hoe reageren broedvogels? *De Levende Natuur* 108: 52-57.

Van Turnhout C. & Aarts B. 2007. MUS: een nieuw meetnet voor broedvogels in stedelijk gebied. *Limosa* 80: 40-43.

Van Dijk A., Hustings F., Koffijberg K., Van Turnhout C., Van der Weide M., Zoetebier D. & Plate C. 2007. Kolonievogels en zeldzame broedvogels in Nederland in 2003-05. *Limosa* 80: 49-67.

Van Turnhout C., Aben J., Beusink P., Majoor F., Van Oosten H. & Esselink H. 2007. Broedsucces en voedselecologie van Nederland's kwijnende populatie Tapuiten. *Limosa* 80: 117-122.

Felix R. & Van Turnhout C. 2008. Observation of African Stonechat *Saxicola torquata albofasciata* in Mgahinga National Park, south-western Uganda. *Scopus* 27: 41-42.

Van Turnhout C. & Van Roomen M. 2008. Drieteenstrandlopers in Nederland: steeds meer wad-, steeds minder strandvogel? *Limosa* 81: 1-10.

Van Turnhout C.A.M., Schekkerman H., Ens B.J. & Koffijberg K. 2008. Nut en noodzaak van broedbiologisch onderzoek voor natuurbeheer en -beleid. *De Levende Natuur* 109: 158-162.

Boele A., Hustings F., Koffijberg K., Van Turnhout C. & Plate C. 2008. Populatietrends van terrestrische wintervogels in 1980-2006: habitat, trekgedrag en verschillen tussen Hoog- en Laag-Nederland. *Limosa* 81: 50-61.

Voslamber B. & Van Turnhout C. 2008. Invloed van terreinbeheer op het wel en wee van Grauwe Ganzen in de Ooijpolder. *Limosa* 81: 74-76.

Van den Bremer L., Van Turnhout C., Van Roomen M. & Voslamber B. 2009. Natuurontwikkeling in uiterwaarden: hoe reageren trekkende en overwinterende watervogels? *De Levende Natuur* 110: 231-234.

Van Turnhout C., Van Winden E., Troost G., Koffijberg K. & Hustings F. 2009. Veranderingen in timing van zichtbare najaarstrek over Nederland: een pleidooi voor hernieuwde standaardisatie van trektellingen. *Limosa* 82: 68-78.

Ens B.J., Van Winden E.A.J., Van Turnhout C.A.M., Van Roomen M.W.J., Smit C.J. & Jansen J.M. 2009. Aantalontwikkeling van wadvogels in de Nederlandse Waddenzee in 1990-2008. Verschillen tussen Oost en West. *Limosa* 82: 100-112.

Van Strien A., Van Turnhout C. & Soldaat L. *submitted.* Composing annual breeding bird atlases through site-occupancy modeling. *Bird Census News.*

Book chapters and proceedings

Van Turnhout C. & Vergeer J.W. 2002. Het atlaswerk: opzet, uitvoering en volledigheid. In: SOVON Vogelonderzoek Nederland 2002. Atlas van de Nederlandse Broedvogels 1998-2000. Nederlandse Fauna 5. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & EIS-Nederland, Leiden. pp. 11-32.

Hustings F., Van Turnhout C. & Vergeer J.W. 2002. Hoe vergaat het de Nederlandse broedvogels? In: SOVON Vogelonderzoek Nederland 2002. Atlas van de Nederlandse Broedvogels 1998-2000. Nederlandse Fauna 5. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & EIS-Nederland, Leiden. pp. 33-50.

Van Turnhout C. 2002. Zomertortel *Streptopelia turtur*. In: SOVON Vogelonderzoek Nederland 2002. Atlas van de Nederlandse Broedvogels 1998-2000. Nederlandse Fauna 5. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & EIS-Nederland, Leiden. pp. 266-267.

Van Turnhout C. 2002. Rietgors *Emberiza schoeniclus*. In: SOVON Vogelonderzoek Nederland 2002. Atlas van de Nederlandse Broedvogels 1998-2000. Nederlandse Fauna 5. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & EIS-Nederland, Leiden. pp. 494-495.

Geertsema W., Schotman A., Meeuwsen H., Van Swaay C. & Van Turnhout C. 2004. Spatial arrangement of woody habitats and the distribution of birds and butterflies in agricultural landscapes in the Netherlands. In: Smithers R. (ed.). Landscape ecology of trees and forests. Proceedings of the 12th annual IALE conference. pp. 69-75.

Van Duinen G.A., Van Kleef H.H., Nijssen M., Van Turnhout C.A.M., Verberk W.C.E.P., Holtland J. & Esselink H. 2004. Schaal en intensiteit van herstelmaatregelen: hoe reageert de fauna? In: Van Duinen G.A. et al. (red.). Duurzaam natuurherstel voor behoud van biodiversiteit. 15 jaar herstelmaatregelen in het kader van het Overlevingsplan Bos en Natuur. pp. 189-240.

Van Turnhout C. 2005. Leefgebieden: agrarisch Hoog-Nederland. In: Van Beusekom R., Huigen P., Hustings F., de Pater K. & Thissen J. (red.). Rode Lijst van de Nederlandse Broedvogels. Tirion Uitgevers B.V. i.s.m. Vogelbescherming Nederland en SOVON Vogelonderzoek Nederland. pp. 18-24.

Van Turnhout C. 2005. Leefgebieden: kust en duin. In: Van Beusekom R., Huigen P., Hustings F., de Pater K. & Thissen J. (red.). Rode Lijst van de Nederlandse Broedvogels. Tirion Uitgevers B.V. i.s.m. Vogelbescherming Nederland en SOVON Vogelonderzoek Nederland. pp. 49-57.

Foppen R., Saris F. & Van Turnhout C. 2007. Veranderingen in vogelstand: basis voor bescherming. In: Saris F. Een eeuw vogels beschermen. KNNV Uitgeverij, Zeist. pp. 297-311.

Hustings F., Van Turnhout C. & Foppen R. 2010. Aves – vogels. In: Noordijk J., Kleukers R.M.J.C., Van Nieukerken E.J. & Van Loon A.J. (red.). De Nederlandse biodiversiteit. Nederlandse Fauna 10. Nederlands Centrum voor Biodiversiteit Naturalis & European Invertebrate Survey Nederland, Leiden. pp. 296-302.

English reports

Van Turnhout C. 1999. Evaluation of the monitoring scheme for common breeding birds in the Wadden Sea. SOVON-onderzoeksrapport 1999/07. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Willems F., Van Turnhout C. & Van Roomen M. 2001. Evaluation of the monitoring scheme for waterbirds in the Dutch Wadden Sea: a study on the representativeness of the Spring Tide Counting-sites. SOVON research report 2001/02. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Willems F., Van Turnhout C., Van Kleef H. & Felix R. 2002. Breeding birds of Medusa Bay, Taimyr, Russia. Methods for biological monitoring in the Arctic with results of 1998 and 1999. WIWO-report 77, Foundation WIWO, Zeist.

De Nobel P., Van Turnhout C., Van der Winden J. & Foppen R. 2002. An Alert System for bird population changes on a national level and for EU Bird Directive monitoring: a Dutch approach. SOVON research report 2002/04. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C. & Van Kleunen A. 2003. Habitat use of European breeding birds: allocation of EUNIS-habitat types to a selection of European breeding birds. A report by the European Bird Census Council under subcontract to Wetlands International as partner of the European Topic Centre on Nature Protection and Biodiversity.

Ens B., Van Roomen M., Van Turnhout C. & Blew J. 2009. Exploring contrasting trends of migratory waterbirds in the international Wadden Sea. Wadden Sea Ecosystem No. 26. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Joint Monitoring Group of Migratory Birds in the Wadden Sea, Wilhelmshaven, Germany.

Dutch reports

Van Turnhout C. & Hagemeijer W. 1995. Kentallen voor overwinterende ganzen in de Zuidhollandse Delta. SOVON-onderzoeksrapport 1995/05. SOVON, Beek-Ubbergen.

Van Turnhout C., Hustings F., Sierdsema H. & Verstrael T. 1995. Punt Transect Tellingen van wintervogels in seizoen 1993/94 in Nederland. SOVON-monitoringrapport 1995/04. SOVON, Beek-Ubbergen.

Van Turnhout C., Hustings F., Sierdsema H. & Verstrael T. 1997. Punt Transect Tellingen van wintervogels in seizoen 1994/95 in Nederland. SOVON-monitoringrapport 1997/01. SOVON, Beek-Ubbergen.

Hustings F., Van Turnhout C., Vogel R. & Van der Weide M. 1997. Aantalsontwikkelingen van karakteristieke broedvogels op de Nederlandse waddeneilanden. In: Van der Have T.M. & Osieck E.R. (red.) 1997. Aantalsontwikkelingen van en beheersmaatregelen voor karakteristieke vogels van het Waddengebied. Technisch Rapport Vogelbescherming Nederland 18, Zeist.

Van Turnhout C. & Verstrael T. 1998. Twintig jaar Punt-Transect-Tellingen van wintervogels in Nederland. Evaluatie en aanbevelingen voor de toekomst. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C. & Verstrael T. 1998. 15 jaar Punt-Transect-Tellingen van wintervogels in Nederland. Resultaten van de PTT-evaluatie. Achtergronddocument. SOVON-onderzoeksrapport 1998/02. SOVON Vogelonderzoek Nederland/Centraal Bureau voor de Statistiek. Beek-Ubbergen/Voorburg.

Van der Weide M. & Van Turnhout C. 1998. Handleiding Atlasproject Broedvogels 1998-2000. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C. 1998. Voorstudie Atlasproject Broedvogels 1998-2000. SOVON-onderzoeksrapport 1998/04. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Boele A., Van Turnhout C., Sierdsema H. & Meijer R. 1998. Punt Transect Tellingen van wintervogels in Nederland in het seizoen 1995/96. SOVON-monitoringrapport 1998/03. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Voslamber B. & Van Turnhout C. 1998. Aantalsontwikkeling van Kuifeend *Aythya fuligula* en Tafeleend *A. ferina* op enkele Nederlandse zoetwatermeren en rivieren in de periode 1966 t/m 1997. SOVON-onderzoeksrapport 1998/07. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Hagemeijer E.J.M. (Ward), Van Turnhout C.A.M., Van Winden E.A.J., Zoetebier T.K.G. (Dirk) & Van Roomen M.W.J. 1998. Vogelaantallen en vogelmassa in Nederland: 2D-kaarten van vogeldagen en vogelkilodagen voor heel Nederland op atlasblokniveau (5×5 km) (voor het vaststelling van aanvaringsrisico's). SOVON-onderzoeksrapport 1998/05. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C. 1999. Naar een Broedvogelmeetnet voor de Zoete Rijkswateren: Meetplan. SOVON-onderzoeksrapport 1999/01, RIZA-rapport 99.014. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C. 1999. Naar een Broedvogelmeetnet voor de Zoete Rijkswateren. Achtergronddocument bij het meetplan. SOVON-onderzoeksrapport 1999/02. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Voslamber B. & Van Turnhout C. 1999. Vergelijkende studie van telmethoden tijdens watervogeltellingen in de Randmeren. RIZA-rapport BM99.06, SOVON-onderzoeksrapport 1999/04. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Voslamber B. & Van Turnhout C. 1999. Vergelijkende studie van land- en vliegtuigtellingen van watervogels in het IJsselmeergebied. RIZA-rapport BM99.01, SOVON-onderzoeksrapport 1999/08. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Boele A., Koffijberg K., Van Turnhout C. & Meijer R. 1999. Punt Transect Tellingen van wintervogels in Nederland in 1996-97. SOVON-monitoringrapport 1999/08. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Bosman W., Van Turnhout C. & Esselink H. 1999. Effecten van herstelmaatregelen op diersoorten: "Eerste versie van Standaard Meetprotocol Fauna (SMPF) en Richtlijnenprogramma Uitvoering Herstelmaatregelen Fauna (RUHF)". Rapport Stichting Bargerveen, Nijmegen.

Beemster N., Van Dijk A.J., Van Turnhout C. & Hagemeijer W. 1999. Het voorkomen van moerasvogels in relatie tot moeraskarakteristieken in Nederland. Een verkenning aan de hand van het Baardmannetje. SOVON-onderzoeksrapport 1999/13. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C. & Van Winden E. 2000. Analyse van wadvogeltellingen in steekproefgebieden in de Nederlandse Waddenzee in 1980-98. SOVON-onderzoeksrapport 2000/02. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C. & de Nobel P. 2000. Trends van 16 broedvogelsoorten in de Nederlandse duinen (excl. de Amsterdamse Waterleidingduinen) in 1965-99. Intern document. SOVON, Beek-Ubbergen.

Bink F., Van de Bund C., Esselink H., Sierdsema H., Stuijfzand S. & Van Turnhout C. 2000. Heidebeheer en heidefauna in de praktijk. Handleiding OBN-excursie naar De Hoge Veluwe. Rapport Stichting Bargerveen, Nijmegen.

Schekkerman H., Klok C., Voslamber B., Van Turnhout C., Willems F. & Ebbinge B.S. 2000. Overzomerende grauwe ganzen in het noordelijk Deltagebied. Een modelmatige benadering van de aantalontwikkeling bij verschillende beheersscenario's. Alterra-rapport 136, SOVON-onderzoeksrapport 2000/06.

Van Roomen M.W.J. & Van Turnhout C. 2000. Projectvoorstel evaluatie monitoring-opzet watervogels Nederlandse Waddenzee. Intern document. SOVON Vogelonderzoek Nederland.

Van Turnhout C., Van der Hut R., Van Dijk A.J. & Foppen R. 2001. Het voorkomen van de Snor in relatie tot moeraskarakteristieken en moerasbeheer in Nederland. SOVON-onderzoeksrapport 2001/07. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Roomen M., Van Turnhout C., Nienhuis J., Willems F. & Van Winden E. 2002. Monitoring van watervogels als niet-broedvogel in de Nederlandse Waddenzee: evaluatie huidige opzet en voorstellen voor de toekomst. SOVON-onderzoeksrapport 2002/01. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C. 2002. Naar een betere monitoring van de Steenuil in Nederland. SOVON-onderzoeksrapport 2002/06. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C., Van der Weide M. & Kurstjens G. 2002. Toepassings- en presentatiemogelijkheden van het Broedvogelmeetnet Zoete Rijkswateren. SOVON-onderzoeksrapport 2002/11. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C. 2003. De situatie omtrent het Korhoen in Nederland en omliggende landen. SOVON-notitie, Beek-Ubbergen.

Foppen R., Loos W.B., Van Winden E. & Van Turnhout C. 2003. High Nature Value Farming Areas: important bird areas. Intern document. SOVON, Beek-Ubbergen.

Van Turnhout C. 2003. Status en knelpunten van de Duinpieper in Nederland en omliggende landen. SOVON-informatierapport 2003/09. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C., Stuijfzand S., Nijssen M. & Esselink H. 2003. Gevolgen van verzuring, vermesting en verdroging en invloed van herstelbeheer op duinfauna. Basisdocument. Rapport EC-LNV nr. 2003/153, Wageningen

Bakker T., Everts H., Jungerius P., Ketner-Oostra R., Kooijman A., Van Turnhout C. & Esselink H. 2003. Preadvies stuifzanden. Rapport EC-LNV nr. 2003/228-O, Wageningen.

Van Duinen G.J., Bink F., Lemaire A., Strijbosch H., Van Turnhout C., Peeters T. & Esselink H. 2003. Eesti somaastikud – Verkenning van veenlandschappen in Estland. Rapport Stichting Bargerveen, Nijmegen.

Van Turnhout C., Van Dijk A.J. & Van der Weide M. 2003. Jaar van de Roerdomp 2003. SOVON-onderzoeksrapport 2003/07. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Stuijfzand S., Van Turnhout C. & Esselink H. 2004. Gevolgen van verzuring, vermesting en verdroging en invloed van herstelbeheer op heidefauna. Basisdocument. Rapport EC-LNV nr. 2004/152-O, Wageningen

Soldaat L., Van Winden E., Van Turnhout C., Berrevoets C., Van Roomen M & Van Strien A. 2004. De berekening van indexen en trends bij het watervogelmeetnet. SOVON-onderzoeksrapport 2004/02. SOVON/CBS.

Van Turnhout C. & Vogel R.L. 2004. Natuurtoets Vliegende Vennen Noordoost (Gemeente Gilze en Rijen). VOFF-rapport 2004-4. Vereniging Onderzoek Flora en Fauna, Nijmegen.

Oosterhuis R., Dijksen L.J., Ens B.J., Foppen R., de Jong M., Kats R.K.H., Koks B.J., Van Turnhout C. & Willems F. 2004. Naar een reproductiemeetnet voor broedvogels in de Waddenzee. Alterra-rapport 944, Wageningen & SOVON-onderzoeksrapport 2004/03, Beek-Ubbergen.

Leopold M.F., Smit C.J., Goedhart P.W., Van Roomen M.W.J., Van Winden E. & Van Turnhout C. 2004. Langjarige trends in aantallen wadvogels in relatie tot de kokkelvisserij en het gevoerde beleid in deze. Eindverslag EVA II (Evaluatie Schelpdiervisserij tweede fase), deelproject C2. Alterra-rapport 954, Wageningen & SOVON-onderzoeksrapport 2004/07, Beek-Ubbergen.

Van Turnhout C., Majoor F. & Willems F. 2004. Broedsucces en conditie van algemene moerasvogels in Constant Effort Sites. SOVON-onderzoeksrapport 2004/09, Beek-Ubbergen.

Voslamber B., Van Turnhout C. & Willems F. 2004. Effect van aantalsregulatie op overzomerende Grauwe Ganzen. SOVON-onderzoeksrapport 2004/12, Beek-Ubbergen.

Van der Jeugd H.P., Voslamber B., Van Turnhout C., Willems F., Teunissen W. & Foppen R. 2004. Overzomerende ganzen in Nederland: grenzen aan de groei? – projectplan. SOVON-intern rapport 2004/141. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Geertsema W., Grashof C.J., Meeuwsen H.A.M., Schotman A.G.M., Van Turnhout C. & Van Swaay C.A.M. 2004. Kwaliteit van groenblauwe dooradering en voorkomen van vogels, vlinders en planten. Alterra-rapport 1095. Alterra, Wageningen.

Van Roomen M., Van Winden E., Koffijberg K., Boele A., Hustings F., Kleefstra R., Schoppers J., Van Turnhout C., SOVON Ganzen- en zwanenwerkgroep & Soldaat L. 2004. Watervogels in Nederland in 2002/2003. SOVON-monitoringrapport 2004/02, RIZA-rapport BM04/09. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Hustings F., Borggreve C., Van Turnhout C. & Thissen J. 2004. Basisrapport voor de Rode Lijst Vogels volgens Nederlandse en IUCN-criteria. SOVON-onderzoeksrapport 2004/13. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Dijk A.J., Dijksen L., Hustings F., Koffijberg K., Schoppers J., Teunissen W., Van Turnhout C., Van der Weide M.J.T., Zoetebier D. & Plate C. 2005. Broedvogels in Nederland in 2003. SOVON-monitoringrapport 2005/01. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C., Van Winden E. & Van Roomen M. 2005. Bijschatten van ontbrekende watervogeltellingen in de Zoute Delta in de periode 1975-87. Intern rapport, SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van der Weide M., Van Turnhout C., Foppen R. & Koffijberg K. 2005. Ruigtevogels en natuurontwikkeling. In: Reeze A.J.G., Buijse A.D. & Liefveld W.M. (red.). Weet wat er leeft langs Rijn en Maas. Ecologische toestand van de grote rivieren in Europees persepectief. RIZA-rapport 2005.010. RIZA, Lelystad.

Odé B., Van der Weide M., Van Turnhout C. & Foppen R. 2005. Ecologische indicatoren voor dynamiek. In: Reeze A.J.G., Buijse A.D. & Liefveld W.M. (red.). Weet wat er leeft langs Rijn en Maas. Ecologische toestand van de grote rivieren in Europees persepectief. RIZA-rapport 2005.010. RIZA, Lelystad.

Odé B., Van der Weide M., Van Turnhout C. & Foppen R. 2005. Kwaliteit van land-waterovergangen. In: Reeze A.J.G., Buijse A.D. & Liefveld W.M. (red.). Weet wat er leeft langs Rijn en Maas. Ecologische toestand van de grote rivieren in Europees persepectief. RIZA-rapport 2005.010. RIZA, Lelystad.

Boele A., Hustings F., Van Kleunen A., Van Turnhout C. & Plate C. 2005. Een kwart eeuw Punt-Transect-Tellingen van wintervogels in Nederland (1980-2004). SOVON-monitoringrapport 2005/02. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C. & Van Roomen M. 2005. Effecten van strandsuppleties langs de Nederlandse kust op Drieteenstrandloper en kustbroedvogels. SOVON-onderzoeksrapport 2005/05. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Foppen R., Van Diek H., Van der Weide M. & Van Turnhout C. 2005. Voorlopige evaluatie van mogelijke effecten van vliegbewegingen vanuit Airport Weeze op de broedvogels van Vogelrichtlijngebied Maasduinen. SOVON-onderzoeksrapport 2005/08. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Kooijman A.M., Besse M., Haak R., Van Boxtel J.H., Esselink H., ten Haaf C., Nijssen M., Van Til M. & Van Turnhout C. 2005. Effectgerichte maatregelen tegen verzuring en eutrofiëring in open droge duinen. Eindrapport fase 2. Rapport DK 2005/dk008-O, Ede.

Van Kleunen A., Sierdsema H., Van der Weide M., Van Turnhout C. & Vogel R. 2005. Soortbeschermingsplan Nachtzwaluw Noord-Brabant. SOVON-onderzoeksrapport 2005/09, Beek-Ubbergen.

Van Dijk A.J., Dijksen L., Hustings F., Koffijberg K., Oosterhuis R., Van Turnhout C., Van der Weide M.J.T., Zoetebier D. & Plate C. 2006. Broedvogels in Nederland in 2004. SOVON-monitoringrapport 2006/01. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C., Loos W.B., Foppen R.P.B. & Reijnen M.J.S.M. 2006. Hotspots van biodiversiteit in Nederland op basis van broedvogelgegevens. SOVON-onderzoeksrapport 2006/01. SOVON Vogelonderzoek Nederland, Beek-Ubbergen. WOT Natuur & Milieu, werkdocument 33.

Van der Jeugd H., Voslamber B., Van Turnhout C., Sierdsema H., Feige N., Nienhuis J. & Koffijberg K. 2006. Overzomerende ganzen in Nederland: grenzen aan de groei? SOVON-onderzoeksrapport 2006/02. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C., Van Manen W. & Vergeer J.W. 2006. Jaar van de Tapuit 2005. SOVON-onderzoeksrapport 2006/04. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Willems F., Van Turnhout C., Loos W.B. & Zoetebier D. 2006. Belang van het Nederlandse duin- en kustgebied voor broedvogels. SOVON-onderzoeksrapport 2006/07, Beek-Ubbergen.

Van Turnhout C., Van Kleunen A. & Foppen R. 2006. Effecten van de aanleg van de Betuwelijn op broedvogels. SOVON-onderzoeksrapport 2006/10, Beek-Ubbergen.

Van Turnhout C. 2006. Meetplan M.U.S. (Meetnet Urbane Soorten). SOVON-onderzoeksrapport 2006/13, Beek-Ubbergen.

Van Turnhout C. & Van Diek H. 2006. Handleiding Meetnet Urbane Soorten (MUS). SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Roomen M., Van Winden E., Koffijberg K., Ens B., Hustings F., Kleefstra R., Schoppers J., Van Turnhout C., SOVON Ganzen- en zwanenwerkgroep & Soldaat L. 2006. Watervogels in Nederland in 2004/2005. SOVON-monitoringrapport 2006/02, RIZA-rapport BM06/14. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Dijk A.J., Boele A., Van den Bremer L., Hustings F., Van Manen W., Van Kleunen A., Koffijberg K., Teunissen W., Van Turnhout C., Voslamber B., Willems F., Zoetebier D. & Plate C. 2007. Broedvogels in Nederland in 2005. SOVON-monitoringrapport 2007/01. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C., Aben J., Beusink P. & Geertsma M. 2007. Broedsucces en voedselecologie van Tapuiten in de Nederlandse kustduinen. SOVON-onderzoeksrapport 2006/14, Beek-Ubbergen en Stichting Bargerveen / Radboud Universiteit, Nijmegen.

Van den Bremer L., Voslamber B., Van Winden E. & Van Turnhout C. 2007. Veranderingen in de verspreiding van Smienten in relatie tot wijzigingen in het faunabeleid. SOVON-onderzoeksrapport 2007/04, Beek-Ubbergen.

Van Turnhout C. 2007. Het gebruik van vogelvides door Huismussen op vier locaties in 2007. SOVON-informatierapport 2007/14. Beek-Ubbergen.

Koffijberg K. & Van Turnhout C. 2007. Vogelbalans 2007. Thema klimaatverandering. SOVON, Beek-Ubbergen.

Van Turnhout C., Van Winden E. & Van Roomen M. 2008. Het gebruik van losse meldingen t.b.v. trendbepaling Zeearend en andere schaarse soorten. SOVON-notitie 2008/102, Beek-Ubbergen.

De Leeuw C.C., Grootjans A.P., Lammerts E.J., Esselink P., Stal L., Stuyfzand P.J., Van Turnhout C., ten Haaf M.E. & Verbeek S.K. 2008. Ecologische effecten van duinboog- en washoverherstel. Een verdiepende ecologische studie naar de mogelijke effecten van duinboog- en washoverontwikkeling op de Waddeneilanden Vlieland, Terschelling en Schiermonnikoog. RUG, Groningen.

Roodbergen M., Van Turnhout C. & Teunissen W.A. 2008. Meetnet Agrarische Soorten (MAS). Plan van aanpak voor Flevoland en verkenning voor een landelijke implementatie. SOVON-informatierapport 2008/03. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Van Turnhout C., Brouwer E., Nijssen M., Stuijfzand S., Vogels J., Siepel H. & Esselink H. 2008. Herstelmaatregelen in heideterreinen. Samenvatting OBN onderzoek en maatregelen met betrekking tot de fauna. Rapport DK nr. 2008/042-O. Directie Kennis, Ede.

Van Oosten H., Van Turnhout C., Beusink P., Majoor F., Hendriks K., Geertsma M., Van den Burg A. & Esselink H. 2008. Broed- en voedselecologie van Tapuit: Opstap naar herstel van de faunadiversiteit in de Nederlandse kustduinen. Stichting Bargerveen & SOVON Vogelonderzoek Nederland.

Koffijberg K. & Van Turnhout C. 2008. Vogelbalans 2008. Thema natuurgebieden. SOVON, Beek-Ubbergen.

Van Oosten H.H., Beusink P., de Boer P., Van den Bremer L., Dijksen L., Klaassen O., Majoor F., Van Turnhout C. & Waasdorp S. 2008. De laatste karakteristieke vogels van het open duin: de dynamiek van populaties op de rand van uitsterven – en oplossingen. SOVON-onderzoeksrapport 2008/17, Beek-Ubbergen.

Van den Bremer L., Van Turnhout C. & Van Vliet A.J.H. 2009. Evaluatie van waarnemingen vogelfenologie binnen De Natuurkalender en aanbevelingen voor de toekomst. SOVON-onderzoeksrapport 2009/01, Beek-Ubbergen.

Van Roomen M., Van Kleunen A., Van Winden E. & Van Turnhout C. 2009. Trends van vogels in het Beneden Rivierengebied in vergelijking met Nederland en Natura 2000 doelen. SOVON-onderzoeksrapport 2009/15, Beek-Ubbergen.

Arens S.M., Van den Burg A.B., Esselink P., Grootjans A.P., Jungerius P.D., Kooijman A.M., de Leeuw C., Löffler M., Nijssen M., Oost A.P., Van Oosten H.H., Stuyfzand P.J., Van Turnhout C.A.M., Vogels J.J & Wolters M. 2009. Preadvies Duin- en Kustlandschap. Rapport DK nr. 2009/dk113-O, Ede.

Van Oosten H.H., Versluijs R., Klaassen O., Van Turnhout C. & Van den Burg A.B. 2010. Knelpunten voor duinfauna. Relaties met aantasting en beheer van duingraslanden. DK-LNV rapport 2010/dk129-O., Ede.

Nijssen M., Riksen M.P.J.M., Sparrius L.B., Bijlsma R.J., De Waal R., Jungerius P.D., Ketner-Oostra R., Kooijman A.M., Kuiters A.L., Van den Burg A., Van Dobben H.F., Van Turnhout C. & Van Swaay C. 2010. Onderzoek naar effectgerichte maatregelen voor het herstel en beheer van stuifzanden. Ministry of Agriculture, Nature and Food Quality, Ede. Report.

Koffijberg K., Van Turnhout C., Foppen R., Hustings F. & Schekkerman H. 2010. Vogelbalans 2010. Thema biodiversiteit. SOVON, Beek-Ubbergen.

Authors’ addresses

Rob G. Bijlsma
Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, the Netherlands

Christiaan Both
Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, the Netherlands

Arend J. van Dijk
SOVON Dutch Centre for Field Ornithology, PO Box 6521, 6503 GA Nijmegen, the Netherlands

Hans Esselink
†

Ruud P.B. Foppen
SOVON Dutch Centre for Field Ornithology, PO Box 6521, 6503 GA Nijmegen, the Netherlands

Ward J.M. Hagemeijer
Wetlands International, PO Box 471, 6700 AL Wageningen, the Netherlands

A. Jan Hendriks
Radboud University Nijmegen, Institute for Water and Wetland Research, Department of Environmental Science, PO Box 9010, 6500 GL Nijmegen, the Netherlands

Gijs Kurstjens
Kurstjens Ecologisch Adviesbureau, Rijksstraatweg 213, 6573 CS Beek-Ubbergen, the Netherlands

Rob S.E.W. Leuven
Radboud University Nijmegen, Institute for Water and Wetland Research, Department of Environmental Science, PO Box 9010, 6500 GL Nijmegen, the Netherlands

Calijn L. Plate
Statistics Netherlands, PO Box 24500, 2490 HA The Hague, the Netherlands

Henk Siepel
Radboud University Nijmegen, Institute for Water and Wetland Research, Department of Animal Ecology & Ecophysiology, PO Box 9010, 6500 GL Nijmegen, the Netherlands

Centre for Ecosystem Studies, Alterra, Wageningen University and Research Centre, PO Box 47, 6700 AA Wageningen, the Netherlands

Arco J. van Strien
Statistics Netherlands, PO Box 24500, 2490 HA The Hague, the Netherlands

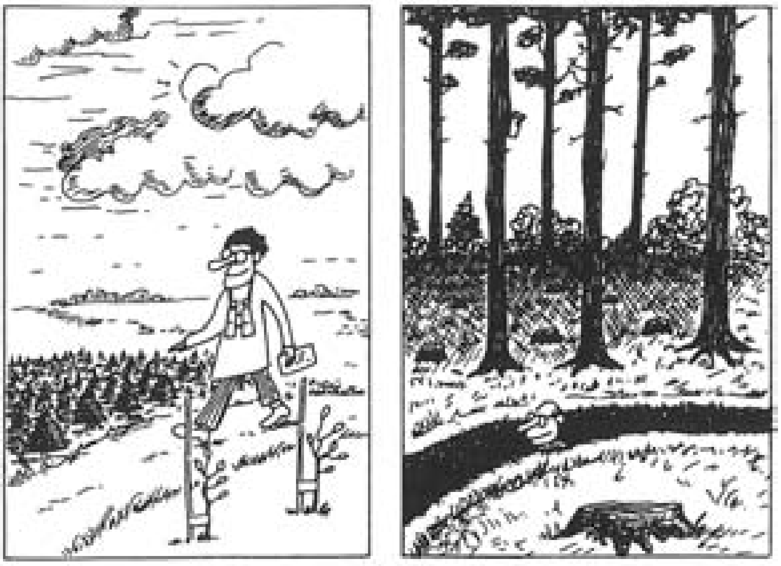
Wolf A. Teunissen
SOVON Dutch Centre for Field Ornithology, PO Box 6521, 6503 GA Nijmegen, the Netherlands

Frank J. Willems
Kasanka Trust, PO Box 850073, Serenje, Zambia

Chris A.M. van Turnhout
SOVON Dutch Centre for Field Ornithology, PO Box 6521, 6503 GA Nijmegen, the Netherlands

Radboud University Nijmegen, Institute for Water and Wetland Research, Department of Animal Ecology & Ecophysiology and Department of Environmental Science, PO Box 9010, 6500 GL Nijmegen, the Netherlands

chris.vanturnhout@sovon.nl



1985 2025

Houd jaarlijks een vaste route aan

Verschenen in de serie '*Mechanisms and constraints in biodiversity conservation and restoration*'

1. Verberk W.C.E.P. 2008. Matching species to a changing landscape – aquatic invertebrates in a heterogeneous landscape.
2. Remke E. 2009. Impact of atmospheric depostion on lichen-rich, coastal dune grasslands.
3. Van Kleef H.H. 2010. Identifying and crossing thresholds in managing moorland pool macroinvertebrates.
4. Vermonden K. 2010. Key factors for biodiversity of urban water systems.
5. Van Turnhout C.A.M. 2011. Birding for science and conservation. Explaining temporal changes in breeding bird diversity in the Netherlands.
6. Schipper A.M. 2011. Multiple stressors in floodplain ecosystems. Influences of flooding, land use and metal contamination on biota.

Het samenwerkingsverband tussen Natuurplaza en de Radboud Universiteit Nijmegen (IWWR) ontwikkelt, bundelt en verspreidt kennis op het gebied van herstel en behoud van biodiversiteit en ecosystemen.

In Natuurplaza participeren:
- Vereniging SOVON Vogelonderzoek Nederland
- Stichting Bargerveen
- Stichting reptielen, amfibieën en vissenonderzoek Nederland (RAVON)
- Stichting floristisch onderzoek Nederland (FLORON)
- Zoogdiervereniging
- Vereniging onderzoek flora en fauna (VOFF)

Deze combinatie van organisaties verbindt het verspreidingsonderzoek met het wetenschappelijk onderzoek. De koppeling van veldwaarnemingen in ruimte en tijd met ecologische lab-, veld- en beheerexperimenten resulteert in innovatieve kennis. De Natuurplaza partners hebben een breed en actief netwerk van vrijwilligers. Hierdoor is er een continue vernieuwing, ontwikkeling en doorstroom van kennis, waardoor maatschappelijke vraagstukken snel en adequaat aangepakt kunnen worden.

SOVON Vogelonderzoek Nederland volgt de ontwikkelingen in aantal en verspreiding van alle in ons land in het wild voorkomende vogelsoorten. Dit gebeurt door middel van signalerend onderzoek (monitoring) en door uitvoering van veld- en bureaustudies die bijdragen aan het verklaren van de gesignaleerde ontwikkelingen. Onze drijfveren zijn kennisontwikkeling en het door middel van informatievoorziening ondersteunen van natuurbeleid, natuurbeheer en natuurbescherming. Daarbij zorgen we voor goede borging van de kwaliteit, onafhankelijkheid en objectiviteit. SOVON coördineert, stimuleert en ondersteunt systematisch veldonderzoek door vrijwilligers.

SOVON is met de andere Natuurplaza partners gehuisvest binnen de Radboud Universiteit Nijmegen en werkt nauw samen met de afdelingen Dierecologie en -ecofysiologie, Milieukunde, Aquatische ecologie en Milieubiologie.

Radboud Universiteit Nijmegen

SOVON
Vogelonderzoek Nederland

NATUURPLAZA
van waarneming tot wetenschap

Stichting Bargerveen
Voor systeemgericht natuurherstel