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Long-Term Population Developments in Typical Marshland Birds in The Netherlands

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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 paper 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.

METHODS

Species selection

We arbitrarily 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*).

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 3374 different BMP-plots were covered, ranging from around 300 per year in 1984 to a maximum of around 1750 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 2000 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 popula-

tion 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 1674 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) (Hagemeyer & 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.

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	Est/Ind	Start year	Number of plots		Number of territories	
			<1990	≥1990	<1990	≥1990
Great Cormorant <i>Phalacrocorax carbo</i>	E	1952				
Great Bittern <i>Botaurus stellaris</i>	I	1968	25 (4)	96 (23)	32 (20)	74 (34)
Little Bittern <i>Ixobrychus minutus</i>	E	1965				
Night Heron <i>Nycticorax nycticorax</i>	-	1950				
Little Egret <i>Egretta garzetta</i>	E	1950				
Great Egret <i>Casmerodius alba</i>	E	1950				
Purple Heron <i>Ardea purpurea</i>	E	1970				
Eurasian Spoonbill <i>Platalea leucorodia</i>	E	1961				
Greylag Goose <i>Anser anser</i>	I	1984	79 (36)	319 (103)	77 (124)	2046 (1571)
Red-crested Pochard <i>Netta rufina</i>	E	1954				
Western Marsh Harrier <i>Circus aeruginosus</i>	E	1950				
Water Rail <i>Rallus aquaticus</i>	-					
Spotted Crane <i>Porzana porzana</i>	-					
Black Tern <i>Chlidonias niger</i>	E	1955				
Bluethroat <i>Luscinia svecica</i>	I	1963	45 (41)	423 (114)	272 (342)	1738 (533)
Common Grasshopper Warbler <i>Locustella naevia</i>	I	1977	29 (15)	121 (28)	83 (48)	371 (101)
Savi's Warbler <i>Locustella luscinioides</i>	I	1966	32 (13)	123 (32)	79 (43)	281 (95)
Sedge Warbler <i>Acrocephalus schoenobaenus</i>	I	1965	98 (40)	325 (76)	986 (337)	3430 (1666)
European Reed Warbler <i>Acrocephalus scirpaceus</i>	I	1965	132 (67)	435 (84)	1490 (1355)	5590 (1127)
Great Reed Warbler <i>Acrocephalus arundinaceus</i>	I	1968	35 (6)	53 (11)	86 (45)	53 (20)
Bearded Reedling <i>Panurus biarmicus</i>	-					
Penduline Tit <i>Remiz pendulinus</i>	E	1950				
Common Reed Bunting <i>Emberiza schoeniclus</i>	I	1965	30 (15)	99 (20)	480 (327)	1533 (333)

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 by using dashed lines before 1990 and solid lines after 1990 in Figure 1. 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 1100 breeding pairs in two colonies (Coomans de Ruiter 1966). After legal protection in 1965 the population initially recovered slowly. In 1978 4470 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 *Ixobrychus minutus* 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

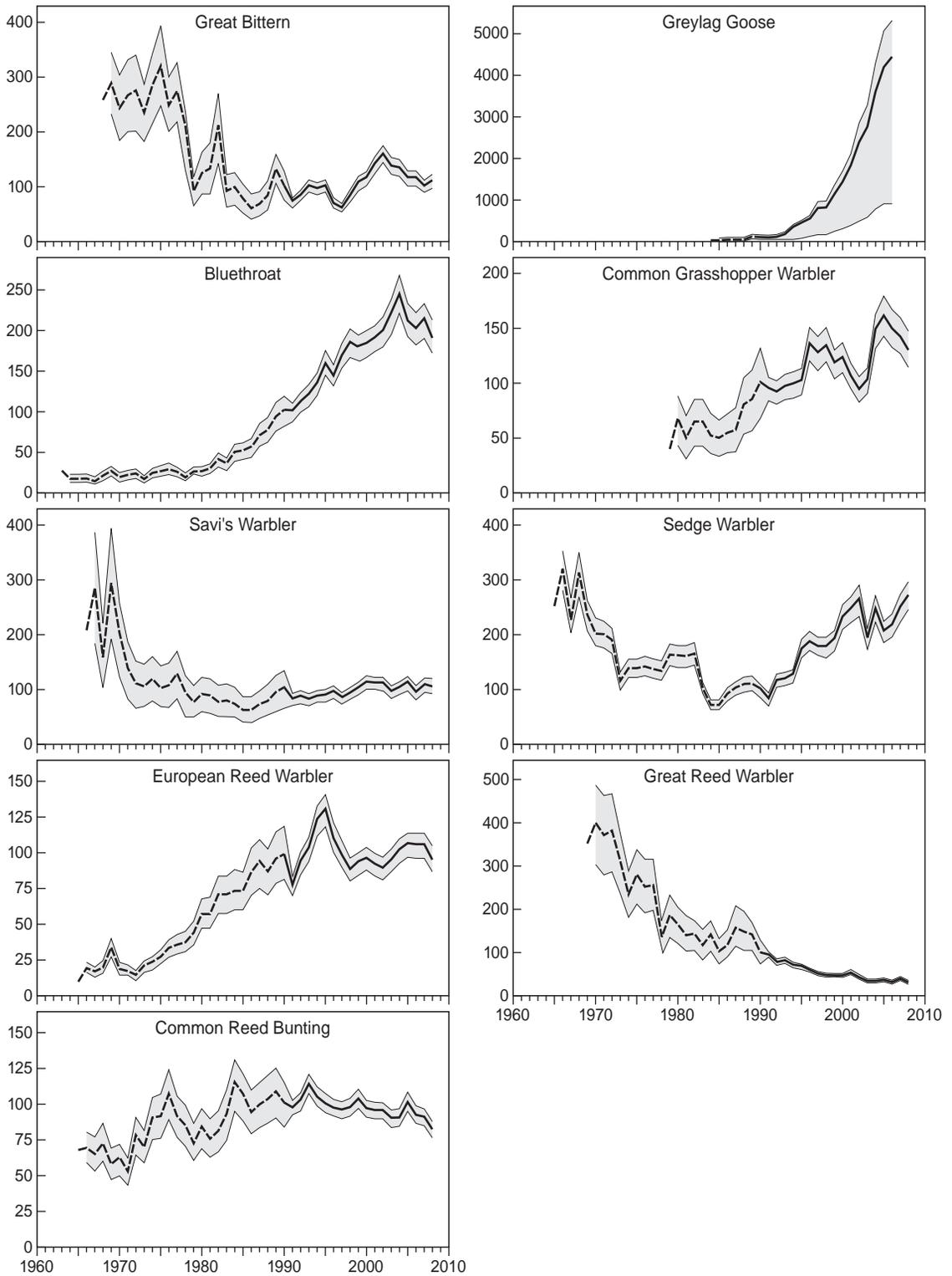


Figure 1. Population indices (\pm SE) for nine breeding birds of marshland in The Netherlands, 1960–2008.

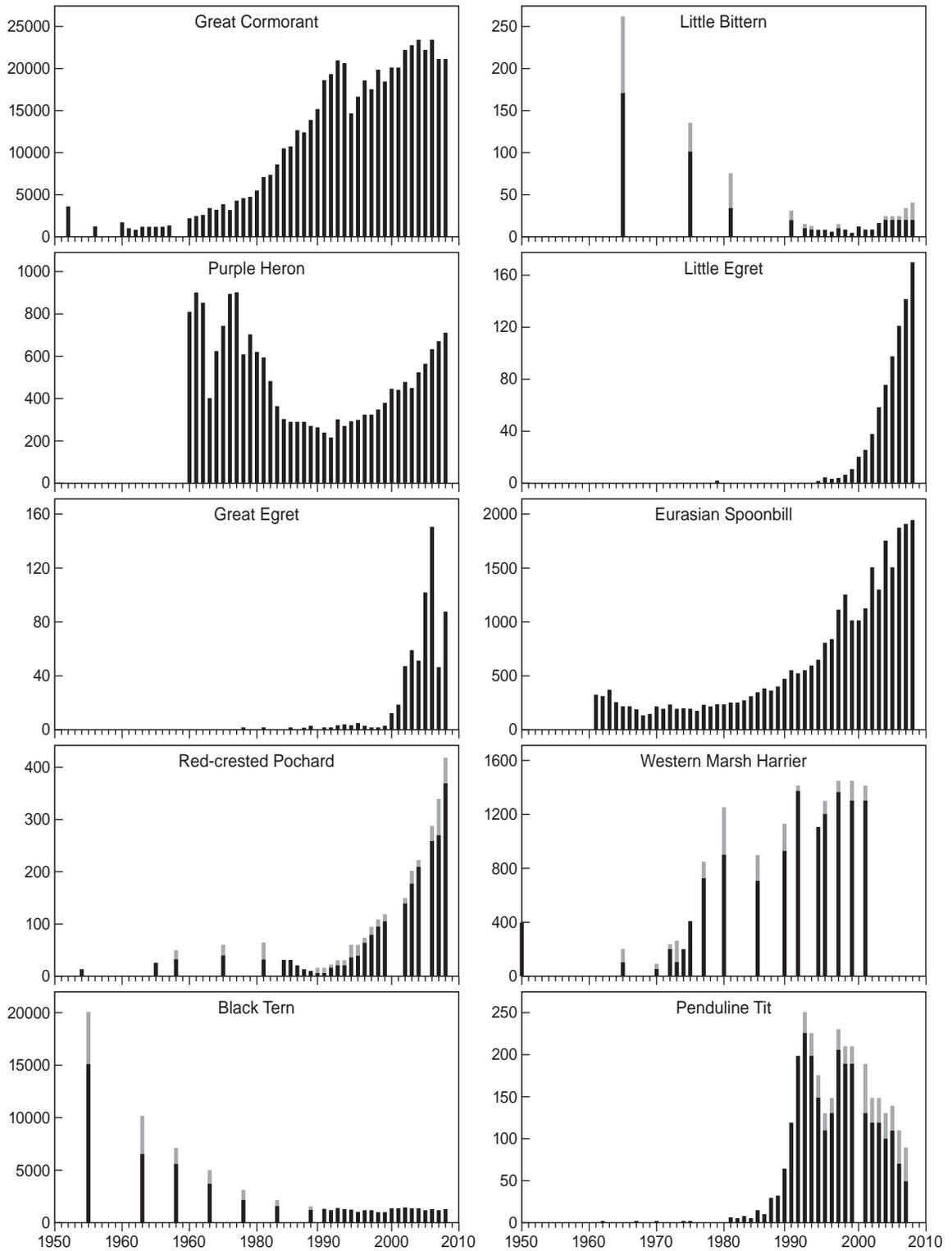


Figure 2. Total population estimates for ten breeding bird species of marshland in The Netherlands, 1950–2008. Estimates are given per year or for periods of years (Little Bittern, Red-crested Pochard, Western Marsh Harrier, Black Tern), including or excluding minimum and maximum estimates.

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 dropped to 46 pairs, as a result of drought in the main breeding site, Oostvaardersplassen (>90% of Dutch population, Voslamber *et al.* 2010). In 2008, the national population recovered to 86–90 breeding pairs, distributed over five sites.

Major colonies of **Purple Heron** *Ardea purpurea* 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** *Platalea leucorodia* 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 1900–2000 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,b). 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 8000–9000 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, 900–1250 in 1980 and 1370–1410 in 1991–92 (Bijlsma 1993, Vogt 1994). Numbers stabilized in the 1990s (1300–1450 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 2000–3600 pairs in 1973–85 and 2500–3200 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 800–1100 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** *Chlidonias niger* 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 2200–3000 in 1976–80. Since the 1990s the population has stabilized around 1000–1400 breeding pairs (van der Winden *et al.* 1996). The most recent estimate is 1200–1300 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 fluvial 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 3000 pairs in 1980, 6500 in 1990 (the two strongholds containing half of the population at that time) and 9000–11,000 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 3000–5000 pairs in 1979–85 to 4000–6000 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 3500 breeding pairs in 1973–77, 1350–2050 in 1989–91 and 1700–2100 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 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 7000 breeding pairs in Zuidelijk Flevoland, and 7500–8000 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 750–1350 pairs in 1989–91, 1800–2000 in 1995–97 and 1200–2000 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 under-sampling 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 paper. 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 paper. Immediately after reclamation, large-scale sowing of Reed 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 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.* 2007). 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.

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 *Phragmites australis* 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 *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 transparency of the water has increased and stoneworts have returned at many sites (Ruiters *et al.* 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

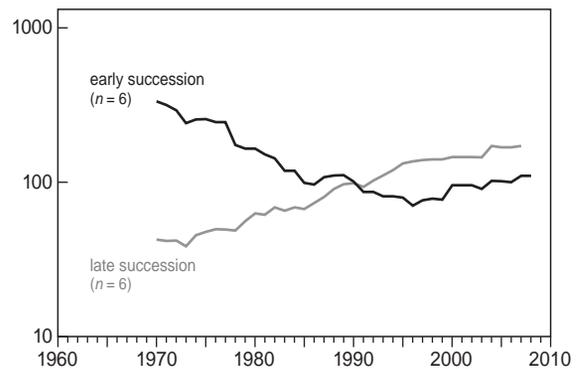


Figure 3. Aggregated population trends in 1970–2008 for six marshland birds typical for early succession stages (particularly reed beds in water: Great Bittern, Little Bittern, Purple Heron, Black Tern, Savi's Warbler, Great Reed Warbler), and for six marshland birds typical for late succession stages (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.

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 paper, 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 (Fig. 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.

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 (Hagemeyer *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).

Agricultural intensification (including reallocation, 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).

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.

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SAMENVATTING

Nederland is – ook op grotere schaal bekeken – een belangrijk land voor moerasvogels. Van 23 moerasbewonende soorten wordt in dit overzicht de Nederlandse trend in de afgelopen halve eeuw gereconstrueerd. Hiertoe werd gebruikt gemaakt van langlopende monitoringsprogramma's, verspreidingsstudies en literatuurbronnen. Twaalf soorten namen vanaf de jaren vijftig van de vorige eeuw in aantal toe: Aalscholver *Phalacrocorax carbo*, Grote Zilverreiger *Casmerodius alba*, Kleine Zilverreiger *Egretta garzetta*, Lepelaar *Platalea leucorodia*, Grauwe Gans *Anser anser*, Krooneend *Netta rufina*, Bruine Kiekendief *Circus aeruginosus*, Blauwborst *Luscinia svecica*, Sprinkhaanzanger *Locustella naevia*, Kleine Karekiet *Acrocephalus scirpaceus*, Buidelmees *Remiz pendulinus* en Rietgors *Emberiza schoeniclus*. Negen soorten vertoonden in dezelfde periode een afname: Roerdomp *Botaurus stellaris*, Woudaapje *Ixobrychus minutus*, Kwak *Nycticorax nycticorax*, Purperreiger *Ardea purpurea*, Zwarte Stern *Chlidonias niger*, Snor *Locustella luscinioides*, Rietzanger *Acrocephalus schoenobaenus*, Grote Karekiet *Acrocephalus arundinaceus* en Baardmannetje *Panurus biarmicus*. Waterral *Rallus aquaticus* en Porseleinhoen *Porzana porzana* gaven grote jaarlijkse schommelingen te zien zonder duidelijke trend. Vooral karakteristieke soorten van overjarig waterriet namen in aantal af, terwijl de meeste soorten met een voorkeur voor drogere moerashabitats met opslag van struweel en bos en soorten met een brede habitatkeuze in aantal toenamen. De achterliggende oorzaken van de gevonden aantalveranderingen, voor zover bekend, zijn zeer uiteenlopend. In het verleden speelde habitatvernietiging (drooglegging van moerassen) een grote rol, nog versterkt door vervolging van schadelijk geachte soorten en gebruik van persistente bestrijdingsmiddelen. De aanleg van de polders in het IJsselmeergebied zorgde in die periode voor enig respijt. De tijdelijke beschikbaarheid van grote oppervlaktes moeras resulteerde in een explosie van moerasvogels (veel broedbiotoop, waarschijnlijk ook hoge reproductiecijfers en verbeterde overleving). Zodra echter de polders in cultuur werden gebracht, verdwenen deze moerasvogelbolwerken, waarbij mogelijk de omringende moerassen als tijdelijke opvangplaats hebben gefungeerd. Op dit moment gaan nog steeds moerassen verloren en gaat de kwaliteit van de resterende moerassen achteruit, voornamelijk door veranderingen in waterpeilbeheer, verdroging, verlanding en eutrofiëring. De aanleg van 'nieuwe natuur' kan dat proces maar deels compenseren. Los van dit alles hebben de langeafstandstrekkers onder de moerasvogels te maken met de omstandigheden die ze tegenkomen op trek en in hun overwinteringsgebied. Langdurige droogte in de Sahel heeft in de jaren zeventig en tachtig van de vorige eeuw een diepgaand effect gehad op soorten die daar overwinterden, waaronder Purperreiger en Rietzanger. Hoewel de regencijfers in de Sahel recent zijn aangetrokken, liggen ze nog steeds niet hoger dan het eeuwgemiddelde. Verder is de aanleg van dammen in rivieren een grote bedreiging voor de Sahel-vloedvlaktes. De resulterende verkleining van het overwinteringsgebied vertaalt zich in een structurele vermindering van de populatieomvang van soorten die ervan afhankelijk zijn.