Responses of autumn staging waterbirds to wetland restoration and water levels in a Danish river delta

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Abstract

A 2,200 ha wetland in the Danish Skjern River valley was restored between 1999–2002, partly to re-establish a rich community of migratory waterbirds, in a project which aimed to restore the nutrient retention capacity of the area and to improve its overall value for wildlife and humans. Numbers, distribution and foraging activity of waterbirds were monitored over the first four years after restoration, between late August and late November in 2002–2005. The restoration turned the western part of the project area into important feeding and roosting habitat especially for dabbling ducks, but also for herons, swans, coots and waders during their autumn migration. A total of 109 waterbird species were observed inside the restoration area. Dabbling ducks exploited the area extensively, with Wigeon *Anas penelope* as the most numerous species reaching up to 12,600 individuals. There was no clear increase or decrease in the number of bird-days for geese, swans, dabbling ducks and Coot *Fulica atra* over the first four years after restoration, except for Gadwall *A. strepera* and Shoveler *A. clypeata* which were not numerous in the first autumn. The number of bird-days increased over the study period for three species of diving ducks and decreased for two species of waders. The proportion of dabbling ducks recorded feeding during the day was high in three years (range of annual means for six species = 29–76%) but low in one year (range = 9–44%). Many ducks also flew at dusk to feed in adjacent fields and other wetlands. In shallow lakes numbers of Coot and some species of dabbling ducks decreased with increasing water levels, whereas diving duck numbers increased.

Key words: foraging activity, Mallard, Pintail, wetland mitigation, Wigeon.

The severe loss of wetlands world-wide has highlighted the importance of conserving those that remain and the need to exploit opportunities for restoring wetlands lost in earlier times. Waterbirds are one of many groups of wetland-dependent organisms that may benefit from wetland restorations schemes, being highly mobile and potentially able to rapidly exploit new opportunities. They are also potential dispersal vectors for aquatic plants and animals, so their presence in the short term can contribute to the development of local biodiversity (Santamaría & Klaassen 2002). Planning of wetland restoration is rarely simple because of the opposing demands of the many different stakeholders involved in the process and the highly contrasting aspirations and outcomes that each brings to the process. Experience of the effects on waterbirds of decisions taken during planning of wetland restoration can be helpful for future restoration projects. We therefore describe here the results of a waterbird monitoring programme made following a major Danish wetland renovation scheme recently completed in west Jutland.

The lower reaches of the Skjern River valley and its surrounding meadows was an extensive and very important wetland area for waterbirds (Tåning 1936) until the river was straightened, the area drained and lowland areas converted to intensive agriculture in the early 1960s. In 1987, the Danish Parliament decided to restore the lower reaches of the Skjern River and its valley. The objectives of the restoration project were: 1) to restore the nutrient retention capacity of the river and its valley, reducing discharge into the adjacent Ringkøbing Fjord, 2) to restore an internationally important wetland and associated habitats for migratory birds, 3) to promote fishery in the downstream estuary (Ringkøbing Fjord), and 4) to increase the recreational and tourist potential of the area (Pedersen *et al.* 2007).

For many waterbirds access to food resources is constrained by water depth (Velasquez 1992; Elphick & Oring 1998; Clausen 2000; Isola *et al.* 2000) and preferred foraging depths vary widely between species (Pöysä 1983). Consequently, variation in a wetland's water depth within and across seasons can have great effects on the numbers of waterbirds present (Mesleard *et al.* 1995; Boertmann & Riget 2006). The present paper describes the waterbirds' use of the restored wetland in the Skjern River valley during the first four autumns after restoration. In particular, it presents information on the numbers of common species, their foraging activity and how they responded to variable water levels in the largest lake. Although all waterbirds were monitored, this paper focuses on dabbling ducks because they were the most numerous group in the area.

Methods

Study area

The Skjern River is the largest river in Denmark in terms of volume of water flowing to the sea. It drains 2,500 km^2 of cultivated land and discharges into Ringkøbing Fjord, a shallow fjord (or lagoon) on the North Sea coast. The project area (Fig. 1) covered 22 km^2 of the original

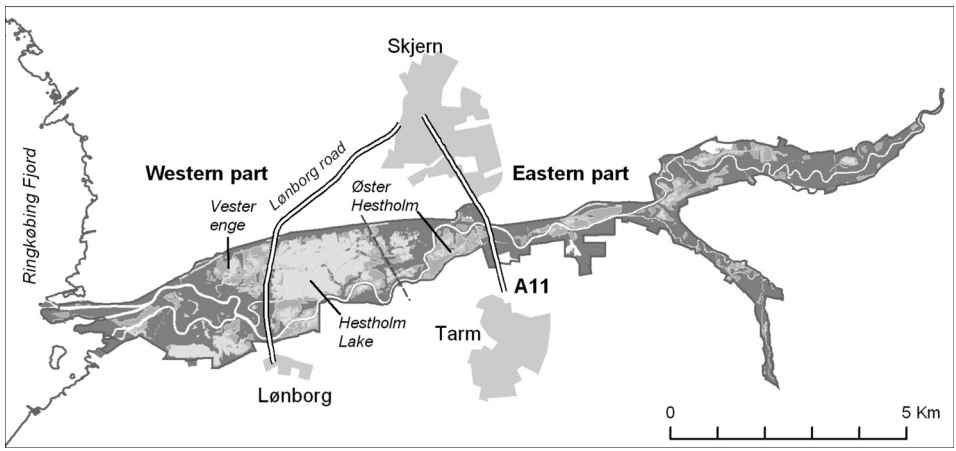

Figure 1. The Skjern River restoration area, following restoration in 1999–2001. The area west of the main road A11 (west of the towns Skjern and Tarm) is referred to as the western part and the area to the east of the A11 as the eastern part. The border between Hestholm Lake and Øster Hestholm is denoted with a dashed line. Habitats inside the restoration area are denoted as follows: white = river; light grey = permanent water; intermediate grey = swamp; dark grey = dry land. Outside the restoration area: white = arable land (except for water in Ringkøbing Fjord to the west); intermediate grey = towns.

40 km^2 that was claimed from wetlands in the 1960s. The Danish Forest and Nature Agency purchased 19.5 km^2 of this area from the farmers in the mid-1990s; the remaining 2.5 km^2 remains in private ownership. During 1999–2002 the cultivated river valley was restored as a meandering river with wetlands, meadows and shallow lakes (Fig. 1). The restoration works included "re-meandering" a 19 km stretch of river and attempts to re-establish natural water level fluctuations in the river and its valley. Details of the restoration of the Skjern River and its valley are given in Pedersen *et al.* (2007).

After restoration, water levels generally were low in summer, but gradually rose during the autumn season. Water levels in the lakes and meadows changed slowly over prolonged periods of the year, but flooding could lead to increases in water levels of more than 10 cm within 10 h (Falck-Rasmussen unpubl. data). Water levels in Skjern River and the surrounding lakes and meadows were determined mainly by the construction of the landscape, precipitation, evaporation and wind conditions. Mean water depth in Hestholm Lake, the largest lake in the valley, was *c.* 60 cm at normal water levels in autumn, with the deepest section reaching 130 cm.

A management plan was developed for the restored river valley with the objective of establishing and preserving the floodplain as an internationally important area for waterbirds, with freshwater meadow ecosystems, low vegetation and shallow lakes. In particular, the plan aimed to

provide a mixture of shallow lakes, meadows and wetlands that were typical of the Skjern River valley before the canalisation of the river in the 1960s. The main management activity in the restored area was cattle grazing, which now occurs across most of the valley. By 2005, 800 cattle grazed across 12 km^2 of the site, with mechanical mowing of the vegetation undertaken over an additional 3 km^2. Public access to the river valley was mainly along roads and paths; in some sections of restored wetland members of the public were also free to walk off the paths, though few actually did so. Hunting was permitted inside *c.* 50% of the restored wetland east of Hestholm Lake on three days in a row (two evenings and one morning hunt), followed by a period of 2.5 weeks without hunting. The activity of the hunters and their disturbance of waterbirds is described in detail in Bregnballe *et al.* (2005).

Bird numbers and activity

Waterbirds inside the restoration area (Fig. 1) were counted from 30 fixed elevated points (including dykes and observation towers) during daylight hours (09:00–17:00 h) between 28 August and 25 November in 2002–2005. Counts were also made outside the main observation period in 2003 to describe phenological patterns in dabbling duck numbers. Counts of the entire area were carried out 1–3 times per month (7–11 counts per autumn) by the same two field-ornithologists (employed full time to conduct waterbird counts), one counting the eastern part and the other simultaneously covering the western part of the restoration area. Extra counts in the western section were carried out in 2002–2004, with waterbirds at Hestholm Lake being counted on 23–30 days in these autumns. All visible waterbirds (except gulls, of which few were present) were counted using Leica 32 × 77 and 20–60 × 77 spotting scopes and 10 × 42 binoculars. The number of individuals seen feeding during the counts was also recorded for most species. For larger flocks, numbers foraging were sometimes estimated from an overview of the proportion foraging rather than being recorded for each individual in the flock. Although measures of feeding activity were not precise for large flocks, trials where an independent observer made detailed counts of foraging activity whilst the bird counter estimated the proportion feeding found that the estimates generally gave a reliable indication of the number of birds feeding. The locations of birds and flocks were plotted on detailed maps.

The development in bird usage of the area was expressed as the number of bird-days, determined both for the entire area (only including counts covering the entire area) and for Hestholm Lake (including all counts covering the lake). Since counts were at regular intervals each autumn, bird-days were calculated as the average number of birds multiplied by the number of days from 28 August to 25 November. The mean proportion of individuals engaged in foraging activity was calculated for each autumn and each species as the mean of the proportion foraging on days where the activity had been recorded for at least 30 individuals on at least three different days during autumn. All activity data were arcsine transformed before analysis, to meet the assumption that the data were samples from

a normal distribution. ANOVA and Tukey's tests were used to test for differences among years in the proportion of dabbling ducks foraging.

In order to illustrate how bird usage of the Hestholm Lake was related to water levels in the lake, numbers of bird-days were converted to indices, setting the number of bird-days in the year with the highest number of bird-days at 100. Indices for other years were then calculated from the number of bird-days in those years, measured as a proportion of the highest number of bird-days recorded. The mean of the water levels recorded at Hestholm Lake during the bird counts was used as a measure of the general water level in each autumn.

Results

Overall waterbird use

In the first four years following the Skjern River valley restoration, 109 different species of waterbirds were observed inside the project area. Dabbling duck were the most numerous group of birds (Table 1), with up to 12,600 Wigeon *Anas penelope*, 5,200 Teal *A. crecca*, 3,400 Mallard *A. platyrhynchos*, 1,400 Pintail *A. acuta*, 520 Shoveler *A. clypeata*, 170 Gadwall *A. strepera*, and 85 Garganey *A. querquedula*. Generally they were present in good numbers throughout the autumn (counts for 2003 are provided as an example in Fig. 2). By far the largest concentrations of dabbling duck were recorded in the Hestholm area (Hestholm Lake and Øster Hestholm) with the wet meadows Vesterenge to the west of the lake being the second most important area (Fig. 3). Only a small proportion used the narrow, eastern part of the river delta during day-time (Fig. 3) but large numbers of dabbling ducks were recorded flying east at dusk, especially in periods when the eastern meadows were partially flooded, and hunting bag data suggest that many dabbling ducks fed there at night. Although dabbling ducks flew at dusk to forage in damp fields and other wetlands, a fairly large proportion was recorded feeding during the daytime counts. Daytime feeding activity was highest for Pintail (66% of counted birds seen to be feeding), Gadwall (63%), Shoveler (52%) and Wigeon (48%) and lowest for Teal (29%) and Mallard (24%; Table 2).

Diving ducks were not numerous, but up to 265 Tufted Duck *Aythya fuligula*, 109 Pochard *A. ferina* and 74 Goldeneye *Bucephala clangula* were recorded. Their distribution was restricted to the three deepest lakes (Hestholm Lake and two other lakes in the western part) which were also used for foraging (Table 2). Coot *Fulica atra* were present in high numbers during each autumn, except for 2004 when numbers had declined markedly by early October. More than two-thirds of all coot-days were recorded in Hestholm Lake. Coot was the species with the highest proportion of birds seen foraging (Table 2).

Among fish-eating birds Great Cormorant *Phalacrocorax carbo* and Grey Heron *Ardea cinerea* dominated with herons feeding inside the restoration area and cormorants mainly foraging at the mouth of the river and in the fjord.

Mute Swan *Cygnus olor* numbers were stable during the autumn and the birds fed almost exclusively inside the restoration

Table 1. Maximum count and number of bird-days recorded each autumn (28 August–25 November) from 2002–2005 in the Skjern River restoration area. Except for Goldeneye, waterbird species are included only if ≥ 100 individuals are recorded on at least one count.

		Maximum numbers				Number of bird-days			
Species group	**Species**	**2002**	**2003**	**2004**	**2005**	**2002**	**2003**	**2004**	**2005**
Cormorants	Great Cormorant	191	37	40	63	3,398	851	1,260	1,209
Herons	Grey Heron	112	115	92	39	1,800	2,986	1,826	1,620
Swans	Mute Swan	509	419	273	305	7,538	20,831	12,163	11,456
	Whooper Swan	1,626	439	75	165	8,213	5,228	964	2,469
	Pink-footed Goose	140	1,812	300	500	1,643	15,513	3,870	2,846
Geese	Greylag Goose	510	1,211	896	1,034	15,548	35,133	24,557	25,599
	Barnacle Goose	1,802	575	110	1,060	20,633	8,476	1,414	13,744
Dabbling Ducks	Wigeon	6,329	12,613	5,612	6,019	101,565	389,185	180,013	147,446
	Gadwall	51	122	151	173	720	4,459	4,359	5,053
	Teal	5,214	3,585	2,811	3,638	94,939	148,541	125,409	136,491
	Mallard	3,374	2,186	1,597	2,600	78,255	83,757	79,521	85,603
	Pintail	1,370	469	310	412	17,021	12,215	10,273	11,224
	Shoveler	282	415	325	523	2,835	12,829	11,649	16,161
Diving Ducks	Pochard	73	70	101	109	765	900	2,546	3,420
	Tufted Duck	170	138	274	265	2,475	867	8,254	8,370
	Goldeneye	63	37	74	45	180	237	1,736	1,093
Coots	Coot	2,516	4,422	3,700	3,450	80,258	150,865	99,566	83,006
Waders	Golden Plover	2,600	1,150	200	644	22,061	21,960	1,723	1,041
	Lapwing	3,392	1,520	1,964	1,016	16,065	45,671	54,720	19,453
	Dunlin	599	660	45	176	7,954	7,765	643	219
	Ruff	337	415	159	126	3,870	2,217	5,336	2,764
	Common Snipe	174	231	112	42	2,610	3,927	4,166	1,144

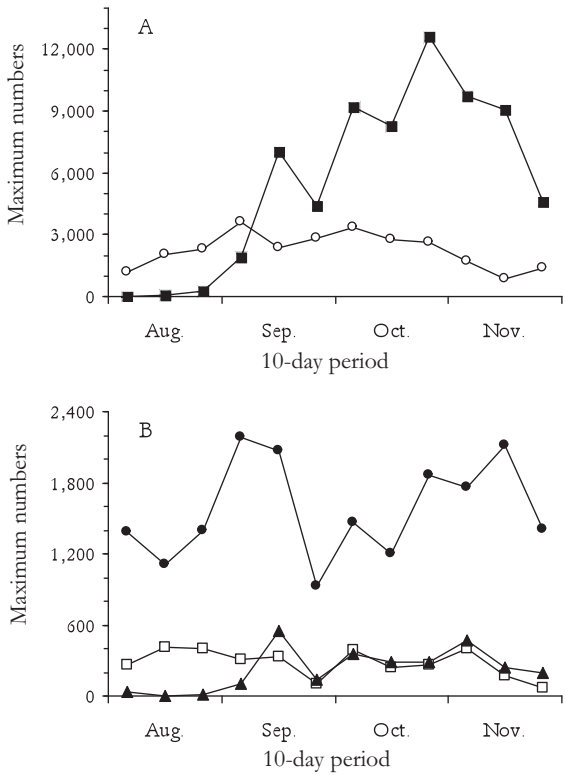

Figure 2. Maximum numbers recorded for five species of dabbling ducks counted in each 10(11)-day period in the Skjern River restoration area from August–November 2003. A: Wigeon (■), Teal (○). B: Mallard (●), Shoveler (□) and Pintail (▲).

area, whereas Whooper Swans *Cygnus cygnus* occurred there in highly variable numbers and regularly flew to the surrounding fields to feed. Pink-footed Goose *Anser brachyrhynchus* numbers were also highly variable inside the restoration area, which they used mainly for roosting, bathing and drinking (Table 2). Greylag Geese *A. anser* frequented the area throughout each autumn but, like the Pink-footed Geese, used it mainly as a roost in between foraging in surrounding fields. Barnacle Geese *Branta leucopsis* occurred sporadically but were mainly seen to be feeding when inside the restoration area.

The most numerous species of waders were Golden Plover *Pluvialis apricaria* and Lapwing *Vanellus vanellus*. Their use of the restoration area varied markedly within and across seasons. Golden Plover sometimes used the area to roost for part of the day whereas Lapwings were present most of the day for several days or weeks and also used the area for foraging in at least two years (Table 2). Other waders such as Dunlin *Calidris alpina*, Ruff *Philomachus pugnax* and

Table 2. Proportion (%) of birds recorded foraging in the Skjern River restoration area during 2002–2005. The first number in parentheses gives the number of days on which activity was recorded for ≥ 30 individuals (≥ 10 individuals for Pochard); the second is the mean number of individuals for which activity was recorded per day. A dash (–) = years where the criterion for calculating a mean value was not met.

		Mean proportion (%) foraging					
Species group	**Species**	**2002**	**2003**	**2004**	**2005**	**Mean**	**s.d.**
Swans	Mute Swan	55.2 (25; 177)	54.1 (21; 234)	60.3 (26; 104)	44.3 (10; 155)	53.3	6.7
	Whooper Swan	70.3 (9; 421)	26.2 (3; 55)	56.5 (3; 55)	25.1 (3; 83)	44.5	22.5
Geese	Pink-footed Goose	0.9 (7; 571)	13.5 (5; 1,379)	11.1 (3; 225)	0.0 (3; 233)	6.2	6.9
	Greylag Goose	19.9 (16; 200)	30.7 (18; 443)	9.1 (22; 278)	22.9 (10; 408)	20.6	9.0
Dabbling ducks	Wigeon	59.7 (25; 2,321)	60.7 (23; 5.821)	53.6 (31; 1,912)	19.1 (21; 1.811)	48.3	19.7
	Gadwall	72.7 (3; 36)	69.8 (14; 72)	76.3 (16; 87)	33.2 (16; 92)	63.0	20.1
	Teal	38.0 (25; 1.453)	41.2 (23; 1,894)	10.1 (29; 1,033)	26.8 (19; 994)	29.0	14.1
	Mallard	36.5 (24; 1,595)	30.7 (23; 1,283)	20.3 (32; 662)	9.4 (21; 716)	24.2	11.9
	Pintail	69.7 (24; 371)	82.2 (20; 222)	43.9 (25; 126)	68.7 (17; 143)	66.1	16.0
	Shoveler	71.3 (14; 119)	65.5 (22; 229)	48.6 (17; 156)	24.9 (13; 177)	52.6	20.1
Diving ducks	Pochard	19.1 (3; 27)	30.5 (5; 29)	38.6 (12; 36)	37.4 (7; 46)	31.4	9.0
	Tufted Duck	26.3 (9; 80)	15.8 (6; 117)	24.4 (21; 102)	33.5 (11; 94)	25.1	7.2
Coots	Coot	74.8 (14; 1.387)	87.3 (20; 1,719)	93.3 (19; 1.123)	73.7 (11; 803)	82.3	9.6
Waders	Golden Plover	0.0 (4; 1,102)	3.9 (5; 588)	0.0 (5; 77)	0.4 (4; 238)	1.1	1.9
	Lapwing	2.2 (16; 417)	10.4 (14; 642)	15.8 (11; 648)	0.0 (17; 335)	7.1	7.4
	Dunlin	45.6 (12; 132)	90.5 (5; 180)	–	–	68.0	31.8
	Ruff	–	52.5 (5; 209)	22.4 (5; 161)	–	37.4	21.3

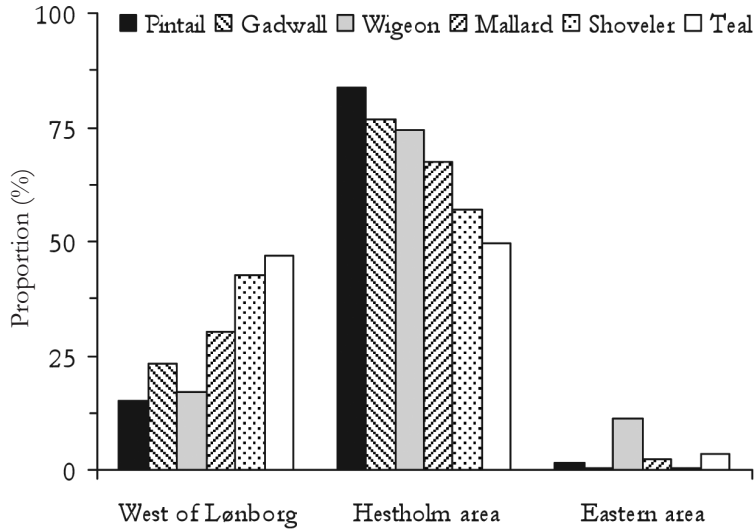

Figure 3. Distribution of five species of dabbling ducks among the three sectors in the Skjern River restoration area during autumn 2002–2005.

Common Snipe *Gallinago gallinago* were present throughout the day and used the area for feeding as well as roosting (Table 2).

Effects of water level

The number of bird-days in Hestholm Lake was calculated each autumn for the species listed in Table 1 and compared with the lake mean water level during autumn. There appeared to be a relationship between mean water level and the number of bird-days for at least six species. The number of bird-days for Wigeon, Shoveler and Coot was 2–10 times higher in 2003, when the mean autumn water level was < 40 cm, so lower than in the other three years when mean water levels were > 50 cm (Fig. 4, upper figure). Conversely, Tufted Duck and Goldeneye numbers were lowest in 2003, when water levels were low (Fig. 4, lower figure). Lapwing numbers were at their lowest in 2004 when water levels were at their highest (Fig. 4, upper figure).

Post-restoration changes

Most species of waterbirds observed using the restoration area during autumn migration occurred in high numbers in the first autumn after restoration. An exception was Gadwall and Shoveler for which the number of bird-days was 4–7 times higher in the 2nd–4th autumn than in the first autumn (Fig. 5a). The number of bird-days also increased markedly for Tufted Duck, Pochard and Goldeneye from the first two to the last two of the four post-restoration years (Fig. 5a, Table 1), whereas the opposite pattern was observed for Whooper Swan, Golden Plover and Dunlin (Table 1).

There was no trend for either an increase or decrease in the number of bird-days over the first four years for Great Cormorant,

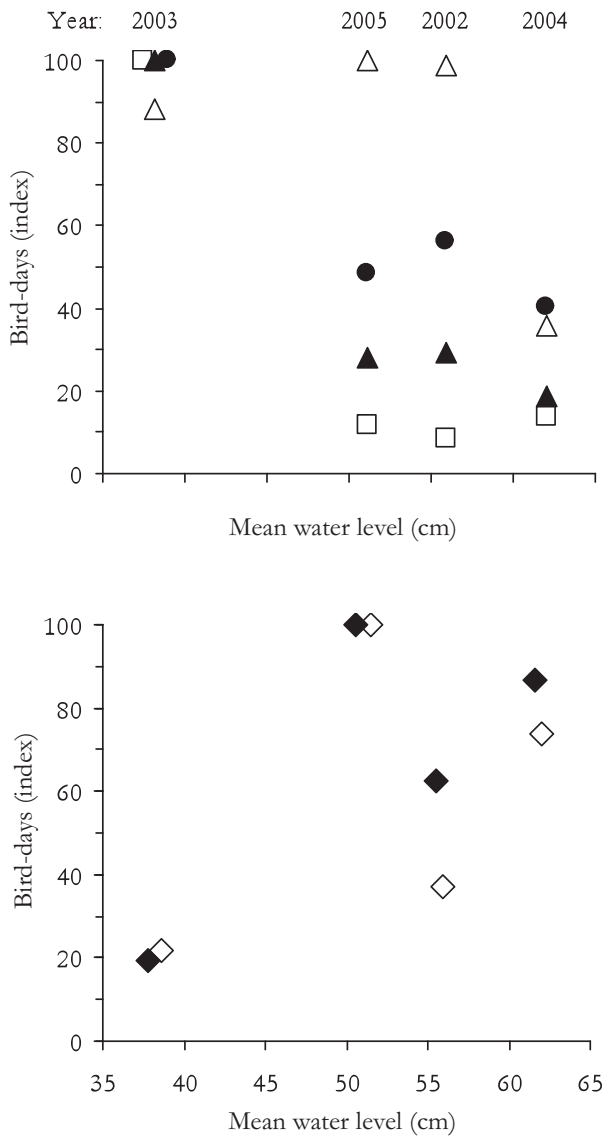

Figure 4. Numbers of bird-days in Hestholm Lake for seven species of waterbirds in relation to mean water level during autumn 2002 (mean water level = 55.9 cm), 2003 (38.2 cm), 2004 (62.0 cm) and 2005 (51.1 cm). Numbers of bird-days were converted to indices, setting the number of bird-days in the year with the highest number of bird-days at 100. Upper figure: Coot (●; maximum number of bird-days = 111,186), Shoveler (▲; max. bird-days = 13,896), Wigeon (□; max. bird-days = 444,522), and Lapwing (△; max. bird-days = 7,770). Lower figure: Goldeneye (♦; max. bird-days = 1,460) and Tufted Duck (◇; max. bird-days = 6,070). The year is denoted at the top in the upper figure.

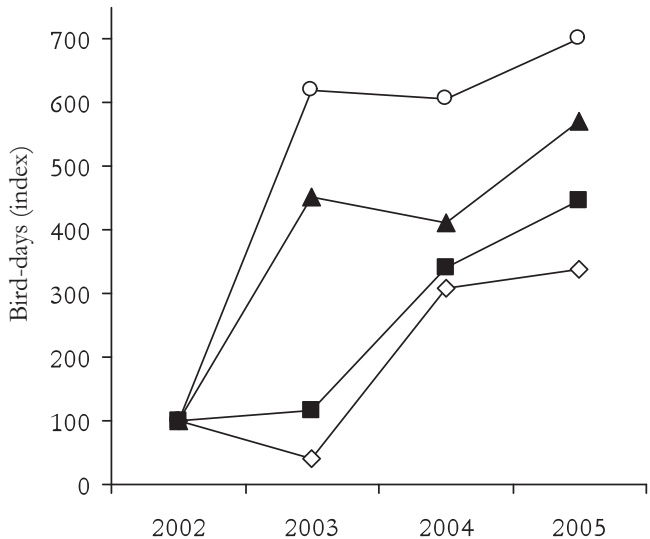

Figure 5. Changes in the number of bird-days recorded in the Skjern River restoration area during the autumns of 2002–2005 for four species of waterbirds: Gadwall (○), Shoveler (▲), Tufted Duck (◊), and Pochard (■). Number of bird-days are given relative to the number of bird-days in 2002; exact number of bird-days are given in Table 1.

Grey Heron, Pink-footed Goose, Greylag Goose, Barnacle Goose, Wigeon, Teal, Mallard, Pintail, Coot, Lapwing, Ruff and Common Snipe (Table 1).

The proportion of birds recorded foraging varied significantly among years for all six species of dabbling ducks included in Table 2 (One-way ANOVA, $5.90 < F_{3,45–96} < 11.88$, $0.0001 < P < 0.05$). Tukey's test showed that significantly fewer of the Wigeon present were foraging in 2005 than in other years ($P < 0.05$). The proportion of Gadwall, Mallard and Shoveler foraging was also significantly lower in 2005 than in two of the other three years. The foraging activity of Pintail and Shoveler was significantly lower in 2004 than in 2002 and 2003, but not significantly different from 2005.

Discussion

Value of the restoration project

A wetland of high value for a number of waterbird species was created when the 2,200 ha of drained fields and canalised streams and rivers were restored into a meandering river, wetlands meadows and shallow lakes. The present study documents that the western part of Skjern River and its valley became an important feeding and roosting area especially for dabbling ducks, but also for herons, swans, coots and waders during their autumn migration. The high diversity of waterbird species recorded in the western part is probably explained mainly by the size of the area and the presence of a mosaic of small and relatively large, and to some extent

topographically variable, but generally shallow wetlands.

Other studies have shown that the largest species diversity of waterbirds is found in large wetlands with a varied topography, dominated by areas with a water depth ranging from 1–25 cm, on average 15–20 cm (Colwell & Taft 2000). These conditions were mainly found in the western part of the restoration area. Three lakes had areas deeper than 25 cm which apparently favoured diving ducks. The value of the different types of wetlands appeared to vary within and among years, partly reflecting variation in water levels.

The extensive use of the wetland by dabbling ducks is probably also explained by the proximity of the restoration area to other extensively used large wetlands located on the autumn migration route of dabbling ducks along the west coast of Jutland (for instance Ringkøbing Fjord, the Tipper Peninsula and West Stadil Fjord). That the presence of neighbouring wetlands was of some importance is supported by regular observations of dabbling ducks and other species of waterbirds that commuted between the restoration area and the shallow lagoon of Ringkøbing Fjord. It is also likely that a part of the attractiveness of the area to Mute Swans, geese, dabbling ducks and Lapwings can be explained by the large Hestholm Lake being completely closed to human activity and to humans rarely visiting the extensive areas of wet meadows at Vesterenge.

The high proportion of dabbling ducks seen to be foraging indicates that the restoration area is of value not only as a suitable disturbance-free daytime roost for these species but also as an attractive feeding site. The western part of the restoration area was also an important foraging area for Mute Swan and Coot.

The planning of a wetland restoration project and its subsequent management can have marked consequences for its long-term value for waterbirds (Taft *et al.* 2002). The present restoration project was successful in providing large inter-connected shallow lakes and grazed meadows in the western part of the restoration area. Furthermore, the management plan ensured that no hunting took place in Lake Hestholm or in the wet meadows to the west of the lake. Furthermore, other types of human activity were also forbidden on the lake and most pedestrians visiting meadows to the west used the public paths where their disturbance of waterbirds was much reduced (Bregnballe *et al.* 2009). The eastern part of the restoration area was of rather limited value to waterbirds during day-time in autumn, probably because it was a narrower area with generally drier meadows and regular hunting.

In summary, the present study suggests that the value of the restoration project for waterbirds was highest in those parts where shallow lakes and wet meadows were extensive, had a variable water depth and were protected against human disturbance.

Post-restoration changes

The probability that a wetland will support a rich and abundant waterbird community will depend on the distribution, abundance and availability of resources such as seeds, tubers, invertebrates and fish (Isola *et al.* 2000; McKinstry & Anderson 2002; Taft *et*

al. 2002). The abundance of such resources may change rapidly in a newly restored wetland due to colonisation and competition among species, *i.e.* due to natural succession. Monitoring of other species in the Skjern River valley showed that, following restoration, the new river and the surrounding meadows and lakes were rapidly colonised with plants, invertebrates and fish from upstream reaches (Pedersen *et al.* 2007). Post-restoration changes have been recorded, for example, in the fish community in Hestholm Lake where large changes in the size composition and stocks of Pike *Esox lucius* have occurred (Falck-Rasmussen & Iversen unpubl. data; Pedersen *et al.* 2007).

It is not possible to test the reasons for the observed changes in bird numbers because food availability and the birds' diet were not recorded during the study. So although likely, it is not known for sure whether the decline in numbers of Whooper Swans and Dunlin and the increase in Gadwall, Shoveler, Pochard, Tufted Duck and Goldeneye was related to changes in food abundance in the area. There may also be a time delay in the response of some species to the restoration because individuals may have established patterns of using other wetlands as their staging or wintering sites. Other studies have shown that numbers of dabbling ducks and other waterbirds at managed sites continue to increase over several years following the establishment of hunting and disturbance-free reserves, indicating that birds take some time to adjust to changes in habitat management programmes (Madsen 1998).

The numbers of all species of dabbling ducks remained high over the first four years, suggesting that the value of the area to dabbling ducks did not deteriorate rapidly despite likely changes in abundance of some food items such as chironomid larvae and seeds from annual plants. However, the proportion of dabbling ducks seen feeding during the day declined in the last 1–2 years, suggesting that food abundance and/or food availability was lower in 2004 and/or 2005 than in 2002–2003. Further studies are needed to determine whether this reflects a decline in food abundance for some dabbling duck species due to natural succession.

Water levels

The sensitivity of some species to changes in water levels, together with large inter-annual variation in water levels as well as timing and extent of flooding of meadows, appeared to cause inter-annual variation in total numbers of bird-days and in the proportion of birds exploiting different parts of the restoration area. In the meadows, numbers of waders decreased as the meadows became increasingly flooded, whereas numbers of dabbling ducks increased. However, dabbling duck numbers tended to decline again if water levels at flooded meadows remained high for several weeks. In the lakes, numbers of some wader and dabbling duck species tended to decrease when water levels rose above a certain level whereas diving duck numbers tended to increase. This was expected because waterbirds have evolved flexible behaviour to take advantage of water level fluctuations at a variety of scales and waterbirds can move frequently among

individual wetlands to find suitable habitat (Kushlan 1989; Warnock & Takekawa 1996; Haig *et al.* 1998). An example from the present study is an increase in Wigeon numbers by 3,690 individuals within three days of increasing water levels in an 80 ha large meadow. The large size and varied topography of the restoration area ensured that a number of species could find alternative feeding and roosting sites even though water levels changed during the season.

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References

Boertmann, D.M. & Riget, F. 2006. Effects of changing water levels on numbers of staging dabbling ducks in a Danish wetland. *Waterbirds* 29: 1–8.

Bregnballe, T., Amstrup, O., Bak, M., Bøgebjerg, E. & Hounisen, J.P. 2005. Vandfugle i Skjern Enge – Forekomst i træktiden og forsøg med reguleret jagt. Research Notes from the National Environmental Research Institute, Report No. 218, Danmarks Miljøundersøgelser, Rønde, Denmark. [In Danish.]

Bregnballe, T., Speich, C., Horsten, A. & Fox, A.D. 2009. An experimental study of numerical and behavioural responses of spring staging dabbling ducks to human pedestrian disturbance. *Wildfowl* Special Issue 2: 131–142.

Clausen, P. 2000. Modelling water level influence on habitat choice and food availability for *Zostera*feeding brent geese *Branta bernicla* in non-tidal areas. *Wildlife Biology* 6: 75–87.

Colwell, M.A. & Taft, O.W. 2000. Waterbird communities in managed wetlands of varying water depth. *Waterbirds* 23: 45–55.

Elphick, C.S. & Oring, L.W. 1998. Winter management of Californian rice fields for waterbirds. *Journal of Applied Ecology* 35: 95–108.

Haig, S., Mehlman, D.W. & Oring, L.W. 1998. Avian movements and wetland connectivity in landscape conservation. *Conservation Biology* 12: 749–758.

Isola, C.R., Colwell, M.A., Taft, O.W. & Safran, R.J. 2000. Interspecific differences in habitat use of shorebirds and waterfowl foraging in managed wetlands of California's San Joaquin Valley. *Waterbirds* 23: 196–203.

Kushlan, J.A. 1989. Avian use of fluctuating wetlands. *In* R.R. Sharitz & J.W. Gibbons (eds.), *Freshwater Wetlands and Wildlife, Conference–8603101, Department of Energy Symposium Series No. 61*, pp. 593–604. US DOE Office of Scientific and Technical Information, Oak Ridge, Tennessee, USA.

Madsen, J. 1998. Experimental refuges for migratory waterfowl in Danish wetlands. II. Tests of hunting disturbance effects. *Journal of Applied Ecology* 35: 398–417.

McKinstry, M.C. & Anderson, S.H. 2002. Creating wetlands for waterfowl in Wyoming. *Ecological Engineering* 18: 293–304.

Mesleard, F., Grillas, P. & Ham, L.T. 1995. Restoration of seasonally-flooded marshes in abandoned ricefields in the Camargue (southern France) – preliminary results on vegetation and use by ducks. *Ecological Engineering* 5: 95–106.

Pedersen, M.L., Andersen, J.M., Nielsen, K. & Linnemann, M. 2007. Restoration of Skjern

River and its valley: Project description and general ecological changes in the project area. *Ecological Engineering* 30: 131–144.

Pöysä, H. 1983. Morphology-mediated niche organization in a guild of dabbling ducks. *Ornis Scandinavica* 14: 317–326.

Santamaría, L. & Klaassen, M. 2002. Waterbird-mediated dispersal of aquatic organisms: an introduction. *Acta Oecologica* 23: 115–119.

Tåning, Å.V. 1936. Ringkøbing Fjords fugle. *In* R. Spärck (ed.), *Ringkøbing Fjords naturhistorie i brakvandsperioden 1915–1931*, pp. 149–219. Andreas Frederik Høst og Søn. København, Denmark. [In Danish.]

Velasquez, C.R. 1992. Managing artificial saltpans as waterbird habitat: species' responses to water level manipulation. *Colonial Waterbirds* 15: 43–55.

Warnock, S.E. & Takekawa, J.Y. 1996. Wintering site fidelity and movement patterns of Western Sandpipers *Calidris mauri* in the San Francisco Bay estuary. *Ibis*: 138: 160–167.

