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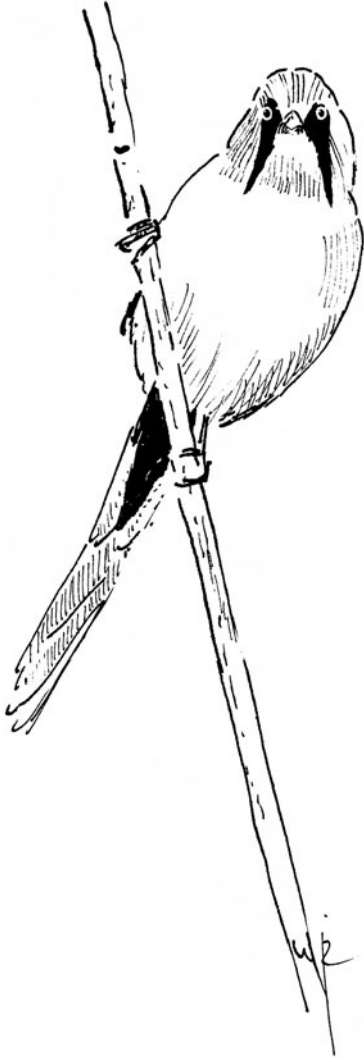
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Early successional stages of Reed *Phragmites australis* vegetations and its importance for the Bearded Reedling *Panurus biarmicus* in Oostvaardersplassen, The Netherlands

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A study on Bearded Reedling *Panurus biarmicus* feeding habits in combination with a sample-wise breeding bird survey of the marshland zones of the Dutch wetland Oostvaardersplassen shows clear-cut spatial differences in densities and habitat use. The more mature stands of Reed *Phragmites australis* constitute the main nesting area, while the more open, younger stands, particularly when inundated and grazed by moulting Greylag Geese, provide the main feeding areas. Arthropod, and especially Chironomid, densities were generally higher in grazed Reed stands and frequent feeding flights were carried out by parent birds between grazed and ungrazed parts of the area during chick raising. Chironomids also proved to constitute the main prey items brought to the nests. Apart from higher prey densities in grazed stands, better detectability as well as better accessibility of the lower vegetation layers are also likely to contribute to the habitat preference of insect-feeding Bearded Reedlings. When in winter the birds shift to Reed seeds, patches with higher seed index hold higher densities of feeding birds. When seed index drops below a certain level, density of birds is low and independent of seed index. The highest seed production is associated with rejuvenated Reed stands, recovering from previous grazing. Bearded Reedlings thus highly depend on the early successional stages of Reed stands. Temporal and spatial habitat diversification is mediated by changing water levels and rejuvenation caused by grazing geese. A number of other marshland bird species depend on this type of vegetation, and wetland management should therefore aim at favouring the natural processes governing Reed succession.

Key words: Reed succession, vegetation structure, food availability, management

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North-west European freshwater marshes on a mineral soil are generally dominated by a more or less extensive vegetation of the helophyte Reed *Phragmites australis*. These Reed marshes constitute an important habitat type for a wide range of marshland bird species, which use it as breeding or wintering habitat. Reed stands easily expand, causing a rapid overgrowth of shallow water and water-logged soil. Early successional stages of Reed are characterised by a high productivity and

within a few years a closed vegetation may develop, covering virtually the entire area (Bakker & Bieuwinga 1957). Some years after a Reed vegetation has become established, productivity normally decreases (van der Toorn & Hemminga 1994). Larvae of noctuid moths play a major role in the degeneration of Reed stands (van der Toorn & Mook 1982). On wet sites productivity is lowered by the stem boring larvae of *Archanara geminipuncta* (Mook & van der Toorn 1985, Tschamtk

1990). The accumulation of litter may eventually cause Reed to disappear because of the invasion of other plant species (Graneli 1989). On the other hand, Reed stands may be rejuvenated by grazing activities of herbivorous mammals (Pelikán 1978) or waterbirds (e.g. moulting Greylag Geese *Anser anser*), particularly when permanently inundated (Iedema & Kik 1986, Zijlstra *et al.* 1991, Loonen *et al.* 1991). When affected by grazing for a series of years, a Reed vegetation tends to be more open, occurring in tussocks, but when a Reed vegetation recovers from grazing it may be highly productive again for some years (van Eerden *et al.* 1997).

After the embankment of the Dutch polder Zuidelijk Flevoland in 1968, extensive Reed beds developed over a vast area (van der Toorn 1972, van Dobben 1995). Many characteristic marshland birds almost immediately colonised the new habitats thus created and often, although temporarily, succeeded in establishing astonishingly high populations (Vulink & van Eerden 1998). One of the most remarkable bird responses to this phenomenon was a dramatic explosion of the numbers of breeding Bearded Reedlings *Panurus biarmicus* in the area, which led to mass emigrations of these birds after the breeding season to other marshland areas, both within The Netherlands as elsewhere in western Europe (Axell 1966, O'Sullivan 1975, Zink 1981, Wawrzyniak & Sohns 1986). Although by now, most of the new polder has actually become cultivated, the remains of this vast freshwater marsh in the northernmost corner are being preserved as the nature reserve Oostvaardersplassen (Fig. 1) and, apart from many other marshland species, still hold remarkable numbers of breeding Bearded Reedlings (Beemster 1997).

The Bearded Reedling is a characteristic inhabitant of temperate freshwater marshes in the Western, Central and Eastern Palearctic (Cramp & Perrins 1993). Some of its ecological features turn it into an interesting example of the importance of early successional stages of Reed for marshland birds. The ecology of the species is closely tied to the single plant species Reed, in which it almost exclusively breeds and winters. The food chiefly consists of arthropods in summer and mainly seeds of Reed in late autumn and winter (Spitzer 1972, Bibby 1981). The Bearded Reedling's dependence on just one plant species, for breeding in spring and summer as well as for food in winter, makes the species vulnerable. The large temporal and spatial fluctuations in numbers shown by the species have been linked to this peculiar dependence by several authors (Spitzenberger 1963, Spitzer 1974, Bibby 1981, 1983). In this paper, an analysis is made of the factors that govern this rather erratic pattern of spatial and

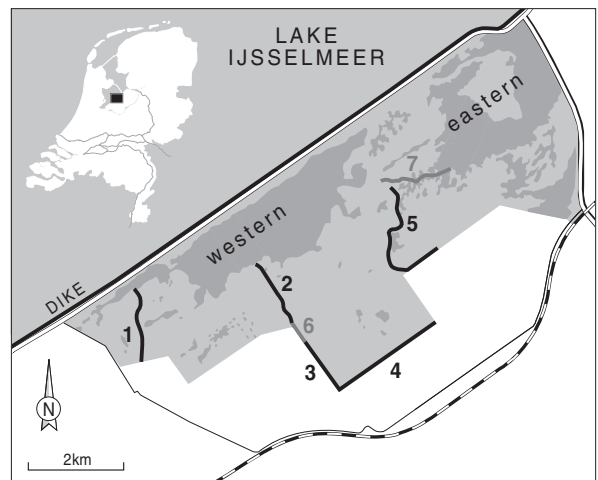


Figure 1. Overview of marshland nature reserve Oostvaardersplassen, The Netherlands, with western and eastern compartment. Breeding bird transects (1–6) and wintering bird transects (2, 3, 5–7) are indicated (1=Willemsvaart, 2=Grote Plas, 3=Kade Stort, 4=Kade Beemdlanden, 5=Drempel, 6=Grote Plas – Kade Stort, 7=Krenteplas – Drempel).

temporal occurrence by focusing on the Bearded Reedling population of Oostvaardersplassen and the particular role of early successional stages of Reed in its ecology. Since the ecological needs of the Bearded Reedling may be considered to constitute an extreme example for those of a far wider range of marshland bird species, the unravelling of the relationships between different types of Reed and the occurrence and behaviour of Bearded Reedling at different stages of the annual cycle is also likely to enhance our insight in how marshland birds in general may respond to various types of wetland management.

METHODS

Study area

The study area, the reserve of Oostvaardersplassen (52°26'N, 5°19'E), nowadays consists of a 3600 ha freshwater marsh on a clayey soil, surrounded by a dam to preclude desiccation, and a 2000 ha border zone, constituting complementary habitat types and serving as a buffer against possible negative influences of cultivation. Up until the early 1980s the heterogeneity of the Reed vegetation was thought to be warranted by the grazing activities in late May and June of moulting Greylag Geese (Zijlstra *et al.* 1991), which maintained the open character of large extents of the lowest and therefore wettest stands of Reed (Jans & Drost 1995,

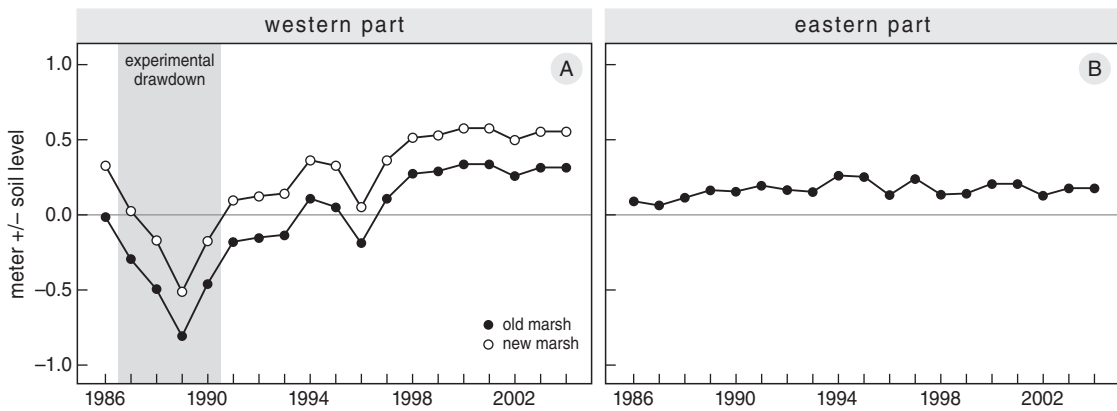


Figure 2. Average water level in May (in m +/- soil level) in the western (A) and eastern (B) compartment of Oostvaardersplassen in 1986–2004.

van Eerden *et al.* 1995, Vulink & van Eerden 1998). However, it became clear that the lack of dynamics in seasonal water level fluctuations was causing a significant decrease in the mosaic pattern of closed Reed beds, sparsely vegetated areas and shallow water devoid of vegetation. Water levels in summer were too high to allow grazed stands of Reed to recover, while the drier parts never became subject to grazing. Thus, the overall pattern became more and more dominated by closed stands of Reed and large extents of shallow water, with almost no gradients left. The lowest water level in summer is on average 20 cm (range 10–30 cm) lower than the highest water level in winter.

In order to allow Reed and other helophytes to rejuvenate and recover (part of) their former range, it was decided to artificially lower the water level of the western part of the marsh (2100 ha) during a period of four years. During this drawdown period (1987–90), helophytes, among which Reed was the most important species, indeed expanded their range and from 1991

onwards the water level was allowed to rise again (Fig. 2A; Jans & Drost 1995, van Eerden *et al.* 1995, Vulink & van Eerden 1998). Meanwhile, in the eastern compartment of the marsh (1500 ha) water tables were maintained at the original high spring level or even somewhat higher (Fig. 2B). In February 1998, the low dike between the two compartments was cut through and since then water tables were more or less similar for both parts. However, as the soil compacted in the western compartment during the drawdown period, the actual water level (in m above the soil) in each of the vegetation zones is about 0.20 m higher than in the eastern part. The drawdown experiment enabled the study of large scale effects of water table management on the abundance and breeding performance of marsh birds in relation to vegetation development and food supply.

Bird censuses and vegetation zones

In order to study the relationships between vegetation development and occurrence of marshland birds, two main vegetation zones were distinguished: ‘old marsh’ and ‘new marsh’ (Table 1). ‘Old marsh’ developed shortly after embankment in 1968, ‘new marsh’ became established during the drawdown of the western compartment in 1987–90. ‘Old marsh’ (Old1, 2 and 3) and ‘new marsh’ (New1, 2 and 3), both dominated by Reed, are each subdivided into three categories on the basis of differences in their history of being grazed by moulting Greylag Geese (Table 1, Fig. 3). Vegetation development was derived from vegetation maps based on false-colour aerial photographs (1985, 1988, 1992, 1996). For the years in between, the surface area of each of the vegetation zones was estimated by oblique aerial photographs.

Table 1. Description of ‘old marsh’ and ‘new marsh’ vegetation zones in Oostvaardersplassen. Old marsh developed shortly after endikement in 1968; new marsh developed during drawdown in 1987–90 (only in western part). June is the main moulting period of Greylag Geese.

Subtype	Age of marsh	
	Old	New
Never grazed by Greylag Geese	Old1	New1
Formerly grazed (in former moulting seasons, but not in preceding moulting season)	Old2	New2
Recently grazed (in preceding moulting season)	Old3	New3

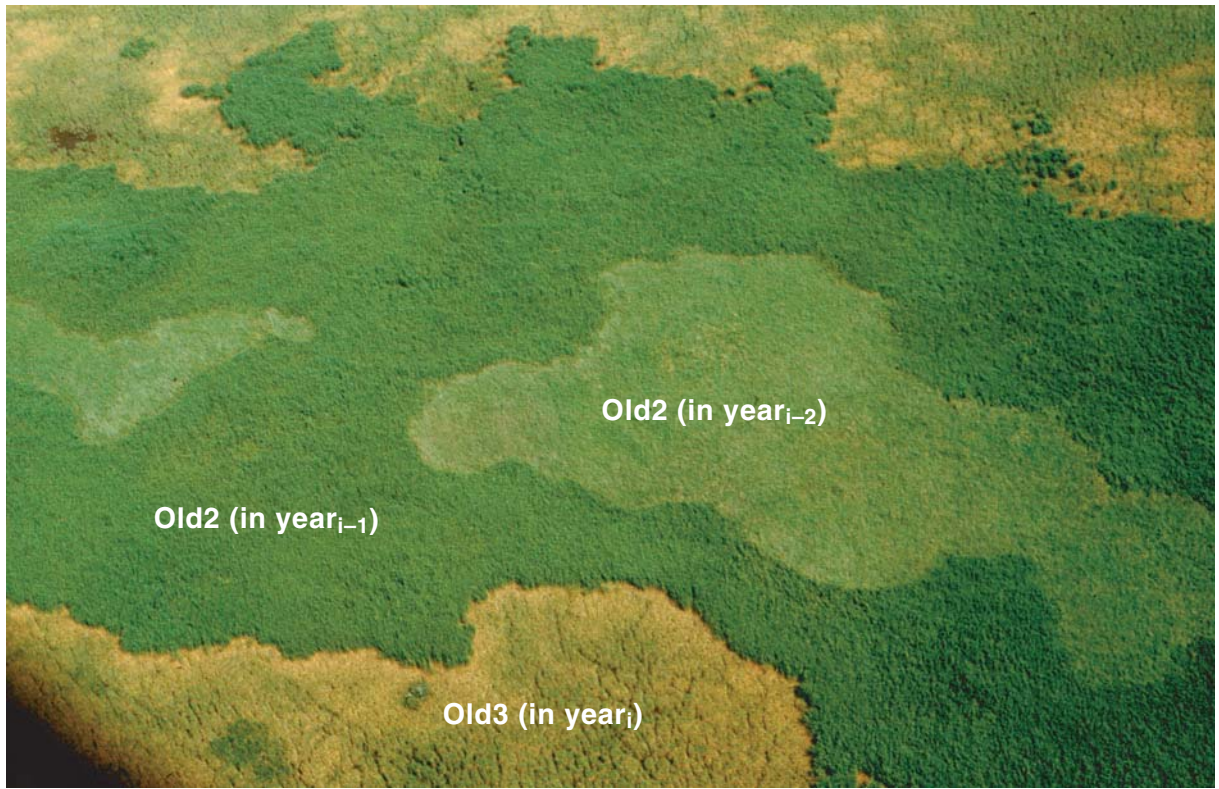


Figure 3. Grazing by moulting Greylag Geese creates variation in structure of Reed vegetation. The picture was taken in the eastern compartment ('Old marsh') and indicated are reedbeds grazed in the previous month (Old3, year_{*i*}), grazed in the previous year (Old2, year_{*i-1*}), grazed two years ago (Old2, year_{*i-2*}). Photograph by Nico Beemster, 13 July 1993.

Counts of breeding birds started in 1987 and occurred along six transects in and along the marsh, three covering the existing gradients in Reed types in the marsh complemented by three more along the border (transects 1–6, Fig. 1). All vegetation zones were represented in the transects. Transects were visited about seven times each breeding season (between 10 April and 5 July). Breeding pairs of Bearded Reedling were counted within a belt of 100 m (transects over low dikes in or along the marsh), or 50 m (transect 'Grote Plas', mudpath through the marsh). Only first breeding attempts of Bearded Reedlings were counted by only considering observations before 25 May. An estimate of the breeding population in the entire marsh was made by multiplication of the breeding bird density per vegetation zone (for eastern and western part) and the surface area per vegetation zone and summing the totals. For the present study counts in 1987–2004 were used. A more detailed description of the breeding bird censuses is given by Beemster (1997).

In order to get information about the distribution of independent 1st calendar-year birds, transect 'Grote Plas' in the western part of the marsh was also regularly visited from 5 July till 25 August (1994–97). Seven counts in July were used, two in 1994, 1996–97 and one in 1995. In the eastern part of the marsh, transect 7 (Fig. 1) was counted twice in July 1997.

Counts of wintering birds took place along five transects in 1996/97–1998/99 (transects 3 and 6 on foot, transects 2, 5 and 7 (partly) by canoe or on foot over ice; see Fig. 1). In 1996/97 (severe winter), all transects were visited once (January 1997). In 1997/98 and 1998/99 (both mild winters), transects 2, 3 and 6, in the western part of the marsh, were visited more or less monthly from late October or mid-November till February, while transects 5 and 7, in the eastern part, were visited once in January. Bearded Reedlings were counted within a distance of 50 m. Visits took place between 10:00 and 16:00 h. All counts were performed at low wind speed (less than 3 Beaufort). The wintering population in January was estimated for the entire marsh in the same way as the breeding population.

Vegetation structure

The structure of 'old vegetation', the remains of growth in previous years, was quantified in 1994. Measurements were carried out in the last decade of April, shortly before new shoots developed. We used a metal rod of 1.5 m length, wrapped with 15 pieces of red tape. From aside, these pieces were visible as squares of 13×13 mm. The metal rod was pushed through the vegetation at heights of 20, 40, 60, 80, 100, 120, 140, 160 and 180 cm above soil level. Afterwards, from a distance of 1 m, an estimate was made of the part of each square visible (categories used 0, 25, 50, 75, 100%). Near each emergence trap (see further on) one measurement was carried out. As the average visibility gradually decreased from low to high in the vegetation, only the measurement at a height of 1 m was used. Horizontal cover was expressed as the percentage of invisible squares at a height of 1 m at a distance of 1 m.

The structural development of 'new vegetation', growth of this year, was measured in 1996 and 1997, by estimating the (vertical) percentage of cover of new shoots. Measurements were carried out in the course of the breeding season during field surveys for breeding birds. Measurements were confined to thirteen locations along the transects 2, 3 and 6 in the western part of the marsh in 1996 (one in Old1, one in Old2, three in New1, seven in New2, and one in New3) and eight of these thirteen locations in 1997 (one in Old1, one in Old2, two in New1 and four in New3).

Food choice and feeding habits

Food choice of Bearded Reedlings was studied in transect 'Grote Plas' (transect 2) in the western part of the marsh, by direct observations from a hide on food deliveries at two nests in 1994 on two days (5 and 6 May, and 11 and 12 May, respectively) during most of the daylight period. Food deliveries by both parents were counted and prey species identified. When a single food delivery consisted of two different prey types, each was counted as 0.5. Since the nest observations suggested that in many cases food was collected from rather great distances, additional observations were carried out on the frequencies and directions of foraging flights of adult birds, in both parts of the marsh. Food choice of adults and fledglings after the nestling period was not investigated. Winter food choice was determined by direct observations of birds during the winter counts.

Food availability

Abundance of arthropods in the breeding season was estimated in 1994 by means of emergence traps (Siepel

1990). The surface area covered by each trap was one square meter, maximum height was three m. Five traps per vegetation zone were used in the eastern part of the marsh and in vegetation zone Old 1 in the western part of the marsh. Along transect 'Grote Plas' in the western part, 9 traps were placed in line from relatively dry to relatively wet, with one trap in vegetation zone Old2, seven traps in New1, and one trap in New3 (cf. Table 1). Vegetation zone New2 was not present in 1994 and, therefore, abundance of arthropods could not be quantified here. Traps in vegetation zone Old2 in the eastern part of the marsh were placed in a section which was grazed for the last time in 1989, for vegetation zone Old2 in the western part this was 1985 or earlier.

Traps were placed over the reed vegetation and all arthropods that emerged from the Reed or out of the water were caught and stored in formaldehyde-ethanol (0.04%). Traps were emptied (and the contents stored in 0.4% formaldehyde-ethanol) and replaced weekly, from the last decade of April till the first decade of August (week number 17–31). All arthropods were collected and those larger than 2 mm were identified up to taxonomic level of order. Within the order of the Diptera a further distinction was made between Chironomidae and other families. After identification and counting, the insects were stored in 70% alcohol.

Winter availability of Reed seed was studied in 1996/97–1998/99. At each sampling site, the following measurements were taken: average panicle density (five measurements per location in 1996/97; twenty measurements per location in 1997/98 and 1998/99) and average panicle length (50 measurements per location in all winters). The seed index was defined as average panicle density × average panicle length. Measurements were carried out in December–January (1997/98 and 1998/99) or April (1996/97) and were confined to thirteen locations along the transects 2, 3 and 6 in the western part of the marsh and one location along transect 5 in the eastern part of the marsh. In the western compartment, in 1996/97 and 1998/99 Reed seed availability was measured on all locations, representing vegetation types Old1 and 2 and New1, 2 and 3. In 1997/98 availability was measured on eight of the thirteen locations in the western part (Old1, Old2, New1 and New3). In the eastern compartment the location was measured in 1996/97 and 1998/99 (Old1).

As larvae of the stem boring moth *Archanara geminipuncta* may affect the formation of panicles (and vegetative cover; van der Toorn & Mook 1982), the percentage of infestation by this species was measured at twelve locations in all vegetation zones along transects

2, 3 and 6 in the western compartment and one location in Old1 along transect 5 in the eastern compartment. Fifty new shoots, with a length more than 50% of the maximum Reed height, were checked during each field visit (1994–2004).

RESULTS

Bird numbers and distribution

The breeding population of the Bearded Reedling in Oostvaardersplassen showed marked annual fluctuations between 1987 and 2004, with a clear difference between the two compartments. Numerical fluctuations were highest in the western part of the marsh. Within this compartment most of the year-to-year differences were due to highly variable breeding numbers in the 'new marsh' vegetation (Fig. 4A).

This 'new marsh' vegetation became established during the years of the drawdown and reached its maximum extension of about 890 ha by 1991, when the western compartment was again inundated (Fig. 4B). Due to a rise in water level in 1994 and a further rise in 1998, in combination with grazing activities of moulting Greylag Geese, a part of the 'new marsh' changed into shallow water uncovered by any vegetation. The extension of 'new marsh' vegetation declined gradually to about 590 ha in 2004. After the re-inundation in 1991 an increasing part of the 'new marsh' vegetation became subject to grazing (New3). However, in 1996 large scale grazing was prevented by low water tables (cf. Fig. 2A). The part of the 'new marsh' vegetation that remained ungrazed (New1) developed into a closed Reed stand. The extension of the 'old marsh' vegetation, both in the western and in the eastern part of the marsh, remained stable over the years (Fig. 4B). In the eastern compartment a variable part of the 'old marsh' vegetation was annually grazed (Old3), the extension being larger in 1988–95, a period with relatively high water tables (Fig. 2B). In the western part of the marsh a small but increasing part of the 'old marsh' vegetation was grazed since 1998.

In the western compartment, the breeding population of the Bearded Reedling was relatively small during the drawdown, strongly increased in the first years after the re-inundation (with about 1500 breeding pairs in 1992–95), but decreased again the years after. This population rise and subsequent downfall was due to the colonisation of the 'new marsh' vegetation from the year of re-inundation (1991) onwards, with a high rate of increase between 1990 and 1992 (Fig. 4A). Up until 1998, the majority of breeding birds

were found in the 'new marsh' vegetation. However, from 1993 onwards, the number of breeding birds in the 'new marsh' vegetation showed a steady decline. A rise in water level in 1998 (Fig. 2A) made breeding in the 'new marsh' vegetation near-impossible. By that time, breeding numbers in the 'new marsh' vegetation had declined strongly, while in 1999, probably because of a relatively high water level in winter 1998/99, breeding was merely confined to the 'old marsh' vegetation. However, in the years after small numbers of breeding Bearded Reedlings returned to the 'new marsh' vegetation. In the eastern compartment the breeding population fluctuated within smaller limits than in the western compartment and was, moreover, considerably lower (estimated maximum about 300 breeding pairs; Fig. 4A).

Breeding Bearded Reedlings were not evenly distributed over the marsh (Fig. 5A). In the eastern part, average breeding density in the years with high breeding numbers in the entire marsh (1991–97) was highest in vegetation zone Old2 and much lower in Old1, while breeding pairs were absent from Old3. In the western part of the marsh, average breeding bird density in 1991–97 was highest in New1 and much lower in Old2 and Old1. Within the transects a relatively large extension of vegetation zone New2 occurred only in 1997, while New3 occurred only in 1995 and 1996 (Fig. 5A, cf. Fig. 4B). In New2, breeding density (in 1997) was of the same level as in New1. In New3 annual variations were considerable: 1996 produced an unprecedented high density (2.61 pairs/ha), whereas in 1995 breeding pairs were absent. The situation in 1996 was exceptional for two reasons. Firstly, the water level in this part of the marsh was extremely low, not only in spring (cf. Fig. 2A) but also in the preceding autumn and winter. This was caused by an artificial lowering of the water level in August 1995, to minimize the effects of an outbreak of botulism, and the exceptional dry winter of 1995/96. Consequently, potential nesting sites in the lowest layers of the Reed remained available and were not inundated as in wetter years. It should be borne in mind that Bearded Reedlings during their first breeding attempt only nest in 'old vegetation', the remains of growth from previous years. Secondly, when affected by grazing, it takes at least two or three years before the structure of Reed becomes very open. All breeding pairs in New3 in 1996 nested in the part that was grazed for the first time in 1995, while no breeding pairs were recorded in the part that was already grazed in 1994. Therefore, the high density in New3 in 1996 was exceptional. Remarkably, average breeding densities in never or formerly grazed 'new marsh' vegetation

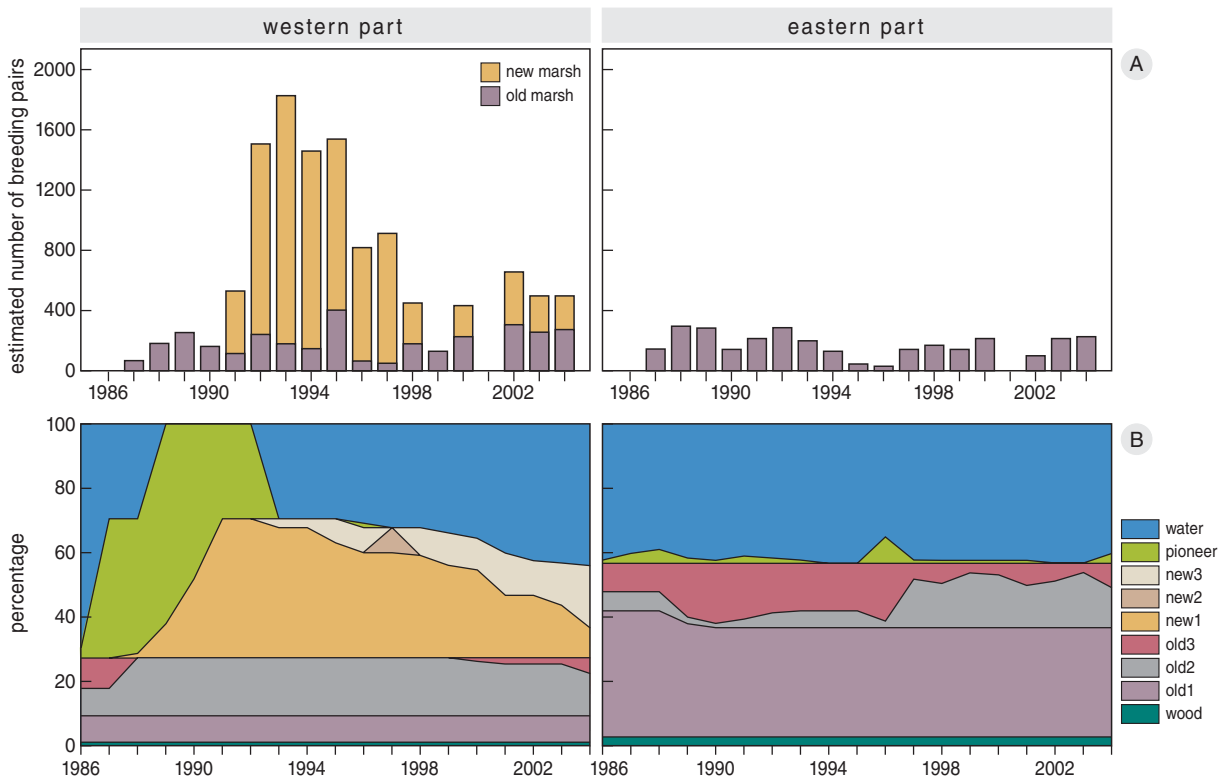


Figure 4. Development of breeding population size of Bearded Reedling (A) and cover of vegetation type (B) in the marshland area of Oostvaardersplassen, divided into a western and eastern compartment, during the period 1987–2004. The western compartment was desiccated in 1987–90, after which re-inundation took place. For an exact description of the vegetation types mentioned see Table 1.

were more than five times higher than in similar ‘old marsh’ vegetation (Fig. 5A). Average densities in ‘old marsh’ vegetation in east and west were about equal (Fig. 5A).

A strong attachment to the recently grazed marsh types also became apparent in the distribution shown by independent 1st calendar-year birds in July. In the western part, young independent birds were absent from the ‘old marsh’ vegetation zones and reached the highest average density (7.73 ± 3.10 birds/ha) in New3 (Fig. 5B). In New1, average density of independent 1st calendar-year birds was much lower, while none were recorded in New2 (only present in July 1996). In the eastern compartment, independent 1st calendar-year birds were mainly observed in Old3, in densities which were apparently lower than in New3 in the western part of the marsh (Fig. 5B).

Also in winter, Bearded Reedlings showed clear-cut spatial preferences, according to Reed vegetation type (Fig. 5C). In the eastern part, apart from some birds along canals, Bearded Reedlings were exclusively found in vegetation zone Old2. In January 1997, when this

vegetation zone in the transect consisted entirely of one-year old Reed (most recently grazed in 1995), density was 1.60 birds/ha. In January 1998 and January 1999, when transect Old2 mainly consisted of two-year old, respectively of three-year old Reed, no birds were counted. In the western part of the marsh by far the highest density was found in New2 in January 1997 (9.64 birds/ha). Locally, Bearded Reedlings reached densities of about 15 birds per hectare. In this winter New2 covered an extensive area and consisted entirely of one-year old Reed (cf. Fig. 4B). In January 1998 New2 was absent within the transect, while in January 1999 the extension was too small to calculate a reliable bird density. In both winters the total area of New2 in the marsh was very small (Fig. 4B). In other vegetation zones the average density in January 1997–99 was less than 1.5 birds/ha (Fig. 5C). Thus, in both parts of the marsh, the preferred vegetation zone entirely consisted of one-year old Reed, grazed in the past. Remarkably, the density in one-year old Reed in ‘new marsh’ in the western compartment was much higher than in ‘old marsh’ in the eastern compartment (Fig. 5C).

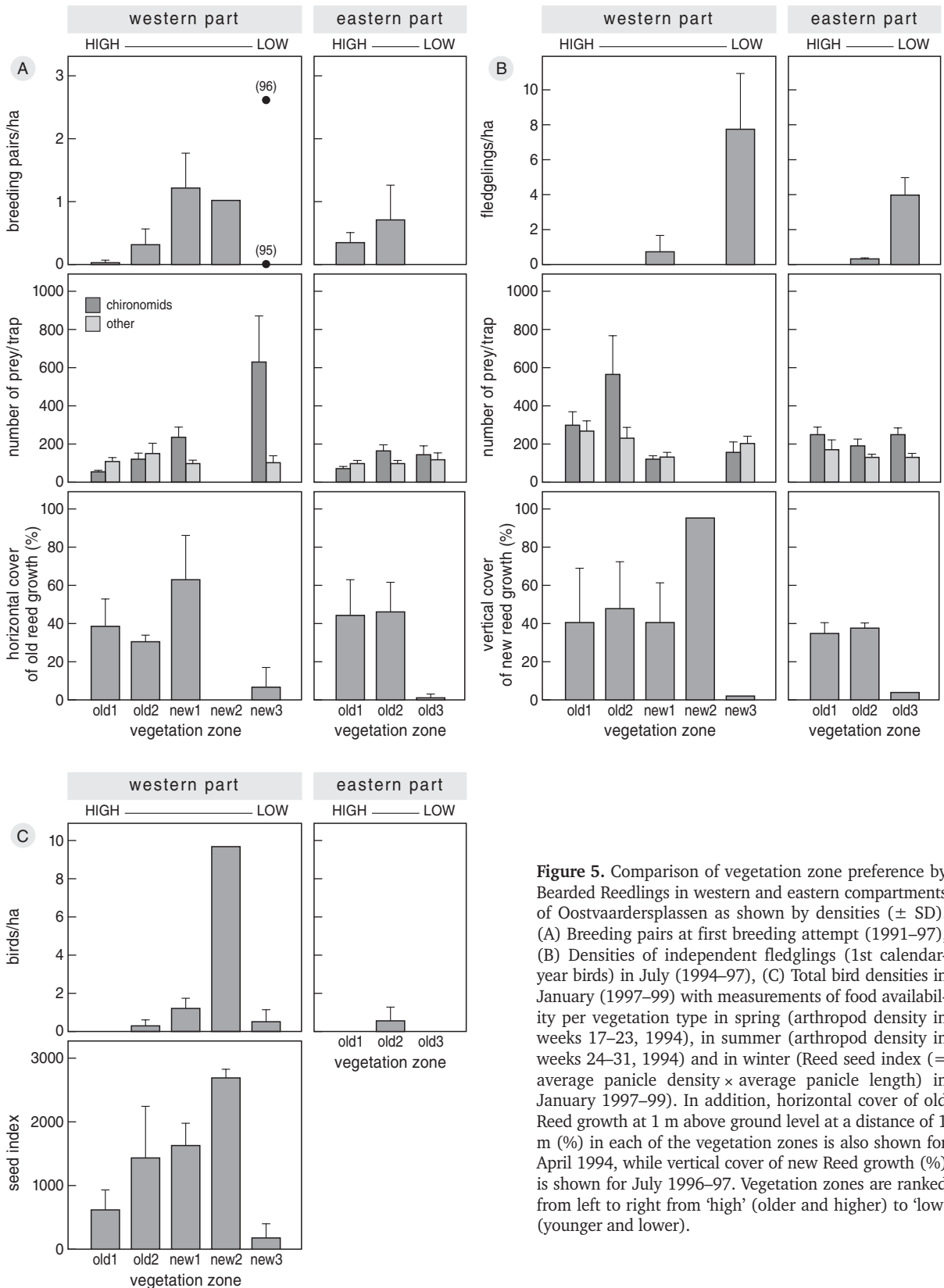


Figure 5. Comparison of vegetation zone preference by Bearded Reedlings in western and eastern compartments of Oostvaardersplassen as shown by densities (\pm SD). (A) Breeding pairs at first breeding attempt (1991–97), (B) Densities of independent fledglings (1st calendar-year birds) in July (1994–97), (C) Total bird densities in January (1997–99) with measurements of food availability per vegetation type in spring (arthropod density in weeks 17–23, 1994), in summer (arthropod density in weeks 24–31, 1994) and in winter (Reed seed index (= average panicle density \times average panicle length) in January 1997–99). In addition, horizontal cover of old Reed growth at 1 m above ground level at a distance of 1 m (%) in each of the vegetation zones is also shown for April 1994, while vertical cover of new Reed growth (%) is shown for July 1996–97. Vegetation zones are ranked from left to right from ‘high’ (older and higher) to ‘low’ (younger and lower).

The wintering population in the marsh was estimated at 2730 birds in January 1997, 1340 in January 1998 and 630 in January 1999. Most of the birds were present in the western compartment (88–99%). In January 1997, 50% of the estimated wintering population was found in New2, on less than 7% of the vegetated part of the marsh.

Food choice and feeding habits

Direct observations at two nests, situated in vegetation zone New1 along transect ‘Grote Plas’, revealed that Chironomids were the major food for nestlings of Bearded Reedling. On average, 68.1% of all food deliveries by adults consisted of Chironomids (Table 2). Chironomids were always brought in seething balls of, at a rough estimate, about 10–20 individuals each. Prey types of minor importance were caterpillars or other larvae (3.9%) and Diptera other than Chironomids (4.1%). A proportion of 14.4% of the food deliveries could only be classified as consisting of small or large prey items. Small unknown prey (7.7%) may well have referred to small beetles Coleoptera, large prey (6.7%) predominantly to spiders Araneae. The difference in food choice between the two nests, about 50 meter apart, was relatively small.

In some 10% of the food deliveries, prey was not seen (Table 2), mostly when attention was being paid to other activities of the birds. There is no reason to believe that prey composition of the food deliveries missed differed significantly from other food deliveries. Assuming prey composition of both categories to be similar, the proportion of Chironomids in the diet for the two nests combined can be estimated at 75%. Many

Table 2. Number of food deliveries per prey type at two nests in 1994. Observations at nest 1 on 5 May (6:15–21:30 MET) and 6 May (6:03–21:35), at nest 2 on 11 May (6:21–21:30) and 12 May (6:00–21:30). Age of the young in the nests during the observations was 7–8 days and 9–10 days, respectively.

Prey type	Nest 1		Nest 2		Total	
	n	%	n	%	n	%
Diptera, Chironomidae	339	67.9	463	68.3	802	68.1
Diptera, other	5	0.9	43	6.5	48	4.1
Lepidoptera, larvae	27	5.4	19	2.7	46	3.9
Small unknown prey (< 4 mm)	36	7.2	55	8.0	91	7.7
Large unknown prey (> 4 mm)	15	3.0	63	9.4	78	6.7
Prey not detected	78	15.6	35	5.0	113	9.6
Total	500		678		1178	

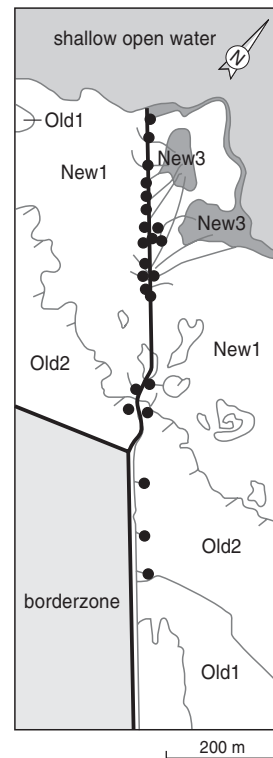


Figure 6. An example of the spatial distribution of nests and favourite foraging areas of breeding Bearded Reedlings in a representative part of Oostvaardersplassen (transects 2, 3 and 6). Direction and length of observed foraging flights are indicated as well as the distribution of vegetation zones.

observations of adults with food for nestlings during breeding bird censuses throughout the years corroborated the observation that Chironomids are the main food source for nestlings of first broods, second broods and probably even third broods.

Bearded Reedlings are non-territorial (Bibby 1983) and were often seen to make foraging flights over considerable distances (up to c. 400–500 m). Figure 6 gives a cross-section of the western part of the marsh, with breeding localities and foraging flights made by breeding birds in May 1994. The majority of the foraging flights made by birds breeding in New1 was directed towards the nearest patch of recently grazed Reed (New3). A minority of the foraging flights made by birds breeding in New1, generally of a shorter distance (up to c. 100 m), was within this vegetation zone. Foraging flights of birds breeding in ‘new marsh’ to ‘old marsh’ were never observed. Breeding birds in the ‘old marsh’ vegetation made foraging flights either to New1 or to the bordering canal. These flights were normally of a relatively short distance (up to 100 m), although

some foraging birds along the border canal were seen to fly to their presumed nest at a distance of up to c. 400 m from the canal. Foraging flights were never directed to other parts of this 'old marsh' vegetation. The density of nests in New1 was generally higher in parts that were close to recently grazed Reed, to where the majority of the foraging flights were conducted. Similarly, a higher density was found in 'old marsh' vegetation close to New1 (Fig. 6).

Observations on foraging flights were carried out in the eastern part of the marsh on 17 May 1994, from a spot on a low dike along the border of Old1 (in which 10 nesting pairs had been localised) and Old3 (in which no nesting pairs had been found). These observations revealed that Bearded Reedlings made frequent foraging flights from their nests in the never grazed Reed vegetation of Old1 to the recently grazed Reed vegetation of Old3. Of 53 flights towards the ungrazed stand, the bird involved carried food in 37 cases. On the other hand, of 45 flights towards the grazed area only two birds did. This difference was statistically significant (Chi-squared test, $P < 0.001$). This clearly suggested that, also in the eastern part of the marsh, Bearded Reedlings nest in the structured Reed stands, fly towards recently grazed Reed stands for food.

In January 1997, during a period of severe frost, 95% ($n = 74$) of the Bearded Reedlings counted in the western part of the marsh and 38% ($n = 16$) of the birds counted in the eastern part were actually seen feeding on seeds of Reed. Within the western compartment 100% ($n = 66$ birds) of the birds counted in New2 were feeding on seeds, while in New1 this was only 50% ($n = 8$ birds). With the exception of one bird feeding on seeds on the ice, all seed-eating birds were

picking seeds from the flower heads. In 1997/98 Bearded Reedlings feeding on seeds of Reed were only observed on 30 October (78%; $n = 41$), while in 1998/99 feeding on seeds of Reed was not observed. In both mild winters, Bearded Reedlings normally foraged low in the vegetation, in the same way as they do in summer, presumably on arthropods.

Response to food availability

Generally, Bearded Reedlings showed two or three fledging peaks each year in Oostvaardersplassen. In 1994, when arthropod densities were regularly measured throughout the breeding period (from late April till early August), three fledging peaks were detected in the western part of the marsh: major ones around 10 May and 25 June and a minor one around 1 August. The first two peaks coincided with periods of high arthropod density (Fig. 7). Arthropod density peaks were mainly caused by peaks in the abundance of Chironomids, which have been shown to constitute the Bearded Reedling's main prey during chick raising. In the eastern part of the marsh arthropod densities were more constant throughout spring and summer (Fig. 7). Arthropod sampling in spring 1994 in each of the different vegetation types showed prey numbers to be higher in 'new marsh' than in 'old marsh' vegetation. Within 'new marsh', the highest prey density was found in the recently grazed New3 (Fig. 5A). Differences in prey abundance among the vegetation types were entirely due to a much higher number of Chironomids, while other arthropods were present in equal numbers throughout the marsh (Fig. 5A). Bearded Reedlings responded by showing a clear preference for breeding in the 'new marsh' vegetation (Fig. 5A) and by making

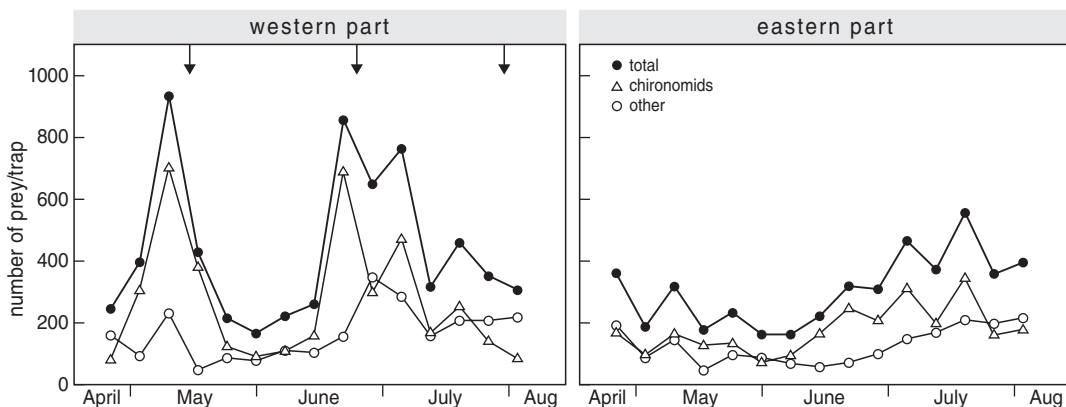


Figure 7. Seasonal variation in the abundance of arthropods in western and eastern compartment of Oostvaardersplassen marshland during 1994. The remarkably high peaks in the western compartment invariably correspond to peak occurrences of Chironomids; the first two peaks also coincide with the fledging peaks of Bearded Reedlings in the western part of the marsh (indicated by ↓) as observed in the field.

regular foraging flights to vegetation zones with the highest prey abundance (Fig. 6). Within the eastern compartment, the preference for feeding in recently grazed Old3 cannot be explained by prey abundance. Probably, the extreme openness of the recently grazed vegetation (Fig. 5A) also plays a role, enabling the birds to easily locate prey.

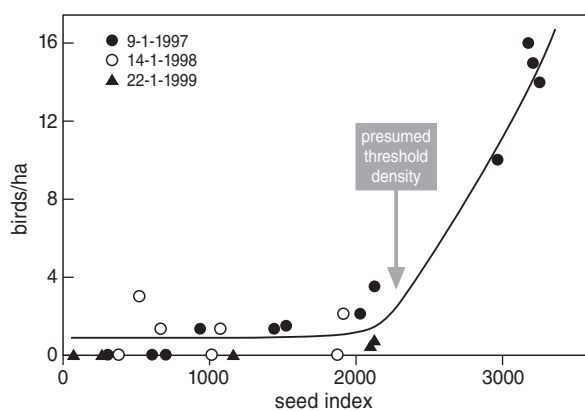


Figure 8. Density of Bearded Reedling in January 1997–99 as a function of seed index of Reed. The curve is drawn by eye.

Later in summer, a different pattern of occurrence was observed in arthropod density. In the western part of the marsh, the highest densities now occurred in Old2 (Fig. 5B), which was re-inundated for the first time that year (cf. Fig. 2A). Once again, in the eastern part no obvious differences in prey abundance were found (Fig. 5B). In spite of the low arthropod density in New3 and Old3, in both parts of the marsh 1st calendar-year birds concentrated almost exclusively in the more open, recently grazed, vegetation zones (Fig. 5B). This preference once more underlines the importance of openness for Bearded Reedlings while foraging.

The seed production of the Reed stands varied strongly according to the vegetation type concerned. Within the western part of the marsh, the highest seed index was found in formerly grazed New2 (Fig. 5C). The response of Bearded Reedlings to these differences in seed availability was a clear preference for New2 (Fig. 5C). Plotting all concurring estimates of seed index and Bearded Reedling densities in January 1997–99 against each other, a clear overall picture emerges: the birds concentrated where seed availability was highest (Fig. 8). Moreover, it is suggested that a threshold seed index exists of well above 2000, below which bird density is low and not affected by seed density. Within the western part of the marsh this threshold was only exceeded in New2 (Fig. 5C).

DISCUSSION

Food choice

In spring, summer and early autumn the food of the Bearded Reedling chiefly consists of arthropods, especially slow-moving species (Spitzer 1972, Bibby 1981, 1983). In Oostvaardersplassen, Chironomids turned out to be the major food for nestlings (Table 2), a similar outcome as was found by Bibby (1981) in England. The first two fledging peaks of Bearded Reedlings coincided with emergence peaks of Chironomids (Fig. 7). Therefore, it seems that Bearded Reedlings time their egg-laying in such a way that chicks can be fed when the availability of food is highest. A similar timing has been found for dabbling ducks: ducklings hatched just after the peak of emergence of Chironomids (Danell & Sjöberg 1977). Actual availability of Chironomids in the wettest Reed types may have been even underestimated in this study, as prey items from the open lake may be transported by wind to the surrounding vegetation (Bibby 1981). The highest density of Chironomid larvae in Oostvaardersplassen was found within 30 meters of the edge of the vegetation (Blomert *et al.* 1996). The diet of adult Bearded Reedlings, not quantified in our study, has been found to contrast markedly with that of nestlings: Chironomids were less frequently caught, while other arthropods as beetles (Coleoptera), spiders (Araneae) and snails (Gastropoda) were more important prey items (Bibby 1981).

In late autumn and winter the food of the Bearded Reedling has been found to consist mainly of seeds of Reed (Spitzer 1972, Bibby 1981). In the latter study, the percentage of Reed seeds in the diet was at its maximum in November–January (68–75%). In both studies it remains unclear to what extent the percentage of Reed seeds in the diet is affected by the differential availability of seeds or arthropods. Our results show that seeds of Reed were the major food source in January 1997, especially in formerly grazed marsh (New2), where the supply was highest. Seeds of Reed were of minor importance as a food source in the winters of 1997/98 and 1998/99, when the supply of seeds was generally lower. Below a certain level of seed production, with a seed index well below 2000, the density of Bearded Reedlings was low and independent of seed abundance (Fig. 8). Below this threshold level of seed production birds do not seem to be able to exploit this food source and are probably forced to feed mainly on arthropods. Wawrzyniak & Sohns (1986) also found foraging Bearded Reedlings in winter most often low in the vegetation, presumably feeding on arthropods. The effect of availability of arthropods in winter on the diet

remains unclear. Finally, also weather may have an effect on food choice. Probably, severe frost affects the availability of some types of arthropods, which in turn may force the birds to feed to a larger extent on seeds.

Feeding and breeding habits and habitat choice

In spring and summer, Bearded Reedlings preferentially forage in recently grazed stands of Reed (Figs 6, 5B). This preference can be explained by a higher availability of food (Chironomids in spring and possibly Aphids in late summer; M.R. van Eerden, pers. obs.) and better foraging conditions because of a lower vegetation cover. Birds hunting by visual clues may have better chances to localise prey in the more open recently grazed Reed than in other vegetation types (cf. Figs 5A, B). Also, highly structured stands of Reed tend to have less sunshine, less wind, more dew and more prolonged periods of overhanging wet leaves after rainfalls (van Eerden *et al.* 1997). All these differences support the preference of feeding Bearded Reedlings for recently grazed stands of Reed.

The lack of structure of recently grazed stands of Reed impedes its use as a nesting site in most years. The majority of nests of Bearded Reedlings were found in highly structured stands of Reed, in both 'old marsh' and 'new marsh', that had been unaffected by goose grazing in the preceding year. Breeding birds were found to undertake frequent and relatively long foraging trips from their nesting sites in more structured Reed stands to the relatively open recently grazed Reed stands. The Bearded Reedling's preference for feeding in the wettest stands of Reed has also been described for other European marshlands, with flying distances of 400–500 m, as found here, also reported by Bibby (1981), and even greater distances of up to a 1000 m mentioned by Hoi (1988) for Neusiedl. The length of foraging flights seems to be related with the distribution of wet and dry parts of Reed beds in a marsh. In Lauwersmeer, which holds the second largest breeding population in The Netherlands after Oostvaardersplassen, foraging flights of more than 200 meters are rarely observed. In this marsh, birds mainly forage in fringes of wet stands of Reed along the edge of former sandflats and breed in dry stands of Reed a short distance away. The situation in Lauwersmeer seems to be characteristic for most wetlands in The Netherlands (Beemster *et al.* 1999) and other parts of north-western Europe (Bibby 1983).

In winter, Bearded Reedlings preferentially forage in one-year old Reed, grazed by Greylag Geese in the recent past, but not in the preceding summer (Fig. 5C). This preference can be explained by a much higher seed

production. One-year old Reed is the only type of Reed with an average seed index above the presumed threshold (Figs 5C, 8). Winter densities of Bearded Reedlings in the 'new marsh' vegetation proved to be much higher than in the 'old marsh' vegetation. In one-year old Reed, the preferred wintering site, the density in January was about six times higher (Fig. 5C). Therefore, the extension of one-year old Reed in the western part of the marsh is probably the most important factor determining the potential number of wintering birds in the marsh. This extension was relatively large in 1996/97, but small in other winters after the re-inundation (Fig. 4B).

Water level, grazing effects and vegetation structure

The vegetation structure of Reed beds changes continuously (Fig. 9). Succession of this pioneer vegetation type generally tends to encroachment of Reed beds by herbs, shrubs and trees from the land side, while shallow water becomes invaded by Reed. An unhampered natural succession would eventually lead to the disappearance of Reed beds and corresponding habitats for Bearded Reedling and other marshland birds.

Marshlands, however, persist because of continuous 'resetting' of this succession by both abiotic and biotic processes, such as water level fluctuations and grazing. High water levels regularly flush the Reed beds, preventing the accumulation of dead organic material (Graveland & Coops 1997), and thereby impede the colonisation of the area by other, more terrestrial plant species. Moreover, high water levels in Oostvaardersplassen have been shown to facilitate the grazing of Reed stands by moulting Greylag Geese (Iedema & Kik 1986, Zijlstra *et al.* 1991, Loonen *et al.* 1991). Low water levels, on the other hand, enable Reed and other helophytes to expand into the lower parts of the marsh, thereby forming wetter, periodically inundated parts of the marsh vegetation (Jans & Drost 1995). Rejuvenation of Reed beds and the slowing down of the rate of succession in Oostvaardersplassen is, thus, mainly governed by fluctuations of the water level.

During the first years, the re-inundation of the 'new marsh' vegetation in the western compartment resulted in a higher density of breeding Bearded Reedlings than in the 'old marsh' vegetation in the eastern compartment (Fig. 5A). This difference is likely to be due to a higher availability of Chironomids, the main food source for nestlings. The spring density of this prey type in recently grazed 'new marsh' in the western compartment was about six times higher than in recently grazed 'old marsh' in the eastern compartment (Fig. 5A). High densities of Chironomids in 'new marsh'

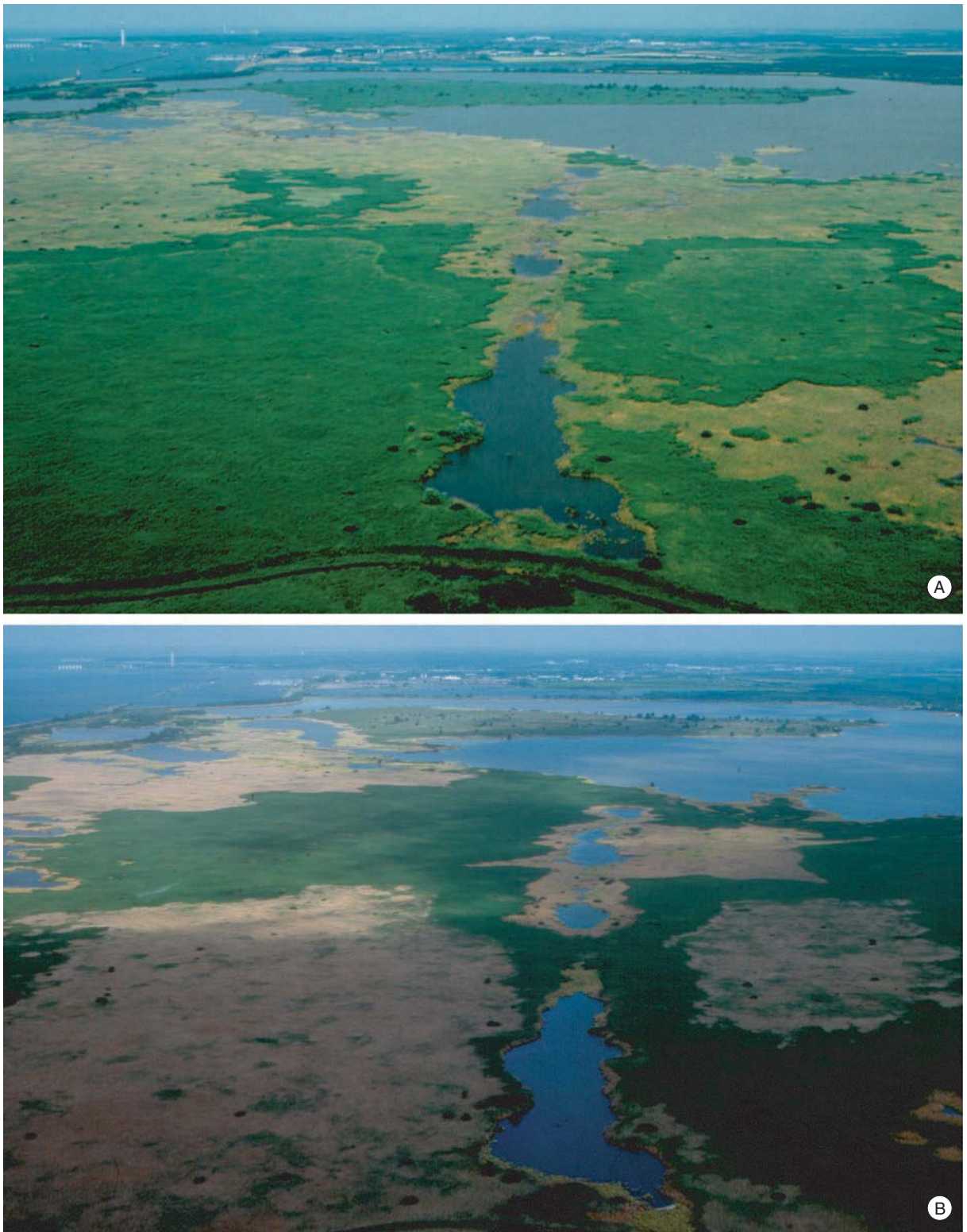


Figure 9. Overview of the Oostvaardersplassen showing large variation in areas grazed by Greylag Geese among years (light patches, (A) in 1993 and (B) in 1996). In 1996 Reed suffered also from infection by the stem-borer *Archanara geminipuncta*. Photographs by Nico Beemster.

vegetation may be explained by the longer inundation time in the latter (cf. Voigts 1976), resulting in a more prolonged predation of the larvae by fish.

Prolonged grazing by Greylag Geese over consecutive years has been shown to cause an increase in shoot density of Reed while shoot diameter decreases (van Eerden *et al.* 1997). With respect to degeneration of Reed stands, a major role is also being played by the stem boring larvae of the moth *Archanara geminipuncta* (van der Toorn & Mook 1982, Mook & van der Toorn 1985, Tscharncke 1990). The relatively high seed production in one-year old Reed can be explained by a revitalising effect of goose grazing on Reed growth (van Eerden *et al.* 1997). Moreover, the grazing activities of geese keep the density of the stem boring larvae low for at least one year. The average percentage of infestation in recently grazed Reed in the western part of the marsh (1994–2004) was extremely low (3%), while other Reed types showed much higher infestation rates, varying between 10% and almost 100%. Thanks to the low infestation rate, recently grazed stands of one-year old Reed, if not grazed again the same summer, produced the highest density of panicles in the following winter. In general, enclosure experiments have shown that panicle density in Reed stands subjected to grazing for fifteen years was much higher than in newly established Reed stands (van Eerden *et al.* 1997). However, as thinner shoots produce on average smaller panicles (van der Toorn 1972), the effect of prolonged grazing on seed abundance in one-year old Reed is not obvious.

Bearded Reedling: an example for other marshland species?

The remarkable biodiversity and numbers of marshland bird species in Oostvaardersplassen has generally been attributed to the heterogeneity in the structure of its dominant helophyte vegetation, e.g. Reed (Iedema & Kik 1986). The dynamic mosaic of shallow open water and bare mud, sparsely vegetated areas and dense, highly structured Reed beds holds the key to these 'natural values' (Vulink & van Eerden 1998). Several characteristic marshland birds are found breeding in Oostvaardersplassen. Populations reacted in three different ways to the re-inundation of the western part of the marsh (Table 3). Four species, all insectivorous, showed an increase, followed by a decrease: Eurasian Coot *Fulica atra*, Spotted Crake *Porzana porzana* and Bearded Reedling showed a pronounced peak in the recently inundated 'new marsh' vegetation, while Sedge Warbler *Acrocephalus schoenobaenus* showed a small peak in the desiccating 'old marsh' vegetation. Four other species showed an increase up to the year 2004. All fish-eaters are found in this category. Finally, five species of birds did not show a clear numerical response to the re-inundation. Breeding populations of these species may be determined by external factors.

Among the marshland passerines, the Bearded Reedling is special because of its non-territoriality, its semi-colonial breeding and its ability to commute over relatively large distances for food. Because of this behaviour, the species is able to exploit the rich food

Table 3. Characteristic reedland birds breeding in Oostvaardersplassen and their numerical response to the re-inundation of the western part of the marsh in 1991. Response refers to the breeding population in the entire marsh. Changes in breeding populations as a reaction to a lower water level in the eastern part of the marsh (1998–2000) are not taken into account. For species that increased, but later decreased, the years with peak numbers are given. For each species the main food for their young in Oostvaardersplassen is noted.

Species		Response to re-inundation	Main food
Little Grebe	<i>Tachybaptus ruficollis</i>	Increase	Fish, insects
Great Crested Grebe	<i>Podiceps cristatus</i>	Increase	Fish
Great Bittern	<i>Botaurus stellaris</i>	Increase	Fish, insects
Greylag Goose	<i>Anser anser</i>	Stable	Plants
Western Marsh Harrier	<i>Circus aeruginosus</i>	Stable	Birds, mammals
Water Rail	<i>Rallus aquaticus</i>	Stable	Insects
Spotted Crake	<i>Porzana porzana</i>	Peak (91–93)	Insects
Eurasian Coot	<i>Fulica atra</i>	Peak (91–92)	Insects
Savi's Warbler	<i>Locustella luscinioides</i>	Stable	Insects
Sedge Warbler	<i>Acrocephalus schoenobaenus</i>	Peak (93–97)	Insects
Common Reed Warbler	<i>Acrocephalus scirpaceus</i>	Increase	Insects
Bearded Reedling	<i>Panurus biarmicus</i>	Peak (92–95)	Insects
Common Reed Bunting	<i>Emberiza schoeniclus</i>	Stable	Insects

supply of open parts along the water side of a marsh, where breeding is impossible. This behaviour, in combination with its relatively high reproductive rate (Bibby 1983), explains why the Bearded Reedling population showed such a pronounced peak after the re-inundation. Thus, the Bearded Reedling nicely illustrates the importance of early successional stages of Reed within a marsh. Peak numbers in Oostvaardersplassen in 1987–2004 were confined to the ‘new marsh’ vegetation of the western compartment. In the ‘old marsh’ vegetation of both parts of the marsh the breeding population was relatively stable (Fig. 4A). The rapid development of the breeding population in the ‘new marsh’ vegetation immediately after re-inundation resembled the development in the entire marsh, shortly after embankment of the polder in 1968 (Vulink & van Eerden 1998). This attractiveness of ‘new marsh’ vegetation seems to be related to the young age of its Reed stands and the corresponding feeding conditions.

Implications for management

Water level fluctuations and reed-grazing by birds or mammals are key operators for breeding birds in a marsh (Weller & Fredrickson 1974, van der Valk & Davis 1978, van Eerden 1997, Vulink & van Eerden 1998, this study). Relatively small fluctuations in water level lead to a variable grazing pressure and thereby to a high diversity of Reed types. The importance of a high diversity of Reed types within a particular marsh is obvious. Both breeding and feeding opportunities are not evenly spread among different vegetation types and, moreover, the different types may be used in different manners at successive stages of the annual cycle or, as in the case of commuting birds, even within the same period of year. Larger fluctuations in water level have more drastic effects. Low water levels stimulate Reed renewal and colonisation of formerly open water, while higher levels counteract encroachment by herbs, shrubs or even trees on the land side and allow erosion and more extensive grazing by waterbirds on the water side. Newly established reedlands are highly productive with respect to arthropods (Voigts 1976, this study) and seeds (van Eerden *et al.* 1997, this study). Reed marshes also serve as refuges for (smaller) fish and the vegetated zone is most accessible in the earlier stages when a more open mosaic pattern enhances the interface between land and water (Weinstein & Balletto 1999). New marsh vegetation therefore constitutes a profitable feeding ground for a wide variety of marshland birds.

Clearly, a dynamic balance between vegetation succession and Reed renewal over the years is necessary to

ensure the continuing existence of populations of typical marshbird species in need of several different Reed types for their survival. Such a balance may be achieved by allowing, or by artificially simulating, ‘natural’ water level fluctuations, both within and across years. Nature management in embanked areas and other wetlands strongly influenced by man, should focus on the continuation of presence of early successional stages. This could either be realised by natural water level fluctuations but, as we observed, drawdown management may be necessary to induce recolonisation.

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SAMENVATTING

De belangrijkste broedplaats voor het Baardmannetje *Panurus biarmicus* in Nederland is gelegen in de Oostvaardersplassen. Het aantal broedende Baardmannetjes vertoonde tussen 1987 en 2004 aanzienlijke schommelingen. De variatie was het meest uitgesproken in het westelijke deel van het moeras, en liep in de pas met het ontstaan en de uitbreiding van jonge moerasvegetaties die volgde op een verlaging van de waterstand in 1987. In 1992–95 telde het werkelijke moeras ongeveer 1.500 paren en het oosterlijke 300. In latere jaren daalde het aantal paren in de nieuw ontstane moerasvegetatie sterk. De vogels nestelden in oude opstanden riet, maar foerageerden voornamelijk in de meer open, natte opstanden, die door ruiende Grauwe Ganzen werden begraasd. De nestdichtheid was groter indien de broedplaatsen in oud riet grensden aan begraasde stukken riet. Tijdens de jongenfase pendelden de broedvogels geregeld heen en weer tussen broed- en foerageerplaats, altijd van oud naar jong riet, over afstanden van 100–400 m. Arthropoden (geleedpotigen) bereikten in het algemeen in de jonge rietvelden een hogere dichtheid en waren daar beter zichtbaar en door de vogels te pakken. Dansmuggen vormden het hoofdvoedsel in de broedtijd. In de winter schakelden de Baardmannetjes veelal over op een menu van rietzaad. De hoogste dichtheid van foeragerende vogels werd dan gemeten waar de zaadindex het hoogst was. Het Baardmannetje is een mooi voorbeeld van een soort die afhankelijk is van een in ruimte en tijd rijk gestructureerd moeras. Dynamiek in een rietmoeras, zoals bewerkstelligd door wisselende waterstanden en begrazing door ganzen, levert het juiste mozaïek op van jonge, oude, natte en droge rietopstanden die Baardmannetjes nodig hebben om te broeden, te foerageren, op te groeien en te overwinteren.