The long-term influence of grazing by livestock on common vole and raptors in man-made wetlands in the Netherlands

Nico Beemster[1,2,*] & J. Theo Vulink[1,2,]**

[1] Rijkswaterstaat, Programma GPO, P.O. Box 24057, NL-3502 MB Utrecht, the Netherlands
[2] Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, NL-9750 AA Haren, the Netherlands

Abstract: Several studies have examined the effects of grazing by wild ungulates or livestock on the abundance of small mammals; some studies have also examined the effects on the abundance of raptors feeding on small mammals. In most studies the abundance of small mammals was negatively affected by grazing, while raptors were found to show a numerical response to the density of small mammals. However, most studies rely on census data from time spans of just 1-4 years. Because there are often large fluctuations in the numbers of small mammals, there is a need for long-term studies. In this study we analyse the long-term effects (3-27 years) of grazing by livestock on vegetation development, vegetation structure, common vole (*Microtus arvalis*) index and density of vole-feeding raptors in man-made wetlands in the Netherlands. The man-made wetlands studied are characterised by a low level of physical perturbation, and without additional management measures their vegetation, of short grasses, will soon be replaced by tall vegetation dominated by reed (*Phragmites australis*), wood small-reed (*Calamagrostis epigejos*) and shrubs. Grazing was initiated while short grasses dominated the vegetation. The intense grazing (summer grazing with a stocking rate of more than 0.8 animals.ha^{-1}), created a homogeneous short vegetation. Grazing with a low stocking rate (year-round grazing with a stocking rate less than 0.6 animals.ha^{-1} or summer grazing with a stocking rate of less than 0.1 animals.ha^{-1}) led to a heterogeneous vegetation. However, after a few years, relatively sharp boundaries developed between short-grazed grassland and closed reed stands and the intermediate stage, characterised by a moderate reed height (between ca. 0.5-1.5 m), increasingly disappeared. In grazed areas relatively high densities of common voles (vole indices 15-35 voles / 100 trap nights) were restricted to parts with a moderate reed height. Such areas only temporarily existed and their disappearance led to a decrease of vole abundance after some years. Vole-feeding raptors showed a numerical response to changing vole densities. Vegetation structure also had an effect on raptor density. Maximum raptor densities were found at sub-maximum vole indices, where average reed height was somewhat lower. The relevance of grazing as a tool for management of vole-feeding raptors in man-made wetlands is highly dependent on the potential of grazing to revert tall vegetation to an earlier successional stage. The regular occurrence of high vole densities and their predators may be achieved by creating a cyclic variation in stocking rates. Years with relatively low stocking rates should be alternated with some years with higher livestock densities.

Keywords: livestock grazing, long-term effects, common vole, *Microtus arvalis*, vole-feeding raptors, reed height, wetlands.

* present address: Altenburg & Wymenga Ecological Consultants, P.O. Box 32, NL-9269 ZR Feanwâlden, the Netherlands, e-mail: n.beemster@altwym.nl

** present address: Rijkswaterstaat, Programma Projecten en Onderhoud, P.O. Box 2232, NL-3500 GE Utrecht, the Netherlands

Introduction

As a result of large hydraulic-engineering works intended to protect against flooding or to reclaim land for agriculture, about 30,000 ha of new wetlands have been established in the Netherlands during the last century (Schultz 1992). Many of these man-made wetlands are of international conservation importance because of the occurrence of large numbers of birds. Many of these bird species, including vole-feeding raptors and owls, are attracted by early stages in vegetation succession (van Eerden 1984, Dijkstra et al. 1995). Since the level of perturbation, such as inundation by salt or freshwater, erosion by ice, or grazing by ungulates, is very low in these wetlands, these early successional stages only exist for a short while. Livestock grazing is one of the management options for stopping or slowing down vegetation succession (e.g. Bakker 1989, Scherfose 1993), with the aim of maintaining early successional stages and their characteristic plant and animal species.

The effects of grazing on vegetation structure and habitat use by birds have attracted a great deal of attention (e.g. Larsson 1969, Soikkeli & Salo 1979, Holechek et al. 1982, van Wieren 1991, Duncan 1992, Vulink & van Eerden 1998). The effects of grazing by wild ungulates (Keesing 1998, Smit et al. 2001) or livestock (Grant et al. 1982, Bock et al. 1984, Heske & Campbell 1991, Hayward et al. 1997, Schmidt et al. 2005, Wheeler 2008, Johnson & Horn 2008, Bakker et al. 2009) on the abundance of small mammals and their avian predators have been less well studied. In most studies the abundance of small mammals was found to be negatively affected by grazing, while raptors were found to show a numerical response to small mammal density. However, except for the work of Hayward et al. (1997) and Bakker et al. (2009), these studies rely on census data from just 1-4 years. Because small mammals often show large fluctuations in numbers, there is a need for long-term studies (Hayward et al. 1997). Microtine rodents are known to show large variation in population size; often these fluctuations are cyclic with peaks every 3-4 years (Krebs & Myers 1974, Hansson & Henttonen 1985). In the Netherlands populations of common voles (*Microtus arvalis*), the main prey species for the majority of raptor species (Dijkstra et al. 1995), are weakly cyclic (van Wijngaarden 1957, Cavé 1968, Dijkstra & Zijlstra 1997). The numerical responses of vole-feeding raptors to changing vole densities may occur either rapidly, without an obvious time lag (Korpimäki & Norrdahl 1989, Korpimäki & Norrdahl 1991, Korpimäki 1994) or with a long delay (Keith et al. 1977, Erlinge et al. 1983).

We examined the long-term effects of grazing by cattle and horses on the abundance of common vole, vole-feeding raptors and one species of owl (hereafter referred to as raptors) in a long-term study (27 years). The effect of vegetation development on the density of raptors is analysed for the entire study period (1969-1995). The effects of (1) grazing on vegetation structure, (2) vegetation structure on vole numbers, and (3) vegetation structure and vole numbers on raptor abundance, are analysed for the second part of the study period (1983-1995).

Methods

Study areas

The study was conducted in two recently reclaimed areas in the Netherlands: Lauwersmeer (53°20'N, 6°10'E) and Oostvaardersplassen (52°26'N, 5°19'E) (figure 1). The Lauwersmeer polder (9100 ha) was reclaimed from the Wadden Sea in 1969. The nature reserve (4500 ha) consists of former tidal flats (2100 ha; hereafter referred to as flats), former accretion works (300 ha) and shallow and deeper waters (2100 ha). Soil types, varying from loamy sand to clay-rich, are related to the elevation of the flats: the higher-lying flats being more sandy than the less-elevated ones. After empoldering, the soils of the flats gradually

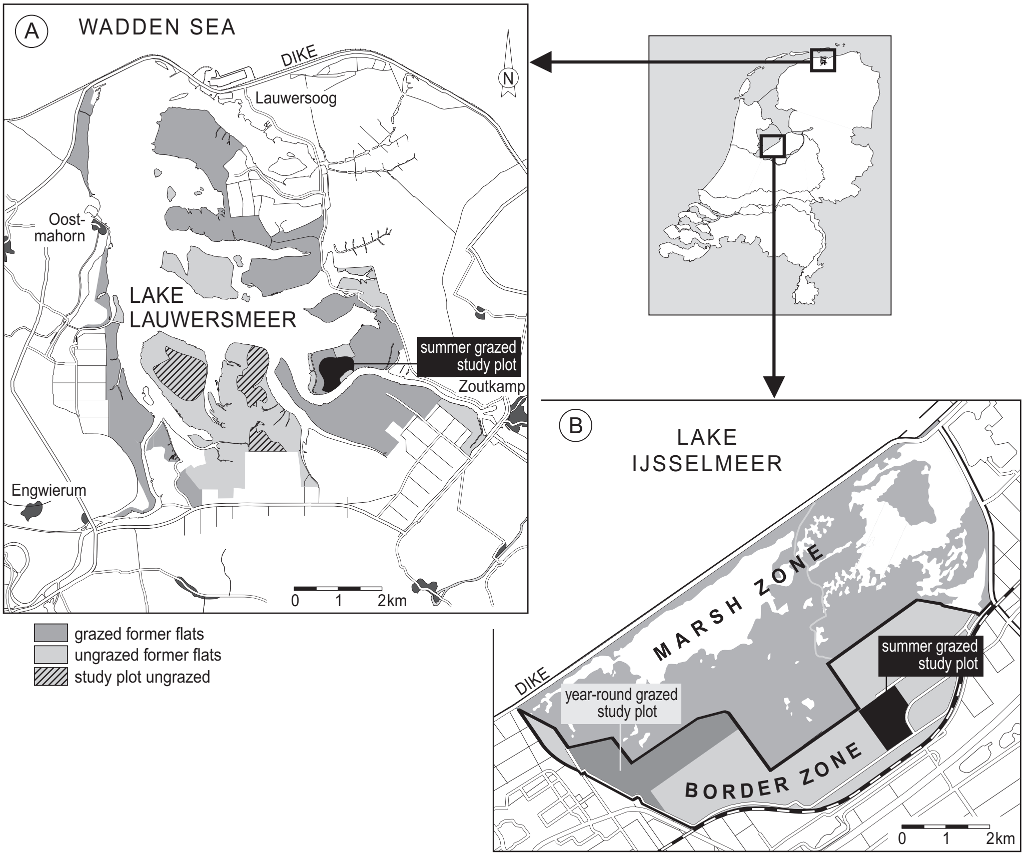

Figure 1. Overview of the study areas in the Netherlands: (A) Lauwersmeer (a former estuary) and (B) Oostvaardersplassen (along lake IJsselmeer, the former Zuiderzee).

desalinated (Joenje 1978, van Rooij & Drost 1996). In the first few years after empoldering, an undisturbed vegetation succession took place (Joenje 1978). In 1982, summer grazing with cattle and horses was started on parts of the flats (1300 ha).

The Oostvaardersplassen study area (5600 ha) is located in southern Flevoland, a polder reclaimed in 1968 from the freshwater lake IJsselmeer. The nature reserve consists of a central reed marsh (3600 ha) and a well-drained border zone (2000 ha). Soils in the Oostvaardersplassen are clayey and therefore more fertile than in Lauwersmeer. In the border zone, grasslands (900 ha) were created on former arable fields by sowing grass mixtures (for a detailed description see Vulink & van Eerden 1998). Some areas in the border zone were managed by summer grazing with cattle and horses between 1982 and 1993. From 1984 onwards, year-round grazing with Heck cattle (*Bos taurus*, crossbred from primitive races) and konik horses (*Equus ferus*, a primitive breed of horse originating from Poland) has taken place. The area with year-round grazing gradually expanded in accordance with growth of the herds.

Study plots

In Lauwersmeer, common voles are more numerous on high-lying flats (>0.65 m above target level) than on less-elevated flats (<0.65 m

Table 1. Study plot characteristics of the summer-grazed and ungrazed study plots in Lauwersmeer, and the summer-grazed and year-round grazed study plots in Oostvaardersplassen.

	Lauwersmeer		Oostvaardersplassen	
Grazing regime	Summer grazing	Ungrazed	Summer grazing	Year-round grazing
Study period	1983-1995	1989-1993	1991-1993	1989-1995
Size (ha)	33	190	120	288
Stocking rate (animal.ha^{-1})	0-1.1	0	1.4-1.7	0.3-0.9
Annual grazing period	1982-1992; 7 June to 30 Sept. 1993-1995; 1 May to 31 Oct.	n.a.	1 May to 31 Oct.	Year-round

above target level). For example, in October 1983 the density of burrows was 65.ha^{-1} on high-lying flats versus 2 burrows.ha^{-1} on less-elevated flats. The reason for this is that low-lying flats are regularly flooded for several days, whilst only parts of the high-lying flats are occasionally inundated. The study on the relationship between grazing, vegetation structure, vole density and abundance of raptors was carried out on high-lying flats of the nature reserve, some grazed and others ungrazed (figure 1A). For the most important characteristics of the study plots, see table 1.

In Oostvaardersplassen, grasses were sown in the summer-grazed study plot in 1989. The vegetation was mown for a period of two years (twice a year), after which the area was summer grazed at high stocking rates for three years (for characteristics of the study plot, see table 1). In the year-round grazed study plot in Oostvaardersplassen grasses were sown in 1982. In the period 1984 to 1988 the density of Heck cattle and konik horses was relatively low and grassland was also mown; 1989 was the first year of grazing without additional mowing (for characteristics of the study plot, see table 1). The locations of the summer-grazed and year-round grazed study plots in Oostvaardersplassen are shown in figure 1B.

Vegetation development

Long-term vegetation development on flats in Lauwersmeer was derived from vegetation maps (scale 1:5000 or 1:10,000) based on the interpretation of satellite photographs (1972, 1975) and aerial photographs (1980, 1984 and 1989), combined with ground surveys that identified the different zones by using data from quadrates (Küchler & Zonneveld 1988). The vegetation composition in 1995 was based on field visits. The original vegetation maps distinguished between 10 vegetation types. In this study, vegetation types are grouped into three categories: vegetation of halophytic pioneers, dominated by glasswort (*Salicornia* spp.), with herbaceous seepweed (*Suaeda maritime*), lesser sea-spurrey (*Spergularia marina*) and greater sea-spurry (*Spergularia media*); vegetation of short grasses, dominated by creeping bentgrass (*Agrostis stolonifera*) and common saltmarsh-grass (*Puccinellia maritima*), with red fescue (*Festuca rubra*), marsh foxtail (*Alopecurus geniculatus*) and reed; tall vegetation, dominated by reed, with wood small-reed (*Calamagrostis epigejos*) and willows (*Salix* spp.). The scientific nomenclature of the plant species follows van der Meijden (1996).

As succession proceeds vegetation dominated by short grasses gradually changes into tall vegetation, dominated by reed on desalinated former flats in Lauwersmeer as well as on grassland in Oostvaardersplassen. Since there is a significant correlation between reed cover and reed height (Huijser et al. 1996), the latter was used as an index for the vegetation structure in the study plots. Reed height was measured in autumn, using a measuring rod. At each vole-trapping station, five measurements were taken with a total of 100 or 150 readings per study plot. Before 1988, measurements in Lauwersmeer were based on visual estimations (estimated to the nearest 5 cm).

Developments in the vegetation structure of short grasses in Oostvaardersplassen in 1989-93 were described in terms of average sward height. Sward height was measured by using a polystyrene disc (radius 50 cm, weight 320 gram). The disc was gently lowered on to the sward, and the height of the vegetation was read off on the measuring staff in the centre. At each vole trapping station, the height was measured five times. The 100 to 150 readings per study plot were averaged.

Vole densities

Vole densities were measured two or three times a year (March, July and October). Small mammals were caught according to the modified method of Hörnfeldt (1978). In each study plot, trap lines were set up at 30 m intervals and randomly assigned to each of the three trapping periods per year. On each trap line 10 trapping stations were situated at 10 m intervals, with five traps at each trapping station. Traps were controlled once a day, for a period of three days. Consequently, the number of trap nights was 150 per trap line. Usually, two trap lines were set up per study plot. In the summer-grazed study plot in Lauwersmeer, the number of trap lines was three after 1985, in the year-round study plot in Oostvaardersplassen the number of trap lines was four in all years. In all study plots, common voles made up more than 95% of the small mammals caught. The vole index was defined as the number of common voles caught per 100 trap nights.

Raptor densities

Counts of raptors in Lauwersmeer were initiated in 1969, the year of reclamation; counts in Oostvaardersplassen were started in 1982, fifteen years after empoldering was completed. In both study areas, counts were organised about once a month. In Lauwersmeer the raptor species (partly) feeding on common voles are hen harrier (*Circus cyaneus*), buzzard (*Buteo buteo*), rough-legged buzzard (*Buteo lagopus*), kestrel (*Falco tinnunculus*) and short-eared owl (*Asio flammeus*). Hen harrier and rough-legged buzzard are mainly present in winter, while buzzard, kestrel and short-eared owl are present throughout the year. Data of the two most common species (hen harrier and kestrel) were selected for detailed analysis in the study plots. In the study areas, the diets of these two species consisted of more than 90% of common voles (Masman et al. 1988, Dijkstra et al. 1995).

Raptor densities were expressed as bird-days.ha^{-1} per year. The number of bird-days was calculated for each interval between consecutive counts as the average of these two counts multiplied by the interval length in days. These values were added up for each year (months from July till June). For the entire flats in Lauwersmeer all birds were included, whilst in the study plots only flight-hunting birds were selected.

Results

The effects of grazing on vegetation structure

On Lauwersmeer flats with a natural succession of the vegetation, parallel to the process of desalination, halophytic pioneers were gradually replaced by short grasses, which in their turn were replaced by tall vegetation (figure 2A). Flats where summer grazing was initiated were, on average, in an earlier successional stage at the onset of grazing than flats which remained ungrazed (cf. figures 2A and 2B). After the initiation of grazing, the successive decrease in the incidence of short grasses and of halophytic pioneers halted for some years, this was in contrast to a steady

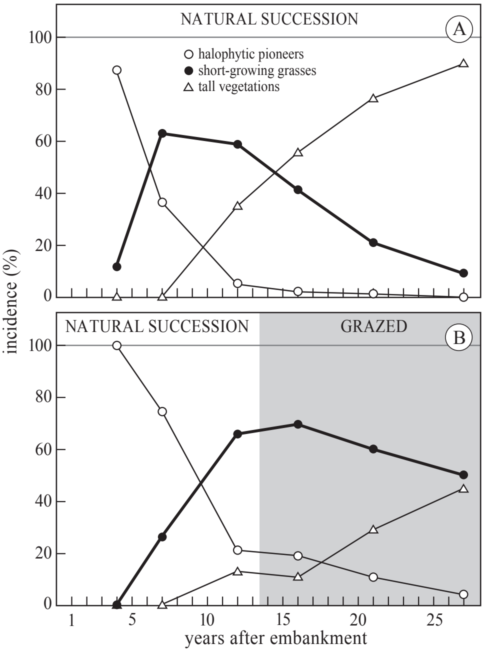

Figure 2. Vegetation succession on former tidal flats in the Lauwersmeer nature reserve (year 1 = 1969): (A) flats with a natural succession of the vegetation (1030 ha), (B) flats with summer grazing (since year 14; 890 ha). The percentage of each vegetation type is presented (= % incidence) for years 4, 7, 12, 16, 21 and 27 after empoldering.

decrease on the ungrazed flats. Thereafter, the proportion of halophytic pioneers and short grasses decreased again, while the proportion of tall vegetation increased. However, even in the last year of the study period, the proportion of tall vegetation was much lower than on ungrazed flats (figures 2A and 2B).

In the summer-grazed study plot in Lauwersmeer, grazing transformed a vegetation of mosaics of reed and short grasses into a large-scale open vegetation. In the first five years of grazing, when the average stocking rate was relatively high (figure 3A1), the average reed height was lower than 0.5 m (figure 3B1). After the fifth year, when the stocking rate was very low, the average reed height sharply increased and gradually levelled off. In the last years of the study period, reed height was only slightly lower than on comparable flats in the ungrazed study plot at Lauwersmeer (1.4 m versus 1.6 m). Gradually, the vegetation in the summer-grazed study plot changed into a closed reed stand, comparable to the ungrazed study plot. On less-elevated flats the vegetation remained open: the average reed height was lower than 0.7 m for the entire period of grazing.

In the summer-grazed study plot in Oostvaardersplassen, grazing at high stocking rates (cf. table 1) resulted in a homogeneous short grassland with a very low reed height (less than 0.1 m) for the entire study period. Average sward height showed only a slight increase in summer (table 2A).

In the year-round grazed study plot in Oostvaardersplassen the average stocking rate strongly increased from about 0.3 to 0.9 animals.ha^{-1} during the study period (table 1). The average stocking rate increased from 0.3 to 1.1 animals.ha^{-1} in summer, but was rather stable in winter (in most years 0.3-0.6 animals.ha^{-1}; figure 3A2). Cattle and horses did not distribute equally over the study plot. In a part of the study plot the animal density was extremely low from the first year of grazing without additional mowing. The area with a reed height higher than 1.5 m therefore increased from 0% in year 1 to 30% in year 7. The gradual increase in stocking rate during the study period resulted in an expansion of heavily grazed grassland (reed height 0-0.5 m) from 40% in year 1 to 60% in year 7. In the same period the percentage of moderately grazed grassland (reed height 0.5-1.5 m) decreased from 60% to 10%. In the last two years of the study period, the area mainly consisted of intensively-grazed grassland (60%) and ungrazed closed reed stands (30%) with rather sharp boundaries between the two. Maximum reed height in the reed stands in Oostvaardersplassen was higher than in Lauwersmeer, due to higher soil fertility. Along the vole-trap lines, situated in the part of the study plot with a moderate grazing intensity, average reed height increased from 0.6 m in the first year of grazing to 0.8-1.0 m

Table 2. A. Average sward height (cm, ±sd) in March, July and October in the summer-grazed and a part of the year-round grazed study plot in Oostvaardersplassen. Measurements were made at vole-trap lines. B. Average vole index (±sd) in March, July and October in the summer-grazed and a part of the year-round grazed study plot in Oostvaardersplassen (*n* refers to the number of trap lines).

A	Sward height	
	Summer grazing	Year-round grazing
March	6.7±7.2 (1992-93; *n*=100)	5.1±8.4 (1991-93; *n*=150)
July	18.8±15.5 (1991-92; *n*=100)	38.6±17.7 (1990-92; *n*=150)
October	6.5±7.4 (1991-93; *n*=150)	19.5±14.1 (1989-93; *n*=250)

B	Vole index	
	Summer grazing	Year-round grazing
March	0.0±0.0 (1992-93; *n*=4)	0.2±0.3 (1992-93; *n*=4)
July	1.0±1.2 (1991-92; *n*=4)	2.5±2.9 (1991-92; *n*=4)
October	0.7±0.6 (1991-93; *n*=6)	12.4±9.7 (1991-93; *n*=6)

in years 3-4, and decreased to about 0.3-0.4 m in years 5-7 (figure 3B2).

There was more seasonal variation in sward height in the year-round grazed study plot than in the summer-grazed study plot (table 2A). In the year-round grazed study plot cattle and horses minimised sward height outside the closed reed stands during the winter, which led to short grassland in early spring. In March, the average sward height was significantly lower than in the summer-grazed study plot (Mann-Whitney U test, $P<0.001$). During summer, sward height in the year-round grazed study plot increased sharply and the average sward height in July and October was significantly higher than in the summer-grazed study plot (Mann-Whitney U test, $P<0.001$ for both periods).

The effect of vegetation structure on vole density

In the summer-grazed study plot in Lauwersmeer, in the first years of grazing, when the stocking rate was relatively high and vegetation was short, the vole index was relatively low (years 2-5: average vole index 2.9±1.5; *n*=9 trap lines; figure 3C1). The vole index increased after the stocking rate was lowered and the reed height increased, and remained high for five consecutive years (years 6-10: average vole index 15.1±7.5; *n*=15 trap lines). In later years, when the reeds were high, the vole index decreased again to a relatively low level (years 11-14: average vole index 3.6±4.6; *n*=12 trap lines). On comparable flats in the ungrazed study plot, the vole index was very low (years 9-12: average vole index 0.3±0.7; *n*=4 trap lines). Considered over the entire study period of fourteen years, high vole indices were restricted to areas with a moderate reed height (between ca. 0.5-1.5 m; figure 4A). The variation in vole density in the summer grazed study plot did not follow the multi-annual cycle found in the border zone of Lauwersmeer Nature Reserve (figure 3C1).

In Oostvaardersplassen the vole index in the year-round grazed study plot showed a larger seasonal variation than in the summer-grazed study plot (table 2B). In the year-round grazed study plot, the vole index increased significantly from March to October (ANOVA: $F_{1,12}=8.02$, $P<0.05$). In the summer-grazed study plot, the vole index was low in all months of trapping and the increase from March to October was not significant. The difference in vole index between the two study plots was only significant for October (Mann-Whitney U test, $P<0.01$). In the year-round

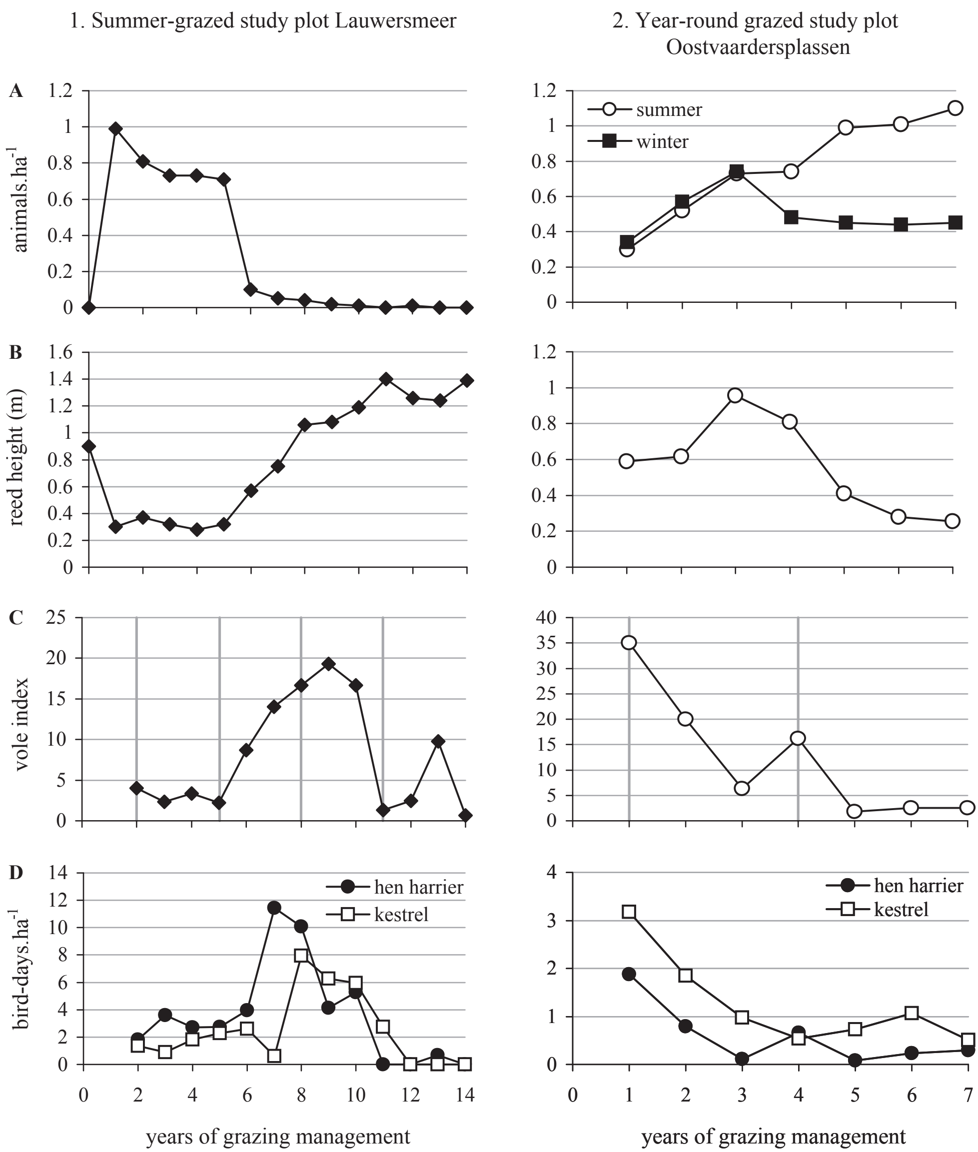

Figure 3. Response of vegetation structure to grazing and consequences for the vole index and raptor density in (1) the summer-grazed study plot in Lauwersmeer (33 ha; grazing by grazing) and (2) the year-round grazed study plot in Oostvaardersplassen (288 ha; grazing by cattle and horses). Data are all expressed as a function of years of grazing management (Lauwersmeer: year 1 = 1982; Oostvaardersplassen year 1 = 1989). (A) Average stocking rate (in year-round grazed study plot in Oostvaardersplassen shown for summer (April-September) and winter (October-March)), (B) Average reed height in October, (C) vole index in October, vertical bars refer to vole peak-years (based on data for October from the well-drained border zone in the Lauwersmeer nature reserve (Dijkstra et al. 1995) and from the borderzone in Oostvaardersplassen (N. Beemster, unpublished data)), and (D) hen harrier and kestrel density, expressed as bird-days.ha^{-1} per year (1 July - 30 June). Only hunting birds were included.

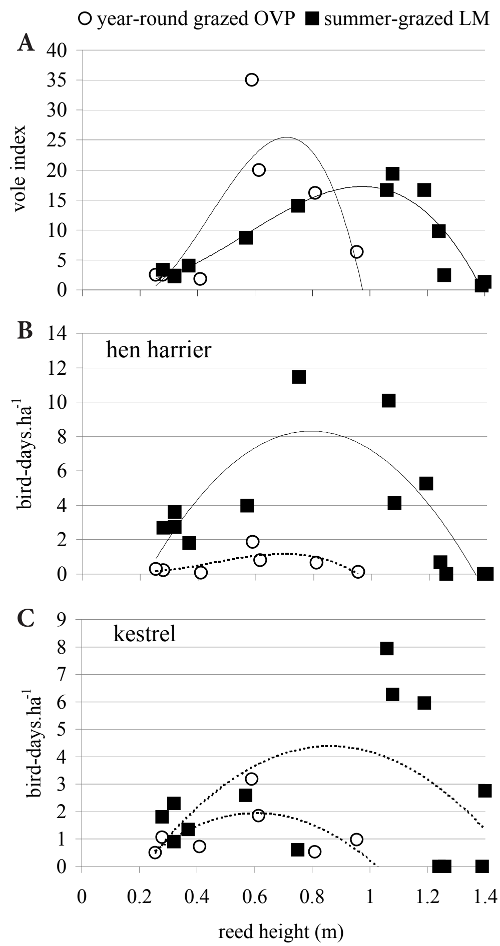

Figure 4. Relation of vole index (A) and raptor density (hen harrier (B), kestrel (C)) to reed height in the summer-grazed study plot in Lauwersmeer (33 ha) and the year-round grazed study plot in Oostvaardersplassen (288 ha). Data are expressed as a function of years of grazing management (summer grazed study plot in Lauwersmeer: year 1 = 1982; year-round grazed study plot in Oostvaardersplassen year 1 = 1989). (A) Vole index in October (summer-grazed study plot in Lauwersmeer: R^2=0.85, P<0.001; year-round grazed study plot in Oostvaardersplassen: R^2=0.69, P<0.05), (B) hen harrier density, expressed as bird-days.ha^{-1} per year (1 July - 30 June). Only hunting birds were selected (summer-grazed study plot in Lauwersmeer: R^2=0.64, P<0.001; year-round grazed study plot in Oostvaardersplassen: R^2=0.54, NS) and (C) kestrel density, expressed as bird-days.ha^{-1} per year (1 July - 30 June). Only hunting birds were selected (summer-grazed study plot in Lauwersmeer: R^2=0.40, NS; year-round grazed study plot in Oostvaardersplassen: R^2=0.21, NS). Insignificant lines are stippled.

grazed study plot, the vole index decreased sharply during the study period (figure 3C2; ANOVA: $F_{1,12}$=23.37, P<0.001). The vole index in the year-round grazed study plot seemed to be somewhat higher in vole peak-years in the borderzone of Oostvaardersplassen in comparison to other years (figure 3C2), however, the differences are not significant because of the small sample sizes. In the summer-grazed study plot, there was no clear change during the three years of study. As with the summer-grazed study plot in Lauwersmeer, high vole indices in the year-round study plot in Oostvaardersplassen were restricted to a moderate reed height (figure 4A). The maximum vole indices in Oostvaardersplassen were higher than in Lauwersmeer.

The effect of vegetation structure and vole density on raptor density

Before grazing was introduced in Lauwersmeer, the numbers of raptors on the flats that were ungrazed throughout, and on flats which were later grazed, were quite similar (figure 5) with the exception of the hen harrier, which showed differences in density over the period 3-13 years after empoldering. These were significantly higher on consistently ungrazed flats (Wilcoxon signed rank test: n=11, P<0.05).

On ungrazed flats with a continuing natural succession of the vegetation, raptor numbers showed a strong increase in the first years

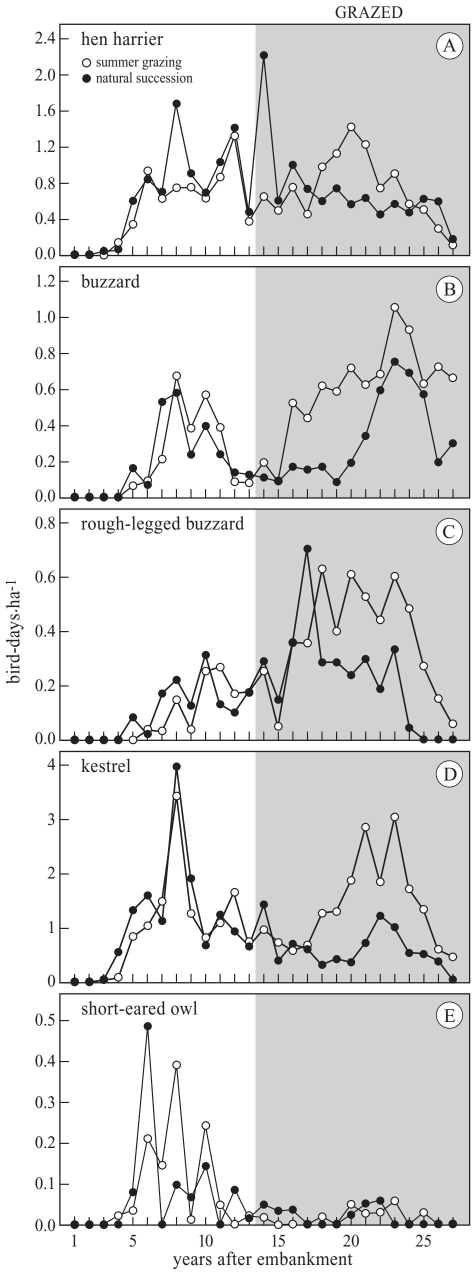

Figure 5. Densities of raptors, depending for a major part of their diet on common voles, on former tidal flats in Lauwersmeer after empoldering (year 1 = 1969); closed dots, flats with a natural succession of the vegetation (1030 ha), open dots, flats with summer grazing (since year 14; 890 ha). (A) hen harrier, (B) buzzard, (C) rough-legged buzzard, (D) kestrel, (E) short-eared owl.

after empoldering, followed by a stabilisation. In the latter half of the study period raptor numbers gradually declined, with some species declining somewhat earlier than others (figure 5). Long-term developments in raptor abundance are related to a change in the extent of the area covered with short grasses (figure 2A) and consequently to a change in food supply of common voles (Dijkstra et al. 1995). Buzzard numbers increased again more than twenty years after empoldering, when a small breeding population became established. These birds mainly find their food outside the ungrazed flats.

At the time grazing was introduced, some species were still numerous (hen harrier and rough-legged buzzard), while others were on the decline (buzzard and kestrel) or had almost disappeared (short-eared owl). After the introduction of grazing, four out of five species showed a temporary increase in number, contrasting with the general decline on the ungrazed flats. The short-eared owl did not respond to this change: the species had almost disappeared before the onset of grazing, and this measure did not result in the return of the species (figure 5E). The following remarks are confined to the four species that responded to the introduction of grazing.

For the entire period of grazing, three out of four species were significantly more abundant on grazed flats than on the consistently ungrazed flats (Wilcoxon signed rank test: n=14 years, buzzard P<0.01, rough-legged buzzard P<0.05 and kestrel P<0.01). However, densities showed a large year-to-year variation. Roughly, three periods can be distinguished. In the first four years of grazing, some species were more abundant on ungrazed flats, while other species were more abundant on grazed flats (the differences are, however, not significant because of the small sample sizes). In the period 5-10 years after the initiation of grazing, raptor densities on grazed flats were relatively high. All the species were now significantly more abundant on grazed flats (Wilcoxon signed rank test: n=6 years, $P<0.05$ for all species). In the last four years of the study period, raptor densities on grazed flats decreased sharply, although the abundance of most species was still higher than on ungrazed flats (but because of the small sample sizes, the differences are not significant).

In the summer-grazed study plot in Lauwersmeer, densities of hen harrier and kestrel were relatively low in the first years after initiating grazing (figure 3D1). Both species were numerous shortly after the stocking rate had been lowered (years 6-10). Later (years 11-14), the densities were again low. Annual variations in the density of hen harrier and kestrel were tested by multiple regression, with average vole index, average reed height + average reed height² as independent variables. Variation in raptor density was significantly correlated with vole index (hen harrier: $R^2=0.49$, $P<0.01$; $n=13$ years; kestrel: $R^2=0.51$, $P<0.01$; $n=13$ years) and reed height + reed height² (hen harrier: $R^2=0.64$, $P<0.01$; $n=13$ years; kestrel: $R^2=0.62$, $P<0.05$; $n=13$ years). The results for the full model were: hen harrier: $R^2=0.67$, $P<0.05$; $n=13$ years; kestrel: $R^2=0.62$, $P<0.05$; $n=13$ years. Hence, both species of raptors showed a clear numerical response to changing vole densities, although maximum raptor densities were found at sub-maximum vole indices, where average reed height was somewhat lower (cf. figures 4B and 4C with figure 4A).

In the ungrazed study plot in Lauwersmeer densities of hen harrier and kestrel were low for the entire study period (four years). The average number of bird-days hunting.ha^{-1} per winter was 0.23 (range 0.14-0.32) for the hen harrier and 0.50 (range 0.14-0.93) for the kestrel.

In the summer-grazed study plot in Oostvaardersplassen, densities of hen harrier and kestrel were also low for the entire study period (three years). The average number of bird-days hunting.ha^{-1} per winter was 0.36 (range 0-0.85) for the hen harrier and 0.59 (range 0.32-0.76) for the kestrel.

In the year-round grazed study plot in Oostvaardersplassen both species were relatively numerous in the first two years of grazing without additional mowing; in later years densities were much lower (figure 3D2). Both species showed a decrease in density during the study period. Annual variations in the density of hen harrier and kestrel were tested by multiple regression, with average vole index and average reed height + average reed height² as independent variables. Variation in raptor density was significantly correlated with vole index (hen harrier: $R^2=0.93$, $P<0.001$; $n=7$ years; kestrel: $R^2=0.75$, $P<0.01$; $n=7$ years). Reed height + reed height² did not have an additional effect. Hence, as was the case in the summer grazed study plot in Lauwersmeer, both species of raptors showed a clear numerical response to changing vole densities. However, in contrast to the summer grazed study plot in Lauwersmeer, no effect of reed height + reed height² could be detected, probably because of the small sample sizes (number of years). In the summer grazed study plot in Lauwersmeer maximum raptor densities were much higher than in the year-round grazed study plot in Oostvaardersplassen, despite lower maximum vole indices.

Discussion

Effects of grazing on vegetation structure

Intense grazing by livestock of reed stands led to a homogeneous short vegetation, as was also found by Vulink et al. (2000). When, after a period of intense grazing or mowing, grazing with a low stocking rate was practised, patches were grazed with a different intensity and a heterogeneous vegetation gradually developed. The development of a patchy vegetation at a low stocking rate has been documented earlier by Bakker et al. (1984) and Bakker (1989). However, after some years, relatively sharp boundaries between short-grazed vegetation and closed reed stands developed and there were almost no areas with a moderate reed height. Annual variation in vegetation structure was more pronounced in the year-round grazed study plot than in the summer-grazed study plots.

Effects of grazing on vole density

In grazed areas, relatively high densities of common voles were restricted to parts with a specific vegetation structure, characterised by a moderate reed height (between ca. 0.5 and 1.5 m). Areas with such a reed height existed only temporarily. Grazing may affect vole abundance in different ways: by trampling, by changing the vegetation structure and/or by influencing the availability of food for voles.

Trampling

Normally, common voles live in burrows in the upper soil and feed above ground. In the case of high densities of ungulates, trampling might well have a serious effect on vole abundance, by destroying burrows and compacting the soil (cf. Heske & Campbell 1991). The risk of trampling is probably higher during wet conditions in winter and therefore higher in year-round grazed areas than in summer-grazed areas. On Lauwersmeer flats, characterised by high water tables in winter and occasionally in summer, common voles are forced to live above the ground for a substantial part of the year. Above-ground, voles live in nests of grass in the vegetation (own observations) and are probably vulnerable to trampling.

Vegetation structure

Herbivores may affect the vegetation structure directly by grazing and trampling, or indirectly by changing the abiotic environment (compacting and thereby salinating the soil, or influencing the level of nutrients (Scherfose 1993)). The vegetation structure is thought to influence vole density (Edge et al. 1995, Peles & Barrett 1996). A uniform, low, vegetation has a negative effect on vole density because it does not offer the voles enough cover. This may have played a role in some of the grazing units. In the summer-grazed study plot in Oostvaardersplassen, vegetation was short-grazed throughout the year and a lack of cover may have been responsible for the low vole densities. In a large part of the year-round grazed study plot, vegetation varied annually between rough grassland in summer and short grassland in winter and early spring. This part of the study plot probably was a favourable habitat for voles in summer, but less so in winter. Flats in Lauwersmeer, characterised by high groundwater tables, undoubtedly need a more structured vegetation for voles to survive in winter than well-drained environments. A lack of cover was probably the main reason for low vole densities in years with a relatively high stocking rate.

In the 14-year study period on former tidal flats in the summer-grazed study plot in Lauwersmeer the vole population did not show the characteristic 3-4 years cycle in density. The absence of this cycle might have been due to large changes in vegetation structure over the years and by high groundwater tables at the flats during winter. Throughout the winter months (October-March) the vole index declined by 95-98% (n=2 winters).

Availability of food

Voles (*Microtus* spp.) often fluctuate greatly in number and food availability plays an important role in limiting their numbers (Hansson 1979). Throughout the year, the diet of the common vole in the study areas mainly consists of the green parts of monocotyledons, with the seeds of monocotyledons and dicotyledons playing a role in summer (Hoogeboom, unpublished data).

Grazing affects food abundance and quality for voles in different ways. Through repeated grazing, grass maturation is prevented and growth stimulated, resulting in a higher food quality. However, the prevention of grass maturation suppresses the production of seeds (McNaughton 1979).

Where grassland in the study areas was intensely grazed, seed production, as indicated by inflorescence abundance, was very low. On Lauwersmeer flats, seed production in creeping bentgrass sharply decreased after the introduction of summer grazing (van Eerden et al. 1997). In grassland with a low grazing pressure, seed production appeared to be relatively high during the stage with a moderate reed height. At this stage common voles were relatively numerous. When grassland changed into a closed reed stand, grass-cover - and hence seed production - sharply decreased. It seems probable that the decrease in vole index at this stage can be explained by a decrease in the availability of food.

Effects of vole density and vegetation structure on raptor density

In the year-round grazed study plot in Oostvaardersplassen and the summer-grazed study plot in Lauwersmeer hen harrier and kestrel showed a clear numerical response to vole abundance. The additional effect of vegetation cover was only detected in the summer grazed study plot in Lauwersmeer and not in the year-round grazed study plot in Oostvaardersplassen, but this was probably due to the small sample sizes (number of years). In Lauwersmeer the highest densities of raptors were found at sub-maximum prey densities, where vegetation cover, as indicated by reed height, was somewhat lower. We conclude that the numerical response of vole-feeding raptors to change in vole availability occurred very rapidly. This holds for the hen harrier, which is mainly a winter visitor, as well as for the kestrel, which is a partial migrant and a common breeding bird in the study areas (Cavé 1968, Masman et al. 1988). These results are in accordance with the results of Korpimäki (1994) and Korpimäki & Norrdahl (1989, 1991), who found that the densities of most avian predators in western Finland tracked vole densities rapidly, without obvious time lags.

Maximum raptor densities in the summer grazed study plot in Lauwersmeer were much higher than in the year-round grazed study plot in Oostvaardersplassen, despite lower maximum vole indices in Lauwersmeer. On Lauwersmeer flats, characterised by high water tables in winter and occasionally in summer, common voles are forced to live above the ground for a substantial part of the year. Above-ground, voles live in nests of grass in the vegetation (own observations) and are probably more vulnerable to predation. Additionally, Lauwersmeer flats have a somewhat more open vegetation, because of a more sandy soil.

Conclusions

In the study areas grazing regimes with relatively low stocking rates created a suitable vegetation structure for common voles and subsequently for vole-feeding raptors, for five years at the most. In man-made wetlands, characterised by a low level of physical perturbation, the relevance of grazing as a management tool for encouraging vole-feeding raptors will greatly depend on the potential of grazing to revert tall vegetation to an earlier successional stage.

Vegetation dominated by reeds can be successfully reverted into a vegetation dominated by short grasses by intense grazing (cf. van Deursen & Drost 1990, Vulink et al. 2000, the present study). Subsequently, the regular occurrence of relatively high densities of common voles and vole-feeding raptors can be achieved by creating a cyclic variation in stocking rate. Years with a relatively low stocking rate should be alternated with some years with a higher one. In the first years after lowering the stocking rate, high densities of common voles and vole-feeding raptors can be expected. In Oostvaardersplassen, in 1997 the area with year-round grazing was extended to the entire border zone and stocking rates in this area gradually increased to about 2.4 animals. ha^{-1} in recent years (in 2011 about 350 Heck cattle, 1150 konik horses and 3300 deer (www.staatsbosbeheer.nl)). The area became short grazed for a large part of the year and densities of hen harrier and kestrel decreased to very low levels (less than 0.1 bird-days.ha^{-1}). In spring 2010 ten small exclosures (10x8 m) were erected in the year-round grazed area of Oostvaardersplassen and vole trapping with life traps in October 2010 showed substantial densities of common voles within the exclosures and no voles in the areas surrounding the exclosures nearby (own observations). In the summer grazed study plot in Lauwersmeer the stocking rates remained very low and the reed stands are nowadays gradually being succeeded by willow species. Since 1995 densities of the hen harrier remained low (less than 2 bird-days.ha^{-1}), and the kestrel became an irregular visitor. Higher stocking rates are needed to revert tall vegetation to an earlier successional stage, before vole feeding raptors are able to profit from the abundance of common voles again.

In addition to vole-feeding raptors, red fox (*Vulpes vulpes*), mustelids (*Mustela nivalis* and *Mustela erminea*) and herons (*Botaurus stellaris*, *Egretta alba* and *Ardea cinerea*) are also able to profit from the abundance of common voles. In years with high stocking rates, raptor densities will be lower, and the area will be more suitable for species that prefer a vegetation of short grasses, such as geese (Vulink et al. 2000, Vulink et al. 2010). If the preservation of vole-feeding raptors is to be a goal of the management of large-scale man-made wetlands, the management should include spatial and temporal variation in grazing pressure, following the pattern of partial migration in natural systems such as the Serengeti (e.g. McNaughton & Banyikwa 1995).

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Samenvatting

De lange termijn-effecten van begrazing met landbouwhuisdieren op de talrijkheid van de veldmuis en de daarvan afhankelijke roofvogels in door de mens gemaakte wetlands in Nederland

Verschillende studies hebben het effect van begrazing door wilde herbivoren of landbouwhuisdieren op de talrijkheid van kleine zoogdieren bestudeerd; sommige studies gaan ook in op het effect van begrazing op de talrijkheid van muizenetende roofvogels. In de meeste studies werd gevonden dat de dichtheid van kleine zoogdieren negatief beïnvloed werd door begrazing, terwijl muizenetende roofvogels meestal een numerieke response lieten

zien op de talrijkheids-index van de veldmuis (*Microtus arvalis*). Echter, de meeste studies waren gebaseerd op gegevens uit een korte onderzoeksperiode (1-4 jaren). Omdat kleine zoogdieren vaak grote aantalsfluctuaties laten zien, is er behoefte aan langjarige studies.

In deze studie analyseren we de lange termijn-effecten (3-27 jaren) van begrazing met landbouwhuisdieren op vegetatieontwikkeling, vegetatiestructuur, talrijkheid van de veldmuis en de daarvan afhankelijke muizenetende roofvogels in recent door de mens gemaakte, grootschalige wetlands in Nederland (Lauwersmeer en Oostvaardersplassen).

De bestudeerde wetlands worden gekenmerkt door een laag niveau van dynamiek, waardoor vroege successiestadia (pioniervegetaties, grazige vegetaties) zonder aanvullend beheer snel vervangen worden door latere successiestadia (riet, duinriet en wilgenstruweel). Begrazing werd in de studiegebieden geïntroduceerd toen de vegetatie nog overwegend bestond uit grazige vegetaties.

Onder invloed van een hoge begrazingsdruk ontstond een homogeen korte grazige vegetatie. Begrazing met een lage begrazingsdruk leidde tot een heterogene vegetatie van grazige vegetaties en riet. Na een aantal jaren ontstonden echter scherpe grenzen tussen kort afgegraasde graslanden en gesloten rietvegetaties. Het intermediaire stadium, gekenmerkt door gematigde riethoogtes (tussen 0,5 en 1,5 m) verdween meer en meer.

Hoge dichtheden van veldmuizen in begraasde gebieden waren beperkt tot gebiedsdelen met gematigde riethoogtes. Gebieden met dergelijke riethoogtes bestonden slechts tijdelijk, waardoor de veldmuisdichtheid na enkele jaren afnam.

Muizenetende roofvogels lieten een numerieke response zien op de veranderende veldmuisdichtheid. Behalve veldmuisdichtheid had ook vegetatiestructuur effect op de roofvogeldichtheid. Maximale roofvogeldichtheden werden gevonden bij een suboptimale veldmuisdichtheid, waar de gemiddelde riethoogte wat lager was.

De relevantie van begrazing als instrument voor het beheer van muizenetende roofvogels in deze wetlands is afhankelijk van de potentie van herbivorie om latere successiestadia weer om te vormen in vroegere stadia. Het regelmatige voorkomen van hoge dichtheden van veldmuizen en de daarvan afhankelijke predatoren kan bereikt worden door het instellen van een cyclisch variërende begrazingsdruk. Jaren met een lage begrazingsdruk zouden afgewisseld moeten worden met enige jaren met een hogere begrazingsdruk.

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