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Grazing as a conservation management tool: Responses of voles to grazer species and densities

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Abstract

Grazing is a widely applied conservation management tool, but the optimal regime for biodiversity conservation is still unknown. The effects of grazers on small mammals are not yet fully understood and mostly restricted to studies which compare grazed with ungrazed areas. We determined the effect of different livestock grazers and densities and a rotation regime, on voles in a conservation area in The Netherlands. We used a 7-year grazing experiment with horse and cattle grazing at two densities namely 0.5 and 1 animal ha^{-1} (equivalent to 0.4 and 0.8 LSU), including a rotation regime i.e. 1 year summer grazing with 1 cattle ha^{-1} followed by 1 ungrazed year. We recorded vole activity signs as a measure for presence (i.e. presence of burrow entrances, droppings, runways and plant clippings) in circular 2 m^2 plots along transects. Low grazer densities, regardless of species, corresponded to higher vole presence. Vole presence tended to be greater with cattle grazing than with horse grazing, but the difference was not significant. The increase in vole presence was greater in the rotation regime than with low or high density cattle grazing. The different vole activity signs provided similar results to each other with the exception of burrow entrances, suggesting that this measure is less accurate in predicting vole presence. Hence, voles clearly responded to the different grazing regimes. Our results have high relevance for conservation, in particular in systems where small mammals contribute to important ecological processes (e.g. bioturbation, seed dispersal) and play a crucial role in the survival of (iconic) higher trophic level taxa such as raptors or mammalian predators. In such systems, conservation management may best implement low-density cattle or rotation grazing.

Keywords: Cattle; Common vole; Horse; *Microtus arvalis*; Nature management; Salt marsh; Vole sign index; Large herbivore grazing

Introduction

Grazing with large herbivores is increasingly applied as a management tool in conservation areas to promote biodiversity (Middleton, Holsten, & Van Diggelen 2006; Van Klink et al. 2016; Lagendijk, Howison, Esselink, Ubels,

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& Smit 2017). Through their foraging activities (i.e. defoliation, trampling and soil compaction) herbivores affect vegetation diversity (i.e. composition and structure), with many effects dependent on grazer species and grazer density (Milchunas, Sala, & Lauenroth 1988; Nolte, Esselink, Smit, & Bakker 2014; Lagendijk et al. 2017). High-density grazing generally results in low plant diversity and homogeneous vegetation structure, while low to intermediate grazing density increases biodiversity of plants and heterogeneity (Milchunas et al. 1988; Bakker, Ritchie, Olff, Milchunas, & Knops 2006; Nolte et al. 2014). The presence of herbivores may also promote both nutrient cycling and plant productivity through the deposition of urine and dung (Tolsma, Ernst, & Verwey, 1987; Rook et al. 2004). In addition, herbivore species also exert different effects on vegetation due to differences in behaviour and physiology (Van der Plas, Howison, Mpanza, Cromsigt, & Olff 2016; Nolte et al. 2017). Thus, the magnitude of grazing effects varies across herbivore species and densities, creating different levels of biodiversity and structural heterogeneity.

Besides the effect on vegetation, the applied grazing regime may also affect organisms of higher trophic levels, such as small mammals (Evans et al. 2015). For example, high density grazing reduces structural vegetation heterogeneity, and thus cover for small mammals, increasing their vulnerability to predation (Steen, Mysterud, & Austrheim 2005; Evans et al. 2006). As a result, habitat becomes less suitable for small mammals, and their direct impacts on the system decline (e.g. soil bioturbation and seed burial; Wijnhoven et al. 2006; Wilkinson, Richards, & Humphreys 2009; Cao et al. 2016). Furthermore, the disappearance of small mammals due to high density grazing may affect higher trophic levels, as small mammals are vital prey for many (meso)predators (Moreno, Villafuerte, Cabezas, & Lombardi 2004). The effects of high-density grazing may therefore have negative effects that cascade to other trophic levels, eventually changing food web diversity and ecosystem functioning (Thébault & Loreau 2003; Finke & Denno 2004).

Here we focus on the effect of grazing on voles (family Cricetidae, subfamily Arvicolinae). Voles are generally sensitive to disturbances, such as fire, floods and agricultural disturbances (Jacob 2003a, 2003b; Morilhat et al. 2007; Plavsic 2014) and known to respond to grazing by large herbivores (Evans et al. 2015; Schieltz & Rubenstein 2016). Burrow formation and persistence may be hampered by large herbivores through soil compaction and trampling (Torre et al. 2007; Ward-Fear, Brown, Pearson, & Shine 2017). As most voles are herbivores, they may have to compete with larger grazers for food (Bakker, Olff, & Gleichman 2009). Grazing reduces vegetation height and thus food resources, in addition to reducing cover for protection against predation and nesting opportunities (Smit et al. 2001; Evans et al. 2006; Bakker et al. 2009). On the other hand, grazing may improve the quality of grasses as regrowth is often more nutritious (McNaughton 1976; Ydenberg & Prins 1981), potentially creating a trade-off between quality and protection.

Most studies focus on the effects of single grazer species, comparing grazed with ungrazed situations without considering different grazing densities (Kaufman, Kaufma, & Clark, 2000; Giuliano & Homyack 2004; Saetnan, Skarpe, & Batzli, 2012, but see for example Evans et al. (2015) for effects of sheep at multiple densities compared with mixed sheep and cattle at equivalent densities and Steen et al. (2005) also for effects with sheep grazing at multiple densities). However, the search for an optimal grazing regime for conservation management in terms of grazer species and densities is still ongoing (Rook et al. 2004; Van Klink et al. 2016; Lagendijk et al. 2017). Here we examine the effect of different grazing species and densities on voles, using a 7-year grazing experiment in a salt marsh ecosystem in The Netherlands. Salt marshes have a long history of livestock grazing (traditionally high densities of 1–2 cattle ha^{-1}; Bakker et al. 1993), but the use of grazing decreased when this became economically less viable in the 20th century (Veeneklaas, Dijkema, Hecker, & Bakker 2013). However, livestock grazing on salt marshes is once again strongly promoted as a conservation management tool to increase biodiversity (Esselink, Zijlstra, Dijkema, & van Diggelen 2000; Ford, Garbutt, Jones, & Jones 2012; Van Klink et al. 2016; Lagendijk et al. 2017). Recently, rotation grazing has been suggested as a potential conservation management tool to enhance and maintain biodiversity, but empirical evidence is scarce (Lagendijk et al. 2017). In this experiment, we focus on the effects of two grazing species (i.e. cattle and horses) at two densities, and compare a rotation regime (cattle summer grazing followed by a year of non-grazing), with the more traditional cattle grazing regimes with yearly summer grazing.

The effects of cattle and horses on vegetation differ, due to their respective foraging behaviour and physiology. Cattle, being ruminants, require less food than horses, which are hindgut fermenters (Duncan, Foose, Gordon, Gakahu, & Lloyd 1990). Horses graze closer to the ground with their teeth, maintaining shorter vegetation as opposed to cattle, which tear grass with their tongue at higher levels and so create greater structural heterogeneity (Menard, Duncan, Fleurance, Georges, & Lila 2002; Nolte et al. 2014). While ruminating cattle remain relatively static on the high marsh, horses are generally more active and mobile, creating greater spatial disturbance on both the low and high marsh (Nolte et al. 2017). Therefore the effect of horses is more pronounced, while densities are the same. These differences in behaviour and feeding between both herbivores are expected to show differential impacts on voles. Lower vole presence is expected at higher densities of large grazers (both cattle and horses), with greater negative impacts caused by horses due to the greater spatial disturbance and reduced structural vegetation heterogeneity.

The aims of this study were threefold. First, we investigated the effects of cattle and horses at two densities (0.5 and 1 animal ha^{-1}) on vole presence over three years using the vole sign index (VSI: i.e. burrow entrances, droppings, runways and plant clippings (Lambin, Petty, & MacKinnon 2000; Wheeler 2008)). Second, we determined if rotation grazing with cattle affects vole presence differently compared with low and high density cattle grazing. Third, as a wide variety of vole signs is used in the scientific literature (both separate and in combination; see for example Lambin et al. 2000; Evans et al. 2006; Wheeler 2008), we evaluated the reliability of different vole signs. This could improve vole sampling efficiency in future research. Specifically, we hypothesised that (a) due to differences in feeding behaviour and disturbance horses suppress vole presence more than cattle, (b) vole presence is lower with higher grazing densities, irrespective of grazer species and (c) voles benefit from rotation grazing because of grazing release.

Materials and methods

Study area

We conducted this study in Noord-Friesland Buitendijks (hereafter NFB: 53°20′N, 05°43′E), a conservation area of 41.8 km^2 in The Netherlands. NFB includes a relatively large mainland salt marsh area (>20 km^2) along the Wadden Sea, a UNESCO world heritage site. The climate is temperate maritime with an average yearly temperature of 11 °C and an average yearly rainfall of 785 mm (2005–2015; FetchClimate n.d.).

The salt marshes of NFB developed during the 20th century from coastal engineering works which used sedimentation fields (Dijkema 1997; de Vlas, Mandema, Nolte, Van Klink, & Esselink 2013). Plant species associated with the high salt marsh are *Agrostis stolonifera*, *Elytrigia atherica*, *Elytrigia repens*, *Festuca rubra* and *Potentilla anserina*. Besides voles, other wildlife includes hares (*Lepus europaeus*), foxes (*Vulpes vulpes*) and roe deer (*Capreolus capreolus*), but only in very low densities (Lagendijk pers. obs.). Predatory birds include common buzzard (*Buteo buteo*), common kestrel (*Falco tinnunculus*), short-eared owl (*Asio flammeus*) and western marsh harrier (*Circus aeruginosus*) (Van Klink et al. 2016).

DNA analyses of droppings indicate a strong presence of common vole (*Microtus arvalis*), as all successfully analysed samples were of this species (Verkuil, Van Guldener, Lagendijk, & Smit 2018). While this does not exclude the possibility that other vole species may be present, focus in this study is on the most abundant species, the common vole.

Experimental set-up

A grazing experiment was initiated in 2010 at two sites (i.e. West and East), which were approximately 2.5 km apart. Each site consisted of experimental fields of 11 ha each, which were roughly rectangular of shape. These fields consisted of approximately $^1/_3$ and $^2/_3$ high marsh in West and East respectively. The remaining area consisted of low marsh. Each site included five different grazing regimes with horses and cattle with 0.5 and 1 animal ha^{-1}, including a rotation regime with 1 cattle ha^{-1}, followed by 1 fallow year (see also Lagendijk et al. 2017). For both livestock species these densities correspond to 0.4 and 0.8 LSU/ha (European Commission n.d.). Grazing regimes were randomly assigned to fields. Grazing took place during the summer season from June to October, after which livestock were removed from the experimental fields. In the rotation regime grazing occurred during the summers of 2011, 2013 and 2015. More replicates of sites were not feasible due to the relatively large size of the experiment. Grazing did not occur in the western replicate from 2000 to 2008. Therefore, to create similar starting conditions both sites were intensively grazed (1.5–3 animals ha^{-1}) in the year prior to the experiment (2009) which resulted in similar conditions with regard to plant species richness and composition (Van Klink et al. 2016; Lagendijk et al. 2017).

Data collection

Voles occur on the high marsh only because of summer water inundations of the low marsh. Due to high floods during winter storms (Nolte, Esselink, Bakker, & Smit 2015), voles are absent from the marsh in winter. Voles thus have to recolonise the high marsh every year from refuge areas, such as the sea wall and the hinterland. In each experimental field, 60 circular plots of 2 m^2 in size, spaced 10–20 m along three to ten transects (depending on the width and length of the high marsh within the experimental field; see also Van Klink et al. 2016) were sampled. Each plot was monitored for vole activity signs which indicated vole presence: burrow entrances (not burrows), droppings, runways and plant clippings (see Villar et al. 2014). Sampling was conducted in October/November (hereafter November) 2013, 2015 and 2016, approximately 2–4 weeks after livestock had been removed from the experiment. Vole presence was scored irrespective of sign, i.e. voles were recorded as present when one of the signs was encountered within the plot. Unfortunately in 2014, the high marsh flooded during a storm before sampling took place. In 2016 we specifically recorded each vole sign separately. This allowed us to test which vole sign would serve best as an indicator (see statistical analyses). During data collection some plots were too wet to sample, and we therefore excluded these from the analyses. The discarded number of plots are indicated per analysis below.

Statistical analyses

All analyses were performed in R 3.4.0 (R Core Team 2017). We used mixed effects logistic regression models (package lmerTest; Kuznetsova, Brockhoff, & Christensen 2016) with a binomial distribution and complementary log-

log link function (cloglog; Zuur, Ieno, Walker, Saveliev, & Smith 2009) for all analyses determining the effects of grazer species and density on vole presence (i.e. measured as vole activity). Density was nested in grazer species as a fixed factor, and experimental field was nested in site as a random factor. 95% confidence intervals were calculated using cloglog-back transformation using 1000 iterations (package aod3; Lesnoff & Lancelot 2013). We first determined the effect of grazer species and density on vole presence (VSI pooled, which are all signs combined) across three years. Here we included year as a separate random factor to account for differences across the years, as voles recolonise the marsh each year due to winter floods. Due to flooding the following number of plots had to be excluded from this analysis; 2013: 24 plots; 2015: 8 plots; 2016: none.

We determined the effect of rotation grazing on vole presence and compared the change in vole presence in rotation with low and high density cattle grazing between 2013 and 2016. We pooled all vole signs per plot in 2016 (i.e. voles were recorded as present when one of the signs was encountered within the plot). As the number of transects differed between 2013 (rotation grazed) and 2016 (rotation ungrazed), we randomly selected 9 transects per regime per year for analysis. We used percentage vole presence per transect and calculated the change in vole presence between 2013 and 2016. Mixed linear effects models (lmerTest package; Kuznetsova et al. 2016) with a Gaussian distribution were used to analyse differences in the change in vole presence between rotation and the other two cattle grazing regimes, by setting the rotation regime as the intercept. Grazing regime was included as a fixed factor, and site as a random factor. Tukey posthoc testing (multcomp package; Hothorn, Bretz, & Westfall 2008) was conducted for the remaining pairwise comparison between low and high density cattle grazing regime. To test whether the observed changes in vole presence were significantly different from zero, thus being genuine changes, we used 1 sample *t*-tests (see also Lagendijk et al. 2017 for this method). Due to flooding the following number of plots had to be excluded from this analysis; 2013: 11 plots; 2016: one.

We then determined the reliability of using different vole signs by examining if grazer species and density affected each vole sign (and combinations thereof) differently using the 2016 data (including all 480 plots). We tested seven signs or combinations thereof, which have been used in other studies (see Appendix A): ‘burrow entrances only’, ‘droppings only’, ‘runways only’, ‘plant clippings only’, ‘plant clippings and droppings’, ‘plant clippings, droppings and runways’, ‘all four signs combined’.

Results

Overall treatment effect 2013–2016

Vole presence differed among regimes: 47–73% of the low-density cattle grazing plots included vole signs (high-density: 26–47%) compared with 18–50% of the low-density horse grazing plots (high-density: 7–34%). Vole presence tended to be greater with cattle grazing than horse grazing, however this was not significant (GLMER: $z = -1.808$, $P = 0.07$; Fig. 1, Table 1). Vole presence was greater in low-density cattle grazing compared with high-density cattle grazing (GLMER: $z = -2.129$, $P = 0.03$), and vole presence tended to be greater in low-density horse grazing compared with high-density, however this was not significant (GLMER: $z = -1.708$, $P = 0.09$).

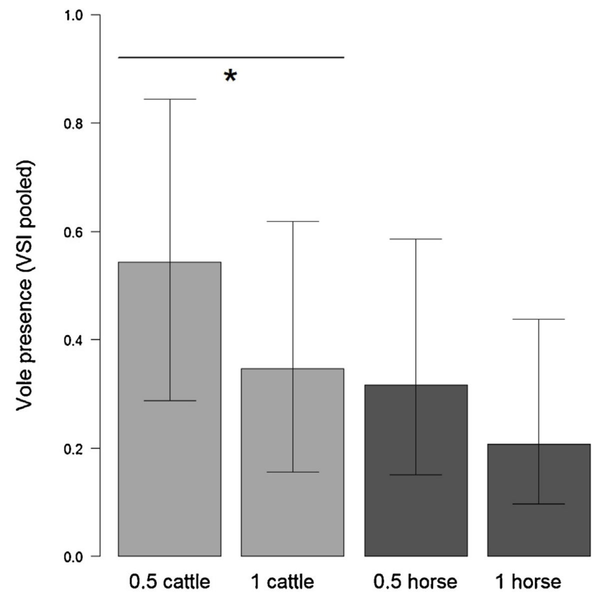

Fig. 1. Mean proportion of vole presence per grazing regime in Noord-Friesland Buitendijks, The Netherlands, across 3 years (November 2013, 2015 and 2016). Vole presence was determined using all vole signs (VSI pooled). Error bars represent 95% confidence intervals based on using grazing regime as a factor; significant differences between grazing densities within species are indicated with an asterisk. $N = 348$ for 0.5 cattle, $N = 360$ for 1 cattle, $N = 353$ for 0.5 horse and $N = 347$ for 1 horse.

The three cattle grazing regimes (including rotation grazing) all showed an increase in vole presence from 2013 to 2016. This increase was affected by grazing regime (LMER: $F_{2,23} = 4.845$, $P = 0.018$; Fig. 2, see Table 2 for absolute values of all transects), with a greater increase in vole presence within the rotation regime than in the low-density (LMER: $P = 0.023$) and high-density (LMER: $P = 0.008$) cattle grazing regimes. The increase in vole presence was similar between the low and high density cattle grazing regimes (Tukey: $P = 0.88$). The change in vole presence was positive in the rotation regime (1 sample *t*-test: $t = 8.0087$, $P \leq 0.0001$; Fig. 2) and under low-density cattle grazing (1 sample *t*-test: $t = 4.6847$, $P \leq 0.01$), but neutral within the high-density cattle regime (1 sample *t*-test: $t = 2.0215$, $P = 0.08$).

Table 1. Summary of model statistics effects of grazer species and densities on vole presence. P-values in bold indicate significant effects. PC = plant clippings, D = droppings, R = runways, BE = burrow entrances, C = cattle.

Vole sign	Year	Grazer species				Density cattle			Density horse			Model	
		Estimate	Test statistic	*P*-value	Positive effect	Estimate	Test statistic	*P*-value	Estimate	Test statistic	P-value	χ^2	*P*-value
PC + D + R + BE	2013 & 2015 & 2016[a]	0.61 ± 0.34	z = −1.81	0.07	–	−0.72 ± 0.34	z = −2.13	**0.03**	−0.60 ± 0.35	z = −1.71	0.09	6.94	0.07
BE	2016	−0.92 ± 0.42	z = −2.17	**0.03**	C	−0.65 ± 0.40	z = −1.62	0.11	−0.18 ± 0.45	z = −0.40	0.69	5.65	0.130
D	2016	−1.09 ± 0.36	z = −3.06	**<0.01**	C	−1.08 ± 0.35	z = −3.05	**<0.01**	−0.38 ± 0.40	z = −0.96	0.33	9.09	**0.028**
R	2016	−0.93 ± 0.44	z = −2.14	**0.03**	C	−0.93 ± 0.44	z = −2.12	**0.03**	−0.49 ± 0.46	z = −1.06	0.29	6.42	0.093
PC	2016	−1.04 ± 0.40	z = −2.62	**<0.01**	C	−0.97 ± 0.40	z = −2.41	**0.02**	−0.67 ± 0.47	z = −1.43	0.15	8.48	**0.037**
PC + D	2016	−1.02 ± 0.37	z = −2.74	**<0.01**	C	−1.02 ± 0.37	z = −2.71	**<0.01**	−0.61 ± 0.42	z = −1.45	0.15	8.86	**0.031**
PC + D + R	2016	−0.93 ± 0.43	z = −2.15	**0.03**	C	−0.95 ± 0.43	z = −2.20	**0.03**	−0.49 ± 0.46	z = −1.06	0.29	6.50	0.090
PC + D + R + BE	2016	−0.93 ± 0.45	z = −2.07	**0.04**	C	−0.96 ± 0.45	z = −2.11	**0.03**	−0.52 ± 0.48	z = −1.08	0.28	6.31	0.100

[a] Effects of grazer species and densities on vole presence across three years.

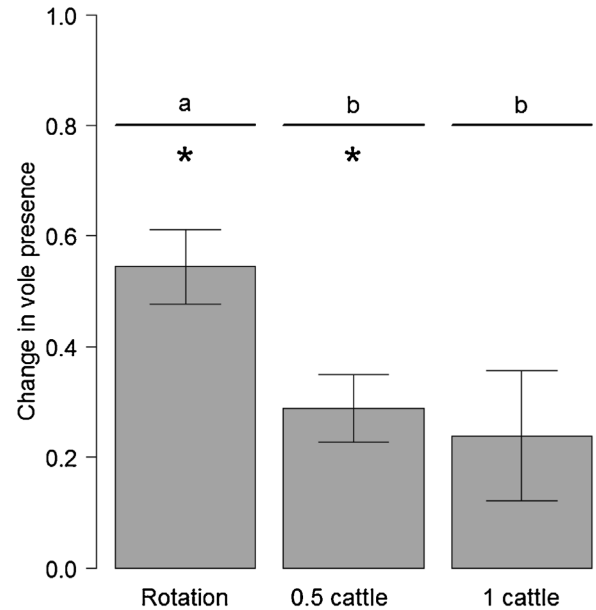

Fig. 2. Three different cattle grazing regimes each showing a proportional increase in vole presence between 2013 and 2016 in Noord-Friesland Buitendijks, The Netherlands. Vole presence was determined using all vole signs (VSI pooled). In 2013 the rotation regime was grazed with 1 cattle ha^{-1}, and in 2016 the rotation regime was ungrazed. Error bars represent mean ± 1SE for each regime; significant differences among regimes are indicated with letters; asterisks indicate changes which were positively different from zero. $N = 9$ transects for each regime each year.

Table 2. Vole presence in three different cattle grazing regimes in Noord-Friesland Buitendijks, The Netherlands, in November 2013 and 2016. Vole presence was determined using all vole signs. Values are number of plots in which vole presence was recorded. The total number of plots sampled per regime and year is given in parentheses.

Grazing regime	Year	
	2013	2016
Rotation	34 (120) grazed	98 (118) ungrazed
0.5 cattle	51 (109)	87 (120)
1 cattle	31 (120)	51 (120)

Testing the reliability of using different vole sign indices in 2016

Most vole signs (separately or combinations thereof) provided similar results to each other, showing an effect of livestock species on vole presence (GLMER: $P \leq 0.039$; Fig. 3, see Table 1 for full model results), with cattle grazing resulting in greater vole presence than horse grazing. Vole presence was generally greater at low-density cattle grazing only (GLMER: $P \leq 0.035$; Fig. 3, Table 1). However, using burrow entrances, cattle density did not affect vole presence (GLMER: $P = 0.11$). Vole presence was not affected by horse density (GLMER: $P \geq 0.15$).

Discussion

Our study focussed on the effect of different grazing regimes (i.e. species and densities) on vole presence. As hypothesised, we found greater vole presence under low density regimes and a tendency for greater vole presence with cattle grazing than horse grazing over three years. Rotation grazing benefits vole presence, at least in the ungrazed year of the rotation cycle. We found very consistent patterns when using different (combinations of) vole signs to determine vole presence, with the exception of burrow entrances, which did not show an effect of cattle grazing density. DNA analyses of the droppings (Verkuil et al. 2018) revealed a strong presence of common vole (*M. arvalis*), which have a widespread distribution within Europe and occur in many different habitat types ranging from natural habitats to more agricultural landscapes (Haynes, Jaarola, & Searle 2003; Jacob, Manson, Barfknecht, & Fredricks 2014). The conservation of common voles on salt marshes is important for ecosystem functioning in terms of processes such as bioturbation and predation, and maintaining biodiversity (Wijnhoven et al. 2006; Torre et al. 2007). In the following, we discuss the potential underlying mechanisms and indicate the relevance of our findings for conservation management.

The effect of grazer species and densities on vole presence

Voles were on average, more abundant in cattle-grazed areas than in horse-grazed areas. Voles were also more abundant in low density grazed areas irrespective of grazer species. Our findings thus corroborate those of Van Klink et al. (2016) from the same study area (based on one year of data) and can be explained by the difference in feeding behaviour between cattle and horses. Cattle create greater structural heterogeneity (Menard et al. 2002; Nolte et al. 2014), providing more opportunities for cover from predators than horses, which maintain large patches of short grass, where high-quality food may be more abundant. In addition, horses are more mobile than cattle and especially at high densities horses cause more disturbance through trampling (Mandema, Tinbergen, Ens, & Bakker 2013). Therefore, cover and thus safety is compromised with horse grazing, and voles seemed to prefer cover above vegetation quality.

Voles clearly preferred low-density grazed areas as also found by e.g. Evans et al. (2015) and Wheeler (2008). These low-density grazed areas are associated with greater structural vegetation heterogeneity (Evans et al. 2006; Nolte et al. 2014), where short patches are utilised by voles for foraging, while tall patches are crucial for cover (Smit et al. 2001; Evans et al. 2006; Bakker et al. 2009). In addition, soil compaction or trampling by livestock affect vole presence, as digging is inhibited and burrows become trampled (Laundré 1989; Hayward, Heske, & Painter 1997; Torre et al. 2007). This effect is reduced in low-density grazing areas, making these areas more suitable for small mammals than high-grazing density areas.

Rotation grazing increases vole presence, at least in the ungrazed year of the rotation cycle. Unfortunately we could only monitor one ungrazed year due to early autumn flooding, which makes it uncertain whether the increase is attributable to direct (less disturbance) or indirect grazing release (response to vegetation). Nevertheless, ungrazed years may provide a window of opportunity for voles to proliferate because there is less disturbance and more vegetation cover, with potential increases in vole populations, and a concomitant increased prey availability for mesopredators and birds (see below). As the change in vole presence over three years was both positive and greater in rotation than in low and high density cattle grazing regimes, rotation grazing is preferred over the more traditional regimes with summer cattle grazing when voles, or other small mammals, are important targets of conservation management.

The use of different vole activity signs

Our results indicated that comparing singular vole signs or combinations thereof, mostly showed similar vole presence patterns in response to grazing with greater vole presence with cattle and low-density grazing with cattle.

Several studies used vole signs, either singular or in combination, to determine vole presence in ecosystems (see references in Appendix A). Out of the sixteen studies examined, only six tested whether the signs showed a relationship with local trapping data (see Appendix A). Five studies selected one sign (plant clippings or droppings) with the strongest correlation, to be used as a density estimate. From the monitored vole signs, burrow entrances are less used as a reliable indicator of vole presence in studies (see Appendix A), as these are affected by many factors such as habitat, season, soil compaction, number of users, risk of predation and trampling (Harper & Batzli 1996; Hayward et al. 1997; Brügger, Nentwig, & Airoldi 2010). Droppings have been used most often in the literature as a proxy for vole density, followed by runways and plant clippings combined with droppings (see Appendix A). These three indices also provided similar results in our study: greater presence with cattle, and at low density grazing with cattle. Hence, runways or droppings seem reliable measures, especially in wetter environments (as plant clippings may quickly decompose); these signs are also relatively quick and easy to detect.

The use of individual vole signs is practical (Wheeler 2008) and less invasive compared to trapping. However, the selection of a reliable vole sign may be dependent on habitat, geographical area, and targeted vole species or community (Hansson 1979). For example, some species deposit most droppings within burrows which will be missed when using only droppings as a vole sign. In addition, to correlate the vole sign data with trapping data also includes an error of miss-

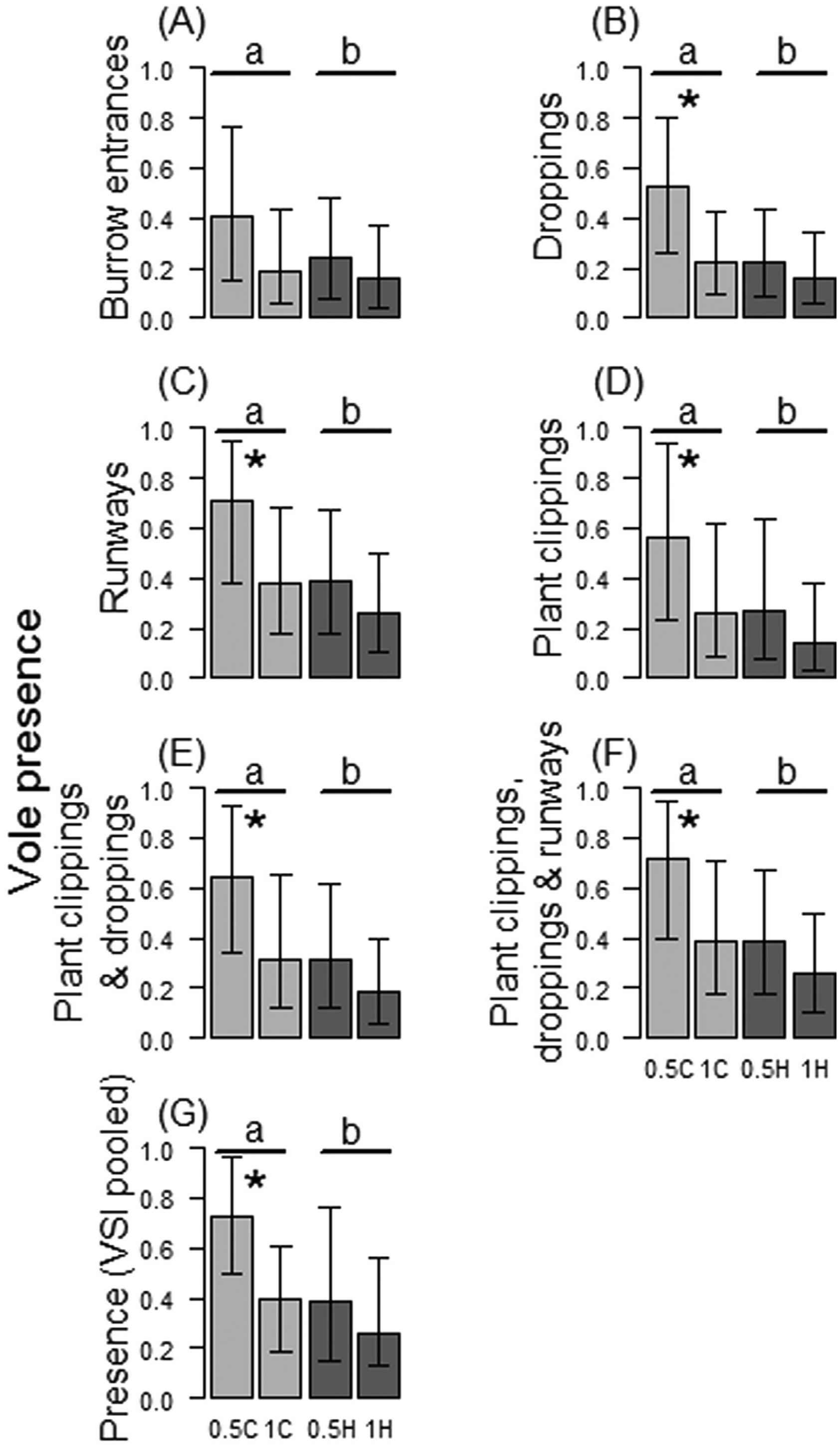

Fig. 3. Mean proportion of vole presence per grazing regime in Noord-Friesland Buitendijks, The Netherlands (November 2016), using different vole signs and combinations thereof: (A) burrow entrances, (B) droppings, (C) runways, (D) plant clippings, (E) plant clippings and droppings, (F) plant clippings, droppings and runways and (G) plant clippings, droppings, runways and burrow entrances combined (VSI pooled). Error bars represent 95% confidence intervals based on using grazing regime as a factor; significant differences between livestock species are indicated with letters; significant differences between grazer densities are indicated with asterisks. $N = 120$ for each grazing regime. 0.5C = 0.5 cattle ha^{-1}, 1.0C = 1.0 cattle ha^{-1}, 0.5H = 0.5 horse ha^{-1}, 1.0H = 1.0 horse ha^{-1}.

ing the trap-shy species or individuals in areas with several species (Wijnhoven, Van Der Velde, Leuven, & Smits 2005). Species confirmation is often not possible using vole signs, but DNA analyses of faecal samples can provide certainty about which small mammal species are present (Verkuil et al. 2018). Thus, as an additional non-invasive method, DNA analyses complement the information acquired from assessing individual vole signs.

Trophic cascades: vegetation, predation by foxes, owls and raptors

Grazing affects vegetation (e.g. height, species composition; Nolte et al. 2014; Lagendijk et al. 2017) with effects cascading to other trophic levels, such as small mammals and predators (Wheeler 2008; Evans et al. 2015). The presence of voles benefits other taxa. For example, reptiles, invertebrates and other small mammals may use the burrow systems as refugia (Jacob et al. 2014; Ward-Fear et al. 2017). Furthermore, voles themselves are an important food item for raptors, owls and foxes (Evans et al. 2015; Ward-Fear et al. 2017). The Wadden Sea coastal zone is an important breeding area for raptors such as short-eared owls and (marsh and hen) harriers (Bos, Engelmoer, Feddema, & Koffijberg 2015; Koffijberg et al. 2015), which are dependent on voles for prey (Kleefstra, Barkema, Venema, & Spijkstra-Scholten 2015). These raptors will thus be negatively affected by high density grazing (Johnson & Horn 2008; Wheeler 2008), due to lower prey availability and increased trampling risk of ground nests. Raptor and fox activity has been observed in our experimental fields, and remains of small mammals have been found on the field fences (Lagendijk pers. obs.). This indicates that predatory birds are successful in hunting small mammals in our study area, although no effect of grazing regime on raptors was found in an earlier study (Van Klink et al. 2016), which may be attributable to the spatial scale of the experiment; raptors use much larger areas for hunting than the experimental fields of 11 ha (Village 1987).

To properly predict the suitability of an area for predators that depend on voles requires the inclusion of factors driving predation success, such as prey density and detectability (Ontiveros, Pleguezuelos, & Caro 2005; Evans et al. 2006), as well as the dietary needs of the predator (Lambin et al. 2000). Prey detection and accessibility by predators is affected by vegetation. While voles may be more abundant in ungrazed (Evans et al. 2015) or low-density grazed areas, the accessibility of the voles to predators may actually be reduced in such tall and dense vegetation (Ontiveros et al. 2005). We also showed greater vole presence in low density grazed areas, but cannot make predictions regarding vole densities as vole signs were not calibrated with trapping data for density estimations. Also the quantification of predation success in our study area requires more study. How different grazing regimes or specific grazer species affect the success rate of vole predation by predatory birds remains unclear. For example, Johnson and Horn (2008) found a higher attack rate in ungrazed areas (where small mammal abundance is greater; Evans et al. (2015), Lagendijk pers. obs.), but similar success rates between ungrazed and grazed areas. Maintaining cover with moderate structural vegetation heterogeneity associated with low density grazing (Nolte et al. 2014) and a diverse landscape thus seems imperative to both predator and prey, and thus to biodiversity.

We showed that grazing regimes with different species and densities have differential effects on vole presence in salt marshes. Vole presence can thus easily be manipulated through the implementation of specific grazing regimes. This is particularly relevant when small mammals play a crucial role in the survival of (iconic) specialist predators (Moreno et al. 2004). Low density cattle grazing or rotation regimes are thus constructive in ecosystems where small mammals, such as voles, promote ecosystem processes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2018.10.007.

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