

1 **Effects of grazing management on biodiversity across trophic levels – The**
2 **importance of livestock species and stocking density in salt marshes**

3
4 Roel van Klink^{*1,2§}, Stefanie Nolte^{1,3§}, Freek S. Mandema¹, D. D. Georgette Lagendijk^{1,4},
5 Michiel F. WallisDeVries^{5,6}, Jan P. Bakker¹, Peter Esselink^{1,7}, Christian Smit¹

6 *Corresponding author, Tel.: ++41 768233056, email: roel.vanklink@gmail.com

7

8 §The first two authors contributed equally to this work

9 ¹ Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences,
10 University of Groningen, P.O. Box 11103, 9700 CC, Groningen, The Netherlands

11 ² Present address: Conservation Biology Group, Institute of Ecology and Evolution,
12 University of Bern, Balzerstrasse 6, 3012, Bern, Switzerland

13 ³ Present address: Applied Plant Ecology, Biocenter Klein Flottbek, University of Hamburg,
14 Ohnhorststr. 18, 22609 Hamburg, Germany

15 ⁴ School of Life Sciences, University of KwaZulu-Natal, Westville Campus, Private Bag
16 X54001, Durban 4000, South Africa

17 ⁵ De Vlinderstichting/Dutch Butterfly Conservation, P.O.Box 506, 6700 AM, Wageningen,
18 The Netherlands

19 ⁶ Laboratory of Entomology, Wageningen University, P.O.Box 16, 6700 AA, Wageningen,
20 The Netherlands

21 ⁷ PUCCIMAR, Boermarke 35, 9481 HD, Vries, The Netherlands

22

23 Keywords: Cattle, horses, plants, birds, butterflies, flower-visiting insects, vegetation,

24 wetland,

25

26 Highlights:

- 27 • Optimal grazing management on salt marshes for plants and animals is unclear
- 28 • A grazing experiment with cattle and horses at two stocking densities was set up
- 29 • Plants, pollinators, birds and voles all responded idiosyncratically
- 30 • Choice of livestock species is of less importance than stocking density
- 31 • We recommend concurrent application of different grazing regimes

32

33 **Summary**

34 European coastal salt marshes are important for the conservation of numerous species of
35 specialist plants, invertebrates, breeding and migratory birds. When these marshes are
36 managed for nature conservation purposes, livestock grazing is often used to counter the
37 dominance of the tall grass *Elytrigia atherica*, and the subsequent decline in plant species
38 richness. However, it remains unclear what is the optimal choice of livestock species and
39 stocking density to benefit biodiversity of various trophic levels.

40 To fill this knowledge gap, we set up a triplicate, full factorial grazing experiment with cattle
41 and horse grazing at low and high stocking densities (0.5 or 1 animal ha⁻¹) at the mainland
42 coast of the Dutch Wadden Sea. Here, we present the results after 4 years and integrate these
43 with previously published results from the same experiment to assess effects of livestock
44 grazing on various trophic groups.

45 Stocking density affected almost all measured variables: high stocking densities favoured
46 plant species richness and suppression of *E. atherica*, whereas low stocking densities
47 favoured abundances of voles, pollinators and flowers. Densities of different functional
48 groups of birds showed no significant response to the regimes, but tended to be somewhat
49 higher under 0.5 horse and 1 cattle ha⁻¹.

50 Choice of livestock species had fewer and smaller effects than stocking density. Horse
51 grazing was detrimental to vole density, and showed an interactive effect with stocking
52 density for Asteraceae flower abundance. Multidiversity, a synthetic whole-ecosystem
53 biodiversity measure, did not differ among regimes. These results are discussed in the light of
54 other results from the same experiment.

55 Because of these contrasting effects on different trophic groups, we advise concurrent
56 application of different grazing regimes within a spatial mosaic, with the inclusion of long-
57 term abandonment. High density horse grazing, however, is detrimental to biodiversity.

58 **1. Introduction**

59 To maintain high plant species richness and to counter the encroachment of tall,
60 competitive plant species, livestock grazing is a frequently used management tool in
61 European semi-natural grasslands. It is becoming increasingly clear, however, that not all
62 trophic groups respond equally positively to this type of management. Grazing is often
63 beneficial to plant species richness (Olf and Ritchie, 1998), but detrimental to species
64 richness of many arthropod groups (Foster et al., 2014; van Klink et al., 2015), molluscs
65 (Boschi and Baur, 2007) and small mammals (e.g. Villar et al., 2014), while mixed effects are
66 reported for species richness of meadow birds (e.g. Atkinson et al., 2005; WallisDeVries et
67 al., 2007). Holistic management approaches, designed to benefit various trophic and
68 taxonomic groups are therefore urgently needed (WallisDeVries et al., 2002).

69 Coastal salt marshes in north-western Europe represent a case in point. These
70 ecosystems are of high conservation interest because of the numerous plant- and invertebrate
71 species confined to this specific habitat, some of which are endemic to the region, and
72 therefore protected under the EU Habitats Directive (Doody, 2008; EC Habitats Directive,
73 1992). Additionally, salt marshes are of high importance to large numbers of breeding and
74 migratory birds, among which several species classified as vulnerable on the Dutch, German
75 and British red lists, such as Redshank (*Tringa totanus*) and Oystercatcher (*Haematopus*
76 *ostralegus*).

77 Mainland salt marshes have been used for livestock grazing for millennia, because of
78 their productive clay soils. However, over the past 50 years many marshes fell to
79 abandonment as livestock grazing became less profitable (Bakker et al., 2002). Abandonment
80 usually results in a dominance of competitive plant species such as the tall-statured Sea couch
81 grass (*Elytrigia atherica*) on higher salt marshes, Sea purslane (*Atriplex portulacoides*) on
82 lower marshes (Bos et al., 2002; Wanner et al., 2014), or Common reed (*Phragmites*
83 *australis*) on brackish marshes (Esselink et al., 2000). Such encroachment endangers

84 populations of short-statured plants (Bos et al., 2002) and some invertebrate species (van
85 Klink et al., 2013), and changes nesting and foraging conditions for birds, which are key
86 issues according to the EU Habitats Directive. Livestock grazing can maintain species-rich
87 plant communities and prevent, or decrease, the dominance of *E. atherica* (Bakker et al.,
88 2002), but will under high stocking densities create a homogeneous short-grazed vegetation
89 structure, which is unfavourable to many species of invertebrates (Pétillon et al., 2007;
90 Rickert et al., 2012) and breeding birds (Mandema et al., 2015; Norris et al., 1998). Therefore
91 it remains unclear, how grazing can be implemented best with respect to stocking density and
92 livestock species to benefit various trophic and taxonomic groups, and to prevent the
93 dominance of competitive plant species, thus promoting biodiversity. To fill this knowledge
94 gap and to optimise salt-marsh conservation management, we installed a four-year grazing
95 experiment on a mainland salt marsh at the Dutch Wadden Sea coast, using cattle and horse
96 grazing at 0.5 and 1 animal per hectare, each. Here, we present new findings on plant, bird,
97 pollinator and vole communities at the field scale, and compare these to previously reported
98 results on vegetation structural complexity, nest survival, staging geese, survival of flowering
99 forb *Aster tripolium*, and sediment accretion.

100 On salt marshes, the most important mechanisms by which livestock grazing affects
101 biodiversity are biomass removal (defoliation) and trampling (Bakker et al., 1985). The
102 impacts of both these processes increase with stocking density, but can also be expected to
103 differ between livestock species due to differences in digestive system and mouth
104 morphology. Horses, as hind-gut fermenters, have higher food intake rates than ruminants of
105 the same size, and are able to digest more low-quality, high-fibrous grasses (Illius and
106 Gordon, 1992; Menard et al., 2002). Additionally, horses can forage closer to the ground and
107 are more active than cattle (Menard et al., 2002). Therefore, we hypothesise that the effects of
108 horse grazing on the system will be greater than those of the more placid cattle.

109 The direct effects of livestock on their habitat can be expected to cascade up the food-
110 chain (Evans et al., 2015). We hypothesise that plant species richness benefits from higher
111 stocking densities as grazing opens the canopy and decreases light competition (Borer et al.,
112 2014). Such a short and open vegetation canopy will be beneficial for spring staging geese, as
113 these small herbivores require high-quality forage (Mandema et al., 2014b). By contrast,
114 protective cover for voles will decrease under high stocking densities (Villar et al., 2014),
115 hence, voles are hypothesised to be more abundant under low stocking densities. Also
116 pollinators can be expected to be more abundant under low stocking densities, as their most
117 important floral resource, *Aster tripolium*, is sensitive to grazing (Kiehl et al., 1996; Nolte et
118 al., 2013). The thus expected high abundance of invertebrates and seeds under low stocking
119 densities should in turn be attractive for breeding and wintering birds foraging on the salt
120 marsh. By contrast, birds that forage on the intertidal flats, but roost on the salt marsh, are
121 hypothesised to utilise the more heavily grazed marsh, because of the higher detectability of
122 predators. Raptors and owls, in turn, can thus be expected to forage under low stocking
123 densities, where their vertebrate prey, such as voles, are most abundant (Baker and Brooks,
124 1981). Our aim was therefore to determine which grazing regime (i.e. species and stocking
125 density) is most optimal in terms of biodiversity.

126

127

128 **2. Material and Methods**

129 *2.1 Study area and experimental design*

130 We established a triplicate grazing experiment in 2010 (year 1) on the salt marshes of
131 Noord-Friesland Buitendijks at the mainland coast of the Dutch Wadden Sea (N53°20',
132 E5°43'). The site is a typical example of a Western European mainland salt marsh, which has

133 established on marine clay deposits (up to 80% clay and silt) within man-made sedimentation
134 fields. The average yearly temperature is 11 °C, with an average yearly rainfall of 785 mm
135 (2005-2015; Royal Dutch Meteorological Institute). The study area is characterised by a
136 distinct vegetation zonation from the frequently flooded pioneer zone, over the low marsh, to
137 the higher elevated and seldom flooded high marsh, and is managed for nature-conservation
138 purposes. The historic management of the experimental area was cattle grazing at relatively
139 high densities (Esselink et al., 2009), with several rotations per year. This management type
140 was continued until the start of the experiment in the central and eastern replicates, but in the
141 western replicate grazing was ceased for eight years prior to 2009. In 2009 (year 0), high-
142 density grazing was installed in the western replicate for one season to enhance comparability
143 with the other two replicates at the start of the experiment in 2010.

144 Each replicate was subdivided into five paddocks of approximately 11 ha (Fig. 1), in
145 each of which a different summer grazing regime (June-October) was installed: horse and
146 cattle grazing at two stocking densities each (0.5 and 1 animal ha⁻¹), and a rotational grazing
147 regime (one fallow year followed by 1 cattle ha⁻¹; not considered here due to limited data).
148 Livestock were obtained from local farmers. Cattle were all 2-3 year old non-lactating cows
149 (breed: Holstein-Friesian; ca. 600 kg). The horse herds consisted of animals of both sexes, all
150 above 2 years of age (breed: Dutch Warmblood (KWPN); ca. 700 kg). The regimes were
151 randomly assigned to the paddocks, with the restriction that horse grazing was not applied to
152 two adjacent paddocks to avoid interactions between the two herds. Ungrazed paddocks were
153 not included in the experiment, since the effects of grazing cessation on various biotic groups
154 have been studied extensively elsewhere (e.g. Ford et al., 2013; Irmiler and Heydemann,
155 1986; Kiehl et al., 1996; Wanner et al., 2014). In addition, the ecological changes are most
156 pronounced under such a severe management regime, making it an ineffective control. The

157 high density cattle grazing regime thus best reflects the historic management, and can be
158 regarded as control regime.

159 2.2 Data collection

160 2.2.1 Vegetation

161 The spread of *E. atherica* was assessed by vegetation mapping of each paddock in
162 year 0 and 4, based on aerial photographs. Vegetation types were identified according to the
163 Trilateral Monitoring and Assessment Program (TMAP) vegetation classification (Esselink et
164 al., 2009). The maps were digitised and the area of the *E. atherica* vegetation type (>50%
165 cover of *E. atherica*) was calculated using ArcGIS 10.1. We analysed change in the
166 percentage cover of the *E. atherica*-type per paddock between year 0 and year 4.

167 To study changes in plant species richness, permanent plots (PPs, 4 m x 4 m) were
168 installed in year 0. In each paddock eight PPs were placed, stratified equally over the high
169 and the low marsh (Appendix A). PPs within the same block and marsh zone were positioned
170 on a comparable surface elevation along the gradient, within homogeneous vegetation. The
171 minimum distance between PPs and the fence was ten metres. Each year in late August /
172 early September (year 0-4) the vegetation height was measured to the nearest cm at five
173 random locations within each PP using a Styrofoam drop disc (diameter 25 cm, weight 75 g),
174 and all plant species were recorded. Nomenclature of plant species follows Van der Meijden
175 (2005). We analysed mean vegetation height and plant species richness per PP.

176 2.2.2 Flowers and pollinators

177 Pollinators were chosen to represent invertebrates because they play an important role
178 in plant reproduction, and are easily visually assessed at the scale of our experimental
179 paddocks. This contrasts to other invertebrate groups, which are typically trapped at small
180 scales and are difficult to identify. Because very few pollinator species can reproduce on the
181 salt marsh, all individuals should be considered immigrants in the system.

182 Pollinator and flower abundance were assessed three times per year (early June, mid-
183 July and around September 1st of years 2-4), along 500 m long transects laid out diagonally
184 through each paddock (Appendix A). Using a modified version of the Pollard walk (Pollard,
185 1977) all Macrolepidoptera (butterflies and day-active moths) were counted and identified by
186 walking along each transect at moderate speed and counting all specimens within a 5 m x 5 m
187 x 5 m imaginary cube. Every 25 m, for one minute all pollinators (Macrolepidoptera to
188 species level, bumblebees, honeybees and hoverflies at family level) in a 2 m x 2 m sub-plot
189 were counted, and flower abundance of all forb species was estimated on a simple scale: 1: 1-
190 10; 2: 10-50; 3: 50-100, 4: >100 (see WallisDeVries et al., 2012). For analysis, we used total
191 pollinator abundance per paddock per year. Total flower abundance per species per paddock
192 was calculated by summing the minimum value of its abundance class over all sub-plots.
193 Flower abundance can thus be seen as a lower boundary estimate.

194 2.2.3 Birds

195 From April of year 1 to December of year 4, bird censuses were conducted biweekly
196 at sunrise along a permanent transect in each paddock (Appendix A). All birds sighted (i.e. on
197 the ground, flying up or landing), except overflying birds, were identified and their locations
198 marked on a map, which was later digitised.

199 All observed birds were classified into one of five functional groups, based on
200 whether they use the salt marsh for foraging or not, viz.: (1) foraging (PB-forag) and (2) non-
201 foraging potential breeding birds (PB-nonforag), (3) foraging (NB-forag) and (4) non-
202 foraging non-breeding birds (NB-nonforag), and (5) raptors (including owls). The functional
203 group of PB was only used for observations in the breeding season (April 1st - July 31st) for
204 those species known to breed at the site according to Bos et al. (2015), excluding raptors (no
205 raptors bred within the experimental area during the research period). Outside this period,
206 these species were classified as NB. The analyses were also performed for Meadow Pipits

207 (*Anthus pratensis*), the only species observed in each paddock each year, and all bird species
208 combined. The complete list of all bird species, their classification and their total abundances
209 can be found in Appendix B.

210 2.2.4 Voles

211 Voles (predominantly *Microtus arvalis* and to a lesser degree *M. agrestis*) occur on
212 the high marsh and only during the summer season (C. Smit unpublished data). This is due to
213 frequent inundations of the low marsh, and floods during winter storms. Therefore, the effects
214 of grazing on voles were only assessed on the high marsh. In October of year 4, 60 circular
215 plots of 2 m², spaced 10-20 m apart along three to ten transects depending on the width and
216 length of the high marsh within the paddock, were surveyed once within each paddock
217 (Appendix A, Fig. A1). Each plot was scanned for signs indicating the presence of voles:
218 runways, fresh plant fragments, or faecal pellets (see Villar et al., 2014). For analysis, the
219 proportion of subplots with vole presence was calculated per paddock (N = 3 replicates per
220 treatment). In the eastern replicate, 24 plots (10%) were excluded from analysis, due to
221 flooding at the time of sampling.

222 2.3 Statistical analysis

223 All analyses were done in R 3.2.5 (R Core Team, 2016). For all analyses of species
224 richness, presence, abundance, and plant vegetation height, we used generalised linear mixed
225 models (GLMM) with backward model selection based on Akaike's Information Criterion
226 (AIC) using the lme4 package (Bates *et al.* 2014). As explanatory variables in all models we
227 used livestock species (cattle or horse), stocking density (0.5 or 1 animal ha⁻¹) and their
228 interaction, and as random factors we included a nested design of paddock nested in block.
229 Year was included as a separate random factor (except for voles, which were only assessed in
230 year 4) to account for yearly differences, and possible non-linear cumulative effects. For the
231 analyses of treatment effects, data from year 1-4 were used. We checked for differences in

232 plant diversity among paddocks before the experiment started (year 0), and found no
233 differences ($P = 0.31$). Final model significance was compared to the null-model of no
234 explanatory variables. Multiple comparisons between all four regimes were done post-hoc by
235 running the GLMM with the same random structure, but with 'regime' (factorial, four levels)
236 as explanatory variable. On this model Tukey's HSD test was performed to test specifically
237 for differences among the four grazing regimes, using the Multcomp library (Hothorn et al.,
238 2008).

239 For the change in cover of *E. atherica* and vegetation height (log transformed to
240 correct for heteroscedasticity) the error structure followed a normal distribution. The models
241 for plant species richness, flower abundance, pollinator abundance, and bird species richness
242 and abundance had a Poisson error structure, and the presence of voles was analysed using
243 the binomial distribution. Overdispersion of the residuals in the Poisson and binomial models
244 was dealt with using individual level random effects and tested for significance against the
245 model not accounting for overdispersion for improvement of fit.

246 For the analysis of plant species richness and vegetation height per PP, we included
247 marsh zone (high or low) and its interactive effects as additional fixed variable, and PP in the
248 random structure (PP nested in paddock nested in block). When marsh zone showed a
249 significant interaction with any other variable, the dataset was split and analysed separately
250 per marsh zone.

251 The relationship between the abundances of pollinators and floral resources was
252 assessed using linear models with log-transformed pollinator abundance as dependent
253 variable, and flower abundance and year (factorial) as explanatory variables. Log
254 transformation provided a better fit of the data than a Poisson error distribution. Four
255 different classes of flowers were assessed, viz.: (1) total flower abundance, (2) flower

256 abundance of *A. tripolium* (i.e. the most abundant Asteraceae species), (3) abundance of all
257 Asteraceae flowers (*A. tripolium*, *Cirsium arvense*, *Sonchus arvensis* and *Leontodon*
258 *autumnalis*), (4) flowers of other forbs (mostly *Potentilla anserina*, *Glaux maritima* and
259 *Spergularia* spp.).

260 We used distance sampling (Thomas et al., 2009) to estimate total density of all bird
261 functional groups within the experimental paddocks. In order not to inflate density estimates
262 due to flocking behaviour, only incidence data were used to obtain estimates. From the
263 mapped positions, perpendicular distances to the transect line were calculated using ArcGIS
264 10.1, after which density per 11 ha paddock was estimated using the Distance package for R
265 (Miller, 2015). Model selection of the appropriate distance function (half-normal or hazard
266 rate) and covariates (livestock species, stocking density, replicate or paddock) was based on
267 AIC. For three out of five functional groups (PB-nonforag, NB-nonforag and Raptors), no
268 individuals were seen in some paddocks in some years, therefore estimates were obtained by
269 pooling all four years per paddock for these groups. The estimated densities were then
270 entered into mixed effects models with the structure described above. Probability
271 distributions and model parameters can be found in Appendix C.

272 To obtain a synthetic number of biodiversity per year for each paddock, we calculated
273 multidiversity (Allan et al., 2014) over plants, butterflies and the five functional bird groups
274 using their total species richness per paddock per year. This is a novel diversity metric
275 covering multiple taxonomic or functional groups. For each group, the proportion of species
276 relative to the maximum observed number of species was calculated for each paddock, after
277 which these proportions were averaged over all groups.

278 **3 Results**

279 *3.1 Vegetation*

280 The cover of the *E. atherica* vegetation type tended to be lower under high stocking
281 densities ($P = 0.08$; Table 1), but differed strongly among replicates. In the eastern replicate
282 the *E. atherica* vegetation type was not present in three paddocks after four years. By
283 contrast, in the western replicate, and to a lesser extent in the central replicate, the *E. atherica*
284 type was already widespread at the start of the experiment.

285 In total 38 plant species were recorded, among which 18 halophytes (Appendix B).
286 On both the high and the low marsh, mean vegetation height was higher under low stocking
287 densities, but was not affected by livestock species (Table 1, Fig. 2a,c). Plant species richness
288 differed among the regimes on the high marsh only, and was higher under high stocking
289 densities (Table 1, Fig. 2b,d).

290 *3.2 Flowers and pollinators*

291 Over years 2-4, we counted 15 flowering plant species and 11 butterfly species over a
292 total of 598 individual butterflies. Additionally, 1874 hoverflies, 143 bumblebees and 42
293 honey bees were counted (Appendix B). Total flower abundance was lower under high
294 stocking densities, but did not differ between livestock species (Table 1). Abundance of
295 Asteraceae flowers did not differ between stocking densities under cattle grazing, but was
296 under horse grazing highest under low density grazing (Table 1, Fig. 3a). Flower abundance
297 of the most abundant Asteraceae species, *A. tripolium*, was significantly higher under low
298 stocking densities than under high densities (Table 1). Abundance of non-Asteraceae flowers
299 was not affected by the regimes (Table 1).

300 Pollinator abundance was highest under low stocking densities (Table 1). However,
301 post hoc comparisons among the four specific treatments showed only effects of stocking

302 density under horse grazing (lower pollinator abundance at high stocking density), but not
303 under cattle grazing (Fig. 3b). There was a strong positive relationship between flower and
304 pollinator abundance (Fig. 3c). Of all floral groups tested, the pooled Asteraceae reached the
305 highest explanatory power ($t = 8.50$, $P < 0.001$, adjusted $R^2 = 0.86$, Fig. 3c), whereas the
306 abundance of pollinators was not related to the flower abundance of other species ($P = 0.87$).
307 The abundance of *A. tripolium* alone also had strong explanatory power for pollinator
308 abundance ($t = 6.91$, $P < 0.001$, $R^2 = 0.82$), whereas all flowers combined had less explanatory
309 power ($t = 2.83$, $P < 0.008$, $R^2 = 0.64$). Year was a highly significant factor in all models
310 ($P < 0.001$) due to strongly differing weather conditions. Year 2 was characterised by cold and
311 wet weather, resulting in very low pollinator numbers. In contrast, year 4 was warm and dry
312 with a ‘blanket’ of pollinators covering the area, with little discrimination among regimes
313 (Fig. 3c).

314 3.3 birds

315 Over the four years, 4870 observations of 60 bird species over 14423 individuals were
316 made (Appendix B). Overall, effects of the grazing regimes on bird densities were weak.
317 Although the models of several functional groups showed significant estimates for some of
318 the factors, including the interaction between livestock species and density, the models did
319 not significantly differ from null models at the 5% level (Table 1, Fig. 4).

320 3.4 Voles

321 Overall, voles were present in 29% of the 696 plots checked. Vole presence was
322 significantly higher under low stocking densities ($P < 0.001$), and under cattle grazing
323 ($P < 0.001$; Table 1, Fig. 5).

324 3.5 Multidiversity

325 Multidiversity did not significantly differ among the grazing regimes (Table 1).
326 Graphs of the species richness of each group per paddock can be found in Appendix A (Fig.
327 A2).

328 4 Discussion

329 Overall, we found significant effects of stocking density on almost all measured
330 variables, and some differences between livestock species. Our hypothesis that effects of
331 horse grazing are always greater than those of cattle at the same stocking density was not
332 supported, since for most variables no differences or differences contrasting over the two
333 densities were found. Evidence for cascading effects beyond pollinators and voles were not
334 found. The multidiversity metric showed no differences among regimes, which was probably
335 caused by the contrasting trends for plants and pollinators in combination with non-
336 significant differences for all bird groups (Fig. A2). Its usefulness in conservation science
337 thus needs further validation.

338 We found a trend for suppression of the grass *E. atherica* under high density grazing,
339 but high variability between the replicates makes it hard to draw strong conclusions. In a
340 large scale experiment such as ours, such variability (i.e. *E. atherica* well established in the
341 western replicate, but little cover in eastern replicate) is impossible to avoid. Nevertheless,
342 this trend concurs with research at other sites showing that high-density grazing can prevent
343 the spread of *E. atherica* (Bakker, 2014).

344 4.1 stocking density

345 Stocking density had strong effects on almost all variables measured here and in other
346 publications on the same experiment (summarised in Table 2). This is in agreement with
347 experiments both on salt marshes (e.g. Andresen et al., 1990; Kiehl et al., 1996; Rickert et al.,

348 2012) and in other grassland systems (e.g. Dennis et al., 1997; Evans et al., 2015; Kruess and
349 Tschardtke, 2002; WallisDeVries et al., 2007).

350 As hypothesised, plant species richness was higher under high stocking density, as
351 vegetation height decreased. This suggests that competitive exclusion among plant species is
352 indeed strong under low stocking densities, which may lead to future plant species losses.
353 However, this was only found on the high marsh, while on the low marsh no differences in
354 species richness were found. This is probably due to the already low overall plant species
355 richness of the low marsh (average 7 and maximum 12 species per 16 m²), and the short
356 duration of the experiment relative to the gradual effects of competitive exclusion on plant
357 species richness. The greater plant species richness on the high marsh may also be due to the
358 lower cover of *E. atherica* under high stocking densities.

359 Suppression of the competitive grass *E. atherica* tended to be most successful under
360 high stocking densities. However, under such conditions, vegetation structural heterogeneity
361 and complexity is strongly reduced (Nolte et al., 2014), with unfavourable consequences for
362 other biota. Structurally heterogeneous vegetation supports more invertebrate species (Dennis
363 et al., 1997; van Klink et al., 2013), and nest sites for birds (Mandema et al., 2015, 2014a;
364 Norris et al., 1998) than homogeneous short-grazed vegetation does, and is thus preferable
365 from a conservation perspective. By contrast, staging geese may benefit from a homogeneous
366 short-grazed vegetation structure because of its high nutritional value (Mandema et al.,
367 2014b), and can thus be expected to become less abundant on marshes grazed at low stocking
368 densities where the vegetation is higher (Bos et al., 2005).

369 As was also predicted, the abundance of voles and pollinators decreased with
370 increasing stocking density due to a decrease in vegetation cover and flower abundance. For
371 the pollinators, this was explained by the abundance of Asteraceae flowers, which are a high
372 quality resource. This was expected, since for pollinators reproduction does not take place on

373 the salt marsh, and thus the abundance of floral resources together with weather conditions
374 will determine the abundance of pollinators on the salt marsh. Because of their importance
375 for plant reproduction and as potential food source for birds, a decrease in pollinator
376 abundance can have severe consequences for ecosystem processes. The results of voles
377 should be interpreted with some caution, as we sampled voles only once (at peak population),
378 while voles show multi-annual cycle dynamics (Villar et al., 2014). However, we are
379 confident that our results give a good representation of the relative effects of the grazing
380 regimes, since the processes by which the voles are affected (most importantly defoliation
381 and trampling) should be independent of vole population cycles.

382 Our experimental regimes had no significant effect on the abundances of the different
383 functional groups of birds. This was surprising, since we previously found strong evidence of
384 habitat deterioration in the short-grazed vegetation, especially under high density horse
385 grazing: decreased vegetation height and heterogeneity (Nolte et al., 2014), increased nest
386 trampling risk (Mandema et al., 2013), and decreased prey abundance (van Klink et al.,
387 2014). It must be noted, however, that also under low stocking densities, nest trampling can
388 be substantial (Sharps et al., 2015). Such a lack of detectable effects on birds is not
389 uncommon in grazing experiments (e.g. WallisDeVries et al., 2007), but somewhat contrasts
390 other research, where highest densities of breeding Meadow Pipits and other breeding birds
391 were found under intermediate (Evans et al., 2006) or high sheep grazing densities (Loe et al.,
392 2007). However, these studies were conducted with a different livestock species and in
393 different biotopes, complicating generalisations.

394 Several factors may have contributed to the general absence of detectable effects on
395 birds. First, the scale of our experimental paddocks in comparison to the foraging range and
396 nest density of birds was relatively small. The number of breeding territories counted in year
397 2 was ca. 1 and 0.5 territories per hectare in the central and eastern replicates, respectively

398 (data from Esselink et al., 2015). Second, the complex relation between abundance and
399 accessibility of food resources in grazed systems (Evans et al., 2006) may have obscured the
400 relation between birds and their resources. Also the different grazing histories of the
401 replicates may factor into this, if the resource abundance was differently affected by grazing
402 in the different replicates. A final reason may be that breeding sites had been chosen before
403 grazing commenced in late May/early June.

404 *4.2 livestock species*

405 Choice of livestock species was of less importance than stocking density, which is in
406 line with previous research (e.g. Boschi and Baur, 2007; Jerrentrup et al., 2015; Öckinger et
407 al., 2006). However, we did find some significant differences between cattle and horses. The
408 foremost difference is that more trampling takes place under horse than under cattle grazing
409 (Mandema et al., 2013). This results in higher probabilities of bird-nest losses, and can also
410 account for the lower densities of voles and lower sediment accretion rates (Nolte et al.,
411 2015). Additionally, trampling was shown to significantly affect flower abundance of *A.*
412 *tripolium* (Nolte et al., 2013). Here, trampling interacted with dietary differences: under high
413 stocking densities *A. tripolium* was damaged more by horses due to their greater mobility, but
414 under low densities more by cattle due to their selective foraging for *A. tripolium*.
415 Experimental grazing on German salt marshes has shown that sheep have an even higher
416 preference for *A. tripolium*, and can almost completely remove the species from the system
417 (Kiehl et al., 1996). Trampling and consumption of *A. tripolium* have strong detrimental
418 effects on its rich herbivorous insect community (van Klink and van Schroyen Lantman,
419 2015) and its pollinators. Lastly, some evidence was found that cattle induce a more fine-
420 grained vegetation patchiness compared to horses (Nolte et al., 2014).

421 *4.3 relevance to other systems and conclusion*

422 Many of our results are likely applicable to a range of other grassland types where
423 grazing is used for conservation management. Despite the obvious differences in species pool
424 characteristics, environmental conditions such as productivity and soil type, and ecological
425 complexity, the mechanisms involved can be expected to be similar. Consequently, the
426 responses of the studied species groups to different grazing regimes (low vs. high stocking
427 density, ruminant vs. hindgut feeder) may be comparable. Additionally, our results highlight
428 the importance of studying different trophic groups in order to avoid erroneous management
429 decisions based on single taxa.

430 No single management type (i.e. grazing regime) was beneficial to all studied groups.
431 Horse grazing at high densities does not provide many benefits to biodiversity and can
432 therefore be discarded as a management option for conservation purposes. In contrast, long-
433 term abandonment, which has been intensively studied elsewhere, proves to have beneficial
434 effects on many, but not all invertebrate species (Rickert et al., 2012; van Klink et al., 2013).
435 Therefore we thus recommend several types of management to be applied concurrently,
436 including long-term abandonment, in order to maximise the biodiversity potential of an area.

437

438 **Acknowledgements**

439 We thank It Fryske Gea for permission to conduct this experiment and in particular
440 Gerrit van der Leest and Johannes Westerhof for logistic support. We thank Remco Hiemstra,
441 Sicco Ens, Corinna Rickert and Petra Daniels for their help with data collection, and Rikjan
442 Vermeulen, Bruno Ens and Joost Tinbergen for helpful comments on the experiment. This
443 study was funded by Het Waddenfonds (project WF200451).

444

445 **References:**

- 446 Allan, E., Bossdorf, O., Dormann, C.F., Prati, D., Gossner, M.M., Tschardtke, T., Blüthgen,
447 N., Bellach, M., Birkhofer, K., Boch, S., Böhm, S., Börschig, C., Chatzinotas, A., Christ,
448 S., Daniel, R., Diekötter, T., Fischer, C., Friedl, T., Glaser, K., Hallmann, C., Hodac, L.,
449 Hölzel, N., Jung, K., Klein, A.M., Klaus, V.H., Kleinebecker, T., Krauss, J., Lange, M.,
450 Morris, E.K., Müller, J., Nacke, H., Pasalic, E., Rillig, M.C., Rothenwöhrer, C., Schall,
451 P., Scherber, C., Schulze, W., Socher, S.A., Steckel, J., Steffan-Dewenter, I., Türke, M.,
452 Weiner, C.N., Werner, M., Westphal, C., Wolters, V., Wubet, T., Gockel, S., Gorke, M.,
453 Hemp, A., Renner, S.C., Schöning, I., Pfeiffer, S., König-Ries, B., Buscot, F.,
454 Linsenmair, K.E., Schulze, E.-D., Weisser, W.W., Fischer, M., 2014. Interannual
455 variation in land-use intensity enhances grassland multidiversity. *Proc. Natl. Acad. Sci.*
456 111, 308–313. doi:10.1073/pnas.1312213111
- 457 Andresen, H., Bakker, J.P., Brongers, M., Heydemann, B., Irmeler, U., 1990. Long-term
458 changes of salt marsh communities by cattle grazing. *Vegetatio* 89, 137–148.
459 doi:10.1007/BF00032166
- 460 Atkinson, P.W., Fuller, R.J., Vickery, J.A., Conway, G.J., Tallowin, J.R.B., Smith, R.E.N.,
461 Haysom, K.A., Ings, T.C., Asteraki, E.J., Brown, V.K., 2005. Influence of agricultural
462 management, sward structure and food resources on grassland field use by birds in
463 lowland England. *J. Appl. Ecol.* 42, 932–942. doi:10.1111/j.1365-2664.2005.01070.x
- 464 Baker, J.A., Brooks, R.J., 1981. Distribution patterns of raptors in relation to density of
465 meadow voles. *Condor* 83, 42–47. doi:10.2307/1367598
- 466 Bakker, J.P., 2014. Ecology of salt marshes 40 years of research in the Wadden Sea.
467 Waddenacademie.
- 468 Bakker, J.P., Dijkstra, M., Russchen, P.T., 1985. Dispersal, germination and early

469 establishment of halophytes and glycophytes on a grazed and abandoned salt-marsh
470 gradient. *New Phytol.* 101, 291–308. doi:10.1111/j.1469-8137.1985.tb02836.x

471 Bakker, J.P., Esselink, P., Dijkema, K.S., van Duin, W.E., de Jong, D.J., 2002. Restoration of
472 salt marshes in the Netherlands. *Hydrobiologia* 478, 29–51.
473 doi:10.1023/A:1021066311728

474 Bates, D., Maechler, M., Bolker, B.M., Walker, S., 2014. lme4: Linear mixed-effects models
475 using Eigen and S4.

476 Borer, E.T., Seabloom, E.W., Gruner, D.S., Harpole, W.S., Hillebrand, H., Lind, E.M., Adler,
477 P.B., Alberti, J., Anderson, T.M., Bakker, J.D., Biederman, L., Blumenthal, D., Brown,
478 C.S., Brudvig, L.A., Buckley, Y.M., Cadotte, M., Chu, C., Cleland, E.E., Crawley, M.J.,
479 Daleo, P., Damschen, E.I., Davies, K.F., DeCrappeo, N.M., Du, G., Firn, J., Hautier, Y.,
480 Heckman, R.W., Hector, A., HilleRisLambers, J., Iribarne, O., Klein, J.A., Knops,
481 J.M.H., La Pierre, K.J., Leakey, A.D.B., Li, W., MacDougall, A.S., McCulley, R.L.,
482 Melbourne, B.A., Mitchell, C.E., Moore, J.L., Mortensen, B., O'Halloran, L.R., Orrock,
483 J.L., Pascual, J., Prober, S.M., Pyke, D.A., Risch, A.C., Schuetz, M., Smith, M.D.,
484 Stevens, C.J., Sullivan, L.L., Williams, R.J., Wragg, P.D., Wright, J.P., Yang, L.H.,
485 2014. Herbivores and nutrients control grassland plant diversity via light limitation.
486 *Nature* 508, 517–520. doi:10.1038/nature13144

487 Bos, D., Bakker, J.P., de Vries, Y., van Lieshout, S., 2002. Long-term vegetation changes in
488 experimentally grazed and ungrazed back-barrier marshes in the Wadden Sea. *Appl.*
489 *Veg. Sci.* 5, 45–54. doi:10.1111/j.1654-109X.2002.tb00534.x

490 Bos, D., Engelmoer, M., Feddema, J., Koffijberg, K., 2015. Broedvogels op Noord-Friesland
491 Buitendijks en de invloed van verkwelding op aantallen. *Limosa* 88, 31–42.

492 Bos, D., Loonen, M.J.J.E., Stock, M., Hofeditz, F., van der Graaf, S., Bakker, J.P., 2005.

493 Utilisation of Wadden Sea salt marshes by geese in relation to livestock grazing. *J. Nat.*
494 *Conserv.* 15, 1–15. doi:10.1016/j.jnc.2004.10.001

495 Boschi, C., Baur, B., 2007. The effect of horse, cattle and sheep grazing on the diversity and
496 abundance of land snails in nutrient-poor calcareous grasslands. *Basic Appl. Ecol.* 8, 55–
497 65. doi:10.1016/j.baae.2006.02.003

498 Dennis, P., Young, M.R., Howard, C.L., Gordon, I.J., 1997. The response of epigeal beetles
499 (Col: Carabidae, Staphylinidae) to varied grazing regimes on upland *Nardus stricta*
500 grasslands. *J. Appl. Ecol.* 34, 433–443. doi:10.2307/2404888

501 Doody, J.P., 2008. Management of Natura 2000 habitats. 1330 Atlantic salt meadows
502 (Glauco- Puccinellietalia maritimae).

503 EC Habitats Directive, 1992. Council directive 92/43/EEC of 21 May 1992 on the
504 conservation of natural habitats and of wild fauna and flora.

505 Esselink, P., Bos, D., Daniels, P., van Duin, W.E., Veeneklaas, R.M., 2015. Van polder naar
506 kwelder - tien jaar kwelderherstel Noorderleecech. Vries, The Netherlands.

507 Esselink, P., Petersen, J., Arens, S., Bakker, J.P., Bunje, J., Dijkema, K.S., Hecker, N.,
508 Hellwig, U., Jensen, A.-V., Kers, A.S., Körber, P., Lammerts, E.J., Stock, M.,
509 Veeneklaas, R.M., Vreeken, M., Wolters, M., 2009. Salt Marshes. Thematic Report No.
510 8., in: Marencic, H., de Vlas, J. (Eds.), *Quality Status Report 2009. WaddenSea*
511 *Ecosystem No. 25. Common Wadden Sea Secretariat, Trilateral Monitoring and*
512 *Assessment Group, Wilhelmshaven, Germany.*

513 Esselink, P., Zijlstra, W., Dijkema, K.S., van Diggelen, R., 2000. The effects of decreased
514 management on plant-species distribution patterns in a salt marsh nature reserve in the
515 Wadden Sea. *Biol. Conserv.* 93, 61–76. doi:10.1016/S0006-3207(99)00095-6

516 Evans, D.M., Redpath, S.M., Evans, S.A., Elston, D.A., Gardner, C.J., Dennis, P., Pakeman,

517 R.J., 2006. Low intensity, mixed livestock grazing improves the breeding abundance of
518 a common insectivorous passerine. *Biol. Lett.* 2, 636–638. doi:10.1098/rsbl.2006.0543

519 Evans, D.M., Villar, N., Littlewood, N.A., Pakeman, R.J., Evans, S.A., Dennis, P., Skartveit,
520 J., Redpath, S.M., 2015. The cascading impacts of livestock grazing in upland
521 ecosystems : a 10-year experiment. *Ecosphere* 6, 1–15. doi:10.1890/ES14-00316.1

522 Ford, H., Garbutt, A., Jones, L., Jones, D.L., 2013. Grazing management in saltmarsh
523 ecosystems drives invertebrate diversity, abundance and functional group structure.
524 *Insect Conserv. Divers.* 6, 189–200. doi:10.1111/j.1752-4598.2012.00202.x

525 Foster, C.N., Barton, P.S., Lindenmayer, D.B., 2014. Effects of large native herbivores on
526 other animals. *J. Appl. Ecol.* 51, 929–938. doi:10.1111/1365-2664.12268

527 Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric
528 models. *Biometrical J.* 50, 346. doi:10.1002/bimj.200810425

529 Illius, A.W., Gordon, I.J., 1992. Modelling the nutritional ecology of ungulate herbivores:
530 evolution of body size and competitive interactions. *Oecologia* 89, 428–434.
531 doi:10.1007/BF00317422

532 Irmiler, U., Heydemann, B., 1986. Die ökologische Problematik de Beweidung von
533 Salzwiesen an der Niedersächsischen Küste - am beispiel der Leybucht (RPRT),
534 Naturschutz und Landschaftspflege in Niedersachsen. Niedersächsisches
535 Landesverwaltungsamt, Fachbehörde für Naturschutz, Hannover.

536 Jerrentrup, J.S., Seither, M., Petersen, U., Isselstein, J., 2015. Little grazer species effect on
537 the vegetation in a rotational grazing system. *Agric. Ecosyst. Environ.* 202, 243–250.
538 doi:10.1016/j.agee.2015.01.007

539 Kiehl, K., Eischeid, I., Gettner, S., Walter, J., 1996. Impact of different sheep grazing
540 intensities on salt marsh vegetation in northern Germany. *J. Veg. Sci.* 7, 99–106.

541 doi:10.2307/3236421

542 Kruess, A., Tschardtke, T., 2002. Contrasting responses of plant and insect diversity to
543 variation in grazing intensity. *Biol. Conserv.* 106, 293–302. doi:10.1016/S0006-
544 3207(01)00255-5

545 Loe, L.E., Myrsterud, A., Stien, A., Steen, H., Evans, D.M., Austrheim, G., 2007. Positive
546 short-term effects of sheep grazing on the alpine avifauna. *Biol. Lett.* 3, 109–111.
547 doi:10.1098/rsbl.2006.0571

548 Mandema, F.S., Tinbergen, J.M., Ens, B.J., Bakker, J.P., 2013. Livestock grazing and
549 trampling of birds' nests: an experiment using artificial nests. *J Coast Conserv* 17, 409–
550 416. doi:10.1007/s11852-013-0239-2

551 Mandema, F.S., Tinbergen, J.M., Ens, B.J., Bakker, J.P., 2014a. Spatial diversity in canopy
552 height at Redshank and Oystercatcher nest-sites in relation to livestock grazing. *Ardea*
553 101, 105–112. doi:10.5253/078.101.0205

554 Mandema, F.S., Tinbergen, J.M., Ens, B.J., Koffijberg, K., Dijkema, K.S., Bakker, J.P., 2015.
555 Moderate livestock grazing of salt, and brackish marshes benefits breeding birds along
556 the mainland coast of the Wadden Sea. *Wilson J. Ornithol.* 127, 467–476.
557 doi:10.1676/13-133.1

558 Mandema, F.S., Tinbergen, J.M., Stahl, J., Esselink, P., Bakker, J.P., 2014b. Habitat
559 preference of geese is affected by livestock grazing - seasonal variation in an
560 experimental field evaluation. *Wildlife Biol.* 20, 67–72. doi:10.2981/wlb.13046

561 Menard, C., Duncan, P., Fleurance, G., Georges, J.Y., Lila, M., 2002. Comparative foraging
562 and nutrition of horses and cattle in European wetlands. *J. Appl. Ecol.* 39, 120–133.
563 doi:10.1046/j.1365-2664.2002.00693.x

564 Miller, D.L., 2015. Distance: A simple way to fit detection functions to distance sampling

565 data and calculate abundance/density for biological populations. Version 0.9.3.

566 Nolte, S., Esselink, P., Bakker, J.P., 2013. Flower production of *Aster tripolium* is affected by
567 behavioral differences in livestock species and stocking densities : the role of activity
568 and selectivity. *Ecol. Res.* 28, 821–831. doi:10.1007/s11284-013-1064-7

569 Nolte, S., Esselink, P., Bakker, J.P., Smit, C., 2015. Effects of livestock species and stocking
570 density on accretion rates in grazed salt marshes. *Estuar. Coast. Shelf Sci.* 152, 109–115.
571 doi:10.1016/j.ecss.2014.11.012

572 Nolte, S., Esselink, P., Smit, C., Bakker, J.P., 2014. Herbivore species and density affect
573 vegetation-structure patchiness in salt marshes. *Agric. Ecosyst. Environ.* 185, 41–47.
574 doi:10.1016/j.agee.2013.12.010

575 Norris, K., Brindley, E., Cook, T., Babbs, S., Brown, C.F., Yaxley, R., 1998. Is the density of
576 redshank *Tringa totanus* nesting on saltmarshes in Great Britain declining due to
577 changes in grazing management? *J. Appl. Ecol.* 35, 621–634. doi:10.1046/j.1365-
578 2664.1998.355339.x

579 Öckinger, E., Eriksson, A.K., Smith, H.G., 2006. Effects of grassland abandonment,
580 restoration and management on butterflies and vascular plants. *Biol. Conserv.* 133, 291–
581 300. doi:10.1016/j.biocon.2006.06.009

582 Olf, H., Ritchie, M.E., 1998. Effects of herbivores on grassland plant diversity. *Trends Ecol.*
583 *Evol.* 13, 261–265. doi:10.1016/S0169-5347(98)01364-0

584 Pétilion, J., Georges, A., Canard, A., Ysnel, F., 2007. Impact of cutting and sheep grazing on
585 ground-active spiders and carabids in intertidal salt marshes (Western France). *Anim.*
586 *Biodivers. Conserv.* 30, 201–209.

587 Pollard, E., 1977. A method for assessing changes in the abundance of butterflies. *Biol.*
588 *Conserv.* 12, 115–134. doi:10.1016/0006-3207(77)90065-9

589 R Core Team, 2016. R: A language and environment for statistical computing. version 3.2.5.
590 R Found. Stat. Comput.

591 Rickert, C., Fichtner, A., van Klink, R., Bakker, J.P., 2012. Alpha- and beta-diversity in moth
592 communities in salt marshes is driven by grazing management. *Biol. Conserv.* 146, 24–
593 31. doi:10.1016/j.biocon.2011.11.024

594 Sharps, E., Smart, J., Skov, M.W., Garbutt, A., Hiddink, J.G., 2015. Light grazing of
595 saltmarshes is a direct and indirect cause of nest failure in Common Redshank *Tringa*
596 *totanus*. *Ibis (Lond. 1859)*. 157, 239–249. doi:10.1111/ibi.12249

597 Thomas, L., Buckland, S.T., Rexstad, E. a, Laake, J.L., Strindberg, S., Hedley, S.L., Bishop,
598 J.R.B., Marques, T. a, Burnham, K.P., 2009. Distance software: design and analysis of
599 distance sampling surveys for estimating population size. *J. Appl. Ecol.* 47, 5–14.
600 doi:doi: 10.1111/j.1365-2664.2009.01737.x

601 van der Meijden, R., 2005. Heukels' Flora van Nederland. Wolters-Noordhoff,
602 Groningen/Houten.

603 van Klink, R., Mandema, F.S., Bakker, J.P., Tinbergen, J.M., 2014. Foraging site choice and
604 diet selection of Meadow Pipits *Anthus pratensis* breeding on grazed salt marshes. *Bird*
605 *Study* 61, 101–110. doi:10.1080/00063657.2013.856855

606 van Klink, R., Rickert, C., Vermeulen, R., Vorst, O., WallisDeVries, M.F., Bakker, J.P.,
607 2013. Grazed vegetation mosaics do not maximize arthropod diversity: evidence from
608 salt marshes. *Biol. Conserv.* 164, 150–157. doi:10.1016/j.biocon.2013.04.023

609 van Klink, R., van der Plas, F., Van Noordwijk, C.G.E.T., WallisDeVries, M.F., Olf, H.,
610 2015. Effects of large herbivores on grassland arthropod diversity. *Biol. Rev.* 90, 347–
611 366. doi:10.1111/brv.12113

612 van Klink, R., van Schrojenstein Lantman, I.M., 2015. Effecten van kwelderbeweiding op

613 spinnen en insecten. *Entomol. Ber.* 75, 188–199.

614 Villar, N., Cornulier, T., Evans, D., Pakeman, R., Redpath, S., Lambin, X., 2014.

615 Experimental evidence that livestock grazing intensity affects cyclic vole population

616 regulation processes. *Popul. Ecol.* 56, 55–61. doi:10.1007/s10144-013-0398-x

617 WallisDeVries, M.F., Parkinson, A.E., Dulphy, J.P., Sayer, M., Diana, E., 2007. Effects of

618 livestock breed and grazing intensity on biodiversity and production in grazing systems.

619 4. Effects on animal diversity. *Grass Forage Sci.* 62, 185–197. doi:10.1111/j.1365-

620 2494.2007.00572.x

621 WallisDeVries, M.F., Poschlod, P., Willems, J.H., 2002. Challenges for the conservation of

622 calcareous grasslands in northwestern Europe: integrating the requirements of flora and

623 fauna. *Biol. Conserv.* 104, 265–273. doi:10.1016/S0006-3207(01)00191-4

624 WallisDeVries, M.F., Van Swaay, C.A.M., Plate, C.L., 2012. Changes in nectar supply : A

625 possible cause of widespread butterfly decline. *Curr. Zool.* 58, 384–391.

626 doi:10.1093/czoolo/58.3.384

627 Wanner, A., Suchrow, S., Kiehl, K., Meyer, W., Pohlmann, N., Stock, M., Jensen, K., 2014.

628 Scale matters: Impact of management regime on plant species richness and vegetation

629 type diversity in Wadden Sea salt marshes. *Agric. Ecosyst. Environ.* 182, 69–79.

630 doi:10.1016/j.agee.2013.08.014

631

632 Table 1. Summary statistics of all GLMMs. *P*-values in bold indicate significant effects at *P* < 0.05.

			livestock density			livestock species			species*density			MODEL		
	unit	distribution	estimate	test statistic	<i>P</i>	estimate	test statistic	<i>P</i>	estimate	test statistic	<i>P</i>	χ^2	<i>P</i>	
Plants														
Cover change <i>E. atherica</i>	% per paddock	Gaussian	-0.19±0.09	t = -1.99	0.08			ns			ns	3.99	0.046	
Log mean vegetation height (cm)	high marsh	per PQ	Gaussian (log)	-1.02±0.26	t = -3.98	<0.01		ns			ns	11.12	<0.001	
	low marsh	per PQ	Gaussian (log)	-1.21±0.38	t = -3.19	0.01					ns	7.40	0.006	
Plant species richness	high marsh	per PQ	Poisson	0.40±0.09	z = 4.39	<0.001		ns			ns	11.13	<0.001	
	low marsh	per PQ	Poisson			ns		ns			ns	0.27	0.6	
Flowers and pollinators														
Total flower abundance	per 80 m ²	Poisson ¹	-0.28±0.14	z = -2.09	0.04			ns			ns	3.55	0.06	
Asteraceae flower abundance	per 80 m ²	Poisson ¹	-0.06±0.04	z = -1.61	0.1	0.90±0.42	z = 2.12	0.03	-0.13±0.05	z = -2.42	0.02	15.83	0.001	
<i>A. tripolium</i> flower abundance	per 80 m ²	Poisson ¹	-0.18±0.04	z = -4.44	<0.001			ns			ns	12.03	<0.001	
Other flower abundance	per 80 m ²	Poisson ¹			ns			ns			ns	1.71	0.19	
Pollinator abundance	per 500 m transect	Poisson ¹	-0.12±0.03	z = -3.5	<0.001			ns			ns	6.83	0.004	
Birds														
Meadow pipit (density)	all year	per paddock*	Poisson ¹	0.73±0.44	z = 1.65	0.1	0.64±0.50	z = 1.29	0.19	-1.24±0.64	z = -1.95	0.05	6	0.097
PB foraging on marsh (density)	(spring)	per paddock*	Poisson ¹			ns			ns		ns	4.01	0.26	
PB not foraging on marsh (density)	(spring)	per paddock**	Poisson ¹			ns			ns		ns	0.02	0.88	
NB foraging on marsh (density)		per paddock*	Poisson ¹	0.23±0.18	z = 1.29	0.2	0.44±0.21	z = 2.14	0.03	-0.59±0.26	z = -2.26	0.02	4	0.246
NB not foraging on marsh (density)		per paddock**	Poisson ¹	2.00±0.70	z = 2.84	<0.01	1.76±0.80	z = 2.20	0.03	-2.35±0.98	z = -2.40	0.02	6.47	0.09
Raptors (density)		per paddock**	Poisson ¹			ns			ns		ns	0.26	0.61	
All birds (density)	all year	per paddock*	Poisson ¹			ns			ns		ns	4.47	0.22	
Voles														
Vole presence	per 60 subplots	Binomial	-0.18±0.04	z = -4.91	<0.001	-1.35±0.19	z = -7.15	<0.001			ns	76.9	<0.001	
Multidiversity														
Multidiversity of 7 functional groups	per paddock	Gaussian			ns			ns			ns	1.84	0.61	

633 * Density estimated by distance sampling per paddock per year. **Estimated per paddock per four years. ¹Overdispersion was corrected using
634 individual level random effects. PP = permanent plot, PB = potential breeding birds, NB = non-breeding birds.

635 Table 2: Summarised effects of livestock species and density in this experimental setup,
 636 reported here and elsewhere: ↓: negative effect, ↑: positive effect, =: no effect, ⇕: interactive
 637 effect, and causal mechanism per group. ‘H’ indicates that the direction of the effect relates to
 638 horse grazing. PB: potential breeding birds; NB: non-breeding birds. Symbols between
 639 parentheses represent marginally significant effects (0.1>P>0.05).

		Effect of increasing stocking density	Effect of livestock species	mechanism(s)	source (if other than this paper)
Plants					
Cover <i>E. Atherica</i> vegetation type		(↓)	=	trampling / defoliation	
Vegetation height	high marsh	↓	=	trampling / defoliation	
	low marsh	↓	=	trampling / defoliation	
Plant species richness	high marsh	↑	=		
	low marsh	=	=		
Patch size		(↑)	↑H	selectivity	a
flowers and pollinators					
<i>Aster tripolium</i> flowers		⇕	⇕	trampling / defoliation	b
Total flower abundance		↓	=		
Asteraceae abundance		⇕	⇕	trampling / defoliation	
Other flower abundance		=	=		
Pollinator abundance		↓	=		
Birds					
Meadow pipits		=	=	defoliation	c
PB foraging on marsh		=	=		
PB not foraging on marsh		=	=		
NB foraging on marsh		=	=		
NB not foraging on marsh		=	=		
Raptors		=	=		
All birds		=	=		
Nest trampling		↑	↑H	trampling	d
Geese abundance	autumn	↑	↑H		e
	spring	=	=		e
Voles					
Presence		↓	↓H	trampling(?)	
Multidiversity					
		=	=		
Sediment accretion					
		↓	(↓H)	defoliation / trampling	f

640

641

642 Sources: (a) Nolte et al. (2014); (b) Nolte, Esselink & Bakker (2013); (c) van Klink et al.

643 (2014); (d) Mandema et al. (2013); (e) Mandema et al. (2014b); (f) Nolte et al. (2015).

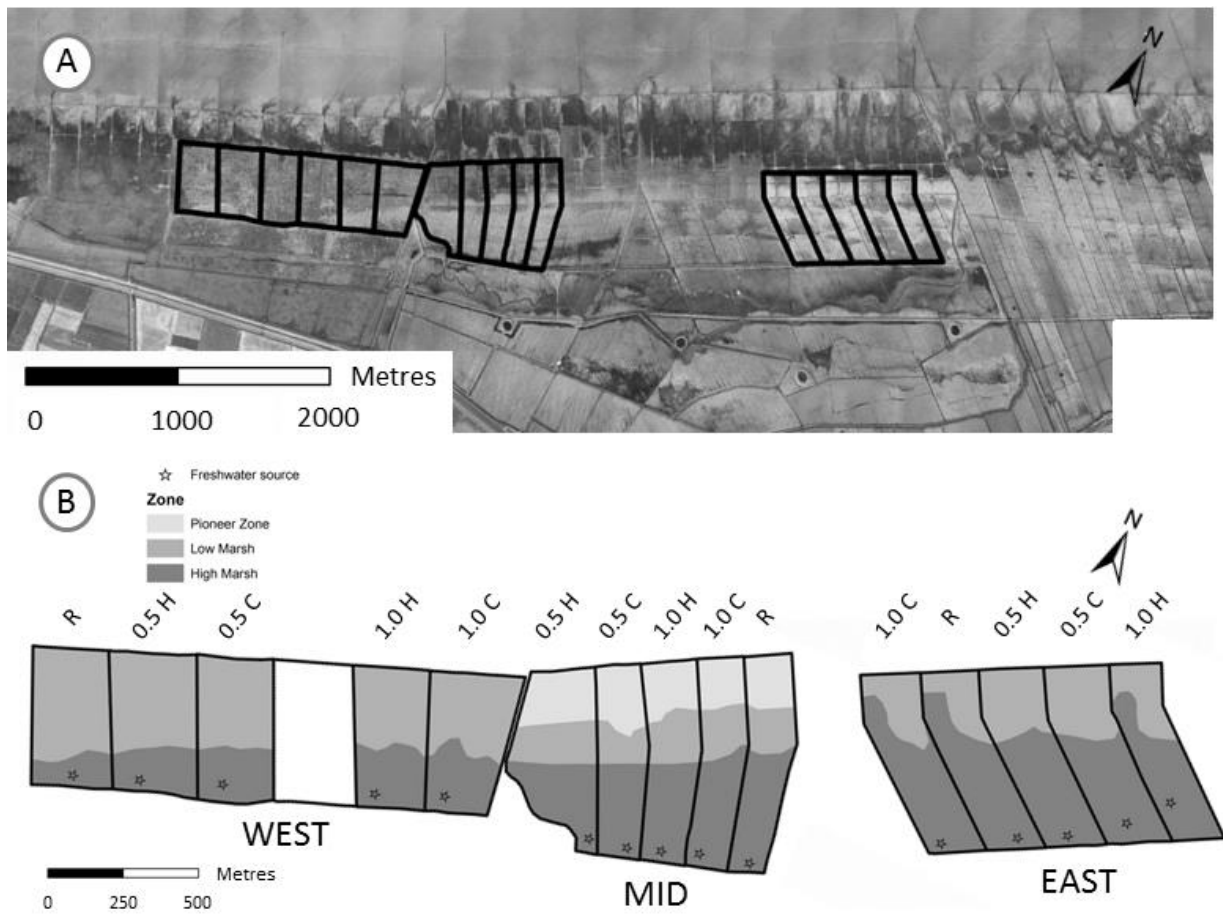
644

645

646

647 **FIGURES**

648



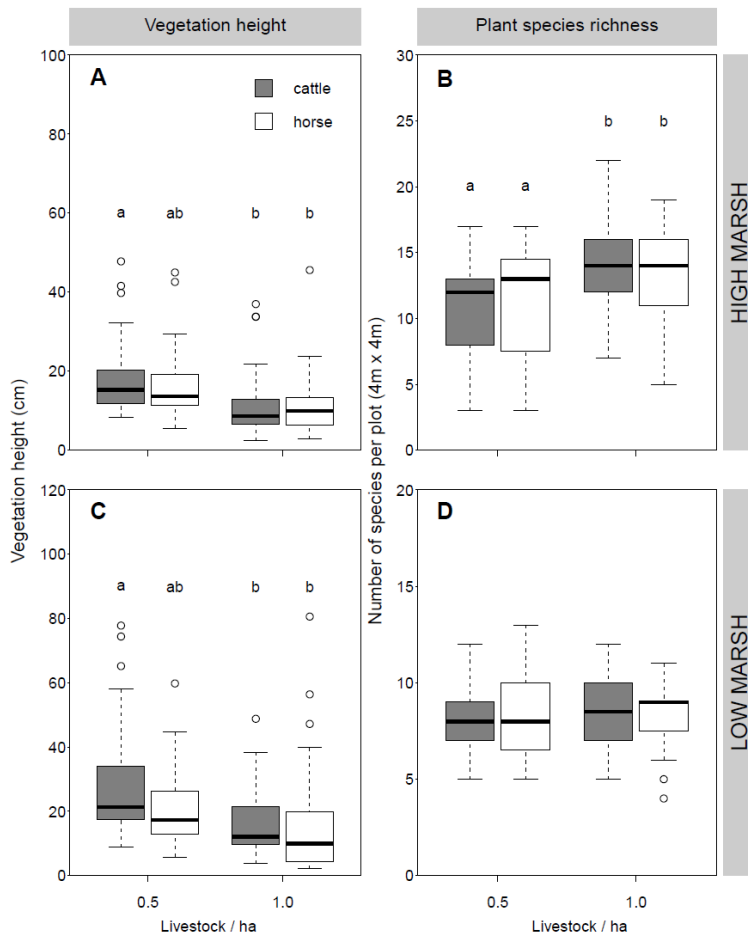
649

650 Figure 1: Overview of the grazing experiment at the salt marshes of Noord-Friesland

651 Buitendijks (A). Experimental setup (B) with grazing regimes indicated as 0.5 = 0.5 animal

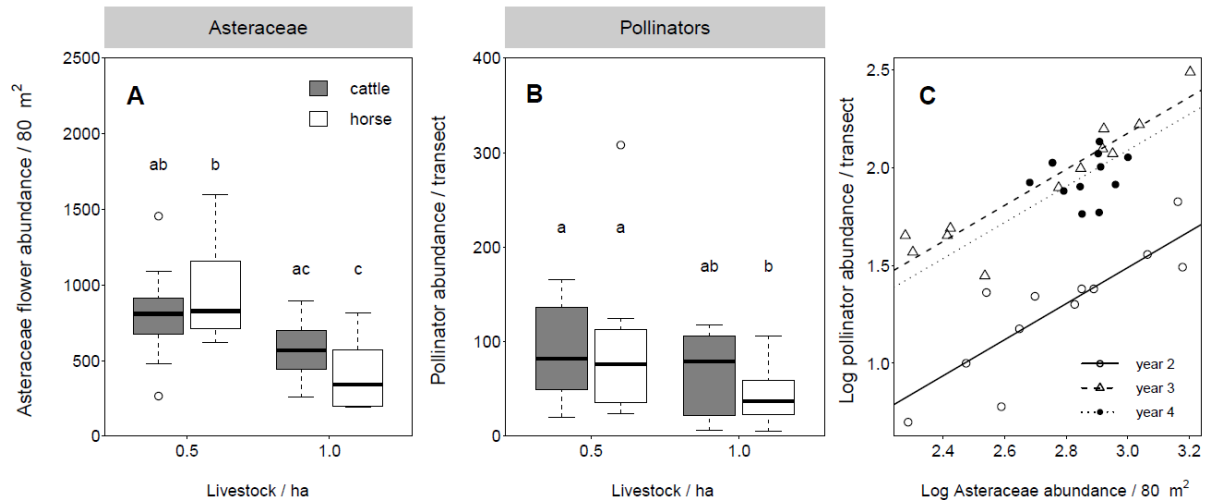
652 ha⁻¹; 1.0 = 1.0 animal ha⁻¹; H = horse; C = cattle and R = rotational regime. Locations of the

653 PPs and pollinator, bird, and vole transects can be found in Appendix A.



654

655 Figure 2: Effects of grazing by different livestock species (cattle or horse) at two densities
 656 (0.5 and 1 animal per hectare) on vegetation height and plant species richness. Boxes
 657 represent the raw data: 25% and 75% quartiles from the median (thick line), whiskers
 658 represent the maximum or minimum values, excluding outliers, and outliers are defined as
 659 more or less than 1.5 times the interquartile range. Significant differences among regimes
 660 indicated by post-hoc Tukey tests with all regimes as separate factors are indicated by
 661 different letters.



662

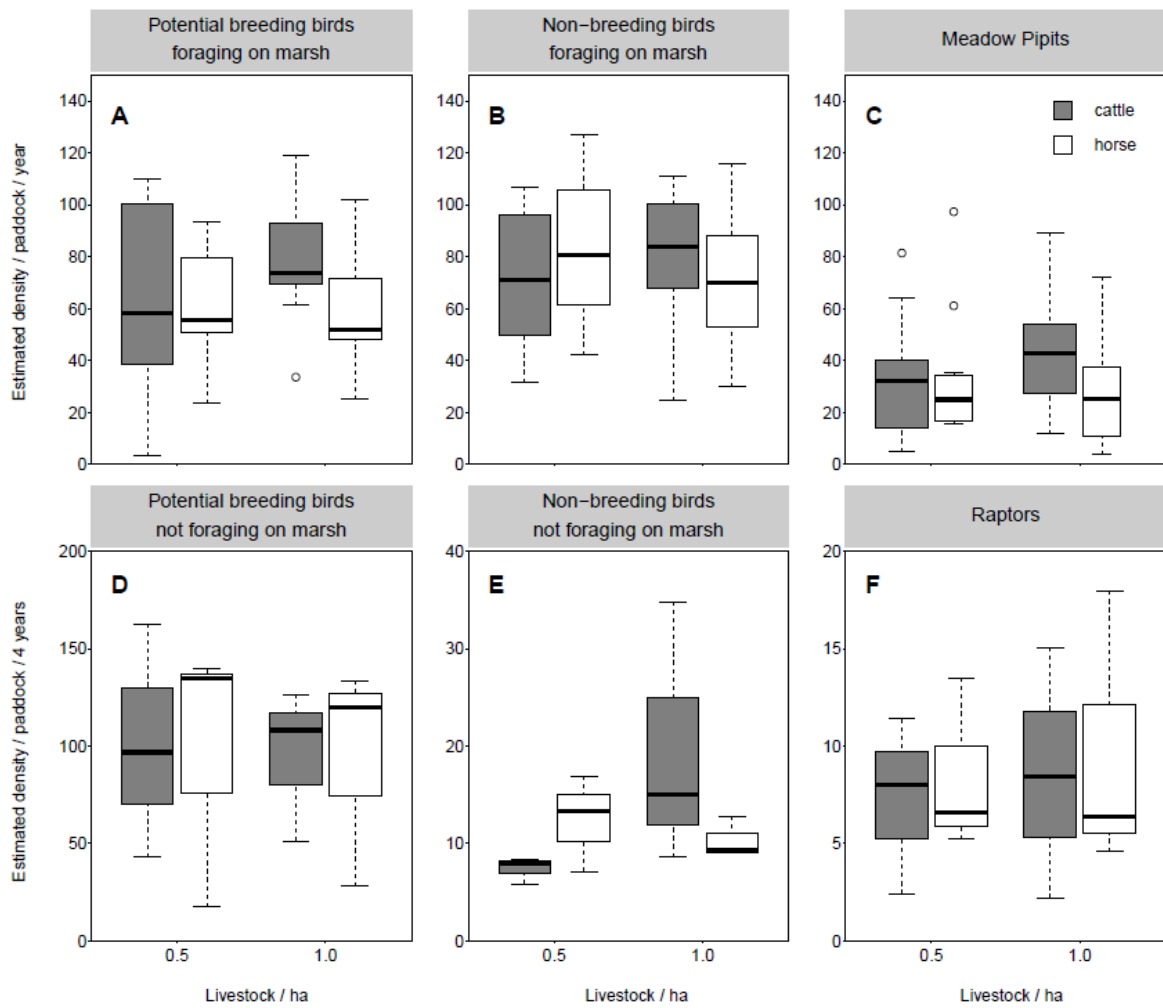
663 Figure 3: The estimated abundance of Asteraceae flowers (A) and pollinators (B) under four

664 grazing regimes. (C) The relationship between Asteraceae and pollinator abundance per

665 transect. The large annual differences can be ascribed to strong differences in weather

666 conditions, where year 2 was particularly cold and wet. Boxplot and letter attributes as in Fig.

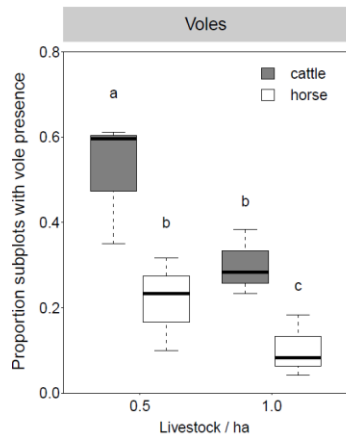
667 2.



668

669 Figure 4: Estimated density of birds (number of individuals per 11 ha) of different functional
 670 groups over the four grazing regimes. Due to low numbers of sightings per year, densities of
 671 the functional groups on the second row were estimated per four years. Boxplot attributes as
 672 in Fig. 2.

673



674

675 Figure 5: Proportion of subplots (60 subplots per paddock) with vole presence in year 4.

676 Boxplot and letter attributes as in Fig.2.

677

678