Habitat preference of geese is affected by livestock grazing - seasonal variation in an experimental field evaluation

Authors: Mandema, Freek S., Tinbergen, Joost M., Stahl, Julia, Esselink, Peter, and Bakker, Jan P.

Source: Wildlife Biology, 20(2) : 67-72

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.13046

Wildlife Biology 20: 67–72, 2014
doi: 10.2981/wlb.13046

Subject Editor: Kjell Einar Erikstad. Accepted 9 September 2013

Habitat preference of geese is affected by livestock grazing – seasonal variation in an experimental field evaluation

Freek S. Mandema, Joost M. Tinbergen, Julia Stahl, Peter Esselink and Jan P. Bakker

F. S. Mandema (f.s.mandema@rug.nl), J. M. Tinbergen, P. Esselink and J. P. Bakker, Centre for Ecological and Evolutionary Studies (CEES), Univ. of Groningen, PO Box 11103, NL-9700 CC Groningen, the Netherlands. – J. Stahl, SOVON, Dutch Centre for Field Ornithology, PO Box 6521, 6503 GA Nijmegen, the Netherlands.

The number of staging geese in northwestern Europe has increased dramatically. Growing goose numbers put strong grazing pressure on agricultural pastures. Damage to agricultural land may be mitigated by managing nature reserves in order to optimally accommodate large numbers of grazing geese. Livestock grazing has been shown to facilitate foraging geese; we take the novel approach of determining the effects of four different livestock grazing treatments in a replicated experiment on the distribution of geese. We present experimental field evidence that livestock grazing of a salt marsh in summer affects the habitat preference of foraging geese during autumn and spring staging. In an experimental field set-up with four different livestock grazing treatments we assessed goose visitation through dropping counts, in both autumn and spring. Grazing treatments included 0.5 or 1 horse ha^{-1} and 0.5 or 1 cattle ha^{-1} during the summer season. The livestock grazing regime affected goose distribution in autumn, just after livestock had been removed from the salt marsh. In autumn, goose visitation was highest in the 1 head ha^{-1} grazing treatments, where grazing intensity by livestock was also highest. In line with this result, goose visitation was lowest in the 0.5 head ha^{-1} livestock grazing treatments, where the grazing intensity by livestock was lowest. The differences in goose visitation among the experimental treatments in autumn could not be explained by the canopy height. In spring we did not find any effect of livestock grazing treatment on goose visitation. Differences in the distribution of geese over the experiment between autumn and spring may be explained by changes in the availability of nutrient-rich vegetation. Livestock summer grazing with a high stocking density, especially with horses, can be used to attract geese to salt marshes in autumn and potentially reduces damage caused by geese to inland farmland. From a nature conservation interest point of view, however, variation in structure of the vegetation is a prerequisite for other groups of organisms. Hence, we recommend grazing of salt marshes with densities of 0.5 head ha^{-1} of livestock when goose conservation is not the only management issue.

Over the past decades the number of staging geese in northwestern Europe has increased dramatically (Fox et al. 2010). An example is the almost exponential growth of the barnacle goose population *Branta leucopsis* from an estimated 267 000 in the 1990s to 770 000 barnacle geese in 2010 (Fox et al. 2010). Growing goose numbers put strong grazing pressure on agricultural pastures, and geese reduce grass yields originally intended for cattle (Patton and Frame 1981, Owen 1990, Vickery 1999). Farmers call for a management of nature reserves in order to optimally accommodate large numbers of grazing geese, as a measure to mitigate goose damage on agricultural land (Owen 1990, Mooij 1991, Percival 1993, Vickery et al. 1994, Vickery 1999).

Livestock grazing is a common tool in nature management (Ebrahimi et al. 2010) and it has been shown to facilitate foraging geese (Van der Graaf et al. 2002, Bos et al. 2005b). With a relatively high stocking density, grass swards are kept short and facilitate the use by grazing geese. (Van der Graaf et al. 2002, Bos et al. 2005b). A short sward enhances intake rates and young shoots are protein rich and provide food of a high nutritional value for small herbivores such as geese (Van de Koppel et al. 1996, Fox et al. 1998, Mayhew and Houston 1999). Previous studies have also shown that canopy height is an important determinant for the distribution of geese on a salt marsh (Drent and Swierstra 1977, Riddington et al. 1997, Vickery 1999), and that the highest numbers of geese will be found at a relatively low canopy height.

Livestock grazing affects canopy height and while the effects of canopy height on geese have been documented, in this study we take the novel approach of determining the effects of four different livestock grazing treatments in a replicated experiment on the distribution of staging geese. With the results from this study we make recommendations on management options for mainland salt marshes with regard to habitat preference of staging geese. In our recommendations we take into account the local goal of increasing biodiversity in the study area. Grazing management resulting in the highest numbers of geese may not necessarily positively affect other bird species, invertebrates or plant diversity.

Methods

Study site

The study site is part of a large connected mainland salt marsh in the north of the Netherlands along the Wadden Sea coast (53 20′N, 5°43′E). The mainland salt marshes of the Netherlands Wadden Sea are largely of anthropogenic origin, because their development has been promoted by the construction of sedimentation fields and ditching (Verhoeven et al. 1980, Esselink et al. 2009). These engineering works nowadays no longer aim at land claim but at conservation of the existing salt marsh. The study area and surrounding marshes are now managed as a nature reserve, with livestock grazing by cattle and horses used as a measure to increase plant diversity. The study area is an important autumn, winter and spring staging site for geese (Fig. 1), especially barnacle geese and, to a lesser extent, brent geese *Branta bernicla*.

Experimental design

In spring 2010 we started a grazing experiment with three 55-ha replicates. Each replicate was divided in four equally sized paddocks with a different grazing treatment in each paddock. The grazing treatments were 1 horse ha^{-1}, 0.5 horses ha^{-1}, 1 cattle ha^{-1} and 0.5 cattle ha^{-1}. The grazing treatments were allocated to the paddocks within a replicate randomly, but we made sure not to place two horse-grazed treatments next to each other, as horses are known to be influenced in their site choice by other horses in adjacent paddocks. Livestock was present from June to October. Within each paddock, we established a transect for goose dropping counts from high to low marsh. High and low marsh were distinguished based on vegetation maps with TMAP typology (Trilateral Monitoring and Assessment Programme; Esselink et al. 2009). Four plots on each transect were placed in vegetation types classified as high marsh vegetation and four plots were placed in low marsh vegetation. The four low marsh plots were always closer to the sea edge than the four high marsh plots. In this manner eight plots per transect, a total of 96 plots, were placed in the entire study area. We marked the middle of the plots with a bamboo stick which protruded not more than 10 cm above the marsh bed.

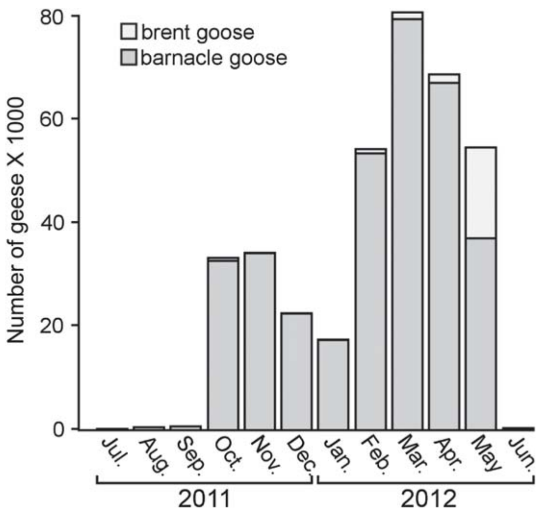

Figure 1. Geese numbers counted during the period of this study in the study area surrounding the experiment show that the study area is extensively used by geese in autumn and spring.

From October to December 2011 (autumn) and from March to May 2012 (spring) we counted goose droppings and removed them from the plots at weekly intervals. For this, we used a 113 cm piece of string, which we attached to the bamboo stick at the centre of each plot. We then circled the stick, counting and removing droppings from a 4-m^2 plot with our string providing a 113-cm radius. Foraging geese defecate at regular time intervals (Owen 1971, Bruinzeel et al. 1997), so the number of goose droppings provides a sound estimate of the total grazing time by geese in a plot (Owen 1971). If the study site was flooded between the weekly dropping counts, these dropping counts were discarded from the analyses, as we could not exclude dropping removal or addition by the tidal water in the preceding interval.

In autumn, three dropping counts, one in October, one in November and one in December, were removed from the analysis, because the study area was flooded prior to the counts. In the spring period, flooding events did not interfere with the dropping counts. We calculated the average number of droppings per weekly interval for each of the 96 plots in both seasons, and used these two average values per plot in the data analyses.

Prior to the first dropping counts in both autumn and spring, the canopy height at each plot was measured to the nearest centimeter four times using a sward stick; for this a styrofoam disc was dropped down along a vertical ruler and the height above ground where it comes to rest was measured (Holmes 1974, Stewart et al. 2001). The canopy height in the plots was used as an explanatory factor for differences in goose visitation between grazing treatments. The four measurements of canopy height at each plot were averaged.

Analysis

To study the experimental effects of the grazing treatments, the dropping counts averaged over weeks were used as the response variable in a generalised linear mixed effects model with grazing treatment, season (autumn/spring), salt-marsh zone (high or low marsh, based on plant species composition), the interaction between grazing treatment and season and the interaction between grazing treatment and salt-marsh zone as the fixed explanatory variables. The three replicates of the experiment were included as a random effect. With the estimates from the model, pairwise comparisons between the treatments were made using the multcomp package (Hothorn et al. 2008) in R.

We hypothesised that the possible treatment effects on goose visitation were generated by impact of livestock on canopy height. For the season with a significant treatment effect, we therefore fitted a different generalised linear mixed effects model in an attempt to explain the variation in the average number of droppings. In this model the explanatory variables were the average canopy height per plot, square canopy height per plot, salt-marsh zone, and all two-way interactions. The three replicates of the experiment were again included as a random effect. Both statistical models were reduced by backwards elimination and by an evaluation of models at every step on the basis of AIC values (Zuur et al. 2009). The statistics were performed in R, using the lme4 package (Bates et al. 2011) to create the linear mixed effects models.

Results

Overall patterns in livestock grazing

The summed numbers of goose droppings found over the entire study area are rather similar in autumn and spring (Appendix 1). With the linear mixed model used in this study we found significantly fewer goose droppings on the low marsh, compared to the high marsh (Table 1).

Experimental treatment effects

We found that the effects of livestock grazing treatment on the number of geese droppings differed per season (Table 1). In autumn we found differences in goose droppings between treatments using pairwise comparisons (Fig. 2). The highest numbers of goose droppings were found in the 1 head ha^{-1} treatments, while the fewest were found in the 0.5 head ha^{-1} treatments (Fig. 2). In the spring we did not find any significant differences in numbers of goose droppings among the treatments. Treatment effect was strongest directly after the livestock had been removed from the experiment in autumn (Table 2).

Does canopy height explain the treatment effects?

The differences in numbers of goose droppings in autumn between grazing treatments could not be explained through average canopy height (Table 3). With an additional linear mixed effects model we did not find any significant relation between average canopy height and the number of goose droppings in autumn ($\chi^2 = 1.45$, $p = 0.23$).

Discussion

Effects of grazing treatments

Livestock grazing treatments with high stocking densities were preferred by staging geese in autumn, while in spring grazing treatments did not seem to affect the distribution of foraging geese over the experiment. This confirms the study by Aerts et al. (1996) who found that barnacle geese were more evenly distributed over different habitat types in spring than in autumn.

At the point of completion of the growing season, at the beginning of autumn, the vegetation on a salt marsh is relatively tall and mature, and plant digestibility is low due to high fibre contents in the shoots (Demment and Van Soest 1985, Aerts et al. 1996). Summer grazing, especially in high stocking densities, keeps the vegetation short and at young growth stages. Grazing induces the growth of secondary shoots and new leaves, which are relatively nitrogen rich

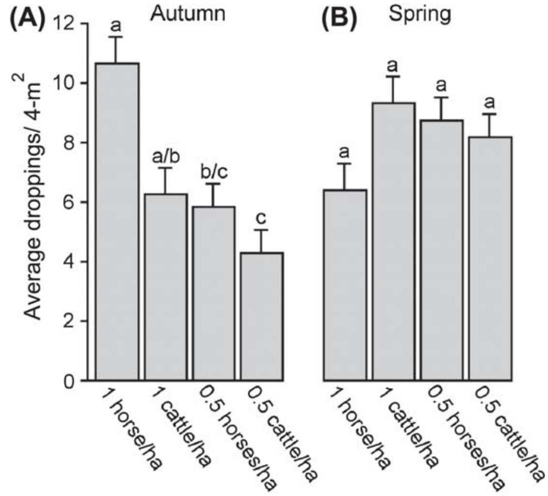

Figure 2. The average number of droppings per 4-m^2 in autumn and spring in four different grazing treatments. The numbers indicate clear differences in the use of different grazing treatments by geese in autumn (A). In spring we did not find significant differences between the same grazing treatments (B). Letters above the bars indicate significant differences between the treatments in each panel. Note that the generalised linear mixed model used to analyse the data takes into account variance between the replicates. The averages shown in the figure, therefore, are a simplification of the underlying data, which may explain why, perceived large differences between the 1 horse ha^{-1} treatment and the 1 cattle ha^{-1} treatment in both autumn and spring are not significant.

Table 1. Significance of fixed model parameters calculated by comparing a full model with models where one of the variables was removed. DF represents the change in degrees of freedom compared to the best model, with 11 DF. AIC shows the AIC values of the models without each variable. AIC value of the best model was 412.80. Models were created with the lme4 package (Bates et al. 2011) in R. Note that the interaction between grazing treatment and marsh is significant, indicating that the effects of grazing treatment vary between the seasons.

Variable	χ^2	DF	AIC	p-value
Marsh zone	14.38	1	421.70	< 0.001
Grazing treatment × Season	28.62	3	431.34	< 0.0001

Table 2. Estimates and standard errors for the generalised linear mixed model showing the effects of grazing treatment on number of goose droppings. Note that the differences in the estimate for the grazing treatments in autumn are larger than the differences in the estimates for the grazing treatments in spring. This suggests that the differences between the treatments are more pronounced in autumn than in spring.

	Estimate	Standard error
1 horse ha^{-1} spring	1.83	0.65
1 cattle ha^{-1} spring	2.23	0.46
0.5 horses ha^{-1} spring	2.09	0.65
0.5 cattle ha^{-1} spring	2.06	0.65
1 horse ha^{-1} autumn	2.32	1.09
1 cattle ha^{-1} autumn	1.92	0.65
0.5 horses ha^{-1} autumn	1.65	1.09
0.5 cattle ha^{-1} autumn	1.18	1.09
low marsh vs high marsh	−0.35	0.09

Table 3. Canopy heights ± SE per treatment, averaged over the three replicates of the experiment.

Grazing treatment	Average autumn	Average spring
1 cattle ha^{-1}	13.8 ± 2.3	2.5 ± 0.3
1 horse ha^{-1}	8.5 ± 1.9	1.6 ± 0.3
0.5 cattle ha^{-1}	21.1 ± 4.6	3.8 ± 0.4
0.5 horses ha^{-1}	3.5 ± 2.6	3.5 ± 0.3

(Demment and Van Soest 1985, Van de Koppel et al. 1996, Fox et al. 1998, Mayhew and Houston 1999), and are high-quality food for small herbivores, such as geese (Ydenberg and Prins 1981, Summers and Critchley 1990). A preference of geese for high-quality food in short canopies (Vickery 1999, Olff et al. 1997), may explain goose preference for the 1 head ha^{-1} grazing treatments in autumn (Fig. 2).

In spring new growth of vegetation occurs over the entire marsh. Previous studies have shown that geese can selectively forage on patches of high quality food in areas of lower quality food (Bos et al. 2005a). In spring geese may, therefore, spread over larger parts of the study area to forage on patches of high quality spring growth. Additionally, in autumn tall vegetation on the salt marsh may be avoided by foraging geese (Aerts et al. 1996), because predators are harder to detect (Underwood 1982, Loughry 1993, Kuijper and Bakker 2008). In winter, the salt marsh is regularly flooded during storms. These flood events destruct and flatten the vegetation and in spring, differences in vegetation structure/canopy height among grazing treatments have become much smaller. Therefore, tall vegetation may no longer present a problem for foraging geese. This corresponds to our finding that the geese use all grazing treatments evenly in spring.

Livestock grazing may also change the plant species composition of a salt marsh (Bakker et al. 1993, Olff et al. 1997) and with that the food availability for geese (Aerts et al. 1996). Previous studies showed that the preferred food of geese differs between seasons. Brent geese prefer *Puccinellia maritima* in winter, *Salicornia* sp. leaves and seeds in autumn and *Trichlogin maritima*, *Plantago maritima* and *Aster tripolium* in spring (Prop and Deerenberg 1991, Summers et al. 1993, Rowcliffe et al. 1995, Van der Wal et al. 2000). This seasonal variation in diet preference combined with effects of livestock grazing on plant-species composition could be an alternative explanation for the effects of livestock grazing in autumn and spring found in the present study. However, Nolte (unpubl.), using data from permanent plots over three years, showed that within the study area within the timeframe of this study, plant-species composition did not change significantly in the grazing treatments. Possibly, the grazing experiment has been running too short to find effects of livestock grazing on plant-species composition (Bakker et al. 1996, Nolte unpubl.).

Implications for management

Salt marshes are a natural habitat for staging geese and grazing management can be applied to conserve salt marsh habitat for geese. Succession of the salt marsh may lead to higher canopy heights and eventually the dominance of the tall grass species *Elytrigia atherica* over a salt marsh (Bakker et al. 1993). This would make salt marshes unsuitable for grazing geese. Grazing management may retard the succession of a salt marsh (Olff et al. 1997), preventing *Elytrigia atherica* from overgrowing a marsh. In this study we show that as long as livestock grazing retards succession, the exact grazing management has little effect on the distribution of geese in spring.

The type of management action recommended for an area is, however, very much dependent on the goals set for nature management. In our study area, the management goal is to increase biodiversity. Biodiversity is higher in moderately grazed areas opposed to intensively grazed areas (Bakker et al. 1993). Moderate grazing leads to a higher structural diversity in the vegetation, which in turn supports higher numbers of invertebrates than intensively grazed sites (Olff and Ritchie 1998, WallisDeVries et al. 1999, Balmer and Erhardt 2000, Dennis et al. 2001, Woodcock et al. 2005, Rickert et al. 2012). Many breeding waders in the study area, have different habitat requirements than geese, and prefer structurally diverse vegetation over short-grazed homogeneous vegetation (Norris et al. 1997, 1998, Milsom et al. 2000, Tichit et al. 2005, Verhulst et al. 2011). Along this line Vickery et al. (1997) describe a management conflict in grazed coastal salt marshes for staging geese and breeding waders. Some waders, such as lapwing *Vanellus* vanellus or dunlin *Calidris alpina*, however, prefer shorter vegetation (Niethammer and Von Blotzheim 1966, Clausen and Kahlert 2010). These species may benefit from high density livestock grazing, which would present no conflict with managing a salt marsh for staging geese, although the trampling of nests is lower when an area is grazed with low stocking density (Beintema and Müskens 1987, Fuller and Gough 1999, Mandema et al. 2013). Trampling of nests may be largely prevented by postponing release dates of cattle to the end of the breeding season.

In those areas where geese themselves are of conservation concern e.g. light-bellied brent geese *Branta bernicla hrota* in Denmark (Clausen et al. 2013), our results show that geese in autumn benefit most from high density livestock grazing by horses. Benefits for geese with a conservation concern should in these areas be carefully weighed against detrimental effects of high density horse grazing for other groups of organisms.

Lastly, livestock grazing may be used to keep geese on salt marshes instead of inland agricultural fields. This will most likely be of little effect; we only found a significant difference between livestock grazing treatments in autumn. The geese inflict most damage to farmland in spring when the grass is growing fastest and is harvested as food for livestock (Mayes 1991, Vickery 1999). Additionally, managing nature areas for geese will, at best, temporarily remove the pressure from agricultural fields. Considering the strong increase in goose numbers over the past decades (Fox et al. 2010), it seems likely that increasing the amount of land that is suitable as foraging habitat for geese will eventually lead to an increase in the number of geese and renewed pressure on farmland. Nonetheless, providing areas of high-quality foraging grounds for geese in autumn may attract geese to salt marshes, at least temporarily relieving some of the stress created by geese on farmland.

Acknowledgements – The study was funded by the 'Waddenfonds'. 'It Fryske Gea' provided us with the possibility to conduct this experimental study on salt marshes within their management and with logistical support. Special thanks go to Gerrit van der Leest and Johannes Westerhof for keeping the experiment running and managing the livestock in the field. We wish to thank Maarten Schrama, Roel van Klink and Remco Hiemstra for help with counting goose droppings. Steffi Nolte provided additional data on canopy heights in autumn. We thank Preben Clausen for useful comments on an earlier version of this manuscript.

References

Aerts, B. A. et al. 1996. Habitat selection and diet composition of greylag geese *Anser anser* and barnacle geese *Branta leucopsis* during fall and spring staging in relation to management in the tidal marshes of the dollard. – Z. Ökol. Naturschutz 5: 65–75.

Bakker, J. P. et al. 1993. Salt marshes along the coast of the Netherlands. – Hydrobiologia 265: 73–95.

Bakker, J. P. et al. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? – J. Veg. Sci. 7: 147–156.

Balmer, O. and Erhardt, A. 2000. Consequences of succession on extensively grazed grasslands for central European butterfly communities: rethinking conservation practices. – Conserv. Biol. 14: 746–757.

Bates, D. et al. 2011. Linear mixed-effects models using S4 classes. R package ver. 0.999375-42. <http://CRAN.R-project.org/package = lme4>

Beintema, A. J. and Müskens, G. J. D. M. 1987. Nesting success of birds breeding in Dutch agricultural grasslands. – J. Appl. Ecol. 24: 743–758.

Bos, D. et al. 2005a. The relative importance of food biomass and quality for patch and habitat choice in brent geese *Branta bernicla*. – Ardea 93: 5–16.

Bos, D. et al. 2005b. Utilisation of Wadden Sea salt marshes by geese in relation to livestock grazing. – J. Nat. Conserv. 13: 1–15.

Bruinzeel, L. W. et al. 1997. Scaling metabolisable energy intake and daily energy expenditure in relation to the size of herbivorous waterfowl: limits set by available foraging time and digestive performance. – Van Zee tot Land 65: 111–132.

Clausen, P. and Kahlert, J. (eds) 2010. Ynglefugle i Tøndermarsken og Margrethe Kog 1975–2009. En analyse af udviklingen i fuglenes antal og fordeling med anbefalinger til forvaltningstiltag. – Danmarks Miljøundersøgelser, Aarhus Univ. – Faglig rapport fra DMU nr. 778. <www.dmu.dk/Pub/FR778.pdf>.

Clausen, K. K. et al. 2013. Grazing management can counteract the impacts of climate change-induced sea level rise on salt marsh-dependent waterbirds. – J. Appl. Ecol. 50: 528–537.

Demment, M. W. and Van Soest, P. J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. – Am. Nat. 125: 641–672.

Dennis, P. et al. 2001. The effects of varied grazing management on epigeal spiders, harvestman and pseudoscorpions of *Nardus stricta* grassland in upland Scotland. – Agric. Ecosyst. Environ. 86: 39–57.

Drent, R. H. and Swierstra, P. 1977. Goose flocks and food finding: field experiments with barnacle geese in winter. – Wildfowl 28: 15–20.

Ebrahimi, A. et al. 2010. A herbivore specific grazing capacity model accounting for spatio temporal environmental variation: a tool for a more sustainable nature conservation and rangeland mangement. – Ecol. Modell. 221: 900–910.

Esselink, P. et al. 2009. Salt marshes. – In: Marencic, H and de Vlas, J. (eds), Thematic report no. 8. Quality Status Report 2009. WaddenSea Ecosystem no. 25.

Fox, A. D. et al. 1998. The effects of simulated spring goose grazing on the growth rate and protein content of *Phleum pratense* leaves. – Oecologia 159: 116–154.

Fox, A. D. et al. 2010. Current estimates of goose population sizes in western Europe, a gap analysis and assesment of trends. – Ornis Svecica 20: 115–127.

Fuller, R. J. and Gough, S. J. 1999. Changes in sheep numbers in Britain – implications for bird populations. – Biol. Conserv. 91: 73–89.

Holmes, C. W. 1974. The Massey grass meter. – In: Dairy farmer annual. Massey Univ., Palmerston North, New Zealand, pp. 26–30

Hothorn, T. et al. 2008. Simultaneous inference in general parametric models. – Biometrical J. 50: 346–363.

Kuijper, D. P. J. and Bakker, J. P. 2008. Unpreferred plants affect patch choice and spatial distribution of European brown hares. – Acta Oecol. 34: 339–344.

Loughry, W. J. 1993. Determinants of time allocation by adult and yearling black-tailed prairie dogs. – Behaviour 124: 23–43.

Mandema, F. S. et al. 2013. Livestock grazing and trampling of birds' nests: an experiment using artificial nests. – J. Coastal Conserv. 17: 409–416.

Mayes, E. 1991. The winter ecology of Greenland white-fronted geese *Anser albifrons flaviostris* on semi-natural grassland and intensive farmland. – Ardea 79: 295–304.

Mayhew, P. and Houston, D. 1999. Effects of winter and early spring grazing by wigeon *Anas penelope* on their food supply. – Ibis 141: 80–84.

Milsom, T. P. et al. 2000: Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. – J. Appl. Ecol. 37: 706–727.

Mooij, J. H. 1991. Hunting – a questionable method of regulating goose damage. – Ardea 79: 219–225.

Niethammer, G. and Von Blotzheim, U. N. G. 1966. Handbuch der Vögel Mitteleuropas. – Akademische Verlagsgesellschaft, Wiesbaden, Germany.

Norris, K. et al. 1997. The density of redhshank *Tringa totanus* breeding on salt-marshes of the Wash in relation to habitat and its grazing management. – J. Appl. Ecol. 34: 999–1013.

Norris, K. et al. 1998. Is the density of redshank *Tringa totanus* nesting on salt marshes in Great Britain declining due to changes in grazing management? – J. Appl. Ecol. 35: 621–634.

Olff, H. and Ritchie, M. E. 1998. Effects of herbivores on grassland plant diversity. – Trends Ecol. Evol. 13: 261–265.

Olff, H. et al. 1997. Vegetation succession and herbivory in a salt marsh – changes induced by sea level rise and silt deposition along an elevational gradient. – J. Ecol. 85: 799–814.

Owen, M. 1971. Selection of feeding site by white-fronted geese in winter. – J. Appl. Ecol. 8: 905-917.

Owen, M. 1990. The damage-conservation interface illustrated by geese. – Ibis 132: 238–252.

Patton, D. L. H. and Frame, J. 1981. The effects of grazing in winter by wild geese on improved grassland in west Scotland. – J. Appl. Ecol. 18: 311–325.

Percival, S. M. 1993. The effects of reseeding, fertilizer application and disturbance on the use of grasslands by barnacle geese, and the implication for refuge management. – J. Appl. Ecol. 30: 437–443.

Prop, J. and Deerenberg, C. 1991. Spring staging in brent geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. – Oecologia 87: 19–28.

Rickert, C. et al. 2012. α- and β-diversity in moth communities in salt marshes is driven by grazing management. – Biol. Conserv. 146: 24–31.

Riddington, R. et al. 1997. The selection of grass swards by brent geese *Brenta bernicla*: interactions between food quality and quantity. – Biol. Conserv. 81: 153–160.
Rowcliffe, J. M. et al. 1995. Cyclic winter grazing patterns in brent geese and the regrowth of salt-marsh grass. – Funct. Ecol. 9: 931–941.
Stewart, K. et al. 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. – J. Appl. Ecol. 38: 1148–1154.
Summers, R. W. and Critchley, C. N. R. 1990: Use of a grassland and field section by brent geese *Brenta bernicla*. – J. Appl. Ecol. 27: 834–846.
Summers, R. W. et al. 1993. Utilisation, diet and diet selection by brent geese *Branta bernicla bernicla* on salt marshes in Norfolk. – J. Zool. 231: 249–273.
Tichit, M. et al. 2005. The role of grazing in creating suitable sward structures for breeding waders in agricultural landscapes. – Livestock Prod. Sci. 96: 119–128.
Underwood, R. 1982. Vigilance behaviour in grazing African antelopes. – Behaviour 79: 81–107.
Van de Koppel, J. et al. 1996. Patterns of herbivory along a productivity gradient: an empirical and theoretical investigation. – Ecology 77: 736–745.
Van der Graaf, A. J. et al. 2002. Short-term and long-term facilitation of goose grazing by livestock in the Dutch Wadden Sea area. – J. Coastal Conserv. 8: 179–188.
Van der Wal, R. et al. 2000. Onfacilitation between herbivores: how brent geese profit from brown hares. – Ecology 81: 969–980.
Verhoeven, B. et al. 1980. Human influences on the landscape of the Wadden Sea area. – In: Dijkema, K. S. et al. (eds), Geomorphology of the Wadden Sea area. Rep. 1 of the Wadden Sea Working Group. – Balkema, Rotterdam.
Verhulst, J. et al. 2011. Seasonal distribution of meadow birds in relation to in-field heterogeneity and management. – Agric. Ecosyst. Environ. 142: 161–166.
Vickery, J. A. 1999. Managing grassland for wild geese in Britain: a review. – Biol. Conserv. 89: 93–106.
Vickery, J. A. et al. 1994. The management of grass pastures for brent geese. – J. Appl. Ecol. 31: 282–290.
Vickery, J. A. et al. 1997. Managing coastal grazing marshes for breeding waders and overwintering geese: is there a conflict? – Biol. Conserv. 79: 23–34.
WallisDeVries, M. F. et al. 1999. The importance of scale of patchiness for selectivity in grazing herbivores. – Oecologia 121: 355–363.
Woodcock, B. A. et al. 2005. Grazing management of calcareous grasslands and its implications for the conservation of beetle communities. – Biol. Conserv. 125: 193–202.
Ydenberg, R. C. and Prins, H. H. T. 1981. Spring grazing and the manipulation of food quality by barnacle geese. – J. Appl. Ecol. 18: 443–453.
Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R. – Springer.

Appendix 1

The average number of droppings per week per 4-m^2 plot in the whole experiment. Note that in autumn three counts were removed from the analysis, because the study area was flooded in the period prior to the weekly count (NA).