Active land use improves reindeer pastures: evidence from a patch choice experiment

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Keywords
agriculture; competition; coupled ecosystems; encroachment; facilitation; sheep grazing; Rangifer tarandus; space use.

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Editor: Andrew Kitchener

Received 24 April 2009; revised 30 June 2009; accepted 8 July 2009

Abstract
The industrialization of agriculture in western societies has often led to either intensified use or abandonment of farmland and open pastures, but experimental evidence on how the dynamics of farmed ecosystems affect space use by large herbivores is limited. We experimentally manipulated farmland patches with cutting and (early summer) low- and high-intensity domestic sheep Ovis aries grazing according to traditional use in north Norway. After treatments, grazing reindeer Rangifer tarandus were exposed to the pastures the subsequent fall (2 months after treatments) and spring (11 months after treatments) as they typically do on their migratory route between summer and winter ranges. The experiment was conducted over 2 subsequent years. We predicted that sheep grazing on farmland during early summer may affect the critical fall and spring range conditions for reindeer either through negative (delayed competition) or positive (grazing facilitation) interactions. We found that the most marked effect of land use on the grazing pattern of reindeer was between no use (the control treatment) and all the other management options involving active land use. The grazing reindeer avoided the pastures no longer in use likely due to senescent plant material. There was a tendency that the lower intensity sheep grazing patches attracted more reindeer than the highest intensity use. These results highlight not only the general principle that large-scale agricultural changes may affect large herbivores in natural ecosystems, but they also increase our understanding of grazing facilitation as a mechanism in large herbivore assemblages.

Introduction
Over much of Europe, the industrialization of agriculture in the last century has often led to either intensified use or abandonment of farmland (Bakker & Berendse, 1999). Such land-use changes have marked effects on the pattern of biodiversity (Gottschalk et al., 2007), and the dynamics of natural and farmed ecosystems are frequently coupled (Liu et al., 2007). Large mammals as a group are often reported to be strongly affected by land-use change (Macdonald et al., 2007; Gorman & Raffaelli, 2008). Although farmlands at northern latitudes are often used for (seasonal) grazing and/or to produce winter fodder for livestock, our knowledge of the effects of this land utilization on cervids is limited. Introduced domestic species may have niches similar to the wild herbivores and livestock often occur in high densities. Some of the most well-documented cases of competition at northern latitudes come from interactions between wild and domestic species using open ranges during the same season (Clutton-Brock & Albon, 1989; Kie et al., 1991; Loft, Menke & Kie, 1991; Loft, Kie & Menke, 1993). However, in cases where wild and domestic stocks do not use the same areas during the same season, the nature of the interaction may be more difficult to predict. One herbivore may improve range quality for subsequent feeding by another herbivore if grasses are allowed to re-grow, so-called grazing facilitation (Arsenault & Owen-Smith, 2002). The mechanisms of facilitation may occur either in the short term (within year) or in the long term (succession over years) (McNaughton, 1979; van der Graaf, et al., 2002).

In northern grazing systems, the late spring and summer is by far the main growing season, being highly productive compared with winter, fall and early spring. Uses of farmland include mowing to produce winter fodder for cattle and sheep, and the farmland is often also used for early grazing by sheep before sheep are released onto open ranges. Because sheep grazing on farmland is often restricted to either early (or very late) in the growing season, the potential exists for between-season facilitation, that is that early summer grazing by sheep improve pastures for other herbivores the following fall and spring. Herds of reindeer in northern Norway migrate seasonally between coastal summer ranges and inland winter ranges. On the migration in spring and autumn, they are frequently found grazing on farmland used for sheep grazing and/or hay production. As for many areas in Europe, the current land use is changing...
rapidly, and it is urgent to know how land use affects reindeer. In particular, in Norway, controversy exists over how reindeer *Rangifer tarandus* are affected by sheep *Ovis aries* grazing (Colman, 2000; Mysterud & Austrheim, 2008), as their dietary overlap is high (∼60%; Skogland, 1989; Mysterud, 2000).

In an experimental setup, we tested whether (fall and spring) patch choice of reindeer would be affected by previous (summer) grazing pressure by sheep and the alternative land-use practices being mowing or no use. For the sheep–reindeer interaction, we predicted P1 avoidance as being indicative of competitive interactions and P2 selection as being indicative of grazing facilitation.

### Materials and methods

#### Study area

The study area is a semi-open farm landscape in Sopnes at sea level, c. 5 km from Langfjordbotn, Finnmark County, Norway (69°59’N, 22°19’E). The area has not been cultivated (plowed, cut or heavily grazed) for over 15 years, representing the common abandoned, ‘old-pasture’ characteristic of the surrounding area and much of the coastal landscape of Finnmark in general. The area has only been sporadically used for low-density reindeer summer grazing and harvested for cattle fodder during 2 years, 5 years before this study. The vegetation was dominated by *Deschampsia cespitosa*, *Alopecurus pratensis*, *Agrostis capillaris*, *Poa pratensis* and *Trifolium repens*. The experimental areas were situated on west-facing slopes surrounded by trees and high shrubs.

#### Experimental design

The setup and fencing was a four-by-four latin square design (Gordon, 1988; Rhodes & Sharrow, 1990; Alpe, Kingery & Mosley, 1999). We ran two replicates each on a 0.3 ha field, termed ‘site’. At each site, there were four replicates of the treatments cutting (mowing), low density of sheep, high density of sheep and a control (i.e. 16 plots for each site; Fig. 1). Site A was 46 × 70 m, providing a plot size of 11.5 × 17.5 m, and Site B was 32 × 100 m, yielding a plot size of 8 × 25 m. In the low and high sheep grazing treatments, respectively, two (ewe and yearling) and four (ewe and three lambs) sheep grazed for 10 days in the beginning of July in 2003 and 2004. In the cutting treatment performed on the same day as sheep were removed, a hay mower cut vegetation to 5 cm in height and the cut grass was removed, similar to what is done when harvesting winter fodder for livestock for round-bales. The controls were left untreated. A given plot received the same treatment throughout the experiment. The fencing within the sites was then removed after treatment and before the introduction of four reindeer (2-year-old males) into each site. In reindeer husbandry, young males represent the main source of meat for harvest and sales. As young males have about the same body size as adult females (in contrast to large adult males), we expect similar grazing behaviour (e.g. Ruckstuhl & Neuhaus, 2005). The reindeer grazed undisturbed for 2 weeks in fall 2003, spring and fall 2004 and spring 2005. Observations of their patch choice were recorded during all these four periods.

#### Direct observation method

The reindeer feeding activities were recorded using the instantaneous scan sampling technique (Altmann, 1974). Observations were made from towers (see supporting information). The observer remained still for 10 min after entering the tower to avoid possible bias caused by their approach. Observations were mostly made by eyesight, although binoculars were used when necessary. Location (plot number) and activities were recorded for each individual reindeer every 10 min. We classified the activities as feeding, standing, walking, running and lying. Because we aimed to test the patch choice related to feeding, the observation period was terminated when more than two animals lay down. The total sample size was 4752 observations from 30 to 32 days and from both the sites.

#### Statistical analyses

We only used data when reindeer were actively feeding. Data are thus feeding observations of four reindeer at the same time. We further pooled the data per day and treatment for each site to avoid strong temporal dependency. This reduced the sample size to 244 data entries. In initial modeling attempts, we tried both binomial and Poisson distributions. However, model fit was low, likely because reindeer do not graze independent of each other, so that the synchronous behaviour does not make this a binomial or a
Poisson process. Therefore, as a response variable, we used proportion of time grazing within each treatment and site for a given day, and transformed with the common standard for proportional data (arc sine-sqrt). Because this yielded varying numbers of reindeer in each estimate of the proportion of grazing time, we weighted the estimate with the (sqrt) number of observations per day. We compared this with results using a quasibinomial distribution, which takes care of the overdispersion found when using a binomial distribution. We used mixed-effect models with 'site' as a random term (Pinheiro & Bates, 2000), using the library lme4 in R. In addition to the treatment variable, we also entered season (spring, fall), year (2003, 2004 and 2005) and time period (fall 2003, spring 2004, fall 2004 and spring 2005) as well as their first-order interactions with the treatment variable. The most parsimonious model based on the AIC was used for inference using a manual selection procedure (Burnham & Anderson, 2002). All analyses were performed in R version 2.6.0 (R Development Core Team, 2007).

Results

There was a marked effect of the treatment on grazing by reindeer (Table 1; Fig. 2). Reindeer spent least time grazing in the controls, while all the other treatments attracted more reindeer grazing. Within the land-use treatments, there was a (non-significant) tendency wherein the lowest intensity use attracted more reindeer than higher intensity use in the sequence: low sheep > high sheep > cutting. This result was robust to the choice of model, as using a quasibinomial distribution and a logit link yielded similar results. Adding interactions between treatment and either year (AIC = 74.13) or time period (AIC = 37.63) resulted in less parsimonious models (only treatment: AIC = 93.64), indicating that the treatment effect was stable over time.

Discussion

Reindeer in north Norway often use agricultural pastures on their migration between summer and winter ranges, leading to a coupling of farmland and natural ecosystems in the region. The most marked effect of land use on reindeer grazing pattern was between no use (the control treatment) and all the other management options involving active use. Pastures grazed by a few or many sheep and mowing in early summer attracted far more grazing reindeer during subsequent autumn and spring than pastures no longer in use, with a tendency for low-intensity use to attract the highest number of reindeer (Fig. 2). These results have implications not only for how large-scale agricultural changes may affect large herbivores in natural ecosystems, but they also increase our understanding of grazing facilitation as a mechanism in large herbivore assemblages. The time scale of interaction is important, as facilitation in one short season may be countered by competition in another season or vice versa (Arsenault & Owen-Smith, 2002; Kujiper et al., 2008). Because reindeer and sheep do not use the pastures during the same season, this may be a case of inter-seasonal grazing facilitation. We have no quantitative documentation of how large the effect of a few weeks’ grazing on pastures might be on the overall reindeer herd productivity. However, spring grazing on pastures is just before calving, which is known to be a critical time for many northern large herbivores. For example, red deer were most affected by climate during late pregnancy (Sims et al., 2007), suggesting that the grazing periods of reindeer on pastures in spring might be especially important. Good grazing conditions in autumn are also important for reindeer growth and hence meat production before harvest in early winter (November and December).

The main evidence for facilitation among northern large herbivores is limited to demonstrating improved forage quality of regrowth (review in Arsenault & Owen-Smith, 2002). In the short term, moderate grazing may improve the quality by keeping especially graminoids in a young phenological stage, which is usually of a higher quality than later and senescent stages (McNaughton, 1984; for northern areas: Alpe et al., 1999; Hebblewhite, Merrill & McDermid, 2008). Clipping experiments and comparisons of grazed and ungrazed meadows have shown the potential of arctic

Table 1 Parameter estimates from the best linear mixed-effects model of (transformed) proportion of grazing reindeer Rangifer tarandus in Finnmark, Norway, for different land-use treatments

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Estimate</th>
<th>Lower</th>
<th>Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0.4053</td>
<td>0.3570</td>
<td>0.4535</td>
</tr>
<tr>
<td>Cutting</td>
<td>0.5100</td>
<td>0.4618</td>
<td>0.5583</td>
</tr>
<tr>
<td>High density of sheep</td>
<td>0.5506</td>
<td>0.5024</td>
<td>0.5988</td>
</tr>
<tr>
<td>Low density of sheep</td>
<td>0.5548</td>
<td>0.5066</td>
<td>0.6031</td>
</tr>
</tbody>
</table>

The model includes a random intercept for site (sd = 3.04 \times 10^{-6}). Addition of interactions resulted in less parsimonious models.

CI, confidence interval.
graminoids to respond positively to grazing (e.g. Ouellet, Boutin & Heard, 1994; Van der Wal et al., 2000). Demonstrating increased plant quality is not sufficient in order for grazing facilitation to occur; the second species must actually choose to graze the site already grazed by the first species. When it comes to predicted responses of the animal populations, the patterns are more limited.

A key aspect of interspecific interactions is therefore patch choice as studied in our case. There are some experimental data manipulating vegetation and observing the resulting space use of herbivores (Gordon, 1988; Van der Wal et al., 2000; Cromsigt & Olff, 2006). Van der Wal et al. (2000) reported that brown hares Lepus europaeus facilitated grazing by brent geese Branta bernicla in salt marshes in the Netherlands by preventing regrowth of the shrub Atriplex portulacoides. Clipping experiments mimicking hare grazing were utilized by brent geese more than twice as frequently as untreated control plots. Positive spatial correlations between reindeer and lemmings Lemmus lemmus were found in Finnmark, Norway (Bråthen et al., 2007; Ims et al., 2007). On the Isle of Rum, Scotland, red deer Cervus elaphus selected summer grazing areas grazed by cattle the previous winter (Gordon, 1988). Our experiment was conducted in a graminoid-rich, mostly soft, moist soil, during summer on coastal pasture. The regeneration of forage is high, and no negative effects of trampling are expected. Avoidance of faeces has been reported as a significant factor in patch choice of herbivores (e.g. Hutchings et al., 1999, 2001; Van der Wal et al., 2000). Parasites are frequently species specific, but semi-domestic reindeer avoid fresh sheep faeces when mixed with their pellets (Moe et al., 1999) and when grazing on outdoor pastures (Colman et al., 2001). The high degree of use of the high sheep density patches indicates no clear aversion towards sheep or reindeer faeces, which was also supported by direct observations. Sheep were removed from pasture about 2 months before reindeer in fall and over 10 months before reindeer entered in the following spring. This suggests that reported aversions of sheep faeces by reindeer (Moe et al., 1999; Colman et al., 2001) are rather short-term effects. The high density of faeces on the intensively grazed areas may instead improve these pastures further by fertilizing the herbaceous vegetation (Moe & Wegge, 2008).

Sheep husbandry can affect wildlife in several ways depending in part on which stages of the production cycle they overlap with a given wildlife species. Sheep in Norway are typically indoors during winter, and they start the grazing season with a short period on farmland in early summer, which is the focus of this experiment. These farmland areas are important in many cases, being at a low elevation and the first to be snow-free in spring. After this, sheep are released to open pastures, where they are free ranging. Depending on the stocking rate, sheep can then compete with cervids, as for example shown for red deer in Scotland (Clutton-Brock & Albon, 1989). However, during the open grazing period, the farmland is used to produce hay for winter fodder for sheep. Access to a high proportion of farmland was beneficial for red deer along the west coast of Norway, yielding a positive correlation with sheep number and red deer body mass most likely being an indirect benefit (Mysterud et al., 2002). In some cases, sheep grazing is used to improve conditions for wildlife (Rhodes & Sharrow, 1990; Mosley, 1994) and birds (Løe et al., 2007).

Our study highlights that lack of maintenance and the re-growth (bush encroachment) of cultural landscape in parts of northern Norway are likely to affect reindeer negatively. These changes have been swiftly advancing in the past 20–30 years due to the declining number of cattle and sheep farms, resulting in less harvesting of the original fields and less pasture utilization by sheep (Elgvin, Colman & Moe, 2004). Such neglected cultural landscapes could maintain a higher productivity by implementing a dual-species management scheme for sheep and reindeer. There are important economical and social benefits of strong and productive reindeer herds, as these herds are semi-domestic and herded by indigenous Sami people. However, this is not necessarily the case in all areas. Agricultural land is legally not reindeer grazing land, and reindeer grazing on pastures is known to cause severe conflicts in regions with a more active farming tradition than in our study area. Further, regulation and limitation of reindeer herd productivity varies regionally (Tveraa et al., 2007). Any effect of pasture grazing on the reindeer will likely depend on the availability of pastures. Agricultural land is a dominant part of the area below the tree line along the coastal areas in northern Finnmark, but not in the alpine areas in the inland also hosting much reindeer (Bråthen et al., 2007). Knowledge of seasonal limiting factors, pasture availability and use and social attitudes towards semi-domestic reindeer in a specific region will therefore be important before implementing such dual-species management schemes.

Acknowledgements

We are grateful to the families Gaup, Jensen and Mikalsen for their trust and extensive support. Alex Mann, Sindre Ef testøl, Ute Hånsch and Ole Petter Hansen provided excellent field assistance. This study was funded through grants by the Research Council of Norway over the programme ’Changing landscapes’, the Reindeer Management Fund and the Trygve Gotaas Fond. We thank one anonymous referee for several useful comments to a previous draft of the paper.

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