



Original article

Experimental evidence that livestock grazing intensity affects the activity of a generalist predator



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ABSTRACT

Grazing by domestic ungulates has substantial impacts on ecosystem structure and composition. In grasslands of the northern hemisphere, livestock grazing limits populations of small mammals, which are a main food source for a variety of vertebrate predators. However, no experimental studies have described the impact of livestock grazing on vertebrate predators. We experimentally manipulated sheep and cattle grazing intensity in the Scottish uplands to test its impact on a relatively abundant small mammal, the field vole (*Microtus agrestis*), and its archetypal generalist predator, the red fox (*Vulpes vulpes*). We demonstrate that ungulate grazing had a strong consistent negative impact on both vole densities and indices of fox activity. Ungulate grazing did not substantially affect the relationship between fox activity and vole densities. However, the data suggested that, as grazing intensity increased i) fox activity indices tended to be higher when vole densities were low, and ii) the relationship between fox activity and vole density was weaker. All these patterns are surprising given the relative small scale of our experiment compared to large red fox territories in upland habitats of Britain, and suggest that domestic grazing intensity causes a strong response in the activity of generalist predators important for their conservation in grassland ecosystems.

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1. Introduction

Domestic ungulate grazing intensity has important impacts on natural communities of grassland ecosystems (Diaz et al., 2007; Fleischner, 1994; Patra et al., 2005; Vickery et al., 2001). In temperate grasslands of the northern hemisphere, increasing livestock grazing has been shown to reduce small mammal abundance across an extensive geographical area that spans from Scandinavia to the Mediterranean (Evans et al., 2006; Munoz et al., 2009; Schmidt et al., 2005; Steen et al., 2005; Torre et al., 2007; Wheeler, 2008). Many vertebrate predators show a strong functional and numerical response to small mammal densities at large spatial scales (e.g. (Hanski et al., 1991; Sundell et al., 2004)), and thus livestock grazing could potentially lead to reductions in a variety of predator populations in these systems (Wheeler, 2008). However, to date there is no experimental evidence of how grazing in these systems affects vertebrate predators.

Here we use data from a replicated grazing experiment in the uplands of Scotland to quantify the impact of grazing intensity on cyclically-fluctuating field voles and an archetypal generalist vole predator in these ecosystems, the red fox (Kjellander and Nordstrom, 2003; Leckie et al., 1998; Lindstrom, 1989; O'Mahony et al., 1999). We use this model system to test the hypothesis that livestock grazing intensity impacts on the activity of generalist vertebrate predators in upland grasslands. Specifically, we predicted that increasing grazing intensity would reduce field vole densities, but that red fox activity would peak at intermediate grazing intensities where the combination of low vegetation cover and intermediate vole abundance might maximise vole availability. Thus, we predicted that fox activity at any given vole density would be larger at intermediate grazing intensities.

2. Materials and methods

2.1. Field methods

2.1.1. Experimental set up

We set up a grazing experiment in Glen Finglas, Scotland (56°16'N, 4°24'W), with four different grazing treatments applied

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to 24 × 3.3 ha plots mimicking realistic management alternatives (Scottish Agricultural College, 2008) and following a replicated, randomized, block design (see (Evans et al., 2006)). Plots were distributed across an altitudinal gradient (220–500 m above sea level) in three clusters of approx 26 ha each and 4 km apart. Each cluster comprised two replicates (hereafter referred as “blocks”) of every grazing treatment: I) 2.7 ewes ha⁻¹; II) 0.9 ewe ha⁻¹; III) mixed sheep and cattle equivalent to 0.9 ewe ha⁻¹; IV) ungrazed. Grazing took place annually from March till October. The site is dominated by continuous acidic upland grasslands, where live-trapping techniques reveals that the field vole is the most abundant vertebrate herbivore prey (Villar, 2010). Though the presence of foxes was evident during the course of the study, systematic behavioural observations of avian predators had to be abandoned due to the low number of sightings recorded. Our study was restricted to the winter months, when there is a scarcity of alternative prey for these predators at the site, other mammals, invertebrates and birds are rare, and seasonal ground nesting birds are absent, though occasional sheep and deer carrion may provide alternative food for foxes. Indices analysed here were collected biannually (October and March 2005–2008). This period roughly corresponds to the low (winter 2005–2006), increase (winter 2006–2007) and peak phases (winter 2007–2008) of a vole population cycle (Figs. 1 and 2).

2.1.2. Vole density estimates

Field vole abundance was estimated using a Vole Sign Index (VSI) previously calibrated by capture-recapture (Lambin et al., 2000) collected biannually (October and March 2005–2008). Every plot had a regular grid of 25 sampling points 40 m apart (except for October 2005 when only five points were sampled), each of them sampled with three replicate 25 cm × 25 cm quadrats. The presence or absence of fresh (green and un-oxidised) grass clippings or droppings was recorded. A VSI score was derived as the proportion of points per plot showing any positive sign, and VSI scores from October and subsequent March were averaged to obtain mean VSI estimates for the winter period.

2.1.3. Fox activity indices

An index of fox activity was estimated from fox scat abundance (Sadler et al., 2004; Webbon et al., 2004). Three regularly spaced line transects were walked by N. Villar across each plot biannually

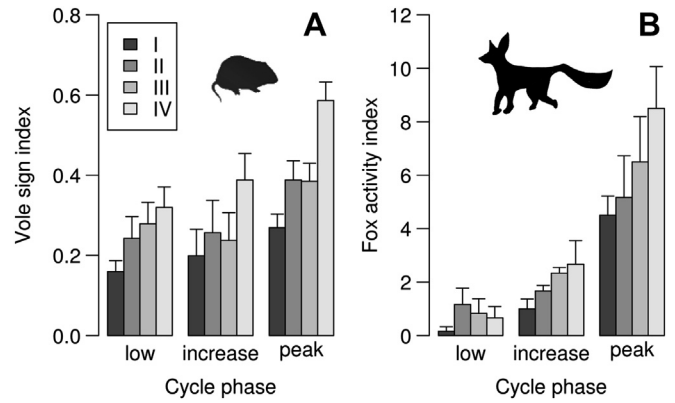


Fig. 2. The effects of grazing treatment and cycle phase on (a) VSI and (b) fox activity indices. The figure shows error bars above treatment means. Treatments: I) 2.7 ewes ha⁻¹; II) 0.9 ewe ha⁻¹; III) mixed sheep and cattle equivalent to 0.9 ewe ha⁻¹; IV) ungrazed.

(October and March 2005–2008), from one extreme of the plot to the other and perpendicular to the orientation of the slope, following the same GPS tracks throughout the study period (total 3000 m per treatment). Outer transects were placed at least 10 m from fence lines to minimize edge effects, and the distance between transects was the same amongst plots in the same replicate block but variable between blocks (minimum 51 m, maximum 98 m). We searched for scats within 5 m of either side of transects, and recorded the location and distance of all the samples found. Scats found were removed, frozen and later identified independently by N. Villar and two expert field ecologists following the guidelines of Bang and Dahstrom (2001). Uncertain identifications (19 out of 230 scats) were discarded from the analyses. Scats accumulated during the October-to-March period were assumed to be indicative of fox activity during winter months.

2.2. Statistical analyses

2.2.1. Validation of equal detection probabilities

We accounted for the possibility of directional biases in scat detection probability between treatments and plots by using standard distance sampling techniques (Buckland et al., 2001) in

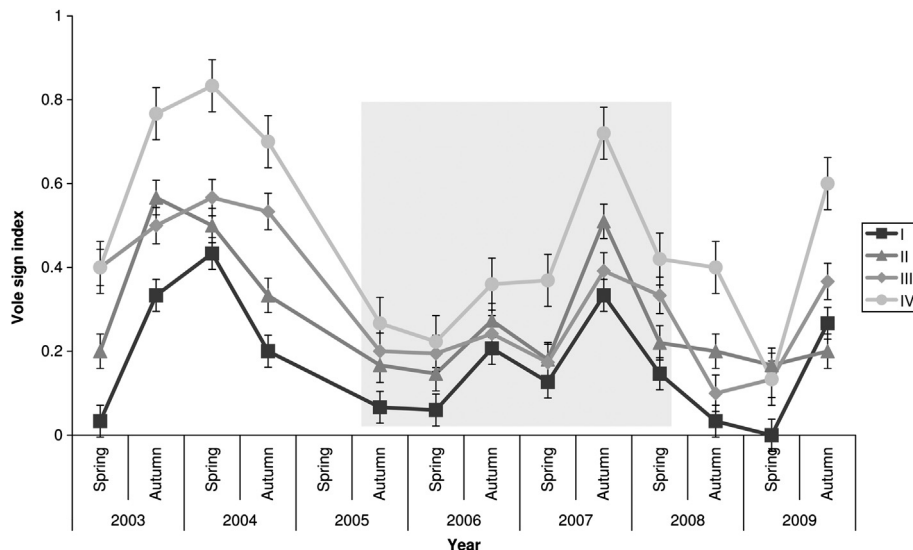


Fig. 1. Long-term VSI fluctuations in the Glen Finglas experiment, with the period analysed in this manuscript highlighted (October 2005–March 2008). The figure shows treatment means and standard errors for all treatments: I) 2.7 ewes ha⁻¹; II) 0.9 ewe ha⁻¹; III) mixed sheep and cattle equivalent to 0.9 ewe ha⁻¹; IV) ungrazed.

software Distance 5.0 (Thomas et al., 2006) (details in Appendix S1, Supporting Information).

2.2.2. The impact of grazing on winter vole densities and fox activity indices

We tested whether grazing intensity had consistent effects on field vole densities across different phases of the cycle by modelling VSI estimates as a function of treatment and phase of the cycle (year) and the interaction between them. We used generalised linear mixed models (GLMMs (Pinheiro and Bates, 2002)) with Gaussian errors and block as a random effect to control for correlations between plots within the same block. The fit of simplified versions of the model to data was explored using information theory i.e. AIC values and weights, and parameter coefficients reported were model averaged (Burnham and Anderson, 2002). The effect of grazing on fox activity indices was examined in a similar fashion: we used fox scat abundance as the response variable and Poisson errors, otherwise following the same model structure, explanatory variables and random effects as for VSI. Statistical analyses were computed in R version 2.12.0 (R Development Core Team, 2010), using the statistical package *lme4* (Bates and Maechler, 2010).

2.2.3. The impact of grazing in the relationship between winter fox activity indices and vole densities

We examined how grazing affected fox activity as a function of vole density by modelling fox activity indices as a function of VSI estimates and treatment and the interaction between them, using GLMMs with block as a random effect. Exploration of this model suggested large residuals and evidence of heteroscedasticity, which may lead to violation of assumptions underlying statistical analyses (Zuur et al., 2007). We fixed this by log transforming fox activity indices, which resolved the problem satisfactorily. Subsequently the fit of simplified versions of the model to data was explored again using information theory.

A side effect of this kind of transformations is that they tend to reduce the power to detect differences between treatments (Zuur et al., 2007). Thus, we additionally explored differences between treatments by modelling logged fox activity indices as a function of VSI estimates for every treatment separately, using GLMMs with block as a random effect and Gaussian errors, and investigated differences between the resulting treatment-specific model estimates.

3. Results

3.1. Validation of equal detection probabilities

The distance sampling analysis supported the assumption that the probability of detecting scats was the same across all plots and treatments (Table A1 in the Appendix).

3.2. The impact of grazing on winter vole densities and fox activity indices

Ungulate grazing caused a strong reduction in both winter vole densities and fox activity indices. In analyses of both vole abundance and fox activity, the models with an additive effect of grazing and phase of the cycle outweighed any alternative model, gathering more than 95% of the possible support ($=0.995$ and $=0.973$ for grazing effects on VSI and fox activity indices, respectively, Tables 1 and 2). Vole densities and fox activity indices increased substantially with decreasing grazing intensity (Fig. 2a and b): moving from high grazing intensities (treatment I) to ungrazed (treatment IV) led to an increase in VSI between 172% and 248% depending on the phase of the cycle, and to an increase in fox activity indices of 209%

Table 1

Model selection results of the effects of grazing treatment and vole cycle phase on VSI and fox activity indices. The number of observations was 72.

Model	VSI			Fox activity index		
	AICc ^a	ΔAICc ^b	w _i ^c	AICc	ΔAICc	w _i
Phase + Treat	-95.3	+0.0	0.995	113.6	+0.0	0.973
Phase*Treat	-84.8	+10.5	0.005	255.3	+141.7	0.000
Treat	-72.5	+22.8	0.000	241.6	+128.1	0.000
Phase	-68.5	+26.75	0.000	120.7	+7.1	0.027
Null model	-55.1	+40.12	0.000	177.6	+64.0	0.000

^a AICc values.

^b AICc differences respect the best model.

^c AICc weights.

across all phases of the cycle (for details, see Table A2 in the Appendix). VSI were similar on both intermediate grazing treatments with and without cattle, but fox activity indices were higher in the presence of cattle (Fig. 2).

3.3. The impact of grazing in the relationship between winter fox activity indices and vole densities

The best model only retained VSI estimates but not grazing treatment as an important explanatory variable ($=0.949$), suggesting that grazing treatment did not affected the relationship between fox activity and vole density. Exploration of treatment specific estimates derived from models fitted to every treatment separately suggested some apparent tendencies consistent with grazing intensity (Fig. 3), though confidence intervals of estimates overlapped. Specifically, fox activity appeared to increased more steeply in response to vole density in the ungrazed treatment (treatment IV, mean[s.e.] slope coefficient = 3.922[0.881]), less steeply in the intermediate grazing treatment with sheep only (treatment II, 2.142 [0.907]), and hardly at all in the intermediate grazing treatment with sheep and cattle combined and in the heavily grazed treatment (treatments III and I, 1.316[1.251] and 1.137[1.519] respectively). Also, fox activity at low vole density as estimated by intercepts appeared to follow the opposite pattern, being larger in the intermediate grazing with cattle and heavily grazed treatments (mean [s.e.] intercept coefficients 0.756[0.416] and 0.553[0.360] respectively), followed by the intermediate grazing treatment with sheep only (0.426[0.303]), and almost null in the ungrazed treatment ($-0.463[0.407]$) – recall the log transformation.

4. Discussion

In our experiment, ungulate grazing intensity had a strong and consistent negative impact on vole densities and fox activity indices. Since foxes are archetypal generalist vole predators in these systems (Kjellander and Nordstrom, 2003; Leckie et al., 1998; Lindstrom, 1989; O'Mahony et al., 1999), it is reasonable to think that the drastic reduction in fox activity recorded with increasing

Table 2

Model selection results of the effects of grazing treatment and VSI on fox activity indices. The number of observations was 72.

Model	AICc ^a	ΔAICc ^b	w _i ^c
VSI	161.9	+0.0	0.949
VSI + Treat	168.1	+6.15	0.044
VSI*Treat	171.7	+9.8	0.007
Null model	177.8	+15.86	0.000
Treat	181.	+19.60	0.000

^a AICc values.

^b AICc differences respect the best model.

^c AICc weights.

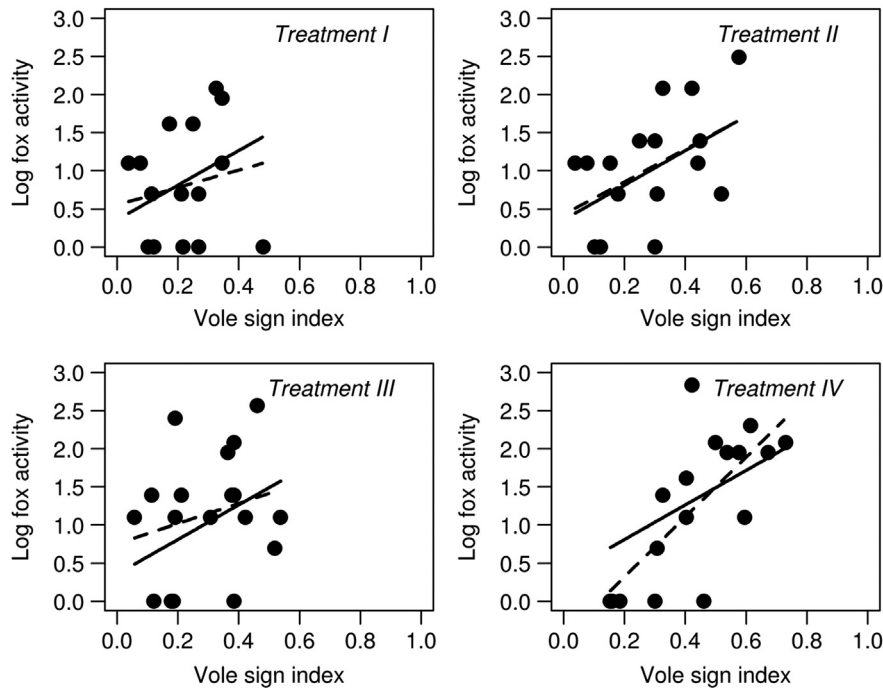


Fig. 3. The effect of grazing treatment on the relationship between fox activity indices and VSI. Points are observations, lines show model fits. Solid lines are derived from a model without a treatment effect, as suggested in the model selection process; dashed lines are derived from models fitted to every treatment separately. Treatments: I) 2.7 ewes ha⁻¹; II) 0.9 ewe ha⁻¹; III) mixed sheep and cattle equivalent to 0.9 ewe ha⁻¹; IV) ungrazed.

grazing intensity is strongly linked to decreased vole densities. In our experiment, the reduction in vole density due to ungulate grazing was as large as the reduction between peak and low phases of the vole cycle (Fig. 2, see also coefficients in Table A2 in the Appendix); this difference is substantial, since in Scotland estimates suggest about one order of magnitude reduction between cycle phases (Lambin et al., 2000). Declines in small mammal densities with increasing livestock grazing had been reported in other upland grassland systems (Steen et al., 2005; Wheeler, 2008), where it has been speculated to have led to a 50% decline in vole predator abundance (Wheeler, 2008). Our results quantify this link for the first time, with livestock grazing leading to a substantial concomitant decline across cycle phases in both vole densities and fox activity indices.

A striking aspect of our results was the strong response of a generalist predator such as the red fox to experimental manipulation of grazing intensity at relatively small spatial scales. Despite the limited size of individual plots (0.033 km²), the relative small size of the experiment (three clusters of 0.264 km² each) compared to large red fox territories in upland habitats of Britain (up to 40 km² (Harris and Yalden, 2008; Webbon et al., 2004)), and the contiguity of treatments and plots, foxes showed a strong response to grazing intensity. Considering the spatial scale of our experiment, the patterns in fox activity recorded most likely reflect a response in individual fox behaviour to grazing treatment at the local scale rather than any population level numerical response of foxes. Hence our results can be interpreted as a strong net reduction in individual fox activity with increasing grazing intensity. If extrapolated to the landscape scale, we would expect increasing domestic grazing intensity to lead to reduced fox population densities, though currently there is no available dataset to test this hypothesis, neither in red foxes nor, to our knowledge, in any other small mammal predator species.

During winter months, sheep and cattle were absent from the experiment, so fox activity was not influenced by their presence. It is possible that occasional sheep and lamb carcasses may have provided alternative food for foxes during wintertime, when other

food resources apart from voles are scarce. However, it is very unlikely that such a process might have influenced our results substantially, otherwise we would expect to have found larger fox activity in the heavily grazed treatment due to the presence of ungulate carcasses, which is the opposite pattern to the one found. Thus we consider that our results are not largely affected by the presence of ungulates or ungulate carrion.

In our experiment, the relationship between fox activity and vole density did not show a substantial change with grazing intensity. However, intercept and slope estimates derived from models fitted to every treatment separately suggested a tendency for grazing intensity to increase fox activity indices at low vole densities but attenuate fox response to vole density (Fig. 3). Increased grazing intensity leading to low vegetation cover might ease vole detection by foxes, but also lead to low vole abundance, with fox activity adjusting to vole availability, which is likely to be a function of both factors. However, this relationship might also have been influenced by the availability of alternative prey and carrion, and perhaps the influence of vegetation structure on other aspects of fox behaviour. It is also possible that large within and between treatment variance might have reduced the power to detect between treatment differences, and that the spatial scale of the experiment might not have been the adequate to test this hypothesis. We conclude that further studies are needed to elucidate whether a three-way interaction between grazing intensity, prey abundance and predator activity or predation rates exists.

5. Conclusions

These results show a strong response of a generalist predator and its main prey to ungulate grazing intensity at small spatial scales, so that the negative impact of grazing on small mammal densities strongly reduces fox activity. By reducing predator activity, it is possible that ungulate grazing at large spatial scales might lead to a substantial reduction in generalist predator densities in upland grasslands.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2013.02.006>.

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