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Population ecology

Positive short-term effects of sheep grazing on the alpine avifauna

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Grazing by large herbivores may negatively affect bird populations. This is of great conservation concern in areas with intensive sheep grazing. Sheep management varies substantially between regions, but no study has been performed in less intensively grazed systems. In a fully replicated, landscape scale experiment with three levels of sheep grazing, we tested whether the abundance and diversity of an assemblage of mountain birds were negatively affected by grazing or if grazing facilitated the bird assemblage. Density of birds was higher at high sheep density compared with low sheep density or no sheep by the fourth grazing season, while there was no clear effect on bird diversity. Thus, agricultural traditions and land use politics determining sheep density may change the density of avifauna in either positive or negative directions.

Keywords: ecosystem function; livestock; biodiversity; birds; facilitation; trophic cascades

1. INTRODUCTION

Large herbivorous mammals often have huge impacts on ecosystem function. Grazing effects on plants have been well studied, while less is known regarding indirect, cascading effects on invertebrates, small mammals and birds (Côté *et al.* 2004). A few studies have demonstrated negative effects of large grazing mammals on the abundance, diversity, and reproductive rates of birds (Fuller 2001) most often explained by reduced food supplies and increased predation risk due to altered habitat structure. However, for insectivorous birds, low-intensity grazing may increase abundance, diversity (Milchunas *et al.* 1998) and possibly catchability (Evans *et al.* 2005) of insect prey, resulting in increased bird abundance (Söderström *et al.* 2001). Bird diversity may be positively affected if more accessible prey relaxes asymmetric competitive relationships among species (see Dunham 1980 for a lizard analogy).

Populations of wild and domestic large herbivores are in general managed which to a large extent determines grazing levels. Grazing effects may consequently vary with management system. The domestic sheep (*Ovis aries* L.) is one of the most common and important domestic herbivores worldwide, especially in marginal habitats. Despite the fact that the ecological impact of sheep probably varies among management systems (Hester 1996), all studies on sheep grazing effects on bird communities are from Scotland (Fuller & Gough 1999) where grazing occurs year-round and usually at extreme densities (from 50–100 up to 1000 per km^2; Simpson *et al.* 1998). In contrast, in Norway, some 2.1 million sheep are released to graze on outlying ranges only during the short summer season, and at densities ranging between 10 and 80 sheep per km^2 (Mysterud *et al.* 2001). Hence, there is a need for studies assessing grazing effects in management regimes with lower densities such as in Norway.

In a fully replicated landscape scale experiment with three levels of grazing spanning the typical range of sheep densities of Norway, we here assess the impact of domestic sheep on densities and diversity of wild mountain birds.

2. MATERIAL AND METHODS

(a) *Study area and the experimental design*

The study area is situated in Hol municipality, southern Norway (between 7° 55′–8° 00′ E and 60° 40′–60° 45′ N). The altitude is between 1050 and 1300 m a.s.l., and above the tree line (Steen *et al.* 2005). Fifty per cent of Norway's land area is mountain habitat, composing the main grazing habitat for sheep.

A fenced enclosure covering 2.7 km^2, split into nine treatment enclosures (termed sub-enclosures A–I) was established in 2001. For each of the three blocks (i.e. three replicates), we randomly assigned the treatments 'control' (no sheep), 'low' (25 sheep per km^2) and 'high' (80 sheep per km^2) densities to the three adjacent sub-enclosures (Fig. S1, electronic supplementary material). These treatments cover the typical variation in densities of sheep on Norwegian mountain pastures. The experiment was run with the same sheep densities each grazing season (from late June to late August/early September) between 2002 and 2005. In 2005, sheep were released into the sub-enclosures on 29 June 2005. Pre-experiment grazing pressure in the study area was low (less than 10 sheep per km^2).

We collected bird data from 7 June to 6 July 2005. Altogether 1324 individuals of 24 species were observed (table S1, electronic supplementary material).

(b) *Statistical analyses*

We analysed separately the density of all birds ($n=1324$), and the three subsets insect eaters ($n=1119$); meadow pipit (*Anthus pratensis*; $n=290$); and willow grouse (*Lagopus lagopus*; $n=64$). We used these subsets because insect eaters was the only functional group with sufficient sample size (table S1, electronic supplementary material), meadow pipit was the most common species and suffers from high grazing pressure in Scotland (Evans *et al.* 2005), and willow grouse is the most important small game species in Norway.

We used distance sampling to estimate bird densities (Buckland *et al.* 2001). The effect of different grazing pressures on densities was evaluated using the count model of Hedley & Buckland (2004), incorporating the study design using nonlinear mixed-effects models. Variation in habitat among sub-enclosures did not affect bird density and there were no edge effects with increased density of birds along fences (see appendix 3 of electronic supplementary material).

We used two classical measures of ecological diversity, the Simpson index and Species richness (Yoccoz *et al.* 2001, box 1). We incorporated unknown species detection probabilities in species richness estimates (Nichols *et al.* 1998). In addition, we used the taxonomic distinctness measure to incorporate taxonomic differences (Yoccoz *et al.* 2001, box 1). We estimated diversity at

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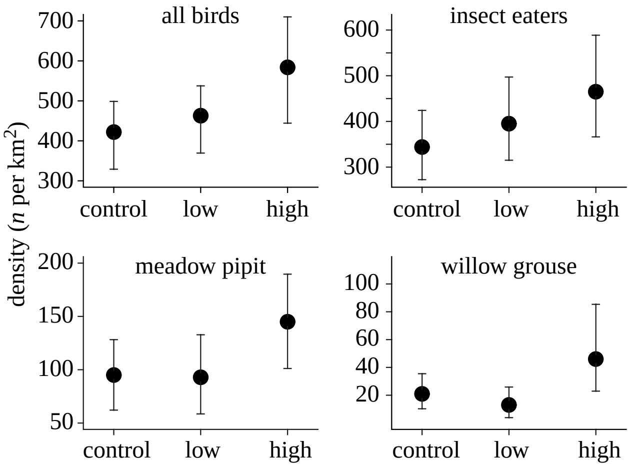

Figure 1. Density estimates (with 95% confidence limits) of all birds and the three subsets, insect eaters, meadow pipit and willow grouse, at the three sheep grazing levels (control, low and high).

Table 1. The difference in bird densities between the three levels of sheep grazing (high, low and control). (Parameter estimates with associated p-values are derived from mixed model. See the electronic supplementary material appendix 3 for details regarding the tests.)

	estimate	s.e.	d.f.	t	p
all birds					
high–control	0.307	0.114	177	2.70	0.008
low–control	0.103	0.115	177	0.892	0.374
high–low	0.204	0.117	177	1.75	0.082
insect eaters					
high–control	0.278	0.116	177	2.41	0.017
low–control	0.138	0.116	177	1.19	0.235
high–low	0.140	0.118	177	1.19	0.234
meadow pipit					
high–control	0.413	0.204	177	2.02	0.044
low–control	−0.0256	0.220	177	−0.116	0.908
high–low	0.439	0.219	177	2.01	0.046
willow grouse					
high–control	0.855	0.429	177	1.99	0.048
low–control	−0.414	0.510	177	−0.812	0.418
high–low	1.27	0.482	177	2.63	0.009

the level of sub-enclosure (A–I) and adjusted for the effect of variable area (see appendix 3 of electronic supplementary material).

We used distance v. 5.0 (Thomas *et al.* 2005) for distance sampling analyses, SPECRICH2 (White *et al.* 1978; http://www.mbr-pwrc.usgs.gov/software) to estimate species richness and R v. 2.2.0 (R Development Core Team 2005) for all other analyses.

3. RESULTS

The grazing levels affected bird densities (mixed model ANOVA; all birds, $F_{2,177}=3.76$, $p=0.025$; insect eaters, $F_{2,177}=2.90$, $p=0.058$; meadow pipit, $F_{2,177}=2.78$, $p=0.065$; willow grouse, $F_{2,177}=4.04$, $p=0.019$). Bird densities were higher at high sheep density compared with low sheep density or no sheep (figure 1; table 1). For diversity, estimates of species richness and taxonomic distinctness appear similar across treatments (figure 2), suggesting neither negative nor facilitation effects of sheep grazing. Only estimates of the Simpson index tended to be higher in high and low sheep density areas than in control areas

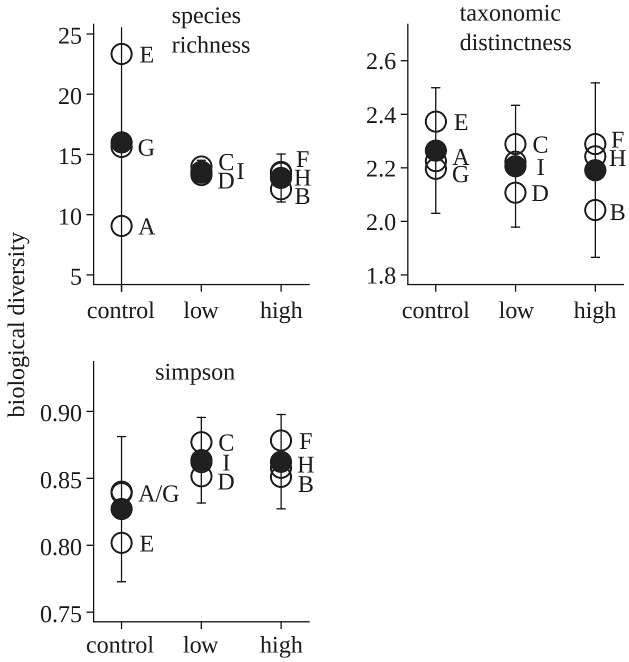

Figure 2. The relationship between the three indices of biological diversity of mountain birds and the sheep grazing levels (none, low and high). Mean value of each index (filled circles) and 95% CI (error bars) are calculated from the estimates of three sub-enclosures (open circles with letters identifying each sub-enclosure).

(figure 2) and was caused by an increased equality in number of individuals per bird species, due to the fact that intermediately common species increase relatively more in numbers than the most common species (Fig. S3; table S1, electronic supplementary material).

4. DISCUSSION

Large herbivores alter ecosystems leading to negative or positive effects on biodiversity (Côté *et al.* 2004). Ecological responses depend on factors such as grazing levels (Steen *et al.* 2005), evolutionary history of grazing (Milchunas & Lauenroth 1993), nutrient levels (Proulx & Mazumder 1998) and scale (Milchunas & Noy-Meir 2002). In contrast to studies from Scotland (Fuller & Gough 1999), we found no negative effect of sheep grazing on abundance and diversity of mountain birds within the fairly low intensity management system in alpine habitats of Norway. Thus, for the same grazer species (sheep), effects on birds may be opposite depending on differences in agricultural traditions and land use policies, although habitat and climatic differences may also play a role.

The lack of a negative grazing impact on birds in our experiment was not due to a general lack of ecosystem effects. Low and high sheep density led to low and moderate grazing pressures (Evju *et al.* 2006). The high grazing levels negatively affected the cover of native vascular plants (Mysterud & Austrheim 2005), the abundance and diversity of beetles (Coleoptera; Mysterud & Austrheim 2005), and the abundance of field voles (*Microtus agrestis*), while grazing increased abundance of the important herbivore food plant *Carex bigelowii* (Steen *et al.* 2005). The majority of birds in our study area are insectivorous and depend heavily on nutritious larvae and adults of Tipulidae (Diptera; Tore Slagsvold 2005, personal communication). Sheep grazing did not affect the abundance and species richness of Diptera or Hemiptera, although Tipulidae larvae were excluded due to the capture technique (Mysterud *et al.* 2005). Grazing may open the habitat making insect larvae more available (Evans *et al.* 2005). Söderström *et al.* (2001) found that small insectivorous birds preferred grazed pastures. As the majority of birds in our study are insectivorous, we suggest that increased catchability of insect prey is the most likely mechanism linking sheep grazing to bird abundance. Similarly, we suggest that relaxed interspecific competition (Dunham 1980) may be the mechanism producing the small increase in the Simpson diversity index.

Low densities of sheep increased meadow pipit abundance in Scotland (Evans *et al.* 2005) and the positive effect at high sheep density levels in this study suggests that Norway is in the lower range of grazing pressure compared to Scotland. Taken to the extreme, grazing must, at some stage, start to detrimental for bird populations. Grazing studies are often conducted in areas where densities are extremely high, and small-scale experiments typically report stronger grazing effects than larger scale experiments (Milchunas & Noy-Meir 2002). This is problematic as management scales are typically large. We used both a large landscape scale, summer grazing only, and applied the low and moderate grazing pressures typical for Norway. Our study documents a short-term positive effect of sheep grazing on the alpine avifauna. However, changes in the vegetation communities may increase responses to grazing at decadal scales. Cleary, long-term monitoring needs to be conducted to evaluate whether sheep grazing has a persistent positive effect on birds or if the observed effect is reversed over time.

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