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Long-term impact of changes in sheep *Ovis aries* densities on the breeding output of the hen harrier *Circus cyaneus*

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Summary

1. Livestock grazing is an important form of land use across the globe and changes in grazing pressure can have profound effects on vertebrate populations.
2. In Scotland, over the last decade sheep numbers in many areas have declined from historically high levels, providing an opportunity to explore the implications of these declines for biodiversity.
3. The hen harrier *Circus cyaneus* is a bird of high conservation importance in the UK, and a species that may be heavily influenced by the indirect effects of sheep on habitat and prey. The hen harrier population on the Orkney Islands in Scotland has been monitored since 1975 and represents an ideal case study for considering the impact of sheep de-stocking on a key predator.
4. Declines in the harrier population were associated with a doubling in sheep numbers between the early 1980s and the late 1990s. Subsequently, as sheep numbers have fallen the harrier population has recovered. These changes indicate an association but no clear mechanism, so we tested whether reductions in sheep numbers have led to increases in harrier prey or preferred foraging habitat. We then tested whether breeding output over the last 33 years correlates with sheep stocking levels or variation in weather conditions (rainfall and temperature).
5. Orkney sheep numbers declined by about 20% between 1998 and 2008. Surveys in 1999/2000 and repeated in 2008 showed increases in rough grassland, the preferred harrier foraging habitat, and increases in a key prey species, the Orkney vole *Microtus arvalis orcadensis*.
6. Overall, hen harrier breeding output over the last 33 years was significantly negatively correlated to both sheep abundance and spring rainfall.
7. *Synthesis and application*. This study provides strong evidence for the consequences of changes in sheep numbers on a top predator. Our results indicate that reductions in sheep numbers are likely to prove beneficial for some upland species, particularly small mammals and their predators.

Key-words: agriculture, grasslands, grazing, grouse moors, Orkney, predation, rainfall, voles

Introduction

The impacts of grazing on vegetation structure and composition, and on ecosystem processes have received considerable attention (Milchunas & Lauenroth 1993; Augustine & McNaughton 1998; Perevolotsky & Seligman 1998; Knapp *et al.* 1999; Cote *et al.* 2004; Hanley *et al.* 2008). In Britain, sheep *Ovis aries* are the principal domestic grazing species in the uplands, and between 1950 and 1990 their numbers rose from 19·7 million to 41·2 million with particularly dramatic increases apparent during the 1980s and the early 1990s (Fuller & Gough 1999; Amar & Redpath 2005; Condliffe 2009). These increases stem from changes to the subsidy and support systems operated through the Common Agricultural Policy (CAP) (Fuller & Gough 1999; Hanley *et al.* 2008).

Increased sheep abundance dramatically affected some bird species, particularly in the uplands, and almost certainly reduced the habitat quality for some ground nesting bird species (Fuller & Gough 1999; Thirgood *et al.* 2000). In contrast,

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increased grazing may have benefited those species preferring shorter or more grass-dominated vegetation (Smith *et al.* 2001; Pearce-Higgins & Grant 2006) and their predators, as well as carrion feeders which would have benefited from the increase in sheep carcasses (Watson, Rae & Stillman 1992; Ratcliffe 1997; Fuller & Gough 1999; Redpath & Thirgood 1999). However, since the late 1990s sheep numbers in Scotland have declined quite dramatically (SAC 2008). The outcome for biodiversity of these declines will inevitably vary between vegetation types and between bird species (Pearce-Higgins *et al.* 2009). There is an urgent need to understand the biodiversity responses to spatial and temporal changes in grazing patterns, indeed understanding the consequences of changes in upland grazing regimes for biodiversity is currently viewed as one of the most important ecological questions of high policy relevance for the UK (Sutherland *et al.* 2006).

Changes to vegetation structure or communities caused by high levels of grazing can have a direct impact on vertebrate and invertebrate species that rely on ungrazed or lightly grazed habitats (Jepson-Innes & Bock 1989; Steen, Mysterud & Austrheim 2005; Evans *et al.* 2006). Reductions in the abundance of these species can in turn influence the abundance of the predators that feed on them, although links between these different trophic guilds have been poorly studied due to their inherent complexities (Duff 1979; Douglass & Frisina 1993; Steenhof *et al.* 1999; Johnson & Horn 2008). For example, small mammal populations are known to be affected by grazing levels (Steen, Mysterud & Austrheim 2005; Evans *et al.* 2006) and avian predators of small mammals, such as hen harriers *Circus cyaneus* whose populations can be strongly influenced by vole abundance (Redpath, Thirgood & Clarke 2002a), may therefore be influenced by changes in grazing densities.

The Orkney Islands in North Scotland are an important breeding area for hen harriers in the UK (Sim *et al.* 2007). Most hen harriers on Orkney breed in the west of the island of Mainland (hereafter referred to as West Mainland) and this population has been monitored on the same area annually from 1975 (Amar *et al.* 2005). A doubling in sheep numbers is believed to have been responsible for a decline in hen harriers between the 1970s and 1990s when the numbers of chicks produced each year declined by 73% (Amar & Redpath 2005; Amar *et al.* 2005). The mechanism for this was thought to have been a reduction in rough grassland (the preferred habitat for foraging harriers) and Orkney voles, reducing the amount of prey available to harriers during the critical pre-laying period (Amar & Redpath 2002, 2005; Amar, Redpath & Thirgood 2003a).

However, since the end of the 1990s the hen harrier population on Orkney has recovered. Between 1998 and 2004, the numbers of breeding females on Orkney increased by 118% from 34 to 74 (Sim *et al.* 2001, 2007), which contributed to an overall population increase for the UK, the Orkney population representing 12% of the Scottish population in 2004 (Sim *et al.* 2007).

In this paper, we describe this population recovery on Orkney to 2008, and quantify the changes in sheep abundance within their breeding and foraging areas. Secondly, we repeat vegetation and prey surveys first undertaken in the late 1990s and test the hypothesis that a reduction in sheep numbers has allowed the amount of rough grassland and the abundance of key prey species to recover. We also test if hen harrier breeding output on Orkney correlates with weather variables because previous work has shown that hen harrier breeding success is influenced by the effect of weather on prey delivery and nestling mortality (Picozzi 1984; Redpath *et al.* 2002b). Lastly, we explore if changes in sheep abundance and/or weather can account for the changes in breeding output of this harrier population over the last 33 years.

Materials and methods

HARRIER DATA

Hen harriers have been monitored on Orkney (59°10' N, 3°12' W) to a varying degree since 1953 (Amar *et al.* 2005). Since 1975 the same areas of moorland on West Mainland have been systematically monitored, with the total number of broods and total number of young produced being the minimum data recorded each year. This population decline dramatically between the 1970s and 1990s and intensive monitoring revealed that the key demographic change during this decline was a reduction in the proportion of breeding females (linked to lower levels of polygny) and a reduction in breeding success of secondary females, with little variation apparent in the brood size of successful nests (Amar *et al.* 2005). Both these factors led to a reduction in the number of broods fledging and a lower number of young produced. Due to the labour intensive methods, data on the proportion of breeding females and levels of polygny are unavailable throughout the whole study period. For this study, we instead used the total number of young produced each year between 1975 and 2008. This measure combines several variables into a single productivity estimate, including numbers of breeding females and breeding success rate, together with the small variation in brood size at fledging. During 1999 and 2000, a supplementary feeding experiment was undertaken and improved the population's breeding performance (Amar & Redpath 2002). Therefore, data from these 2 years are excluded from our analyses examining productivity.

SHEEP AND WEATHER DATA

We obtained the total annual number of sheep from the seven regional areas or parishes (Birsay, Harray, Evie, Rendall, Firth, Orphir and Stenness) with breeding harriers on West Mainland from 1975 to 2008 from the June Agricultural Census data.

Weather data for the same period was extracted from the Met Office MIDAS Land Surface Observation Stations dataset, held by the British Atmospheric Data Centre. All data came from the Kirkwall weather station (58·9°N, 2·9°W), situated about 20 km from the main breeding areas for harriers on West Mainland. Using the same divisions as Redpath *et al.*'s (2002b) analysis of weather on harrier breeding success, we summarized data from March and April as 'spring' and June and July as 'summer'. Rainfall data were the sum of rainfall (mm) in both months in each season. Mean spring and summer maximum and minimum temperatures (°C) were derived from the average minimum and maximum temperatures from both months in each season. Temperature data were missing for a small number of seasons (max. spring = 4; max. summer = 2; min. spring = 4; min. summer = 2), so we used a fuller dataset from Lerwick, Shetland

(60·1°N, 1·1°W), about 100 miles north of West Mainland, to complete the Kirkwall data using predictive linear regressions (Whitfield, Fielding & Whitehead 2008) (R^2 for all correlations > 0·81).

PREY AND HABITAT SURVEYS

Surveys of Orkney voles, lagomorphs (rabbit *Oryctolagus cuniculus* and brown hare *Lepus capensis*), and meadow pipits *Anthus pratensis,* and the area of rough grassland were carried out using line transects within 18 1-km squares. Squares were selected (non-randomly) to allow unobstructed observation of hunting harriers (as part of another study), and were all sited within 5 km of active harrier territories, the locations of which remained similar from year to year (Amar & Redpath 2005; Amar *et al.* 2008). Within each square, surveys were undertaken along two parallel transects, located at 250 m and 750 m from a randomly selected side of each square. Surveys of voles, lagomorphs and rough grassland were carried out in spring, when voles formed the largest component of the hen harrier's diet; surveys of meadow pipits took place in summer, when meadow pipits become an important part of the diet (Amar 2001).

Rough grassland measures, and vole and lagomorph sign indices were recorded simultaneously. Quadrats (25 × 25 cm) were placed every 40 m along the two transect lines within each square, giving 50 quadrats per square. Vole and lagomorph abundance was indexed using the presence or absence of fresh vole or lagomorph droppings in each quadrat, and we recorded the number of quadrats dominated by unmanaged grass. Fresh vole droppings provided the most reliable index of relative vole abundance on Orkney as estimated by simultaneous snap trapping (Oates 1996). Rough grassland was defined by a build up of dead vegetation forming a litter mat under the living vegetation, adequate to conceal a moving vole (Hewson 1982). Original surveys of voles, lagomorphs and rough grassland were undertaken in nine of the 18 squares between 23 and 31 March 1999, with the remaining nine surveyed between 2 and 24 March 2000. Repeat surveys were undertaken between 1 and 10 April 2008.

Meadow pipits were surveyed using standard passerine transects along the same transect routes as the vole and vegetation surveys, between 06:00 and 09:00 h, as this period provided the highest repeatability in estimating passerine numbers (Thirgood, Leckie & Redpath 1995). Numbers of individuals seen within 200 m on either side of the transect line were recorded. Counts were undertaken between 2 July and 6 August in either 1998 or 1999 (all but two counts occurring by 20 July), with the repeat surveys undertaken slightly earlier between 24 June and 9 July 2008. This discrepancy in survey date (average of 10 days between surveys) is unlikely to have influenced our comparison of meadow pipit counts between surveys because we found no correlation between meadow pipit abundance and date ($F_{1,34}$ = 0·29 P = 0·59).

LONGER-TERM VOLE MONITORING

We used longer-term vole abundance data from a separate study (Royal Society of the Protection of Birds unpublished data) to examine whether any changes found between our original and repeat surveys were likely to reflect real changes or larger-scale temporal fluctuations. Vole abundance data collected annually from 1999 to 2008 were available from three 1-km squares in West Mainland. Habitat within these squares was principally heather moorland with some rough grassland with little or no grazing. These surveys used comparable methods to our study, recording the presence of fresh vole droppings within 25 × 25 cm quadrats placed every 20 m (cf. 40 m in our study), along two 1-km transects, giving 100 quadrats per square. Data were collected in July or August, and although this was later than our surveys, previous work in Orkney suggests that vole indices change little between these two time periods (Amar 2001).

STATISTICAL ANALYSIS

Trends in the numbers of young fledged and the numbers of sheep were analysed using linear regression with a normal error structure. Changes in the abundance of prey (count of vole signs or meadow pipits) and in the number of rough grassland dominated quadrats were analysed using a Generalised Linear Mixed Model (GLMM), with a unique identifier for 'square' as a random factor and survey period (original or resurvey) as a categorical fixed effect. For meadow pipit abundance, the GLMM would not converge, so for this analysis we used a Generalised Linear Model with 'square' and survey period as fixed effects. Models were fitted with a Poisson error structures and a log link function and were corrected for over-dispersion. Denominator degrees of freedom for the GLMM were estimated using Satterthwaite's formula (Littell *et al.* 1996). To examine the influence of weather variables and sheep abundance on the number of young fledged, we used a General Linear Model, with a normal error structure and an identify link function. All analyses were carried out in SAS version 9.1 (SAS Institute Inc. 2004).

Results

TRENDS IN HARRIER BREEDING OUTPUT AND SHEEP ABUNDANCE

The number of young hen harriers fledged declined from the end of the 1970s to a low during the 1990s before rising again at the start of the 2000s (Fig. 1). The number of young fledged declined by 79% between 1975 and 1997 ($F_{1,,21}$ = 32·73, P < 0·001) and then increased by 92% between 1998 and 2008 ($F_{1,,9}$ = 6·53, P = 0·03). In contrast, sheep numbers increased by 140% between 1975 and 1997 (1975 – *c.* 20 000, 1997 – *c.* 48 000; $F_{1,,21}$ = 418·96, P < 0·001); and declined by about 20% between 1998 and 2008 (1998 – *c.* 50 000, 2008 – *c.* 40 000; $F_{1,,9}$ = 59·70, P < 0·001) (Fig. 1).

CHANGES IN HABITAT AND PREY ABUNDANCE

We found an increase in the number of quadrats dominated by rough grassland ($F_{1,15}$ = 4·97, P = 0·04) and an increase in quadrats with vole signs ($F_{1,13}$ = 7·25, P = 0·01) between spring 1999/2000 and spring 2008 (Fig. 2). However, no differences in the number of lagomorph signs were found between the two surveys ($F_{1,20}$ = 0·60; P = 0·44). We also found no difference in the number of meadow pipits counted between summer 1998/1999 and summer 2008 ($F_{1,17}$ = 21·25, P = 0·26). Longer-term data on vole abundance from three 1-km squares subject to relatively constant low levels of grazing suggested that a wider pattern of temporal fluctuations in vole abundance was unlikely to explain the increase in voles detected from the 18 squares surveyed in 2008. Indeed, these longer-term data displaying the annual fluctuations, suggested that vole abundance was actually higher in 1999 and 2000 than it was in 2008 (Fig. 3).

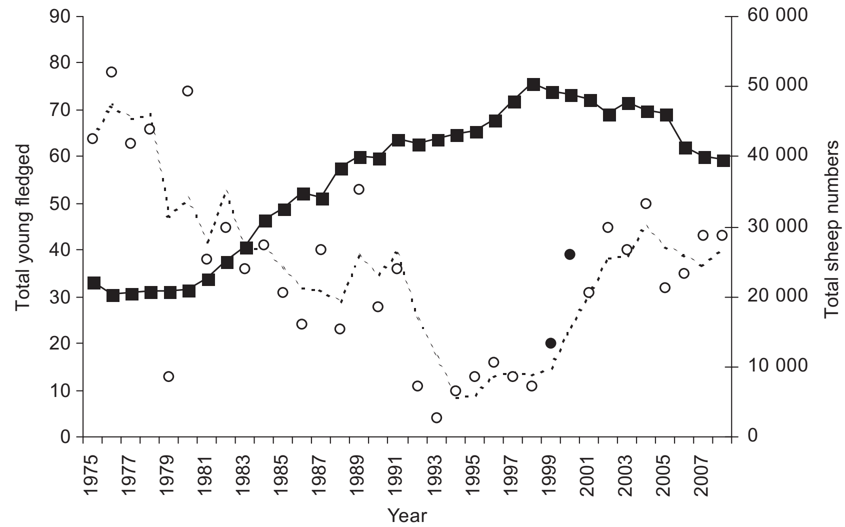

Fig. 1. Graph showing the total number of young hen harriers fledged from West Mainland Orkney (open circles–the two close circles show the years when a diversionary feeding experiment took place) between 1975 and 2008 together with the 3-year running mean (dashed line). Also shown are the total numbers of sheep (closed squares) recorded between 1975 and 2008 from the June Agricultural Census in the seven parishes with breeding harriers.

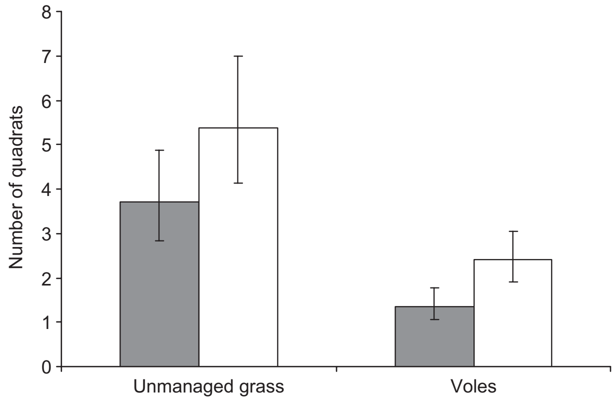

Fig. 2. Changes between 1999/2000 (shaded bars) and 2008 (clear bars) in rough grass abundance and fresh vole signs (per 50 quadrats) within eighteen 1-km squares distributed throughout West Mainland, Orkney. Data are mean (±1 SE) model estimates from the GLMM fitted with survey period as a fixed effect and square as a random term in the model.

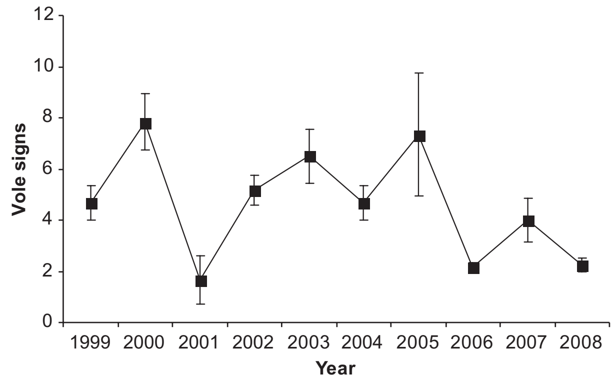

Fig. 3. Graph showing the inter-annual changes in vole signs (per 50 quadrats) between 1999 and 2008 on three 1 km squares. Squares were additional to the main study and were largely un-grazed throughout the period. Data shown are the mean counts taken in July/August across the three squares ± 1 SE. Data indicate that changes in vole abundance between 1999 and 2008 in the main study were not explained by broad-scale between year fluctuations in vole abundance.

RELATIONSHIP BETWEEN CLIMATE, SHEEP DENSITIES AND HARRIER BREEDING SUCCESS

No relationship was found between total young fledged and either spring or summer temperature or summer rainfall (Table 1a, Fig. 4). However, there was a significant negative association between spring rainfall and numbers of young fledged (Table 1a, Fig. 4). Between 1975 and 1997, spring rainfall increased ($F_{1,,21}$ = 5·03, P = 0·04), although there was no trend between 1998 and 2008 ($F_{1,,9}$ = 0·05, P = 0·83). We also found a highly significant relationship between the abundance of sheep and the numbers of young fledged between 1975 and 2008 (Table 1a). Combining these significant terms in a full model, both the abundance of sheep (Fig. 5) and the spring rainfall (Fig. 6) remained significant (Table 1b), with no significant interaction ($F_{1,,28}$ = 1·03, P = 0·31). These two terms in the final model accounted for nearly 40% of the variation in the numbers of young fledged between years (Table 1b).

Discussion

This study provides convincing evidence that the decline and subsequent recovery of the hen harrier population on Orkney was due to changes in sheep abundance. It is important to note that this conclusion is not based on just a one way relationship auto-correlated with time, but with numbers of sheep both increasing and decreasing and harriers following the converse trend. Increases in sheep are thought to have reduced the amount of rough grassland, the habitat preferred by foraging male harriers (Amar *et al.* 2003b; Amar & Redpath 2005) which in turn led to a decrease in the abundance of voles, an important prey species which is heavily dependent on this habitat type (Amar & Redpath 2005). During the period of harrier recovery, sheep numbers declined in the main hen harrier breeding areas on Orkney by over 20%, with the loss of around

Table 1. Relationships between the number of young hen harriers fledged on West Mainland, Orkney and the spring and summer climate variables (rainfall and min. and max. temperature) and sheep abundance recorded on Orkney from 1975 to 2008 (omitting 1999 and 2000), (a) univariate relationships for each term, (b) final full GLM model including only terms significant at the univariate stage. Significant terms are presented in bold

Variable	Intercept	Estimate	d.f.	*F*	*P*	R^2
(a)						
Spring rainfall	**67·05**	**−0·200**	**1,30**	**6·19**	**0·01**	**14·3%**
Summer rainfall	53·31	−0·160	1,30	3·18	0·08	6·6%
Spring max temp	36·83	−0·123	1,30	0·00	0·98	0·0%
Summer max temp	10·05	1·88	1,30	0·19	0·67	0·0%
Spring min temp	30·76	1·469	1,30	0·11	0·74	0·0%
Summer min temp	−2·40	3·901	1,30	0·53	0·47	0·0%
Total sheep	**77·28**	**−0·001**	**1,30**	**15·66**	**< 0·001**	**32·1%**
(b)						
Spring rainfall	**96·16**	**−0·149**	**2,29**	**11·15**	**0·04**	**39·6%**
Total sheep		**−0·001**			**0·001**	

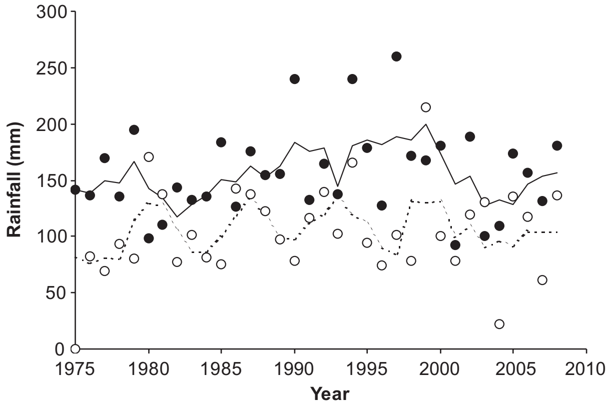

Fig. 4. Annual rainfall data from Kirkwall weather station between 1975 and 2008, together with 3 year running means for spring (sum of March and April daily rainfall) (solid line and circles) and summer (sum of June and July daily rainfall) (dashed line and open circles).

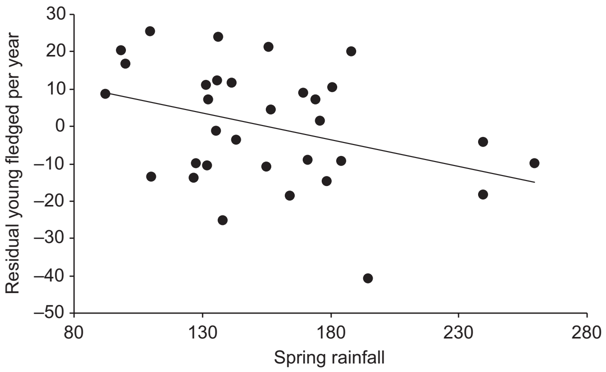

Fig. 6. Relationship between the spring rainfall (mm), and the residuals of the numbers of young hen harriers fledged on West Mainland Orkney between 1975 and 2008 after controlling for the significant relationship between of the total number of hen harriers fledged and the total number of sheep. Data from 1999 and 2000 when a supplementary feeding experiment took place are excluded.

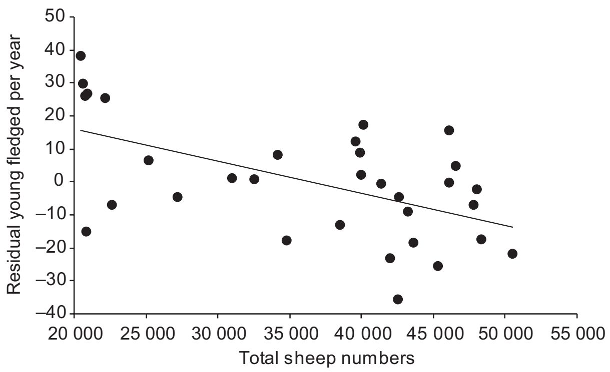

Fig. 5. Relationship between the total number of sheep on the seven parishes on West Mainland containing hen harriers (from the June agricultural records) and the residuals of the numbers of young hen harriers fledged on West Mainland Orkney between 1975 and 2008 after controlling for the significant relationship between of the total number of hen harriers fledged and spring rainfall. Data from 1999 and 2000 when a supplementary feeding experiment took place are excluded.

10 000 sheep. Scottish Natural Heritage (SNH) launched the Orkney Hen Harrier Recovery Scheme in 2002 (http://www.snh.org.uk/pdfs/about/orkneyHH.pdf), and this, together with other agri-environment schemes in Orkney, is likely to have improved habitat conditions for harriers, through sheep removal and exclusion to increase vole abundance and rough grassland. However, the bulk of these sheep declines are probably unrelated to this specific scheme, given that they are typical of wider declines seen across northern and western Scotland, without such schemes. Rather, the decline in sheep numbers is more likely to be due to changes in wider subsidy reforms of the CAP (SAC 2008). Our study provides support for the hypothesis that the decrease in sheep numbers on Orkney has led to an increase in rough grassland habitat with significant increases detected between the late 1990s and 2008. Modelling suggests that only relatively small increases in this habitat type are necessary to improve harrier breeding success (Amar *et al.* 2008).

Previous research has identified that food shortages were most critical for this hen harrier population during the pre-lay and incubation period (Amar & Redpath 2002; Amar, Redpath & Thirgood 2003a), when voles were the most important prey species. The selection of rough grassland habitats by foraging harriers (Amar & Redpath 2005) and the positive relationship between rough grass and breeding success (Amar *et al.* 2008) are thought to be a direct consequence of the higher vole abundance in habitats with more unmanaged and ungrazed grassland. Several non-experimental studies have suggested benefits of reduced grazing on vole densities (Hewson 1982; Hill, Evans & Bell 1992) and these are now supported by experimental studies (Steen, Mysterud & Austrheim 2005; Evans *et al.* 2006). Our study provides further support for these findings, with significant increases in vole abundance also apparent on Orkney over the time that sheep numbers declined and rough grass increased. Furthermore, this study advances our knowledge, by demonstrating how changes in grazing pressure may affect predatory species which depend on voles as a key prey species.

The influence of grazing levels on the vegetation type and structure, and therefore on vole abundance, will vary depending on the original vegetation. For example, some studies on mainland Scotland have demonstrated that higher levels of historical grazing on moorlands can increase the ratio of grass to heather, thus improving the quality of habitat for meadow pipits and field voles *Microtus agrestis*, and therefore favouring higher hen harrier settling densities (Redpath & Thirgood 1997, 1999; Smith *et al.* 2001). The effects of changes in sheep numbers are therefore likely to vary both spatially and temporally. Thus, decreases in sheep numbers might cause improved conditions in the short term, but in some areas, particularly areas where hen harrier home ranges are dominated by heather, these changes could reduce habitat quality for hen harriers in the longer term.

Unfortunately, the June Agricultural Census does not attribute sheep numbers to habitat types and therefore we are unable to determine whether sheep reductions varied between habitats on Orkney. Anecdotal observations suggest that sheep abundance was never very high in most of the moorland nesting areas, especially as most are under conservation management by the Royal Society of the Protection of Birds (RSPB) or are designated Sites of Special Scientific Interest (SSSIs) on which management agreements with landowners have kept grazing levels down. Declines are more likely on marginal habitats, and given that these habitats already contain a higher ratio of grass-to-heather (Amar 2001) than moorland habitats, any reduction in sheep numbers may provide disproportionately positive benefits. Previous grazing in these habitats may have increased the plant species that voles prefer, although until the grazing pressure is relieved the vegetation structure may not have been suitable for voles to colonize. Indeed improvement in vole habitat by limited grazing was considered a possibility from a grazing experiment in Norway where voles appeared to benefit from light grazing over controls with no grazing (Steen, Mysterud & Austrheim 2005) and in Iceland, grazing by sheep increased the cover of *Carex bigelowii*, the main forage plant of both sheep and voles (Jónsdóttir 1991). This might also explain why the recovery of harriers on Orkney was so rapid following the start of the decline in sheep numbers, and we know that voles can respond very quickly to reduced grazing, with effects becoming apparent after only 1 year (Evans *et al.* 2006).

Caution must be applied when comparing two points from a time series since change between points may be due to variation around a long-term trend, rather than being due to the trend itself. The longer-term vole data available from the study area suggested that inter-annual variation was unlikely to account for the contrast in vole numbers between the first and second vole surveys in this study. Data from 2008 did not suggest that this year represented a particular peak in vole abundance in Orkney; indeed this long-term data suggested that 2008 was a year of relatively low vole abundance compared with 1999/2000. Thus, our findings on vole abundance in 2008 may actually underestimate the real level of increase. These data also suggest that although Orkney vole populations appear to show large fluctuations between years, there is no evidence that these fluctuations are cyclic in nature, unlike many other vole populations on mainland Britain (Lambin, Petty & MacKinnon 2000; Redpath, Thirgood & Clarke 2002a) or continental Europe (Oksanen & Oksanen 1992; Lambin, Bretagnolle & Yoccoz 2006).

Although accounting for less variation than sheep numbers, spring rainfall also had an negative influence on hen harrier breeding output, most probably through reducing the amount of time harriers could spend hunting (Newton 1986; Sergio 2003). Harriers rarely hunt in rainy conditions (A. Amar, pers, obs.) and Redpath *et al.* (2002b) found that prey provisioning to nests by male harriers was reduced by rainfall. High rainfall in spring may therefore reduce the amount of food males can supply to their females during the critical pre-lay period in spring. Steenhof, Kochert & MacDonald (1997) found that prey and weather (number of days above 32 °C) interacted to limit golden eagle *Aquila chrysaetos* productivity; in our study however, spring rainfall appeared to act independently of sheep numbers. Thus, even when sheep numbers were low and prey were therefore considered to be more abundant, rainfall had a similar negative effect as when sheep numbers were high and prey was therefore assumed to be less abundant. Should climate change result in increases in spring rainfall our results suggest that this may have negative consequences for the harrier population on Orkney.

National surveys of hen harriers between 1998 and 2004 showed considerable increases on other Scottish islands and in the west of Scotland, with declines only apparent in areas where grouse moor management was most prevalent, presumably due to illegal killing which is heavily associated with management for recreational shooting of red grouse (Etheridge, Summers & Green 1997; Sim *et al.* 2007; Thompson *et al.* 2009; Redpath *et al.* 2010). Many of these western areas have also seen considerable declines in sheep abundance (SAC 2008), and may have also contributed to the increases in these harrier populations. Declines in sheep numbers may have implications for other vole predators of conservation importance. For example, voles are an important component in the diet of kestrels *Falco tinnunculus* (Village 1990), a rapidly declining species in Scotland (Risely, Noble & Baillie 2008). However, voles are also important prey for foxes *Vulpes vulpes* and pine martins *Martes martes*, and these species can be important predators of species of conservation concern, such as curlew (Grant *et al*. 1999) and capercaillie *Tetrao urogallus* (Summers, Willi & Selvidge 2009). Therefore, in theory, changes in grazing pressure may have far reaching indirect effects on other bird species through changing the abundance of their main predators.

Changes to agricultural support mechanisms can influence stocking densities of grazing animals and changes to grazing levels can have profound ecological impacts on vegetation and, as this study demonstrates, these changes can have considerable influence on other grazing species, such as small mammals and their predators. Thus, the large reductions in sheep numbers recorded over the last decade in the Scottish uplands are likely to benefit some species but to have negative effects on others. 'Winning species' may include small mammals and their predators, or other species that benefit from nesting or feeding opportunities created by the changes in sward structure described in this study, such as ground nesting passerines. However, 'losing species' may include species, which prefer shorter vegetation such as golden plover *Pluvialis apricaria* or skylarks *Alauda arvensis*, which benefit from the maintenance of more extensive areas of short, open swards (Pearce-Higgins & Grant 2006). Similar reductions in the abundance of open country bird species have occurred in the Alps (Laiolo *et al*. 2004) and Argentina (Garcia *et al*. 2008) following the loss of livestock. Some have speculated that reduced grazing as a consequence of lower sheep numbers may be compensated by increases in the abundance of deer (Clutton-Brock, Coulson & Milner 2004); Orkney has no wild deer, and this should be considered when transferring these findings to habitats on the mainland where deer are present.

The potential implications of changes in sheep grazing for biodiversity are of broad policy interest. Our results demonstrate that policy-driven changes in grazing intensity, which although not designed with clear biodiversity objectives, nonetheless, can have a large effect on a species of high conservation concern through impacts on the food chain.

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