

Habitat loss and raptor predation: disentangling long- and short-term causes of red grouse declines

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The number of red grouse (*Lagopus lagopus scoticus*) shot in the UK has declined by 50% during the 20th century. This decline has coincided with reductions in the area of suitable habitat and recoveries in the populations of some avian predators. Here we use long-term records of shooting bags and a large-scale manipulation of raptor density to disentangle the effects of habitat loss and raptor predation on grouse populations. The numbers of grouse harvested on the Eskdale half of Langholm Moor in southern Scotland declined significantly during 1913–1990 and grouse bags from the whole moor from 1950 to 1990 exhibited an almost identical but non-significant trend. Hen harriers (*Circus cyaneus*) and peregrine falcons (*Falco peregrinus*) were absent or bred at low densities on this moor throughout this period but heather-dominant vegetation declined by 48% between 1948 and 1988. Harrier and peregrine breeding numbers on Langholm Moor increased to high levels following protection in 1990 whilst grouse density and grouse bags declined year after year until shooting was abandoned in 1998. The prediction of a peak in grouse bags on Langholm Moor in 1996 based on the patterns of bags during 1950–1990 was supported by the observed peaks in 1997 on two nearby moors with few raptors which formerly cycled in synchrony with Langholm Moor. This study demonstrates that, whilst long-term declines in grouse bags were most probably due to habitat loss, high levels of raptor predation subsequently limited the grouse population and suppressed a cycle. This study thus offers support to theoretical models which predict that generalist predators may suppress cycles in prey populations.

Keywords: habitat loss; predation; raptors; red grouse

1. INTRODUCTION

Theoretical models predict that generalist predators can dampen fluctuations in their prey if the predator densities are unrelated to prey densities and predation is density dependent (Hanski *et al.* 1991; Hanski & Korpimäki 1995; Turchin & Hanski 1997). Generalist mammalian predators are thought to have a stabilizing effect on microtine vole dynamics in southern Fennoscandia (Angelstam *et al.* 1984; Erlinge 1987; Korpimäki & Norrdahl 1998) and nomadic avian predators are similarly thought to dampen vole cycles (Korpimäki & Norrdahl 1989, 1991). However, the influence of generalist predators on the dynamics of bird populations remains controversial (Newton 1998). This is particularly the case when the prey concerned has economic value and the predators involved are legally protected. A current example in the UK concerns the effects of predation on red grouse by hen harriers and peregrine falcons (Thirgood *et al.* 2000a). Harriers and peregrines are relatively rare birds in the UK and the range and abundance of harriers is limited by illegal control on grouse moors (Etheridge *et al.* 1997). Income generated by grouse shooting is essential to the economic persistence of many sporting estates and shooting bags have declined by 50% this century (Hudson 1992). Improvements in the population status of harriers and

peregrines in recent decades (Bibby & Etheridge 1993; Crick & Ratcliffe 1995) have raised concerns about the effects of these predators on grouse populations. However, long-term declines in grouse bags have also coincided with large-scale habitat loss—some 20% of heather (*Calluna vulgaris*) moorland has been lost to afforestation and grazing in the UK since the 1940s (Thompson *et al.* 1995).

In this paper, we present the results of a natural experiment, where long-term habitat loss coincided with declines in grouse shooting bags, together with a large-scale manipulation of raptor density, in order to disentangle the effects of habitat loss and raptor predation on grouse populations. We first analyse trends in the numbers of grouse shot on one moor where historical data are available on habitat loss and raptor numbers. We then compare grouse bags on this moor before and after 1990, when harriers and peregrines increased in numbers, to grouse bags on neighbouring moors where these raptors remained uncommon.

2. METHODS

Sporting estates keep annual records of the numbers of grouse shot and previous analyses have demonstrated that shooting bags reflect post-breeding densities of grouse (Hudson 1992). Annual bag records were available from Langholm Moor in southern Scotland from 1913 to 1998 and from two nearby

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moors (F and G) from 1975 to 1998. In 1994 Langholm Moor encompassed 42 km² of heather within an area of 100 km² of land between 100 and 570 m above sea level. Moor F was of similar size with *ca.* 36 km² of heather whilst moor G was smaller with *ca.* 24 km² of heather. Further details of all three moors are given in Redpath & Thirgood (1997).

The long-term trends in grouse bags on Langholm Moor were evaluated from two related data sets. The longer time-series from the western half of the moor (Eskdale) spans the years 1913–1990. The years during and immediately following the Second World War (1939–1948) were omitted from the analysis as the grouse bags during this period were low for reasons unrelated to grouse abundance. The second time-series from the whole of Langholm Moor encompasses the years 1950–1990. Regressing log₁₀-transformed bag data on the year indicated significant first-order autocorrelation in the residuals. We therefore fitted a linear regression and modelled the residuals using a first-order autoregressive model, AR(1). The residuals from both data sets modelled in this way indicated no autocorrelation structure.

Time-series analysis revealed that the most appropriate linear model to fit to the Langholm Moor grouse bag data during the period 1950–1990 was a second-order autoregressive moving average process, ARMA(2,2):

$$X_t - m_t = a_1(X_{t-1} - m_{t-1}) + a_2(X_{t-2} - m_{t-2}) + b_1\zeta_{t-1} + b_2\zeta_{t-2} + \zeta_t \quad (1)$$

This was the most complicated model of the ARMA type in which all the parameters were significant and the residuals from this model exhibited no autocorrelation or partial autocorrelation and did not deviate significantly from normality. X_t is the modelled log₁₀ bag count for year t ($t = 1950$ – 1990), ζ_t is an independent and identically distributed Gaussian noise term with mean -0.0087 and variance 0.0596 and m_t is a function determined by the trend analysis ($m_t = -0.0071t + 17.1$). The estimated parameters (s.e. and p) of the model were $a_1 = 1.107$ (0.033 and $p < 0.001$), $a_2 = -1.00$ (0.033 and $p < 0.001$), $b_1 = 1.00$ (0.113 and $p < 0.001$) and $b_2 = -0.911$ (0.116 and $p < 0.001$). The model was used to forecast grouse bags for the years 1991–1998 together with associated prediction intervals.

As an additional test for a change in the nature of the grouse dynamics from 1991 to 1998, another ARMA(2,2) model was fitted to the log₁₀ bag count for the years 1950–1998. The residuals for the years 1991–1998 were examined for negative bias using a sign test. Predictions of grouse bags on Langholm Moor during 1991–1998 were also made on the basis of the grouse bags at moors F and G during this time from a linear regression relating log₁₀ bags on the different moors during 1975–1990.

Estimates of the grouse density on Langholm Moor in July, immediately prior to shooting, were obtained from 1992 to 1998 (Thirgood *et al.* 2000a). Twelve areas of 0.5 km² were demarcated and the grouse densities estimated from counts with dogs using standardized techniques (Jenkins *et al.* 1963). Temporal trends in the grouse densities were tested by ANCOVA on log-transformed data with area as a factor and time as a covariate.

Historical records of the numbers and breeding success of harriers and peregrines on Langholm Moor and moors F and G were obtained, where possible, from local raptor study groups. During 1992–1998 we recorded the numbers of harriers and peregrines attempting to breed on Langholm Moor by watching from vantage points for displaying harriers and visiting potential

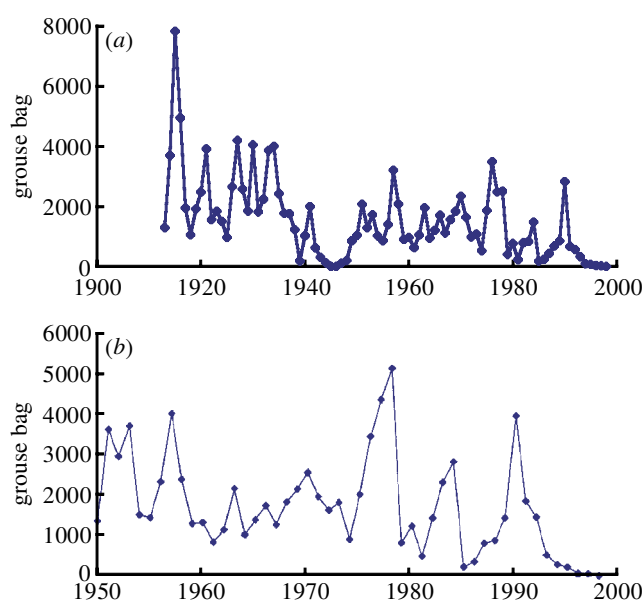


Figure 1. Numbers of red grouse shot on (a) the Eskdale half of Langholm Moor from 1913 to 1998 and (b) the whole of Langholm Moor from 1950 to 1998.

peregrine nests for signs of occupancy. Each raptor nest found in spring was monitored through the breeding season and breeding success recorded.

Aerial photographs were taken of Langholm Moor at a scale of 1:25 000 in 1948 and 1988. The percentage covers of heather and grass were assessed by the same observer from each series of photographs using a stereoscope. Transparent sheets with a 1 ha grid were laid over the photographs and heather cover was categorized in each hectare to the nearest 10%. The 1988 estimates of heather cover were validated in 1994 by an independent observer by walking transects through the moor and assessing dominant vegetation in 1 ha areas around points which could be easily recognized from maps.

3. RESULTS

Linear regression analysis assuming AR(1) residuals revealed evidence that grouse bags on the Eskdale portion of the Langholm Moor declined significantly from 1933 to 1990 (figure 1) (slope = -0.0075 , s.e. = 0.0030 , $t = -2.536$ and $p < 0.007$ and AR(1) term = 0.348 , s.e. = 0.128 , $t = 2.72$ and $p < 0.009$). Similar analysis on grouse bag data from the whole moor from 1950 to 1990 revealed an almost identical but non-significant trend (figure 1) (slope = -0.0073 , s.e. = 0.0064 , $t = -1.141$ and $p < 0.131$ and AR(1) term = 0.340 , s.e. = 0.162 , $t = 2.09$ and $p < 0.05$). A comparison of the aerial photographs taken of Langholm Moor in 1948 and 1988 indicated that the numbers of 1 ha squares with $> 50\%$ heather cover declined by 48% over this time (figure 2). Harriers and peregrines were absent as breeding birds or bred at very low density on Langholm Moor prior to 1990 (figure 3).

The last peak in grouse bags on Langholm Moor was in 1990 when 4038 birds were shot. Grouse bags declined in successive years to zero in 1998 when shooting was abandoned (figure 1). The grouse density estimated in July, at the onset of the shooting season, declined significantly between 1992 and 1998 (figure 4) ($F_{1,67} = 21.4$ and

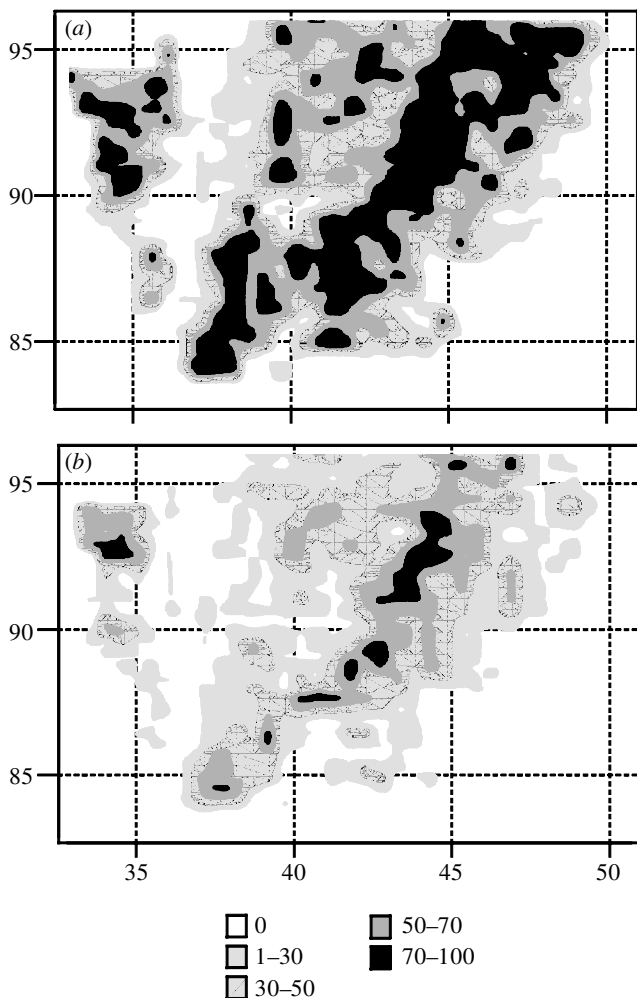


Figure 2. Heather cover on Langholm Moor as assessed from aerial photographs in (a) 1948 and (b) 1988. Heather cover was estimated for 25 ha blocks and divided into five abundance bands. The dotted lines indicate a 100 ha grid.

$p < 0.001$), although this decline was less precipitous than in the grouse shooting bags. The numbers of breeding harriers and peregrines on Langholm Moor increased following the instigation of nest protection in 1990 with a maximum of 20 female harrier and six female peregrine breeding attempts in 1997 (figure 3). The forecasts from the ARMA model fitted to the 1950–1990 bag data assumed no change in the dynamics of grouse cycles on Langholm Moor throughout the 1990s and could therefore be used to test the hypothesis that the observed decline over 1991–1998 was merely the continuation of the long-term trend (table 1). The model predictions for bags during 1991–1998 showed a clear oscillation peaking again in 1996, some six years on from the previous peak in 1990. The observed bags from 1995–1998 fell below the lower 95% (one-step) prediction limits of the forecast bags. Furthermore, analysis of the residuals from an ARMA(2,2) model fitted to the 1950–1998 Langholm Moor data revealed that seven of the eight residuals corresponding to the years 1991–1998 were negative; a sign test rejects the null hypothesis that these residuals have a median equal to zero ($p < 0.032$) suggesting that there was a change in grouse dynamics after 1990, compared to those prior to this time.

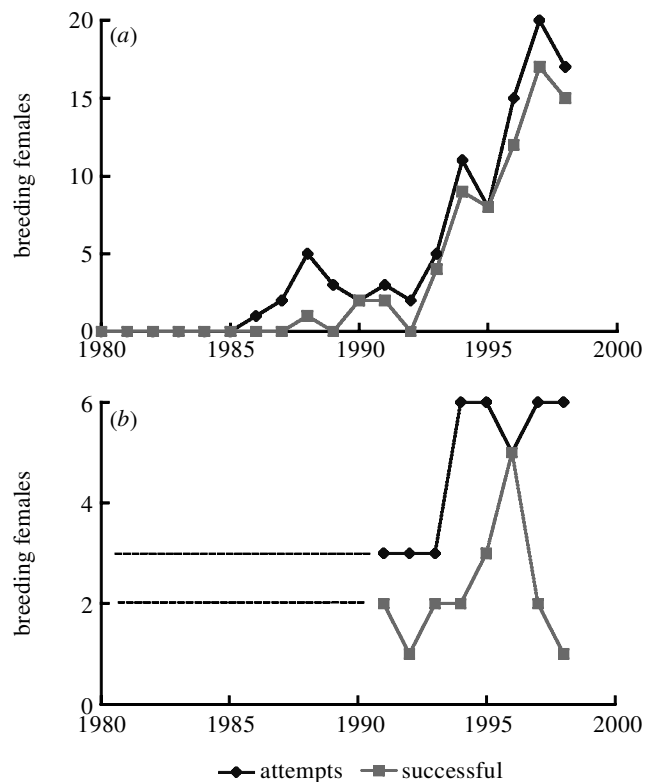


Figure 3. Breeding attempts and successful breeding by (a) female hen harriers and (b) female peregrines on or adjacent to Langholm Moor from 1980 to 1998. Harriers did not attempt to breed prior to 1986. Peregrine breeding attempts prior to 1991 were not rigorously recorded but two to three pairs were believed to attempt to breed throughout the 1980s of which one or two were usually successful.

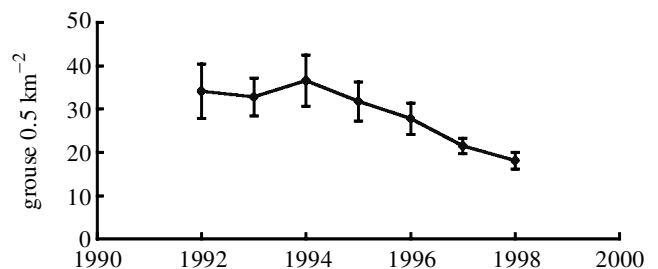


Figure 4. Grouse densities on Langholm Moor in July from 1992 to 1998 as determined by counts with dogs. The values are the means and standard errors of 12 0.5 km² count sites.

Bag records were also available from nearby moors F and G during the years 1975–1998 (figure 5). A comparison of the grouse bags from the three moors during the period 1975–1990 suggested that the bags on Langholm Moor cycled in synchrony with those on moors F and G, with peaks in 1978, 1984 and 1990 or 1991. Grouse bags on all three moors declined following the peak in 1990 or 1991. The bags on moors F and G increased to peaks in 1997 whereas the bags on Langholm Moor continued to decline. Harrier and peregrine breeding numbers increased on Langholm Moor during 1991–1998 whereas the breeding numbers of these raptors on moors F and G remained low. Predictions of grouse bags on Langholm Moor during 1991–1998 were made from bags at moors F and G (table 1). Records from both moors predicted a

Table 1. Prediction of grouse bags and 95% prediction intervals (PI) on Langholm Moor during 1991–1998 based on an autoregressive model from Langholm Moor bags during 1950–1990 and linear regressions relating bags on Langholm Moor to bags on moors F and G during 1975–1990

($\text{Log}_{10}(\text{Langholm Moor}) = 0.241\text{log}_{10}(\text{moor F}) + 5.68$, $r^2 = 23.2\%$ and $\text{log}_{10}(\text{Langholm Moor}) = 0.317\text{log}_{10}(\text{moor G}) + 5.32$, $r^2 = 38.7\%$.)

year	observed Langholm Moor bags	prediction (95% PI) from Langholm Moor bags 1950–1990	prediction (95% PI) from moor F bags 1975–1990	prediction (95% PI) from moor G bags 1975–1990
1991	1879	1434 (476–4315)	1619 (243–10793)	2255 (403–12634)
1992	1473	727 (240–2201)	1418 (214–9396)	1869 (341–10246)
1993	523	538 (178–1629)	930 (134–6475)	1358 (251–7362)
1994	284	751 (247–2281)	1300 (196–8635)	1481 (273–8025)
1995	219	1447 (473–4426)	1830 (271–12364)	2072 (374–11479)
1996	67	2112 (690–6466)	1992 (291–13652)	2280 (406–12792)
1997	51	1638 (534–5026)	2104 (304–14587)	2640 (459–15173)
1998	0	833 (269–2575)	292 (24–3575)	2078 (375–11517)

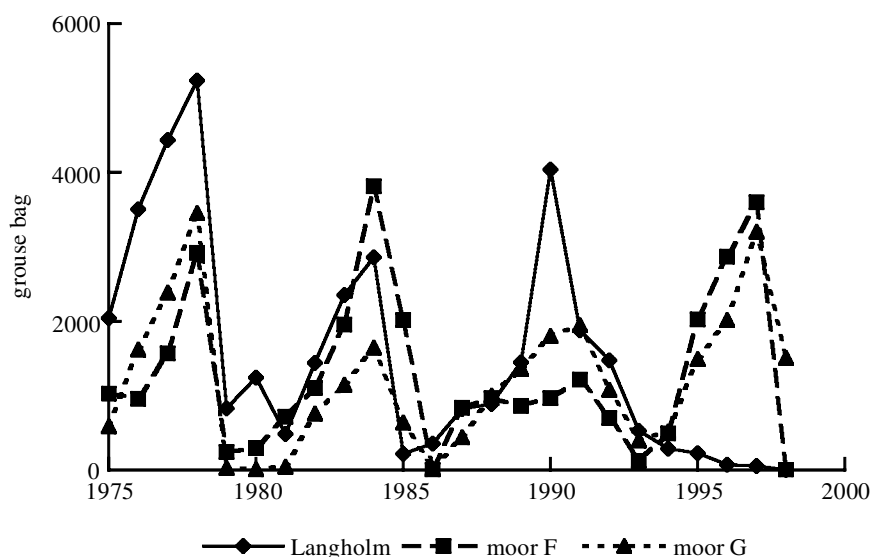


Figure 5. Numbers of red grouse shot on Langholm Moor from 1975 to 1998 in comparison to numbers shot on nearby moors F and G during the same period.

decline in Langholm Moor bags from 1990 to 1993 followed by an increase to a peak in 1997. In both cases the observed Langholm Moor bags in 1995–1998 were less than the lower 95% confidence limit on predicted levels.

4. DISCUSSION

Two results stand out from our analysis. First, there has been a long-term gradual decline in the numbers of grouse shot on Langholm Moor during this century. This decline is statistically significant in the 1913–1990 bags for the Eskdale half of the moor but not in the 1950–1990 bags for the whole moor. However, the two time-series have almost identical negative slopes and the lack of significance in the shorter time-series is largely due to the variability in the time-series in relation to its length. It is extremely unlikely that this decline had anything to do with predation by raptors, as both harriers and peregrines were controlled on this moor and bred at very low densities prior to 1990. The long-term decline in grouse bags coincided with the conversion of nearly half of the heather moorland to grassland during 1950–1990. No

quantitative information is available on habitat loss on Langholm Moor during the first half of this century but anecdotal reports suggest heather cover was even more extensive. Given the associations between red grouse and heather (Brown & Stillman 1993; Stillman & Brown 1994), a link between heather loss and declining grouse bags is strongly suggested. The most likely cause of heather loss on Langholm Moor is heavy grazing by sheep. The situation on Langholm Moor parallels trends across much of the British uplands, where large increases in the numbers of sheep have caused widespread conversion of heather moorland to grassland (Thompson *et al.* 1995; Fuller & Gough 1999). Given that harriers and peregrines have occurred at low density throughout the uplands during this century (Bibby & Etheridge 1993; Crick & Ratcliffe 1995) and that this period coincides with widespread declines in grouse bags (Hudson 1992), the link between grazing, habitat loss and grouse bags identified on Langholm Moor may be repeated elsewhere.

The second important result is that grouse bags on Langholm Moor failed to recover following a cyclic decline in the early 1990s. Predictions of a peak on Langholm Moor in 1996 based on the patterns of grouse

bags during 1950–1990 were supported by the observed peaks in 1997 on two nearby moors which had formerly cycled in synchrony with Langholm Moor. The moors differ in that harriers and peregrines increased to high breeding densities on Langholm Moor following protection in 1990, whereas these raptors remained at low density on the nearby moors due to suspected illegal control. The hypothesis that predation by harriers and peregrines limited the grouse population and suppressed the cycle on Langholm Moor is supported by detailed demographic data and modelling (Thirgood *et al.* 2000a). Predation by harriers and peregrines during the breeding season reduced autumn grouse densities by 50% and models incorporating these losses together with density-dependent winter losses predicted that the removal of raptors would increase both breeding production and breeding density. Harriers and peregrines are generalist predators which occur at high densities on moors where prey such as meadow pipits (*Anthus pratensis*), field voles (*Microtus agrestis*) and pigeons (*Columbia livia*) are abundant (Redpath & Thirgood 1999). If grouse populations fall to low densities on these moors, density-dependent raptor predation may suppress recovery. The raptor–grouse system described here thus supports theoretical models which predict that generalist predators may suppress cycles in prey populations if the predator densities are unrelated to the densities of any one prey and predation on that prey is density dependent (Hanski *et al.* 1991; Hanski & Korpimäki 1995; Turchin & Hanski 1997). This pattern is consistent with the observed effects of generalist predators suppressing vole cycles in southern Fennoscandia (Angelstam *et al.* 1984; Erlinge 1987; Korpimäki & Norrdahl 1989, 1991, 1998). Mammalian predators were predicted to dampen population cycles of red grouse in the model of Hudson *et al.* (1992), but in this model the mechanism was through selective removal of heavily parasitized grouse reducing the effect of the parasite on grouse reproduction which is thought to generate the population cycles (Hudson *et al.* 1998).

The raptor–grouse system described in this paper demonstrates the importance of a temporal scale in consideration of the factors limiting vertebrate populations. In the long term, conversion of heather moorland to grassland over much of this century, which has almost certainly been caused by heavy grazing by sheep, has reduced the area of suitable habitat for grouse and may have also reduced the productivity of remaining areas of heather moorland. The long-term declines in grouse bags can be partially explained by the loss of heather moorland, although other factors such as reductions in the numbers of gamekeepers may also have been involved (Hudson 1992). In the short term, however, there is convincing evidence that predation by harriers and peregrines can limit grouse populations at low density and suppress population cycles. The fact that limitation of grouse populations through raptor predation does not occur more widely can be explained by the illegal control of raptors on grouse moors and the continuing suppression of their densities (Etheridge *et al.* 1997; Thirgood *et al.* 2000b). The raptor–grouse system is of wider interest because of the interaction between the ecological processes which occur on different time-scales. Hen harriers breed at high densities on grouse moors where

meadow pipits and field voles are abundant (Redpath & Thirgood 1999). Meadow pipits and field voles are most abundant on moorland where there is a mosaic of grass and heather (Redpath & Thirgood 1997). It is plausible that habitat change caused by grazing can result in the increased abundance of generalist predators and the limitation of grouse populations by predation. A similar process of habitat fragmentation has been proposed to explain the increased abundance of generalist avian and mammalian predators in the fragmented forests of southern Fennoscandia (Andren 1992; Kurki *et al.* 1998).

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