

Can Raptor Predation limit Red Grouse Populations?

S.J. Thirgood and S.M. Redpath

ABSTRACT

Whether vertebrate predators can limit their prey has long been a controversial question in ecology. This paper summarises a study of predation by Hen Harriers *Circus cyaneus* and Peregrines *Falco peregrinus* on Red Grouse *Lagopus lagopus scoticus* populations in Scotland. Harrier breeding densities were highest in areas and years where passerines and microtines were most abundant. Peregrine breeding densities were highest on southern moors, probably as a result of high pigeon densities. Harriers showed a Type III functional response to grouse chicks. Peregrines showed a Type II response to adult grouse. The implication of these findings is that the greatest proportion of grouse will be removed by raptors from low density grouse populations on southern, grassy grouse moors where alternative prey are abundant. On a moor where breeding densities of harriers and peregrines were high, predation by these raptors during April to September reduced autumn grouse densities by 50% within a single breeding season. On this moor, an increase in raptor densities coincided with a large decline in the numbers of grouse shot. Our data were strongly suggestive that predation by generalist raptors limited Red Grouse populations at low density.

INTRODUCTION

The question of whether predators can limit their prey has long been controversial. An earlier view was that vertebrate populations were limited by habitat constraints and that predators took only the so-called 'doomed surplus' (Errington 1946). However, there is an emerging consensus that predation can in some circumstances limit populations of microtine rodents and lagomorphs (Boutin 1995; Nordahl 1995). Current evidence for predator limitation of bird populations is equivocal - with studies on songbirds suggesting that predation has little effect but studies on waterfowl and gamebirds suggesting that predation can reduce both breeding success and breeding density (Newton 1998).

Red Grouse *Lagopus lagopus scoticus* fall prey to a range of avian and mammalian predators and there has been much debate regarding the impact of predation on grouse populations. Early studies on Red Grouse populations at high density concluded that predators concentrated on non-territorial grouse as opposed to territory owners and that predation was unimportant in limiting populations (Jenkins *et al* 1964; Watson 1985). Later research on Red Grouse populations at low density demonstrated that overwinter survival of territorial and non-territorial grouse was similar,

and suggested that winter predation could be partially additive (Hudson 1992). The importance of the relative densities of grouse and their predators was also highlighted in two studies of predation by Hen Harriers *Circus cyaneus* on grouse chicks. Picozzi (1978) estimated that harriers removed only 7.4% of grouse chicks from a moor where grouse were at high density, whilst Redpath (1991) suggested that on moors with lower grouse densities, harriers could remove up to 17% of grouse chicks.

These studies suggested that the relative abundance of raptors and grouse was important in determining whether raptor predation could limit grouse populations. Little information was available, however, on the mechanisms involved, or on the factors influencing raptor numbers and diet on moorland. Here we summarise a recent study (Redpath & Thirgood 1997), which addressed the following questions:

1. What influences the numbers (numerical response) and diet (functional response) of Hen Harriers and Peregrines *Falco peregrinus* on grouse moors?
2. What impact does predation by Hen Harriers and Peregrines have on grouse populations and grouse shooting bags?

STUDY AREAS AND METHODS

The study was conducted during 1992-96 at Langholm in southern Scotland on a grouse moor where harriers and peregrines had been protected since 1990. We extended the work in part to six other moors where raptors were also protected. On all of these moors mammalian predators and corvids were controlled by gamekeepers. Langholm was historically one of Scotland's finest moors, but in common with many moors, grouse bags had been in decline since early this century at approximately 1.7% per annum. It is very unlikely that raptors were involved in this decline as they were uncommon prior to 1990. Comparison of aerial photographs taken at Langholm during 1948 and 1988 indicates that heather cover declined by 48% in this period and this loss of grouse habitat was considered to be the most likely cause of the long-term decline in grouse bags.

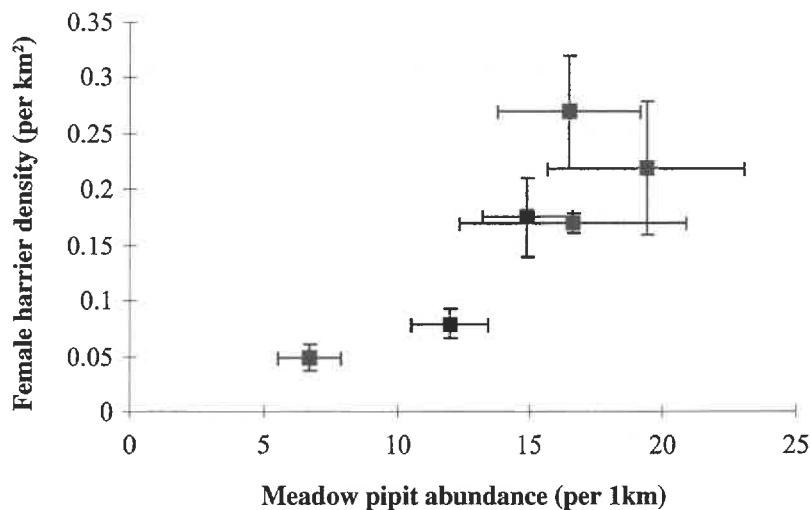
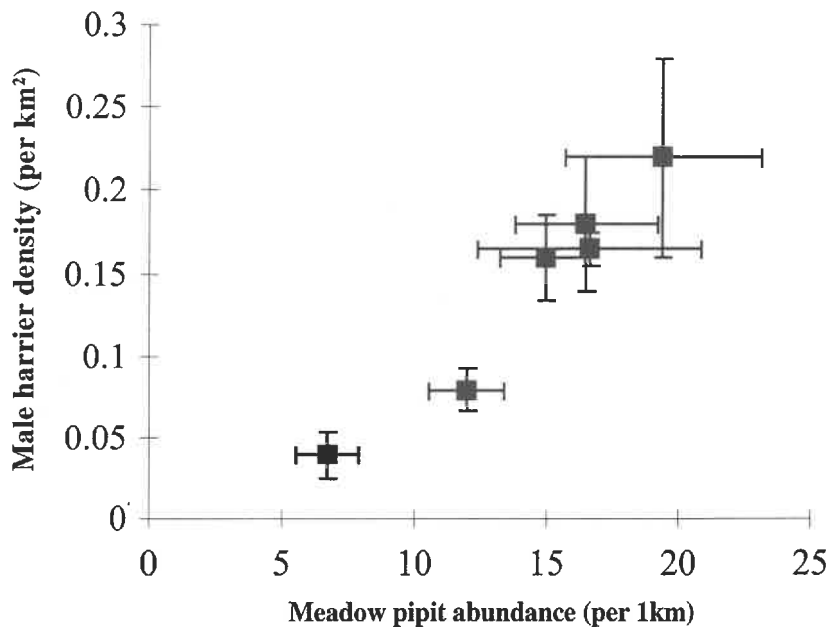
On each moor we estimated the density of Red Grouse and obtained a measure of abundance of moorland passerines and small mammals. Grouse densities were estimated in April, July and October using standard counts with pointing dogs. We also used dogs to obtain estimates of grouse brood size and grouse chick abundance in early June. Passerines were counted in June using line transects on random grid squares. Small mammal abundance was estimated by snap trapping in April. The numbers of harriers and peregrines attempting to breed on each moor were determined in spring by systematically watching the moor from vantage points for displaying harriers and by visiting peregrine nesting sites for signs of occupancy. Harrier diet was assessed during 2678 hours of observations from hides placed at harrier nests. Peregrine diet was assessed from prey remains and pellets collected during regular searches at eyries throughout the breeding season. Intensive studies on the effects of raptor predation on grouse populations and shooting bags were conducted at Langholm. In addition to the estimates of grouse densities described above, we systematically searched for grouse corpses on counting sites throughout each winter 1992-96. We also captured and radiotagged 308 grouse during 1994-96 and monitored their weekly survival. Finally, we had access to detailed bag records of the numbers of grouse shot in each year at Langholm and on neighbouring moors since the late 19th century. Full details of methods used and tests of potential biases are given in Redpath & Thirgood (1997) and references cited therein.

RESULTS AND DISCUSSION

Numerical response of harriers and peregrines

Before considering the numerical response of harriers, we assessed how densities varied after illegal control had stopped. Breeding densities of harriers on our study moors increased year-on-year for four years, on average, following protection. At Langholm, harrier numbers increased from two females in 1992 to 20 females in 1997. Having removed the effects of illegal control, breeding

Figure 1. Mean ($\pm$ se) Hen Harrier density km^2 for (a) males and (b) females in relation to mean ($\pm$) meadow pipit abundance on six study moors.



densities of harriers varied considerably between moors and were not primarily related to grouse density in April. Comparison of harrier densities between moors indicated that densities of males and females were positively associated with Meadow Pipit *Anthus pratensis* abundance and to a lesser extent females were positively associated with small mammal abundance (Figure 1). Within moors, variation in male and female densities from year to year were related to small mammal abundance. This is an important finding, because it has implications for how many harriers we would expect on grouse moors in the absence of illegal control. Meadow pipits and field voles occur at higher densities on moors with a mosaic of heather and grass, so we can expect more harriers on these moors in the absence of control.

Breeding densities of peregrines tended to be more stable from year to year, although at Langholm they increased from three to six pairs over the course of the study. Comparing areas, there was a positive relationship between latitude and the average nearest neighbour distance between peregrine nests (Figure 2). In other words, peregrine nests were further apart at more northerly latitudes. The relationship between grouse density in April and peregrine nearest neighbour distance was not significant, nor was it significant after removing the effects of latitude. Our interpretation of the relationship between peregrine nesting density and latitude is that it is an indirect measure of racing pigeon abundance. Racing pigeons are a major prey of peregrines.

In summary - neither harrier nor peregrine breeding densities were related to grouse densities. In the absence of illegal control, we would expect more harriers on grassy moors where passerines and voles are more abundant and more peregrines on southern moors where racing pigeons are more abundant.

Functional response of harriers and peregrines

Passerines were numerically the most important prey for breeding harriers (63%) and grouse formed only 15% of the prey items identified to species. Of the 263 grouse seen brought to harrier nests, 96% were chicks. The rate at which harriers provisioned grouse chicks varied considerably between different years and different moors. The main factor influencing this variation was the density of grouse chicks, with more grouse chicks resulting in higher provisioning rates. The relationship between grouse chick density and male provisioning was sigmoidal (Type III), with a sharp increase in provisioning of grouse chicks at densities between 50 and 70 chicks per km² (Figure 3). The shape of this relationship indicated that the greatest proportion of grouse chicks were removed by individual harriers at relatively low grouse chick densities.

A total of 868 prey remains was collected during the breeding season from 20 peregrine eyries on six moors. Racing and feral pigeons formed the bulk of the items (49%), whilst Red Grouse formed only 15%. The majority of Red Grouse collected were adults (92%), although the remains of 10 chicks were found. As with the harriers, there was considerable spatial and temporal variation in the occurrence of Red Grouse in the diet of peregrines. The percentage of biomass provided to peregrines by Red Grouse increased with grouse density but levelled off at grouse densities above 20 birds per square km (Figure 4). The shape of this curve suggested that the greatest proportion of adult grouse were removed by individual peregrines at relatively low grouse densities.

In summary - Red Grouse were not the main prey of either harriers or peregrines on grouse moors, though both species took more grouse as grouse became more abundant. The relationships between raptor diet and Red Grouse abundance indicated that individual harriers and peregrines took a greater proportion of grouse at relatively low grouse densities. The implication of this was that grouse populations at low density were more susceptible to limitation through raptor predation.

Impact of raptor predation on grouse populations

The data presented here were derived from counts of grouse with pointing dogs and from systematic searches for grouse corpses. We also radiotagged 308 grouse to look at mortality patterns in more detail. Overall, these data showed that raptors killed on average 30% of the grouse over winter (October - March) and a further 30% during the following spring (April - June) when the grouse were attempting to breed (Table 1). We were unable to distinguish between the kills of harriers

Figure 2. Mean nearest neighbour distance between Peregrine eyries in relation to latitude for seven study moors.

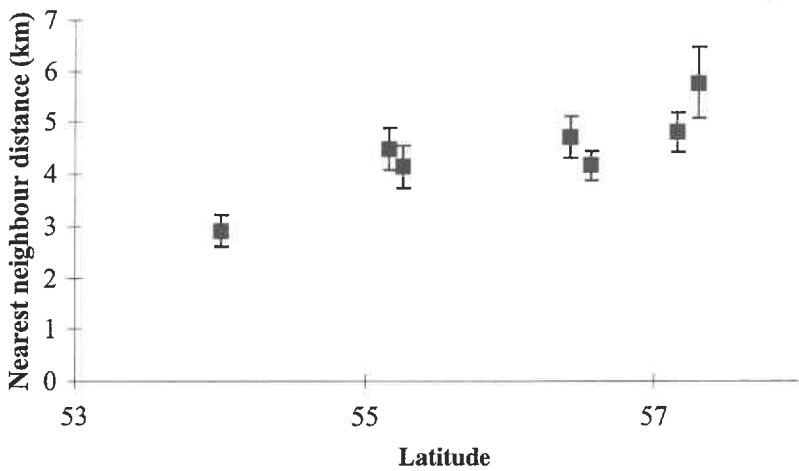


Figure 3. Rate at which Red Grouse chicks brought to harrier nests by male and female harriers combined in relation to the density of grouse chicks. Points represent means ($\pm$ se) for one moor in one year. Line is fitted Type III relationship. Curve fitted to model $Y = 0.21x5.1 / (515.1 + x5.1)$.

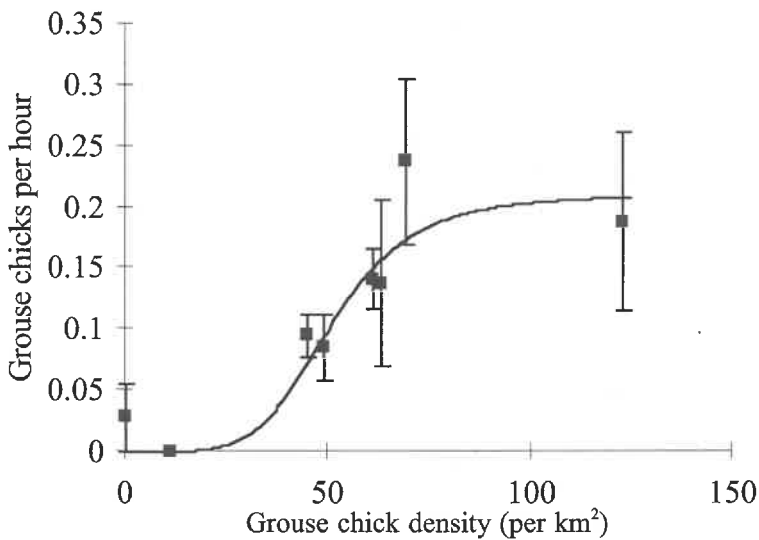


Figure 4. Percentage of Red Grouse in Peregrine prey items (by biomass) in relation to estimates of grouse abundance within a two kilometre radius of each eyrie. Line is fitted Type II relationship. Curve fitted to model $Y = 53.4x / (8.4 + x)$.

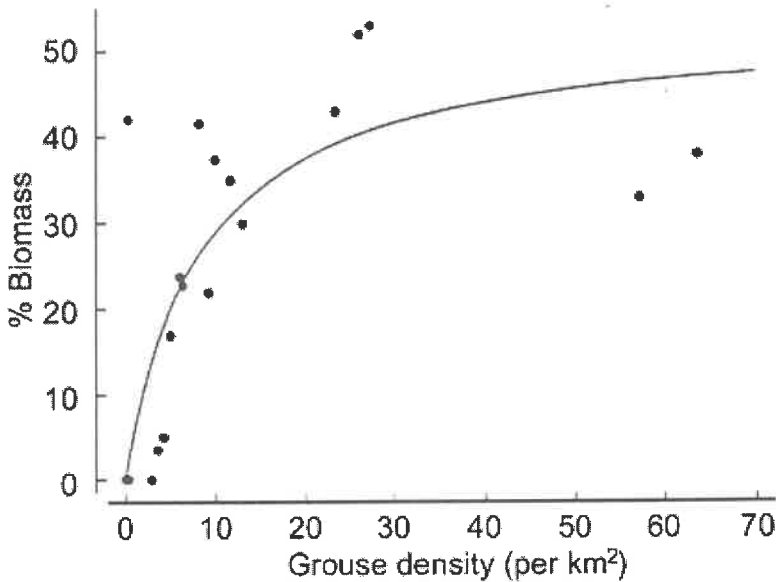
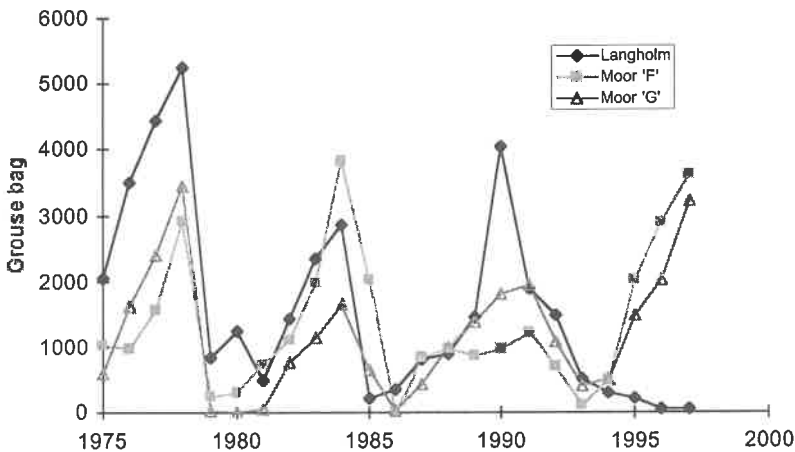


Figure 5. Numbers of Red Grouse shot on Langholm moor during 1975-97 in comparison to numbers shot on nearby moors F and G during the same period. Grouse bags on all three moors fluctuated in synchrony during 1975-93. After 1993, grouse bags on moors F and G increased, while bags on Langholm moor continued to decline. Harrier and peregrine numbers on Langholm moor increased between 1990 and 1997, whereas numbers of these raptors on moors F and G remained low.



and peregrines during these periods. Predation on adult grouse during the summer was low but when harriers were abundant in the latter years of the study they removed up to 40% of the chicks produced by the surviving hens (Table 1). We were unable to determine whether or not the losses to raptors during the winter were compensated by reductions in other losses. However, losses to raptors of adult grouse in spring and grouse chicks in summer appeared to be additive to other mortality and we estimated that they reduced autumn densities of grouse by 50% within a single breeding season. A simple model of the grouse population, combining the estimated reduction in breeding productivity with the observed density dependence in winter loss, predicted that over two years, in the absence of breeding raptors, grouse breeding numbers would have increased by 30% and post breeding numbers by 150%.

Table 1. Grouse mortality to raptors at Langholm during 1995 and 1996. Data on adult mortality derived from radio-tagging studies. Data on chick mortality derived from observations at harrier nests and counts of grouse chicks with pointing dogs. Further details in Redpath & Thirgood (1997).

<i>Year</i>	<i>1995</i>	<i>1996</i>
Live grouse in October (km ²)	49	41
Killed by raptors October - March (%)	28	47
Killed by raptors April - September (%)	30	39
Live grouse chicks at hatch (km ²)	78	71
Killed by raptors June - July (%)	35	39

Impact of raptor predation on shooting bags

Analysis of long-term bag records demonstrated that, in common with many moors, grouse bags at Langholm fluctuated with an approximately six year cyclic pattern. The last peak year at Langholm was in 1990, when more than 4000 grouse were shot, and the next peak was thus expected in 1996. Grouse bags declined year on year from 1990 until only 51 grouse were shot in 1997. A model based on the Langholm bags from 1950-90 suggested that the observed bags in 1995-97 were significantly lower than expected. We compared the grouse bags at Langholm to those from two nearby moors where harriers and peregrines bred at low density because of illegal control (Figure 5). Between 1975 and 1993 the bags from all three moors cycled in relative synchrony. Since 1993, when raptor numbers at Langholm started to increase, grouse bags at Langholm declined. In contrast, grouse bags on the nearby moors increased to high levels. The simplest explanation was that raptors prevented the grouse population at Langholm from increasing to a cyclic peak as expected.

CONCLUSIONS

Whilst raptors were unlikely to be responsible for long-term declines in British Red Grouse populations, they appeared to be capable of holding grouse at low density. Our data were strongly suggestive that predation by the large numbers of harriers and peregrines prevented the grouse population at Langholm from increasing to a cyclic peak and can thus be considered a limiting factor. This suggestion now needs testing through predator reduction experiments.

The numbers of harriers and peregrines were high at Langholm because of the abundance of alternative prey such as meadow pipits, field voles and pigeons. Meadow pipits and voles were abundant because of the mosaic of heather and grass and pigeons were more abundant on southern moors than northern moors. Information on the diet of harriers and peregrines suggests that the greatest proportion of adult grouse and grouse chicks were removed by individual raptors when grouse populations were at low density. The numerical and functional responses suggested that the

potential for harriers and peregrines to limit grouse populations varied between moors. The impact of raptor predation was expected to be greatest on low density grouse populations on grassy southern moors where alternative prey and raptors were at high density. A key area for further research is to determine how many other grouse moors would resemble Langholm, with high harrier densities and low grouse bags, if illegal control of harriers were to cease.

ACKNOWLEDGEMENTS

Many people helped in this research but we particularly thank Ian Newton for his support and guidance throughout. The study was funded by the Buccleuch Estate, Game Conservancy Trust, Game Conservancy Scottish Research Trust, Institute of Terrestrial Ecology, Joint Nature Conservation Committee, Natural Environment Research Council, Royal Society for the Protection of Birds, Scottish Natural Heritage and Westerhall Estate. SJT is grateful to the Royal Society for supporting his attendance at this conference.

REFERENCES

- BOUTIN, S. 1995. Testing predator-prey theory by studying fluctuating populations of small mammals. *Wildlife Research*, 22, 89-100.
- ERRINGTON, P.L. 1946. Predation and vertebrate populations. *Quarterly Review of Biology*, 21, 144-177.
- HUDSON, P.J. 1992. *Grouse in Space and Time*. Fordingbridge: Game Conservancy Trust.
- JENKINS, D., A. WATSON & G.R. MILLAR 1964. Predation and Red Grouse. *Journal of Applied Ecology*, 1, 183-195.
- NEWTON, I. 1998. *Population Limitation in Birds*. London: Academic Press.
- NORDAHL, K. 1995. Population cycles in northern small mammals. *Biological Reviews*, 70, 621-637.
- PICOZZI, N. 1978. Dispersion, breeding and prey of the hen harrier in Glen Dye, Kincardineshire. *Ibis*, 120, 489-509.
- REDPATH, S.M. 1991. The impact of Hen Harriers on Red Grouse breeding success. *Journal of Applied Ecology*, 28, 659-671.
- REDPATH, S.M. & S.J. THIRGOOD 1997. *Birds of Prey and Red Grouse*. London: Stationary Office.
- WATSON, A. 1985. Social class, socially induced loss, recruitment and breeding in Red Grouse. *Oecologia*, 67, 493-498.

S. J. Thirgood
Game Conservancy Trust
Institute of Cell, Animal and Population Biology
University of Edinburgh, Kings Buildings
Edinburgh, EH9 3JT
UK.

S. M. Redpath
Institute of Terrestrial Ecology
Banchory, Kincardineshire
AB31 4BY
UK.