Geographical and seasonal patterns of mortality in red grouse Lagopus lagopus scoticus populations

Authors: Hudson, Peter J., Newborn, David, and Robertson, Peter A.

Source: Wildlife Biology, 3(2) : 79-87

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.1997.010

Geographical and seasonal patterns of mortality in red grouse *Lagopus lagopus scoticus* populations

Peter J. Hudson, David Newborn & Peter A. Robertson

Hudson, P.J., Newborn, D. & Robertson, P.A. 1997: Geographical and seasonal mortality in red grouse *Lagopus lagopus scoticus* populations. - Wildl. Biol. 3: 79-87.

Corpses of red grouse *Lagopus lagopus scoticus* were collected monthly from 10, 1-km^2 study areas on managed grouse moorland for a period of 10 years. Six of the study areas were located in Scotland and four in Northern England. A greater number of corpses were found on the Scottish study areas than on the English and compositional analysis identified the relative importance of death through parasitism in England. Stoat *Mustela erminea* kills were more prevalent in England but fox *Vulpes vulpes* and large raptors were more important in Scotland. Predators were more abundant in Scotland and frequency of sightings positively correlated with number of kills between study areas. There was a seasonal peak in mortality in spring.

Key words: corpses, fox, parasitism, predation, raptors, red grouse

Peter J. Hudson, Unit of Wildlife Epidemiology, Department of Biological and Molecular Sciences, University of Stirling FK9 4LA, Scotland, UK
David Newborn & Peter A. Robertson, Upland Research Group, Game Conservancy Trust, Crubenmore, Newtonmore, Inverness-shire PH20 1BE, Scotland, UK

Received 5 November 1996, accepted 23 May 1997

Associate Editor: Jon E. Swenson

Demographic studies of animal populations aim to estimate rates and patterns of fecundity, mortality and dispersal. Estimating fecundity is usually straight forward but estimating mortality and dispersal (emigration and immigration) is fraught with difficulties. One approach to investigating mortality is to examine the disappearance of marked individuals, however, disappearance may mean emigration or an unrecovered death. In vertebrate studies, accuracy in determining mortality has improved within the past 20 years with the development of radio tags that permit the worker to follow individuals with little disturbance until the time of death. Such studies provide an estimate of mortality rate but only identify the proximate cause of mortality (Kenward 1987, White & Garrott 1990). However, even radio tracking does not provide all the answers; a proportion of radio-tagged individuals are lost due to transmitter failure and emigration and obtaining a large sample size is a time-consuming and costly exercise. Undertaking such studies within a single population is difficult enough but to undertake seasonal, comparative studies on replicated geographic sites over a reasonable period of time becomes prohibitively expensive in effort and cost.

In our detailed and extensive studies of the population dynamics of red grouse *Lagopus lagopus scoticus* we have taken three approaches to estimating mortality and its causes: first, the standardised search for and collection of corpses from study areas in different parts of the species' range, second the use of radio-tagged individuals and third, the experimental manipulation of individuals and mortality factors coupled with predictions of changes in survival (Hudson, Newborn & Dobson 1992b, Hudson 1992). This paper examines the seasonal and geographical variation in the collection of red grouse corpses from

10 study areas in Scotland and England over a period of 10 years.

Materials and methods

Collection of corpses

Ten study areas of 1 km^2 were established on areas of heather moorland, managed for the production of red grouse (Hudson & Newborn 1995); four in North Yorkshire, England and six in Inverness-shire, Scotland. Study sites were selected as representing variations in altitude, moorland habitat and grouse density (Table 1). Most of the study areas were considered to hold separate grouse populations usually because of breaks in habitat between populations, although the two study areas Drumochter 1 and Drumochter 2 were within 2 km of each other and formed part of a contiguous area of grouse moorland. Each area was searched during the third week of each month between July and April for 10 years starting in January 1986 and finishing in December 1995. Searches were not conducted during the months of May, June and July because this would have caused undue disturbance to breeding birds. Searches were postponed if harsh weather conditions made corpse searches worthless.

Initially, each study area was searched on six passes but after three years this was increased to 12 or more passes when visibility was poor due to thick cover or poor weather conditions so the observer felt satisfied the site had been well covered. Each site was covered by a minimum of 6 km at least 170 metres apart and usually took about four man-hours. The searches were undertaken by each of five main field workers although others assisted at times. The direction of search alternated each month (right angles to the previous month), thus ensuring an intensive coverage of each study area. Each pass of the study area was undertaken by walking slowly and scanning the vegetation with binoculars for signs of feathers or corpses. When a sign was noticed, the transect path was left and the worker walked to the sign to search the area for a corpse. If a death was confirmed, standardised notes were taken, the corpse collected and the field worker returned to the transect.

Detailed demographic data were also collected from each study area by counting the number of breeding pairs in spring and by assessing breeding production in July (further details in Hudson et al. 1992b, Hudson 1992). Most shooting occurred during the months of August and September and a post-shooting count was undertaken in October. Table 1 summarises these data.

Identification of corpses

A mortality was recorded if there were red grouse bones, body tissues, guts or primary feathers present. Clumps of feathers without bones or only secondary feathers were ignored because fighting grouse can leave such signs. However, the loss of a significant number of primaries would have made the bird unable to fly and probably resulted in death. All the remains were removed but when there was a preponderance of feathers, a sign (three secondary feathers stuck in the ground) was left so that other workers did not record the mortality on a subsequent visit. Each field worker recorded all details on a standardised record card including a sketch of feathers and other signs. The surrounding vegetation was searched for signs of mammal predators (faeces, urine odour, corpse caching) or raptor predators (mutes, pellets). The relative location of the corpse in the study area was noted, whether the corpse was close to an object

Table 1. Characteristics of 10 study areas with details of grouse demography and environmental variables. For further details on how these characteristics and variables are described see Hudson (1992). Bag records are means from 1980 to 1989.

	Blind Ghyll	*Tarn Moss*	*Dallowgill*	*Danby Low*	*Drumochter 1*	*Drumochter 2*	*Lodge*	*Dalwhinnie*	*Moss*	*Buachalle*
Location	Yorkshire Dales	Yorkshire Dales	Southern Dales	North York Moors	Speyside, Scotland	Speyside, Scotland	Speyside, Scotland	Speyside, Scotland	Speyside, Scotland	Speyside, Scotland
[1]Hens/km^{-2}	35.4	29.6	24	17.2	12.7	10.9	11.0	11.1	4.2	5.22
Young/hen	4.78	4.18	6.04	3.35	4.84	5.04	4.58	4.03	5.5	3.17
Bag/km^{-2}	8	87	146	52	8	8	7	7	4	4
[2]Birds/km^{-2}	80.0	94.3	76.4	59.0	53.4	52.5	38.4	44.7	16.3	17.6
Habitat	Mire	Mire	Heath	Heath	Mire	Mire	Mire	Mire	Heath	Heath
Altitude, m a.s.l.	550	520	350	200	560	520	540	500	410	450
No of wet days	180	180	140	120	180	180	180	180	160	160
Grazing	Moderate	High	Low	Low	Low	Low	Moderate	Moderate	Low	Moderate

[1] The number of hens/km^{-2} is the breeding density
[2] The number of birds/km^{-2} gives the total number of birds in October

it may have collided with or a mound or post on which a predator may have eaten the bird. Each corpse was classified into one of four broad categories: 1) killed by a raptor, 2) killed by a mammalian predator, 3) a thin bird with characteristics of death through parasites or 4) birds that had probably died from a violent cause not associated with a predator, e.g. collision with fence or shot. The last category included any birds where the cause of death was not obvious. Grouse killed by parasites were usually highly emaciated, often with a full crop, no external signs of injury with a lack of leg feathering. In the past we have shown that such deaths were associated with the nematode *Trichostrongylus tenuis* and experimental treatment of infected birds increased survival chances (Hudson 1986, 1992, Hudson, Dobson & Newborn 1992a, Hudson & Newborn 1995). Individuals weakened by parasites and then killed by predators would have been classified as killed by a predator; this is examined in more detail by Hudson et al. (1992a). The accuracy of each classification was determined on a subjective ranked scale of 1 to 5 (Table 2). Corpses classified as ranks 1 and 2 were only based on weak evidence, whereas ranks 3-5 included individuals where there was good evidence supporting the cause of death. Young birds were birds less than nine months of age.

The suspected predator species for each corpse was also recorded if possible according to the evidence available and again the accuracy was subjectively ranked on a scale of 1 to 5 (see Table 2). The cause of mortality of each corpse was assessed independently by a second worker after the corpse was brought back to the laboratory for forensic analyses and any corpse discovered by an inexperienced field worker was examined *in situ* by an experienced field worker. Any differences in the classification of corpses were discussed and an independent assessment by other experienced field workers was sought. When we observed a grouse killed or being eaten by a predator, careful notes and observations were taken and used as a reference for the classification of other grouse corpses collected. Similar techniques have been used and the ability to recover the corpses tested by previous workers (Jenkins, Watson & Miller 1964, Redpath 1989).

Raptor kills were characterised by distinguishing features, in particular the presence of a notched sternum, torn chest muscles, a puff of feathers where the raptor had struck the prey, signs of feathers being plucked, mutes and pellets close to the kill. Peregrine *Falco peregrinus* kills or kills by other large raptors frequently had a broken neck with the head separated from the body by some distance. Peregrine kills also exhibited a characteristic feather pattern reflecting where the bird was struck and later plucked with a strong dismemberment of the corpse, often with the humerus broken. Smaller raptor kills were more carefully eaten, the humerus was not broken and the chest muscles eaten carefully with distinct beak marks. Distinguishing between large raptor kills, such as peregrine, and small raptor, such as hen harrier *Circus cyaneus*, kills was the most difficult task and whereas clear evidence was required for classification, in many instances this was not possible and the kill was not classified further than a raptor kill.

Mammal kills showed characteristics of feathers having been bitten rather than plucked and bones crushed rather than snapped so distinguishing between raptor and mammal kills was relatively simple. Red fox *Vulpes vulpes* kills were quite different from raptor kills, the carcass having been chopped and eaten and often the guts and small parts of the carcass remaining. Foxes frequently crushed the humerus but peregrines would also break this bone. Foxes frequently left the strong smelling caeca behind and occasionally defecated or urinated close by. Stoats *Mustela erminea* tended to partially bury the carcass and eat part of the kill, characteristically starting behind the head and neck and then eating part of the chest muscles while not eating any of the remaining part of the body, leaving a very cleanly,

Table 2. Subjective ranked scale used to identify predator type and predator species when examing corpses of red grouse.

Ranked scale	Description
1	Cause of death unknown
2	Cause of death indicated but evidence weak (predator faeces, marks on the corpse).
3	Cause of death determined from evidence available and at least one obvious sign of cause of death such as notched sternum (raptor) or crunched bones (mammal).
4	Cause of death determined from several obvious signs indicating the type of predator.
5	Cause of death known, kill observed

partly eaten corpse. In Scotland evidence of wild cat *Felis silvestris* and pine marten *Martes martes* kills were recorded but so few were found that these were analysed simply as mammal kills.

Care was taken when identifying kills to ensure the bird had not died from one cause and subsequently been scavenged. The location of the corpse relative to tracks or fences was noted and the signs of more than one predator considered. In such situations it was generally clear which predator had killed the grouse, although if in doubt we considered that the mammal, usually fox, was more likely to scavenge the corpse than a raptor.

The time of death was estimated for each corpse as having occurred either within the past week, within the past month or more than a month ago. Corpses that appeared to have been killed several months previously were assigned to one of the four previous seasons: winter (December-February), spring (March-May), summer (June-August) or autumn (September-November). Corpses assigned to these seasons were later distributed equally among the three months of that season.

Predator presence

Assessing the abundance of predators and the relative predator pressure requires long periods observing an area of moorland and recording the presence and movement of predators. This is time consuming and difficult to record during both day and night. We recorded the amount of time spent undertaking routine field work on each study area and recorded the presence of raptor predators on each visit. If a raptor was seen twice during a bout of field work, it was not always possible to determine if this was the same individual recorded twice or two different individuals. Relative density of raptors was expressed as the number of raptors seen per 100 hours of fieldwork. We also collected and recorded the number of fox faeces as an indirect estimate of fox predator pressure. We express the relative predator pressure as the number of raptors, either hen harriers or peregrines present per 100 hours of field work and the total number of fox scats recorded per 100 hours of fieldwork.

Results

Geographic variation in causes of mortality and predator pressure

A total of 729 corpses were collected on the 10 study areas over the 10 years of this study. The principle cause of mortality on all study areas was predation and in 8 of the 10 study areas the principle cause of predation was raptor predation (Table 3).

Geographically the study areas fall into two discrete groups with different predator species and population dynamics (Hudson 1992) so comparisons were made between study areas at the low spatial scale and between countries at the large spatial scale. Significantly more corpses and kills by predators were recovered on Scottish than on English study areas (Mann Whitney U = 0, P = 0.01), with significantly more raptor kills in Scotland than in England

Table 3. Cause of mortality assigned to red grouse corpses collected in England (N = 125) and Scotland (N = 604)from 1986-1995. Figures are total numbers recovered. Further details in Table 1.

	Cause of mortality				
Study Area	Raptor	Mammal	Parasite	Other	Total
Blind Ghyll	12	8	7	2	29
Tarn Moss	16	19	19	1	55
Dallowgill	12	3	5	2	22
Danby	12	7	0	0	19
England total	52	37	31	5	125
%England	41.6%	29.6%	24.8%	4%	
Drumochter 1	45	67	0	21	133
Drumochter 2	69	66	0	21	156
Lodge	46	24	0	4	74
Dalwhinnie	77	35	0	14	126
Moss	43	17	0	7	67
Buachalle	35	12	0	1	48
Scotland total	315	221	0	68	604
% Scotland	52.1%	36.6%	0%	11.3%	
Total	367	258	31	73	729
% total	50.4%	35.4%	4.2%	10.0%	

Table 4. Predator species associated with red grouse corpses, based on the corpses where the predator species was identified and the accuracy of the identification was ranked as 3 or higher (see Table 2).

Study area	Predator: Medium/Large raptors	Smaller raptors	Fox	Stoat	Total
Blind Ghyll	4	0	3	2	9
Tarn Moss	7	3	9	5	24
Dallowgill	1	1	1	2	5
Danby	1	1	5	1	8
England Total	13	5	18	10	46
%England	28.3%	10.9%	39.1%	21.7%	
Drumochter 1	31	3	53	4	91
Drumochter 2	26	6	57	2	91
Lodge	21	5	12	2	40
Dalwhinnie	33	13	21	0	67
Moss	14	6	14	0	34
Buachalle	13	5	10	0	28
Scotland total	138	38	167	8	351
%Scotland	39.3%	10.8%	47.5%	2.3%	
Total	151	43	185	18	397
% total	38.0%	10.8%	46.6%	4.5%	

(U = 0, P = 0.01), significantly more mammal kills in Scotland than in England (U = 2, P = 0.038), but significantly more parasite kills in England than in Scotland (U = 0, P = 0.01). Since the data in the form of proportions cannot be considered independent, we used compositional analysis (Aitchison 1986), where the proportions were converted to log ratios. Compositional analyses identified significant differences in the proportional cause of death between English and Scottish study areas (F = 21.6, df = 3,6, P = 0.001) with a proportional trend running parasites > raptors > mammals > found dead for the scale of England to Scotland. There was a significantly higher proportion of parasite-related deaths on English than on Scottish study areas (P < 0.05). Whereas there was a numerical difference between Scotland and England, there was no difference in the relative proportion of deaths attributable to the other causes between the two countries. It would appear that corpses are more frequently found on Scottish study areas and more often killed by predators than on English study areas. Proportionately, parasite-induced losses are more common on English than on Scottish study areas, but the other causes of loss occur in similar proportions in the two countries. The relative importance of different predator species also varied between the two countries (F = 15.284, df = 3,6, P < 0.005). Compositional analysis identified stoat kills as being proportionately more common on English than on Scottish study areas; small raptor kills were spread equally between the two countries, whereas fox and large raptor kills were more common in Scotland (P < 0.05 in all cases). Details of corpses recovered where there was clear evidence of the predator species involved (rank > 3) are summarised in Table 4.

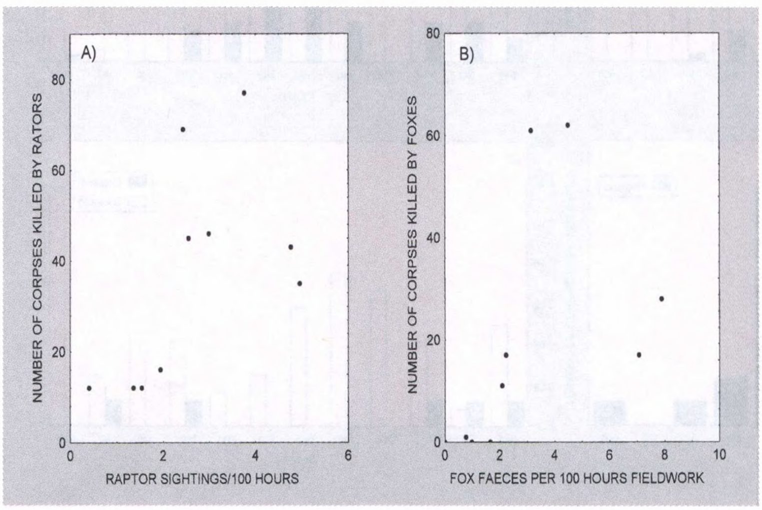

Figure 1. Relationship between number of corpses collected and frequency of predator sightings compared between study areas for: A) raptors and B) foxes.

The larger number of predator kills in Scotland is surprising because densities of grouse, and hence the number available for predation, is consistently greater in England (see

Table 1). However, observations on the study areas indicate that relative abundance of predators was greater on the Scottish study areas (raptor sightings: t = 3.66, df = 8, P < 0.01; fox faeces: t = 2.83, df = 8, P < 0.025): fox faeces were 5.3 times as abundant and raptors 2.7 times as abundant in Scotland than in England. There was a positive relationship between frequency of predator sightings and ranked abundance of corpses collected from the study areas both for raptors and fox faeces (Spearman rank correlation, for raptors: $r_s = 0.644$, $P < 0.05$; for fox faeces: $r_s = 0.824$, $P < 0.005$, Fig. 1).

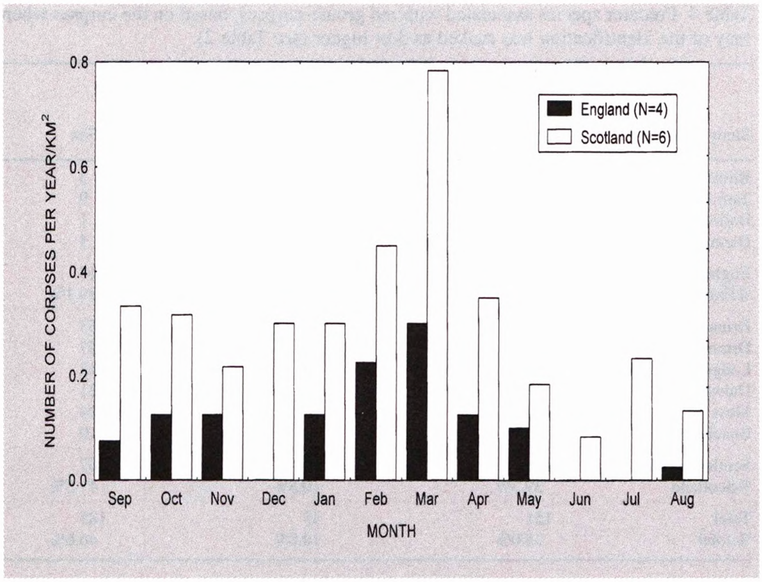

Figure 2. Mean frequency of corpses collected from English (N = 4) and Scottish (N = 6) study areas each month over a period of 10 years. Systematic searches were not undertaken between May and July but corpses found in the study area were removed and their numbers are shown.

Seasonal variation in mortality

There was a general tendency for the proportion of all corpses collected (Fig. 2) and the proportion killed by

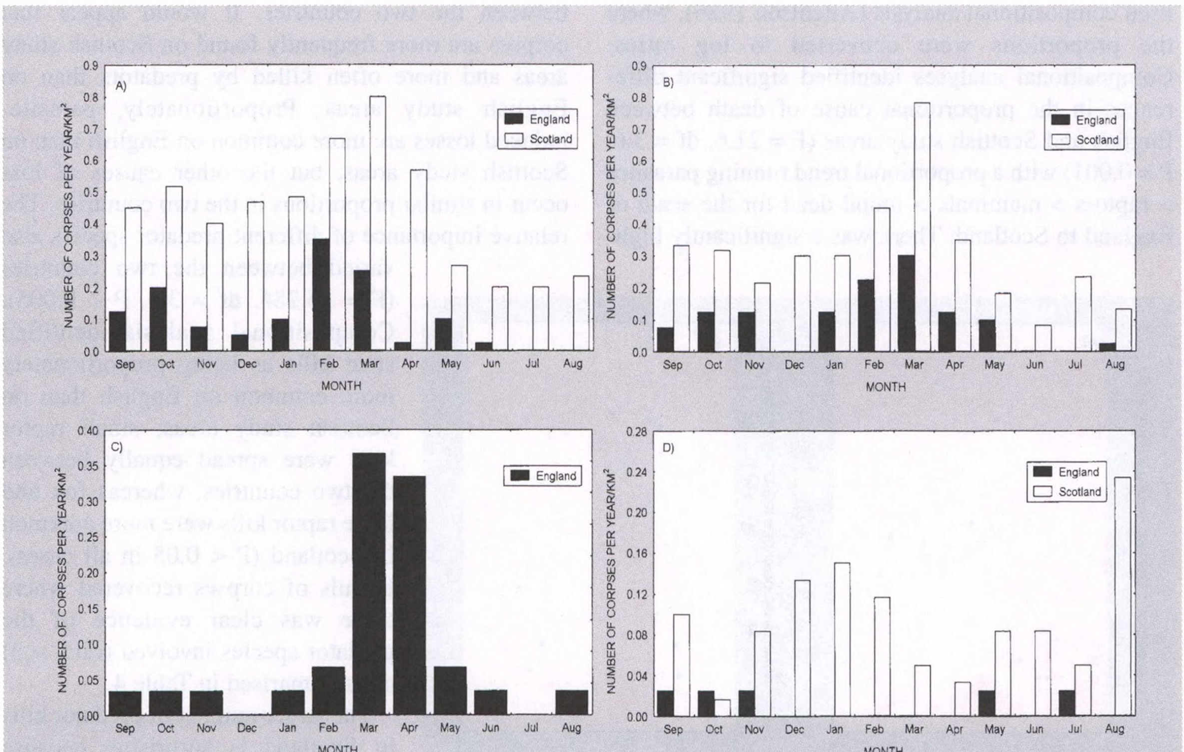

Figure 3. Mean frequency of corpses collected from English (N = 4) and Scottish (N = 6) study areas each month over a period of 10 years related to causes of mortality: A) killed by raptors, B) killed by mammals, C) killed by parasites (England only), and D) 'other'.

predators to peak in early spring both in English and Scottish study areas. There were no significant differences in the seasonal pattern of corpses between study areas in Scotland or England ($F = 3.444$, df = 3,6, $P = 0.092$) nor in the seasonal distribution of predation ($F = 3.077$, df = 3,6, $P = 0.112$). Combining both England and Scotland, there were significant differences in the proportion of total corpses found in each season ($F = 11.403$, df = 3,7, $P = 0.004$) and in the proportions attributable to predation ($F = 15.397$, df = 3,7, $P = 0.002$). In both cases, a significantly higher proportion of corpses ($P < 0.05$) were found in spring, and fewer in autumn compared to winter and summer (see Fig. 2).

The pattern of greatest mortality in February, March and April (deduced from the high proportion of corpses found at this time) holds true for grouse killed by raptors and mammals both in Scotland and England (Fig. 3). Examination of the data on predators at the specific level confirms that these patterns of mortality are reflected in the four main predators recorded during the study (peregrine, hen harrier, fox and stoat) and that this seasonal peak was not a consequence of a single predator species. However, care should be taken when interpreting these data since not all corpses could be assigned to a predator species. Parasite-induced host mortality, although only recorded in England, tended to be concentrated in the spring months largely during March and April (see Fig. 3c). The recovery of grouse in the 'Other' category peaked in August, quite simply because a number of grouse killed by hunters and not recovered were found in the study areas (see Fig. 3d). The relatively high peak in this category during the winter reflected the accidental collision of grouse with fences and other hazards, often associated with snowy conditions (Hudson 1992).

Discussion

An examination of the geographical and seasonal variation in the recovery of red grouse corpses from 10, 1-km^2 study areas over 10 years revealed some interesting patterns. First, the relatively high rate of corpse recovery from the Scottish populations with numerically more corpses associated with predation. Second, proportionately greater parasite-induced mortality on the English study areas. Third, the seasonal peak of mortality in spring. These findings and their possible consequence for grouse population dynamics will be discussed after consideration of the biases involved with the collection of corpses.

Biases in the collection of corpses

Estimating mortality through a single technique is frequently biased and the optimal approach is to apply a variety of techniques. Although seasonal variation in the frequency of corpse collection may reflect seasonal changes in predator pressure, one should not forget that the behaviour of predators also varies during the year. Breeding predators are likely to remove the prey to feed their offspring off the study area during the summer months. As such, the low recovery rate during the summer will reflect both the reduction in the number of standardised searches by field workers and also the behaviour of the predators. We feel that the data from September through to April provide an accurate and comparative data set between study areas. However, whereas we feel the May to August data set provides reasonable data for comparison among sites, we do not feel that strong conclusions should be drawn from comparisons among these and other months.

Parasite differences

The absence of parasite-induced mortality on the Scottish study areas is probably a consequence of density, because parasite burdens tend to be greater on wetter moors and following years of high density (Hudson, Dobson & Newborn 1985, Hudson et al. 1992b, Hudson 1992). Parasite-induced mortality was not identified on the Danby study area in England. This is a relatively dry, freely drained heather moorland and analyses of shot birds also showed relatively few parasites on this study area compared with the other English study areas, which tended to be wetter, and of which two were blanket bogs (Hudson et al. 1985).

Predation differences between England and Scotland

Comparisons between study areas indicate a greater abundance of predators and an apparently greater proportion of birds lost to predators amongst the low density, Scottish populations. Several findings would support the hypothesis that predation could result in the lower breeding density recorded in these populations. These include higher predation rate, the presence of more predators and the between-site relationship that accounted for some of the variation in grouse breeding density from the number of raptor kills. This does not mean that the English populations had a lower overall mortality. Breeding production on the English and Scottish sites was comparable, but there was a greater mortality to hunting (see Table 1, Hudson 1992) and this hunting mortality could have been offset by the predation losses experienced by the Scottish populations. Despite similar total over-winter loss, including hunting, between high and low density populations, this does not rule out winter mortality as a cause of low breeding density in some areas. If the strength of density-dependent winter loss varied among different populations, this may influence spring numbers even though the average percentage loss remained similar. These results do not demonstrate that the lower Scottish densities are a consequence of this predation. Such a hypothesis requires a detailed analysis of population data between sites, coupled with experimental manipulations which will be presented in a later publication.

Alternative hypotheses could account for the differences in the mortality in England and Scotland. Poor habitat quality in the Scottish populations, as a consequence of grazing and other habitat management procedures, could result in reduced carrying capacity within the Scottish populations and consequently the higher mortality through predation would have little impact on the size of the breeding population. This hypothesis is supported by a comparative study of grouse bags between grouse moors in northeast Scotland that found evidence that high-quality underlying rock and heather burning pattern were important factors (Picozzi 1968). However, a more recent study found that such a relationship did not hold true with a more widespread comparison of bag records (Hudson 1992). This is not to say that the quality of food or cover provided by heather is unimportant for the grouse, rather that it appears unlikely to account for the geographic variations in density or mortality. It remains possible that poor heather cover on some moors may increase the susceptibility of grouse to predators, but the impact of predation will also depend on the abundance of predators. The low level of predation and low numbers of predators on the English study areas imply a lower predator pressure.

A third hypothesis is that spacing behaviour determines the density of breeding grouse and the non-territorial, non-breeding birds are lost to predation. Consequently, such losses have no overall effect on breeding density. This hypothesis is supported by the experimental removal and rapid replacement of territorial birds and observations on survival and territorial status (Watson & Jenkins 1968, Watson 1985). Such work was conducted more than 30 years ago when predator pressure was much lower (Jenkins, Watson & Miller 1963, Hudson 1990, Hudson 1992). More recent work found that such large differences in territorial status and survival did not occur and that experimentally removed birds were not replaced (Hudson 1990, Hudson 1992). One may expect this system to operate only at high density, as recorded in several bird species (e.g. review by Davies 1978), although a recent study on a low density population found that the experimental implantation of testosterone resulted in treated birds expanding their territory size and reducing density (Moss, Parr & Lambin 1996). While the data collected in this study do not test this hypothesis, it is difficult to explain the between-area differences in density (Hudson 1992) without incorporating the larger predator pressure in Scotland. One could argue that the high predation losses was simply a compensation for lower rates of hunting on the Scottish areas, but the predation mortality is also correlated with the abundance of predators, suggesting a link. It seems most unlikely that losses to predation would be totally compensated for through spacing behaviour, although low levels of predation when grouse densities are relatively high could result in total compensation.

There still remains the question of why predators are both more diverse and more abundant on Scottish than on English grouse moors? Hudson (1992) suggested that the greater density of gamekeepers in northern England keep predator numbers at a lower level. Although he referred to predators that can be legally controlled, there is evidence that illegal persecution will locally reduce numbers of protected raptors, particularly hen harriers (Bibby & Etheridge 1993). Additionally there is also a greater species richness of upland birds in the Scottish Highlands (Hudson 1988), which may help support a higher diversity and abundance of predators.

We conclude that there are seasonal and geographical variations in the cause of mortality in red grouse. Of all the corpses, parasitism was proportionately more important in England than Scotland, but numerically there were more corpses attributable to predation in Scotland. Since predation is a major cause of mortality, it may well have an influence on the dynamics of grouse populations, but further details and analyses are required on year-to-year changes and patterns of predation.

Acknowledgements - we would like to thank the landowners and keepers for allowing us to work on their estates, particular thanks to John & Eira Drysdale and Lord Peel. Steve Redpath set up the initial kill searches on the study areas and we would like to thank him for his help and guidance throughout the study. Flora Booth, David Howarth, John Renton and other field assistants helped in the collection of the data and we are very grateful to them. Steve Redpath, Simon Thirgood, Nicholas Aebischer and Dick Potts provided constructive criticisms on the manuscript.

References

Aitchison, J. 1986: The statistical analysis of compositional data. - Chapman & Hall, London U.K, 416 pp.

Bibby, C.J. & Etheridge, B. 1993: Status of the Hen Harrier Circus cyaneus in Scotland in 1988-89. - Bird Study 40: 1-11.

Davies, N.B. 1978: Ecological questions about territorial behaviour. - In: Krebs, J.R. & Davies, N.B. (Eds); Behavioural ecology, an evolutionary approach. Blackwell Scientific Publications, Oxford, pp. 317-350.

Hudson, P.J. 1986: The Red Grouse. Biology and Management of a wild gamebird. - Game Conservancy Trust, Fordingbridge, 250 pp.

Hudson, P.J., Dobson, A.P. & Newborn, D. 1985: Cyclic and non-cyclic populations of red grouse: a role for parasitism? - In: Rollinson, D. & Anderson, R.M. (Eds); Ecology and genetics of host-parasite interactions. Linnean Society of London, pp. 77-89.

Hudson, P.J. 1988: Spatial variations, patterns and management option in upland bird communities. - In: Usher, M.B. & Thompson, D.B.A. (Eds); Ecological change in the uplands. Blackwell Scientific Publications, Oxford, pp. 381-398.

Hudson, P.J. 1990: Territorial status in a low density grouse population. Preliminary observations and experiments. - Anonymous RSPB/BES, Sandy, pp. 20-28.

Hudson, P.J. 1992: Grouse in space and time. - Game Conservancy Trust, Fordingbridge, Hants, 225 pp.

Hudson, P.J., Dobson, A.P. & Newborn, D. 1992a: Do parasites make prey vulnerable to predation? Red grouse and parasites. - Journal of Animal Ecology 61: 681-692.

Hudson, P.J., Newborn, D. & Dobson, A.P. 1992b: Regulation and Stability of a Free-Living Host Parasite System-Trichostrongylus tenuis in Red Grouse .1. Monitoring and Parasite Reduction Experiments. - Journal of Animal Ecology 61: 477-486.

Hudson, P.J. & Newborn, D. 1995: Red grouse and moorland management. - Game Conservancy Ltd, Fordingbridge, 170 pp.

Jenkins, D., Watson, A. & Miller, G.R. 1963: Population studies on Red Grouse Lagopus lagopus scoticus (Lath.) in north-east Scotland. - Journal of Animal Ecology 32: 317-376.

Jenkins, D., Watson, A. & Miller, G.R. 1964: Predation and red grouse populations. - Journal of Applied Ecology 1: 183-195.

Kenward, R.E. 1987: Wildlife radio tagging. Equipment, field techniques and data analyses. - Academic press, London, 222 pp.

Moss, R., Parr, R. & Lambin, X. 1996: Effects of testosterone on breeding density, breeding success and survival of red grouse. - Proceedings of the Royal Society of London 255: 91-97.

Picozzi, N. 1968: Grouse bags in relation to the management and geology of heather moors. - Journal of Applied Ecology 5: 483-488.

Redpath, S.M. 1989: The effect of hen harriers and other predators on red grouse populations in Scotland. - PhD Thesis, University of Leeds, 89 pp.

Watson, A. 1985: Social class, socially induced loss, recruitment and breeding of red grouse. - Oecologia (Berlin) 67: 493-498.

Watson, A. & Jenkins, D. 1968: Experiments on population control by territorial behaviour in Red Grouse. - Journal of Animal Ecology 37: 595-614.

White, G.C. & Garrott, R.A. 1990: Analysis of wildlife radio-tracking data. - Academic Press, London, 383 pp.