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Estimating the cause and rate of mortality in red grouse *Lagopus lagopus scoticus*

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We assessed biases in the techniques used to investigate the cause and rate of mortality in two red grouse *Lagopus lagopus scoticus* populations in Scotland during 1985-96. Comparison of the field signs left on grouse carcasses by known predators suggested that whilst it was usually possible to distinguish between grouse killed by mammals and by raptors, it was not possible in most cases to further distinguish between grouse killed by peregrine falcons *Falco peregrinus* and hen harriers *Circus cyaneus*. Similar estimates of the cause and rate of grouse mortality were derived from systematically counting grouse and searching for carcasses and by radio-tagging. Searching for carcasses may provide a useful technique for identifying major causes of mortality in grouse populations inhabiting open habitats.

Key words: carcass searching, field signs, Lagopus lagopus scoticus, mammals, mortality, radio-tagging, raptors, red grouse

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Estimates of the rate and cause of mortality in animal populations are essential to studying many aspects of wildlife ecology (Caughley & Sinclair 1994). Estimates of the rate of mortality may be obtained from radio-tagging, although such studies are costly in terms of time and resources and are often limited in the amount of data that can be collected from a range of sites (White & Garrott 1990). Estimates of the cause of mortality may also be problematic. In most vertebrate populations, few predation events or other causes of mortality are actually witnessed and researchers are often dependent upon careful examination of a small sample of carcasses and field signs left by predators to determine the likely cause of death (e.g. Cresswell & Whitfield 1994).

Population studies on red grouse *Lagopus lagopus* *scoticus* have been conducted for 40 years in Britain (Jenkins, Watson & Miller 1963, 1964, Hudson 1986, 1992, Moss, Watson & Parr 1996). Standardised techniques for estimating mortality rates by systematically counting grouse and searching for carcasses have been developed and have provided large comparative data sets (Hudson 1992, Hudson, Newborn & Robertson 1997), however, few attempts have been made to examine biases in techniques for evaluating cause and rate of mortality. Jenkins et al. (1963, 1967) placed pigeon carcasses on heather moorland to replicate both predator kills and deaths from disease and then recorded recovery rates by naive observers. Recovery rates of 'predator kills' were higher than 'disease deaths' and just over half of all kills were found. Redpath (1989) conducted similar trials with grouse carcasses placed to replicate raptor and mammal kills and concluded that 61% of 'raptor kills' but only 23% of 'mammal kills' were recovered. Subsequently, however, Hudson (1992) demonstrated that the causes of death of grouse recovered during systematic carcass searching were similar to a sample of 49 radio-tagged birds.

The ability to determine the cause of death of grouse from examination of carcasses has also been subject to little critical examination. Whilst some causes of death are obvious, distinguishing the species of predator involved can be more difficult. Although several studies have presented data on the numbers of red grouse killed by different species of predator (Jenkins et al. 1964, Redpath 1989, Hudson 1992), few attempts have been made to verify the causes of death. In most cases, reference has been made to a descriptive account of North American predators (Einarsen 1956).

In this paper we address some of the problems involved in investigating the rates and causes of grouse mortality. We first describe the field signs left on grouse carcasses during predation events and determine whether field signs are reliable indicators of different predators. We then compare estimates of mortality rates and causes derived from grouse counts and carcass searching with estimates derived from radio-tagging.

Methods

The study was conducted from 1992 to 1996 on 100 km^2 of heather moorland near Langholm in southern Scotland. Additional data from observed predation events were available from a study conducted during 1985-1995 in Strathspey in the Central Highlands of Scotland (Hudson et al. 1997). Potential predators of grouse at Langholm included fox *Vulpes vulpes*, stoat *Mustela erminea*, hen harrier *Circus cyaneus*, peregrine *Falco peregrinus*, buzzard *Buteo buteo*, goshawk *Accipiter gentilis* and sparrowhawk *Accipiter nisus*. Additional predators in Strathspey included wildcat *Felis silvestris*, pine martin *Martes martes* and golden eagle *Aquila chrysaëtos*.

Ten areas of 0.5 km^2 were demarcated and used for population studies at Langholm. Grouse densities were estimated on each area during the first week in October and the last week in March from counts with pointing dogs using standard techniques (Jenkins et al. 1963). Briefly, three parallel transects were walked through each area at 150 m intervals and the dog quartered the area to roughly 100 m on either side of the transect pointing all grouse encountered. The same combination of dog and observer were used throughout and counts were only conducted in good weather. Systematic searches for grouse carcasses were conducted monthly on each area from October to March. In October and March, searches consisted of 10 parallel transects at 50 m intervals. Searches throughout the remainder of the winter consisted of six parallel transects walked at 85 m intervals. Observers scanned continuously for feathers and bones during the transects and stopped and searched with binoculars at 100 m intervals. Searches were conducted only in good weather and when there was no snow.

Upon finding a carcass, the perpendicular distance from the carcass to the transect line was recorded. Carcasses were also found on an *ad hoc* basis during radio-tracking and other fieldwork, both on the 'intensive sites' and throughout the rest of the study area. Grouse remains were classified as a carcass only if bones, flesh or primary feathers were present. A 25-m radius was searched around each carcass and any remains found were assumed to come from the same carcass, unless obviously different. Bones and flesh were removed and body feathers were marked to avoid recounting. The following details were recorded: (i) date of recovery and estimated month of death; (ii) grid reference and vegetation details of recovery site; (iii) signs of predators such as pellets or scats; (iv) grouse bone, tissue and feather remains present and whether they were intact or dismembered and whether they had been plucked or bitten.

We captured and radio-tagged 130 grouse between

Table 1. Field signs used to identify different species of predators preying on medium sized birds. Sources: Einarsen (1956), Jenkins et al. (1964), Watson & Millar (1976). Corbet & Harris (1991), Cresswell & Whitfield (1994), Hudson & Newborn (1995).

Predator	Field signs observed
Fox	Puncture wounds on back; most of the meat eaten; intestines often partially eaten; wings or primaries severed and often several metres away from rest of carcass; head and legs often severed; body feathers bitten out in clumps held together by strips of skin; presence of fox scats or smell of urine.
Stoat	Puncture wounds found on neck or chest; meat eaten from the neck and from chest cavity; wings, legs and head all intact; few body feathers removed; often found buried.
Eagle	Most of the meat eaten; intestines often remaining; evidence of a 'powerful predator' with wings and head often torn off, ribs broken and notches in the sternum; body feathers plucked rather than bitten out; line of feathers leading to kill.
Peregrine	Meat partially eaten; intestines often remaining; head and legs often removed; wings articulated; characteristic deep v-notches in sternum; signs of mid-air impact such as rupture or broken back; body feathers plucked and left in long trail from carcass; carcass often on plucking mound or rock in open area.
Harrier	Meat partially eaten with often only neck meat taken; intestines often remaining; head rarely removed; wings articulated; sternum unnotched; few signs of impact; body feathers 'carefully plucked' and left in short trail from carcass.
Sparrowhawk	Meat partially eaten, intestines usually remaining, head remaining, wings articulated and usually entirely clean of feathers, sternum notched, body feathers 'carefully plucked', remains in woodland cover.
Goshawk	Meat partially eaten; intestines usually remaining; evidence of powerful predator with head, wings and legs often removed; sternum notched; body feathers plucked, remains in woodland cover.

3 and 12 October 1994 and 135 grouse between 18 and 22 September 1995 at Langholm. An additional 40 grouse survived the first year of which 25 were re-entered into the second winter survival analysis giving a total of 290 'grouse-winters'. Grouse were captured throughout the 100-km² study area. Grouse were caught at night in hand-held nets after dazzling with strong lights, mass and winglength were measured for an index of body size and classified by age and sex based on plumage characteristics (Hudson 1986, 1992). All grouse were marked in the ptagium with small numbered metal tags and equipped with a necklace radio-tag (Biotrack SS-2). Radio-tags weighed 15 g, were cylindrical in shape measuring 38 × 16 × 16 mm with a 250-mm whip antenna and were attached by a soft cord which was passed around the neck. Tests on the same study area found no effect of radio-tags on grouse survival, although the statistical power of these tests to detect differences in survival was low (Thirgood, Redpath, Hudson, Hurley & Aebischer 1995).

Survival of radio-tagged grouse was monitored weekly from October to March in both winters. Dead grouse were recovered and details recorded as described above. Radio-tagged grouse occasionally could not be found for several weeks prior to their carcasses being located. In these circumstances it was assumed that the bird was killed in the week following its last live observation, unless this was obviously not the case. A number of birds were found dead on the first radio-location following capture and radio-tagging and were excluded from further analysis (6 in 1994 and 13 in 1995). An additional number of birds were never relocated or their radio stopped functioning before the end of each winter and these individuals were also excluded from the analysis (2 in 1995 and 11 in 1996).

Table 2. Field signs left on grouse killed by known predators at Langholm, southern Scotland and Strathspey, Highland Scotland. Values in table represent the proportion of the sample exhibiting the binary variable.

Predator	N	Feathers plucked	Feathers bitten	Feathers trail	Plucking mound	Wings removed	Legs removed	Head removed	Sternum notched	Bones crunched
Fox	6	0.00	1.00	0.00	0.00	0.33	0.00	0.83	0.33	1.00
Stoat	5	0.00	1.00	0.00	0.00	0.00	0.00	0.40	0.00	0.40
Peregrine	20	1.00	0.00	0.30	0.10	0.05	0.15	0.50	0.35	0.20
Harrier ♀	11	1.00	0.00	0.27	0.00	0.09	0.18	0.45	0.18	0.00
Harrier ♂	1	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Goshawk	2	1.00	0.00	0.50	0.50	1.00	1.00	1.00	1.00	1.00
Sp.hawk	2	1.00	0.00	0.50	0.50	0.00	0.00	0.00	0.50	0.00
Buzzard	2	1.00	0.00	0.00	0.50	0.00	0.00	1.00	0.50	0.00

Results

Systematic searching (N = 402), radio-tagging (N = 234) and *ad hoc* discoveries (N = 274) resulted in the recovery of 910 grouse carcasses at Langholm during 1992-96. Of these, 22 were observed raptor kills. An additional 16 carcasses from observed raptor kills were available from a total of 2,340 grouse collected in Strathspey during 1985-95. No mammals were observed killing grouse, although five grouse carcasses were recovered from stoat food caches at Langholm and six grouse carcasses recovered from fox dens at Crubenmore.

Field signs used to identify different species of predators preying on birds of a similar size to grouse were extracted from the literature (Table 1). Some reported field signs could be converted into binary variables whilst others could not or were open to subjective interpretation. Each of the 49 grouse killed by known predators was scored for the following binary variables: 'feathers plucked', 'feathers bitten', 'feather trail', 'plucking mound', 'wings removed', 'legs removed', 'head removed', 'sternum notched', 'bones crunched' (Table 2). Mammals and raptors could be separated with 100% accuracy on the basis of whether feathers were plucked or bitten and as such this analysis was taken no further. Sample sizes were too small to test for differences between specific predators other than peregrines and female harriers. Data for 20 peregrine and 11 female harrier kills were entered into an analysis of variance model with the binary variables noted above. The model could not achieve significant separation of peregrines and female harriers although there was a suggestion ($F_{1,31}$ = 2.57, P = 0.12) that 'bones crunched' could possibly be diagnostic in a larger sample. Even here, however, there was considerable overlap, as 80% of peregrine kills compared to 100% of female harrier kills had no bones crunched.

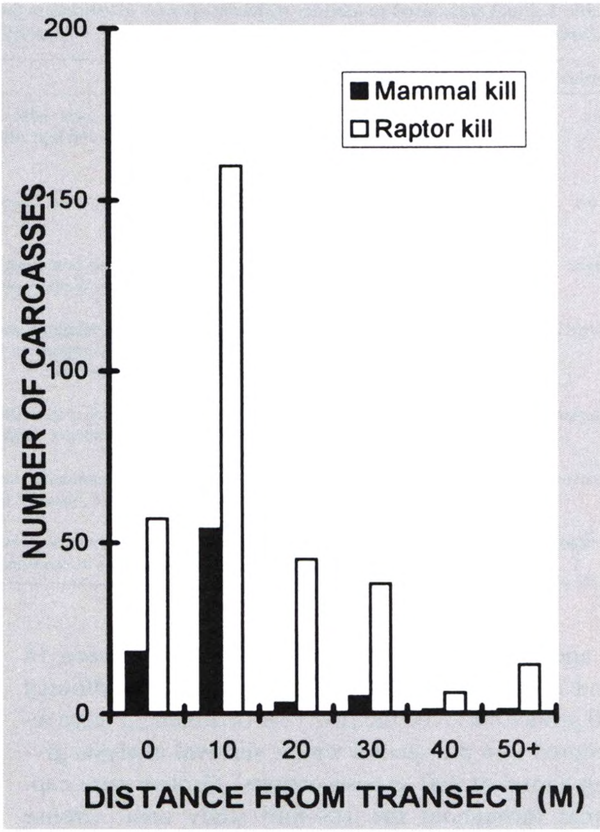

Figure 1. Distribution of sighting distances of grouse carcasses killed by mammals and by raptors recovered during systematic searching at Langholm during 1992-96.

A total of 402 grouse carcasses were recovered during systematic searching of the 10 intensive study sites at Langholm during 1992-96. The distribution of sighting distances of grouse carcasses killed by raptors and by mammals differed significantly (Fig.

Table 3. Estimates of red grouse mortality rates from carcass searching and radio-telemetry at Langholm, Southern Scotland.

	Carcass searching			Radiotelemetry			
Site	October count	March dead	Mortality rate	October tagged	March dead	Mortality rate	G-statistic
1994-95							
LM	54	17	0.31	32	9	0.28	0.058
LC	52	29	0.56	33	19	0.58	0.007
LR	68	36	0.53	30	11	0.37	0.831
LL	18	7	0.39	27	8	0.30	0.007
1995-96							
LM	45	27	0.60	43	29	0.67	0.117
LC	38	20	0.53	31	15	0.48	0.040
LR	67	47	0.70	34	19	0.56	0.441
LD	54	20	0.37	27	20	0.74	3.099
						Cumulative G (df = 8) = 4.600	

Tabel 4. Estimates of the cause of red grouse mortality from carcass searching and radio-telemetry at Langholm, Southern Scotland.

	Carcass searching		Radiotelemetry		
Site	Raptor	Other	Raptor	Other	G-statistic
1994-95					
LM	12	5	6	3	0.042
LC	20	9	14	5	0.125
LR	29	7	9	2	0.009
LL	3	4	5	3	0.582
1995-96					
LM	21	6	26	3	1.481
LC	13	7	9	6	0.092
LR	45	2	18	1	0.031
LD	11	9	14	6	0.965
			Cumulative G (df = 8) = 3.327		

1; G-test, G = 16.0, df = 5, P < 0.01) with 88% of mammal-killed grouse found within 10 m of the transect line in comparison to only 68% of raptor-killed grouse. As the majority of carcasses were found well within the sampling width of the transect, this prompts the question of whether carcass searching underestimates the mortality rate of grouse and biases the estimate of proximate cause to raptor predation.

During the 1994/95 and 1995/96 winters, estimates of the rate and cause of mortality were obtained by both carcass searching and radio-tagging on four areas of approximately 10 km^2 each at Langholm. Each area contained two of the 0.5 km^2 intensive study sites where grouse counts and carcass searches were conducted and on each area the survival of a minimum of 27 radio-tagged grouse was monitored. Estimates of mortality rates derived from grouse counts and carcass searching did not differ significantly from estimates derived from radio-tagging (Table 3; Cumulative G-test, G = 4.60, df = 8, P > 0.5). Causes of mortality were classified as either raptors or all other causes (mammal kills and unknown causes were pooled for statistical analysis). Estimates of the cause of mortality derived from carcass searching did not differ significantly from estimates derived from radio-tagging (Table 4; Cumulative G-test, G = 3.33, df = 8, P > 0.9).

Discussion

The first important finding of this study was that whilst it was possible to use field signs to distinguish grouse killed by mammals and by raptors, it was not possible, within our small sample and selection of field signs, to make clear distinctions between grouse killed by peregrines and by harriers. The shortcomings of the study should be discussed before considering the implications of this finding for grouse researchers.

The study was limited by the small sample of kills in which the predator was observed. In particular, we saw no mammalian predators killing grouse and relied on the recovery of grouse carcasses from fox dens and stoat food caches to compare with raptor killed grouse. It is possible, but considered unlikely, that these grouse were killed by raptors and subsequently scavenged by foxes or stoats. It is likely, however, that few individual predators were involved in these mammal kills and these analyses may suffer from inflated sample size. Additionally, on a small number of occasions, raptors were disturbed from warm grouse carcasses but the actual kill was not observed. In theory, these grouse could have been killed by other predators, but again, this was considered unlikely. In a number of cases, raptors were disturbed from carcasses whilst they were in the process of eating the grouse and thus may have left different field signs to fully satiated birds. By restricting analysis to field signs which could be converted to binary code, some qualitative information regarding the species of raptor may also have been lost. However, qualitative field signs are difficult to rigorously interpret and are particularly prone to bias from inter-observer variation. Finally, we have not included the presence of raptor pellets or feathers, for the simple reason that none were found in our small sample, and in our experience, are rarely found adjacent to kills.

The results of this small sample of known kills suggest that it is difficult to reliably distinguish from field signs between the kills of peregrines and harriers. Several of the field signs suggested in the literature to be diagnostic of peregrines, such as decapitation and notching of the sternum, were also found on some of the kills of harriers. This is perhaps not surprising, as female harriers and male peregrines overlap considerably in weight (male harriers 300-400 g; female harriers 410-708 g; male peregrines 582-750 g; female peregrines 925-1,300 g; Cramp & Simmons 1980) and may thus be expected to exert similar force when killing and consuming a grouse carcass. There was, however, a suggestion that peregrines were more likely to break bones, particularly the humerus, than harriers, although this feature occurred in only 20% of peregrine kills. Bone breaking was also observed in the two available goshawk kills and would almost certainly occur in eagle kills (Jenkins et al. 1964). The presence of a trail of feathers leading to a grouse carcass has often been ascribed to the impact of a peregrine striking a grouse in the air. However, we also observed feather trails at some harrier kills in which the grouse flushed from the ground before the strike and similar feather trails were observed at some suspected harrier kills by Jenkins et al. (1964). It remains a possibility, however, that other field signs not included in this analysis might prove to be diagnostic of the two species of raptor.

Our results suggest that some re-examination of the earlier conclusions of Jenkins et al. (1964), Redpath (1989) and Hudson (1992), who divided kills into eagles, peregrines and harriers, may be appropriate. We cannot comment on the ease of identifying the carcasses of grouse killed by eagles, although Jenkins et al. (1964) suggest that they are readily distinguished from the kills of smaller raptors (male eagles 2,840-4,550 g; female eagles 3,840-6,665 g; Cramp & Simmons 1980). Peregrines were relatively uncommon in the Glen Esk study area of Jenkins et al. during the late 1950s, however at least one peregrine was present on or near the study site during winter in four out of the five years (Jenkins et al. 1964). Both peregrines and harriers were observed during winter on the study areas of Redpath (1989) and Hudson (1992). We suggest that, in these circumstances, and without further evidence of reliable diagnostic features, it may be inappropriate to classify the cause of death to species of raptor. Similar conservative strategies have been adopted in other recent studies of gamebirds where a number of avian predators co-exist (Willebrand 1988, Carroll 1990, Hannon & Gruys 1990, Small, Holzwart & Rusch 1991, Brittas, Marcström, Kenward & Karlbom 1992).

The second key finding of this study was that whilst detection distances from transects of grouse killed by mammals were shorter than grouse killed by raptors, and both were shorter than the assumed sampling width of the transect, similar estimates of the cause and rate of mortality were obtained by carcass searching and radio-tagging techniques. How can this apparent anomaly be explained?

First, why are the observed causes of mortality similar when the detection distances suggest that carcass searching is more likely to overemphasise raptor predation? One possibility is that radio-tagging also overemphasised raptor predation because radio-tags made grouse more vulnerable to raptors. In an earlier study we could find no effect of necklace radio-tags on grouse survival (Thirgood et al. 1995), in agreement with recent studies on willow ptarmigan *Lagopus lagopus* (Schieck 1988), black grouse *Tetrao tetrix* (Willebrand 1988) and pheasants *Phasianus colchicus* (Marcström, Kenward & Karlbom 1989); however, the statistical power of all of these studies to detect differences in survival was low. Another possibility is that the probability of finding a raptor-killed radio-tagged grouse was greater than the probability of finding a mammal-killed radio-tagged grouse because mammalian predators sometimes chewed the radio and could, in theory, impair the signal. However, the number of radio-tagged grouse which were never recovered was relatively low and could not have greatly influenced the results. It seems that whilst the probability of recovering a carcass on any single transect was lower for mammal-killed grouse than for raptor-killed grouse, the frequency of carcass searching combined with the intensity of other field work ensured that most carcasses were found.

Second, why are the rates of mortality suggested by the two techniques similar when most grouse carcasses recovered during systematic searching were seen within 10 m of the transect lines? As suggested above, we believe that we found most carcasses on the study areas because of the intensity of field work. However, grouse numbers on our study areas may have been supplemented by immigration throughout the winter and some of these immigrant birds may have been killed and subsequently found during carcass searching. Thus, whilst carcass searching may provide accurate estimates of mortality rates over the entire population given sufficient sampling, local estimates at the scale of our study areas may be unduly influenced by immigration or emigration.

We conclude with two recommendations. First, whilst it seems possible through examination of carcasses to distinguish between grouse killed by mammals and by raptors, it may be inappropriate to classify the cause of death to species of raptor. Second, systematic searching for carcasses may provide a useful technique for identifying rates and causes of mortality in grouse populations inhabiting open habitats.

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