# Breeding losses of red grouse in Glen Esk (NE Scotland): comparative studies, 30 years on

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Hatching success, brood survival and predation rates of red grouse chicks were examined at four sites in north-east Scotland over two years (1994–1995). Two of these sites have previously been the focus of a large-scale population study on grouse during the late 1950s enabling a comparison to be made. A total of 85 hens were radio-tracked and their breeding success monitored over the two years. Compared with studies undertaken in the 1950s, mean clutch size had risen from 7.2 to 8.6 eggs. Of the 76 nests monitored, 17 (22.4%) broods were lost either through egg or chick predation or by the adult being taken by a predator during incubation. Stoats appeared to be responsible for the largest amount of egg predation. There was a significant increase in predation levels, although hatching success was not significantly different from the 1950s. Chick mortality was highest within the first ten days, a similar result to that found in the 1950s. Overall, mean brood survival from hatching to 20 days was 55.1%. Possible reasons for larger clutch sizes, and the apparent increase in predation levels, are discussed.

## Introduction

Red grouse (*Lagopus lagopus scoticus*) are restricted to the heather (*Calluna vulgaris*) moorlands of the British Isles, an internationally scarce and valuable habitat type (Thompson *et al.* 1995). It is a bird of economic importance as a quarry species and has been the subject of several long-term studies investigating its' ecology, population dynamics and behaviour (e.g. Hudson 1986a, Hudson 1992, Hudson *et al.* 1998, Jenkins *et al.* 1963, 1967, Moss *et al.*

1975, Watson *et al*. 1994, Watson *et al*. 2000). Although periodic crashes in grouse numbers were recorded as far back as the early 19th Century (MacDonald 1883), it was not until the 1950s that the pattern of cyclic changes in grouse numbers were first investigated in detail (Mackenzie 1952). Since then there has been a series of detailed population studies followed by experimental investigations that have examined the possible cause of the cyclic fluctuations in numbers. There are currently two competing hypotheses to explain the cause of the cyclic changes in grouse numbers: (1) that changes in spacing behaviour drives variations in recruitment leading to changes in population size (e.g. Moss *et al*. 1994, Moss *et al*. 1996, Matthiopoulos *et al*. 2000); (2) that parasite induced reductions in grouse breeding production is the principal cause of the cycles (e.g. Hudson 1986b, Hudson *et al*. 1992, Hudson *et al*. 1998). However, these two hypotheses need not be mutually exclusive and indeed both may be operating or even interacting to various degrees in different populations (Hudson *et al*. 2002). A crucial feature in all the work is to examine in detail the features influencing recruitment including breeding success. The factors determining hatch success and chick survival are diverse and vary between sites. Possible factors include: (1) female quality prior to breeding (Jenkins *et al*. 1963, 1967, Moss *et al*. 1975); (2) parasitic infection of the female with the caecal nematode *Trichostrongylus tenuis* (Hudson 1986b); (3) chick infection with the louping ill virus (Hudson *et al*. 1997a); (4) predation of chicks by hen harriers (*Circus cyaneus*) (Redpath 1991, Thirgood *et al*. 2000b); (5) availability of dietary invertebrates (Hudson 1986a, Park *et al*. 2001, Wilson *et al*. 1999). Some of these factors may in turn be influenced by habitat quality.

Red grouse have been extensively studied for nearly 50 years although the longest dataset from a single site is currently just 25 years (Hudson *et al*. 2002). Over this period of time there have been changes in land use practices, wildlife legislation and ecological conditions that have altered conditions on heather moorland and influenced the population ecology of grouse and other birds (Hudson 1992, Robertson *et al*. 2001). Habitat loss, with the conversion of heather moorland to forestry and overgrazing, has been cited as one of the causes of long-term declines in red grouse numbers (Thirgood *et al*. 2000c, Robertson *et al*. 2001). Another change has been an apparent increase in predation pressure following the observed increase in species such as the red fox (*Vulpes vulpes*) (Hewson 1984) and possibly stoat (*Mustela erminea*), and carrion crow (*Corvus corone corone*) (Hudson 1992). At the same time legislation has provided improved protection for raptors and most upland species have shown recovery from the long-term effects of keeper persecution (Thirgood *et al*. 2000a). The aim of this study was to document hatch success and brood survival of red grouse in an area where intensive grouse research was undertaken 30 years previously (Jenkins *et al*. 1963). This would allow us to investigate any changes that may have taken place in the breeding success and predation levels between the two time periods.

## Materials and methods

Female red grouse were captured at night by lamping (Hudson & Newborn 1995) during March and April 1994 and 1995 at four sites in Glen Esk, Angus (NE Scotland; altitude 300–640 m). Two of these study sites were the same as those used by Jenkins *et al*. (1963) and referred to as the *High* and *Low* study areas. Age of the females was not known in either study. A total of 85 hens were fitted with necklace radio transmitters weighing 15 g (Biotrack, Wareham, UK). Previous studies have found no evidence that radio tags have a deleterious effect on the survival or breeding success of red grouse (Thirgood *et al*. 1995). Of the 85 birds tagged, 6 were taken by predators before incubation, and the radio tag failed on one bird. Radio-tagged birds were usually located at least once a week until incubation, using a Telonics TSR-2 receiver (Telonics, Arizona, USA) and a 3-element hand-held Yagi Antenna (Mariner, Lowestoft, UK). If present at the nest, hens were disturbed once during incubation in order to record clutch size. Incubating hens were then located every two days to determine hatch date (mid May to early June). Some nests were taken

**Fig. 1.** Breeding production (= bars) and grouse density (= line) on (**a**) Invermark High and (**b**) Invermark Low, during the period of which the two studies were conducted (Game Conservancy, unpubl. data). There is no observable relationship between young:old ratios and density for either site or with a time lag of one year (*see* text).
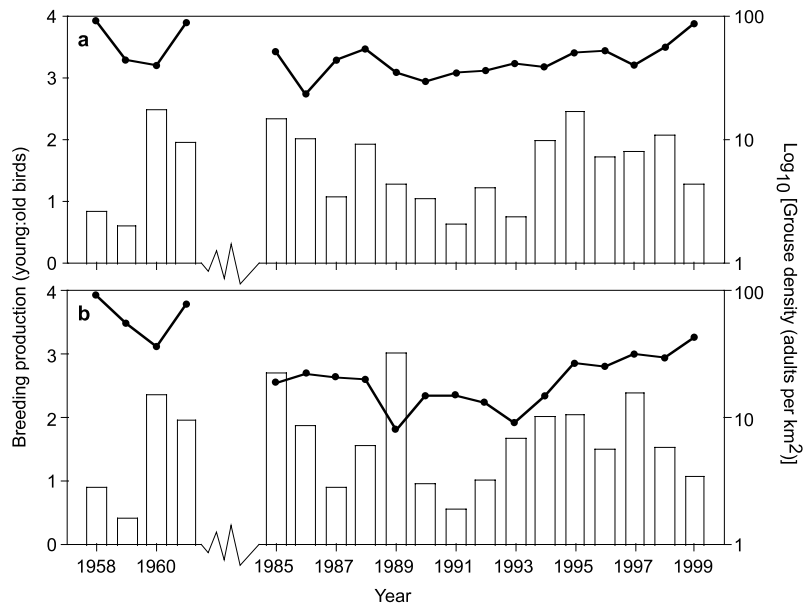
by predators during incubation and these nests and the surrounding area were searched and any remaining egg shells were examined carefully to determine which species caused the predation. Eggs taken and opened by crows are quite distinctive since they show clearly the pecking marks of the crow and leave a distinctive hole through which the contents were eaten. Some of the eggs showed bite marks and these were compared with skulls of stoats and foxes to identify the probable predator. It is possible that some predation events assigned to stoats may infact have been due to weasels, although the former are considered to be the more common mustelid on upland grouse moors. Hatch success is defined here as the number of eggs that hatched, i.e. eggs laid minus the number of eggs taken by predators and those eggs that failed to hatch.

Jenkins *et al*. (1963) calculated hatch success, failure of eggs to hatch, and predation levels from the total number of eggs laid in the study area. As eggs from the same clutch do not represent independent data points, we felt it was more appropriate to examine the proportion of each clutch that hatched, failed or was taken by predators. However, to make direct comparisons between our data and those of Jenkins *et al*. (1963) we also used both methods

(number of eggs, proportion of clutches) to investigate differences between the two time periods 1957–1961 and 1994–1995. Tests using proportion of clutches are reported only where there is a difference between the results of the two methods.

At two sites (High and Low Invermark), data were available from The Game Conservancy Trust, which provided estimates of grouse density and breeding production (1958–1961, 1985–1999; Fig. 1). On each site, red grouse (numbers of hens, cocks and young) in two 1km² blocks were counted in July with pointing dogs to obtain estimates of post-breeding populations (Jenkins *et al*. 1963). The ratio of young:old grouse was used as a measure of breeding success.

Where assumptions of parametric tests were violated, data were transformed (arcsine square root, arcsine, or sine + 1) to achieve normality and homoscedasticity, or non-parametric tests were adopted. General Linear Models, and 2-sample *t*-tests (2-tailed unless otherwise stated) were used to investigate differences between sites and years with MINITAB release 13 (Ryan *et al*. 1985). Data are presented as means ± S.E. or medians and interquartile ranges (IQ RANGES). Power analysis was carried out with the power calculator available on the University of Califor-

nia at Los Angeles' web site (http://ebook.stat. ucla.edu/calculators/powercalc). The significance level was at 5%.

## Results

### Mortality assigned as predation

Most egg losses between laying and hatching could be attributed to specific causes and predator species. After hatching it became harder to assign chick losses to predation rather than to other causes of mortality although in a number of cases there was indirect or suggestive evidence of the cause of mortality. Predation loss is defined here as the direct predation of eggs or chicks, or the loss of the incubating hen to a predator. Of the 78 birds monitored, clutch size was known for 76 nests. A total of 17 entire nests were lost due to predation; and in one other nest two eggs were taken by predators. Of these 18 predation events, 3 were a consequence of predation of the female (by peregrine falcon, *Falco peregrinus*) (1), and fox (2)), 13 were due to egg predation (by stoats (7) and unknown predators (6)), and 2 were due to chick predation by stoats. The proportion of monitored nests (eggs and chicks) which were lost to predation varied from none at Invermark High 1994, to 0.40 (4/10) at Hunthill in 1994 (Table

1). In addition, six radio-tagged hens were killed before incubation (two by foxes, and one each by peregrine falcon, hen harrier, stoat, and unknown predator). We were able to compare predation levels between the two studies. Egg predation levels from 1957 to 1961 ranged from 4.2% to 8.1% of total eggs laid (averaged across the two sites for each year; Jenkins *et al.* 1963). In comparison, 17.7% and 21.8% of eggs (or 15.5% and 23.8% of clutches) were taken by predators in 1994 and 1995 respectively. The proportion of eggs taken by predators from 1994 to 1995 was significantly higher than between 1957 and 1961 ($t_5 = -7.83$, $p = 0.001$).

### Hatching success and brood survival

Mean clutch size during the recent study (1994 to 1995) was 8.6 ± 0.14 eggs (range 6–12), and there were no significant differences in mean clutch size between sites ($F_{3,71} = 0.91$, ns) or years ($F_{1,71} = 0.58$, ns). In comparison, mean clutch sizes from the earlier study, ranged from 5.8 (1959: $n = 58$ nests) to 7.8 (1957: $n = 58$ and 1960: $n = 60$) eggs (averaged across sites; Jenkins *et al.* 1963), with an overall mean size of 7.2 ± 0.9 eggs. Annual mean clutch sizes show that there were significantly more eggs per nest during the 1990s than the late 1950s ($t_5 = 3.43$, $p < 0.05$). In order to ascertain

**Table 1.** The proportion of eggs lost through predation at each site during 1994 and 1995 (present study) and 1957–1961 (Jenkins *et al.* 1963). For comparison purposes only egg predation is considered here (either directly, or indirectly through adult predation). The total number of eggs lost through predation/eggs laid is shown in parentheses. The proportion of clutches lost through predation is also shown for the two years of the present study. All but one of these resulted in the loss of the entire nest (* indicates a nest where only 2 eggs from a clutch of 10 were taken by a predator).

| Site | | Eggs | | Clutches | |
|---|---|---|---|---|---|
| | 1957–1961 | 1994 | 1995 | 1994 | 1995 |
| Invermark Low | 0.06 | 0.02 | 0.15 | 0.02 | 0.15 |
| | (112/1982) | (2/94) | (16/110) | (0.2/11)* | (2/13) |
| Invermark High | 0.05 | 0.00 | 0.24 | 0.00 | 0.25 |
| | (30/624) | (0/47) | (16/68) | (0/6) | (2/8) |
| Millden | n/a | 0.28 | 0.22 | 0.27 | 0.22 |
| | | (28/99) | (17/76) | (3/11) | (2/9) |
| Hunthill | n/a | 0.40 | 0.30 | 0.33 | 0.33 |
| | | (24/65) | (24/81) | (3/9) | (3/9) |

whether density-dependence might be influencing clutch size, records of breeding production and grouse density over the period of these studies (1958–1961, 1985–1999) were analysed for covariance on two sites. At neither Invermark High nor Invermark Low did breeding production co-vary with either grouse density in the same year ($F_{1,12}$ = 0.38, ns; $F_{1,12}$ = 0.04, ns; respectively) or the previous year ($F_{1,12}$ = 0.14, ns; $F_{1,12}$ = 0.34, ns; respectively; Fig. 1).

Of 60 nests in which all eggs were accounted for during the 1994–1995 study, 21 contained some eggs that did not hatch (clear or fertile). Across sites and years, the mean percentage of unhatched eggs in each clutch was 8.3% ± 15.6%, ranging from 0.0% to 75.0%. Between 4.8% (1960: $n$ = 413 eggs) and 28.5% (1959: $n$ = 341) of total eggs laid failed to hatch in the earlier study (Jenkins *et al.* 1963), and there was no significant difference in the percentage of failed eggs between the two time periods ($t_5$ = 1.34, ns). However, the power for this test was very low (~12%).

Overall, a high proportion of each clutch hatched, although some nests were lost through predation, or had very low hatching success (Table 2). There were no significant differences in the proportion of eggs hatching between sites ($F_{3,71}$ = 1.71, ns) or years ($F_{1,71}$ = 2.14, ns). From the total number of eggs laid, we found a hatching success of 75.4% ± 1.9% (per year, across sites, $n$ = 640) compared with 79.8% ± 8.9% ($n$ = 2606) reported by Jenkins *et al.* (1963). Since we found that predation levels of eggs were greater than during 1957–1961, we predicted that hatching success would have decreased and adopted 1-tailed *t*-tests. There was no significant difference between hatching success in the 1950s and that in the 1990s when either number of eggs or proportion of clutch was used ($t_5$ = 1.16, $p$ > 0.05). However, the power of this test was low (~21.6%), so we are unable to ascertain if hatching success has altered or not.

Brood size (proportion alive from hatching) obviously decreased with age, and there were significant differences between the proportion of brood alive at 3, 10 and 20 days (Kruskal-Wallis $H_2$ = 25.44 adjusted for ties, $p$ < 0.0001). Multiple comparison tests showed that the proportion of brood alive at 3 days (5.98 ± 0.33 chicks) was higher than that at 10 days (4.80 ± 0.32; difference = 12.4, $p$ < 0.05) and at 20 days (4.19 ± 0.32; difference = 26.6, $p$ < 0.05), but that there was no significant difference in the proportion of brood alive between 10 and 20 days (difference = –6.6, ns). Data were available for 63 nests for which the brood size at hatching and at 20 days was known. This showed that brood survival from hatching to 20 days was 55.1% ± 3.9% (i.e. by 20 days broods were approximately half the size they were at hatching).

**Table 2.** Clutch sizes, hatching success and brood survival (up to 20 days) at the four sites during 1994 and 1995. Values shown are medians and interquartile ranges. Numbers in parentheses after year indicate the number of independent clutches laid for which hatch success is known. Clutch size was normally distributed but is shown here as medians and interquartile ranges as hatching success and brood survival did not follow a normal distribution.

| Site | Year | Clutch size | Proportion hatched | Proportion survival from hatching to: | | |
|---|---|---|---|---|---|---|
| | | | | 3 day | 10 day | 20 day |
| Invermark Low | 1994 (11) | 8.0 (8.0–9.0) | 1.0 (0.8–1.0) | 1.0 (0.9–1.0) | 0.7 (0.5–0.9) | 0.5 (0.4–0.8) |
| | 1995 (13) | 8.0 (8.0–9.0) | 1.0 (0.8–1.0) | 0.9 (0.8–1.0) | 0.6 (0.4–0.8) | 0.6 (0.4–0.8) |
| Invermark High | 1994 (6) | 8.0 (7.5–8.3) | 0.9 (0.5–1.0) | 1.0 (0.9–1.0) | 1.0 (0.6–1.0) | 0.9 (0.5–1.0) |
| | 1995 (8) | 8.5 (8.0–9.0) | 0.9 (0.2–1.0) | 0.7 (0.3–0.8) | 0.6 (0.3–0.7) | 0.5 (0.3–0.7) |
| Hunthill | 1994 (8) | 8.5 (7.3–9.0) | 0.9 (0.0–1.0) | 0.9 (0.1–1.0) | 0.3 (0.1–0.8) | 0.1 (0.0–0.4) |
| | 1995 (9) | 9.0 (7.5–10.5) | 0.9 (0.0–1.0) | 0.8 (0.5–0.9) | 0.7 (0.3–0.9) | 0.6 (0.1–0.8) |
| Millden | 1994 (11) | 9.0 (8.0–10.0) | 0.9 (0.1–1.0) | 1.0 (0.5–1.0) | 0.8 (0.3–1.0) | 0.7 (0.3–0.9) |
| | 1995 (9) | 8.0 (8.0–9.5) | 0.9 (0.4–1.0) | 1.0 (0.7–1.0) | 0.8 (0.6–1.0) | 0.7 (0.6–0.9) |

## Discussion

Data from this study show that mean clutch sizes of red grouse have significantly increased at the sites investigated in north-east Scotland from 7.2 in the late 1950s to 8.6 in the mid 1990s. The proportion of eggs taken by predators has also increased from an annual level of between 4.2% and 8.1% (Jenkins *et al*. 1963), to 16.1% and 21.8% (in 1994 and 1995 respectively). The low power of the test for hatching success means we are unable to ascertain whether the increase in predation has led to a concurrent decrease in hatching success. Information on chick survival was only available from three weeks of age in the 1957–1961 study, so it was not possible to compare differences in chick survival between the two studies. However, Jenkins *et al*. (1963) indirectly estimated that chick mortality was highest in the first week or two after hatching, a figure that closely resembles that calculated in the present study (between 3 and 10 days). It would be interesting to ascertain whether chick predation levels have increased to the extent that egg predation levels have. The cause of the increased clutch size is not clear, but is likely to be a reflection of hen condition, in turn influenced by improved nutrition and reduced levels of caecal nematode (Hudson 1986b). One possibility is that clutch size may be density-dependent since the more recent grouse densities were lower than previously on the low site (Fig. 1). However, there is no observable relationship between young:old ratios and density for either site or with a time lag of one year, and previous studies have failed to find evidence of density dependent fecundity (Hudson *et al*. 1992). Unfortunately, since age of the hens was not known in either study, it was not possible to control for maternal age. However, Wiebe and Martin (1998) found no significant effect of maternal age of willow ptarmigan (*Lagopus lagopus*) on clutch size, or on nesting or fledging success. They found that the greatest loss of offspring during the breeding season was caused by egg predators during incubation (Wiebe & Martin 1998), but that this loss was not age dependent.

Surprisingly, predation by corvids was not recorded, in contrast to previous studies on nest predation of gallinaceous species (e.g. Erikstad *et al*. 1982). Legal predator control on intensively managed grouse moors such as Glen Esk may reduce densities of corvids to levels where predation is insignificant. Comparative studies on adult grouse survival during winter have highlighted that mortality caused by avian and mammalian predators was greater in some recent studies in the central Highlands (Hudson *et al*. 1997b) compared with the earlier studies of Jenkins *et al*. (1963). Interestingly while these studies of adult grouse highlighted predation by foxes and raptors, the current study has identified the relative importance of stoats in egg predation. Once a nest is located by a stoat, all the eggs are usually taken and the entire clutch is lost. The effect this will have on an individual's breeding success depends to some extent on the timing of the predation event. Three females whose first nests were lost were able to relay as it was sufficiently early in the breeding season. Jenkins *et al*. (1963) discounted nest predation as a factor limiting numbers of grouse. While the present study was not designed to test whether predation was limiting grouse numbers, we did find higher levels of nest predation than previously reported. There are a number of reasons that might explain the apparent increase in predation levels upon red grouse eggs during the breeding season. The first is that stoat populations might have increased, perhaps as a result of increasing rabbit populations — their main prey. In a study investigating stoat diet in the U.K., lagomorphs were present in approximately 65% of stoat guts, an increase from 25% in the early 1960s (McDonald *et al*. 2000). There is, however, no direct evidence that the size of the stoat population has changed significantly over the last 20 to 30 years (Hudson 1992, McDonald & Harris 1999). Detecting changes in mustelid populations is hampered by the fact that most data are in the form of bag records (number of stoats killed by game keepers to control predation). Bag records are heavily reliant on trapping effort, and there is evidence that there has been a reduction in trapping effort over the last 20 to 30 years leading to an apparent reduction in stoat numbers

(McDonald & Harris 1999). We were unable to compare trapping effort in the two periods of this study, and it is possible that the rise in predation levels is due to a reduction in trapping effort at these sites. Alternatively, there may have been a shift in stoat diet towards grouse, increasing predation pressure without an increase in actual stoat numbers. Lastly, it is possible that there have been no significant changes in stoat population size or dietary composition but that grouse are now more susceptible to predation than they were previously, perhaps due to changes in habitat quality or structure (e.g. Johnson & Hines 1999, Storaas *et al.* 1999). Changes in grouse density can also influence the effect that predation has on grouse populations. Both bag records and count data show that there has been a large decrease in grouse density between the late 1950s and mid 1990s in Scotland. Long-term declines can be partially explained by reduction in heather moorland: even on sites actively managed for grouse shooting, the amount of heather cover in the Scottish uplands has decreased from 51% in the 1940s to 41% by the 1980s (Robertson *et al.* 2001). However, it has been suggested that grouse populations can be limited at low density by generalist predators such as hen harriers, peregrines and red foxes (Thirgood *et al.* 2000b). Predation by generalist predators is also believed to be capable of suppressing population cycles (Thirgood *et al.* 2000c), although bag records show that cycles have continued in the Glen Esk population (Game Conservancy, unpubl. data).

This study has demonstrated changes between the 1950s and 1990s in clutch size and predation levels of red grouse during the breeding season. It should be noted that these results are based on brief snap shots of five year and two year studies. Although increased predation levels of grouse have been reported elsewhere, it would be useful to collect similar data in the future to ascertain if these results truly represent long term changes. Due to the time and expense of collecting data over long time periods, it can often be problematic obtaining long-term data on population dynamics. Repeating comparative studies, at regular intervals may be one way of reducing this problem.

## Acknowledgments

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