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Dispersal, survival and causes of mortality in black grouse *Tetrao tetrix* in northern England

Philip K. Warren & David Baines

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Between autumn 1998 and spring 2000, 70 black grouse *Tetrao tetrix* (48 poults and 22 adults) were equipped with radio transmitters in the North Pennines, England. We recorded timing and distances of dispersal, survival rates and causes of death. First-year survival rates differed between years, but in each year were highest in late autumn prior to dispersal, when predation by stoats *Mustela erminea* and raptors accounted for three-quarters of deaths. First-year grouse survival was lower than that of adult birds owing to predation in the autumn and winter by raptors and stoats. The annual adult survival rate of 0.72 was higher than those found in most other European studies. By contrast, breeding success was low. Dispersal was confined to first-year hens, with distinct dispersal periods in late autumn (mean 10.3 km) and again in early spring (mean 5.8 km). Natal dispersal resulted in none of the first-year hens breeding within the study area. Adults of either sex and first-year cocks showed high site fidelity. This has practical repercussions when considering prescriptive management to aid species recovery and range expansion in relation to habitat fragmentation at both the local and regional levels.

Key words: black grouse, dispersal, population, radio telemetry, raptors, survival, *Tetrao tetrix*

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During the last century in most parts of western and central Europe, the black grouse *Tetrao tetrix* has declined in numbers and in some places has gone extinct owing to habitat loss, degradation and fragmentation, caused by changes in land use, chiefly agricultural intensification (Cramp & Simmons 1980, Baines 1994). The range of black grouse within England has in recent decades severely contracted (Sharrock 1976, Gibbons, Reid & Chapman 1993, Baines & Hudson 1995). These processes have resulted in the core of the English population being restricted to the North Pennines. Here, it has

been estimated that 1,700 (95% CL: 800-3,100) males remain (Hancock, Baines, Gibbons, Etheridge & Shepherd 1999). A more recent and comprehensive survey suggests that the true figure is nearer the lower 95% confidence limit at approximately 800 males (J. Calladine, unpubl. data).

Within the North Pennines, England, black grouse habitat is frequently restricted to the mid-slopes of valleys, known locally as dales. Within the North Pennines, there are five main dales within which most of the black grouse are located. Within each dale, suitable

habitat on the valley slopes are separated by more intensively-managed agricultural fields on the lower valley slopes and valley floor. Adjacent dales are separated by heather-dominated upper slopes and watersheds. These lower fields and upper valley slopes and watersheds are habitats where black grouse generally do not occur (Baines 1994) and conceivably could present local barriers to dispersal.

To aid species recovery and range expansion in relation to habitat fragmentation at both the local and regional levels, it is necessary to understand the metapopulation dynamics of black grouse. Dispersal is a key factor in the local dynamics of a fragmented population (Storch 1997), but information on the dispersive capacity and regularity of grouse species is limited. Recent estimates by Caizergues & Ellison (in press), suggest that within the French Alps, first-year hens can disperse up to 29 km (median: 7 km) from their natal site. Distances and frequency of movements may depend on densities of birds within the natal area, e.g. red grouse *Lagopus lagopus scoticus* (Hudson 1992), or be independent of density, e.g. blue grouse *Dendragapus obscurus* (Hines 1986), spruce grouse *Falcapennis canadensis* (Keppie 1979) and willow grouse *Lagopus lagopus* (Smith 1997). In addition, dispersal distances may be determined by the degree of separation of suitable habitat patches within the landscape (Åberg, Jansson, Swenson & Angelstam 1995, Piertney, MacColl, Bacon & Dallas 1998, Marjakangas, Aspegren & Kyllönen 1991). Detailed knowledge of these factors should form the basis for the development of spatial models of the population, which permit predictions to be made that will influence management options for species recovery and range expansion. This study aims to identify the dispersal periods and distances, survival rates and causes of mortality of black grouse within the core of its English range.

Methods

The main study area covers 15 km² at the head of the River Tees valley (Upper Teesdale), County Durham. The landscape and habitats are strongly influenced by the two main land uses: hill farming and red grouse shooting. The hill farms tend to be small, each averaging 150 ha. This size includes common grazing areas where stock from several graziers are present. The farms are predominantly sheep farms, but most still have small numbers of beef cattle.

The study area consists of a coarse mosaic of rough grazing pastures and larger allotments, frequently infest-

ed with rushes *Juncus effusus* and *J. articulatus* surrounded by dry stone walls. Species-rich meadows cut in August for hay and semi-improved pastures are located on the more fertile valley floors. Retention of more traditional forms of farming, typified by low livestock densities, limited use of inorganic fertilisers and delayed cutting of hay crops is actively encouraged and subsidised by government grant aid. The higher valley slopes (500-700 m a.s.l.) are grazed from February to November by sheep and form degraded heather moor dominated by grasses *Nardus stricta*, *Agrostis tenuis*, *Deschampsia flexuosa*, rushes *Juncus squarrosus*, *J. effusus* and sedges *Carex* spp.. At the hill tops, where natural drainage is impeded, blanket bog has formed which, dependent on sheep grazing pressures, may be dominated by heather *Calluna vulgaris* and cotton grass *Eriophorum vaginatum*. These latter areas are managed to maximise numbers of red grouse for sport shooting. Throughout the study area, gamekeepers are employed to manage the heather by rotational burning and to control predators of grouse, chiefly red fox *Vulpes vulpes*, crows *Corvidae*, stoat *Mustela erminea*, rat *Rattus norvegicus* and weasel *M. nivalis* (Hudson & Newborn 1995).

Black grouse were surveyed using two methods: counts of numbers of males attending display grounds or leks in spring and counts of both sexes across the whole area using pointing dogs. Counts of all displaying males, either at established leks or displaying singly away from leks, were made at least twice, once in April and then again in May (Baines 1996). Systematic searches of the whole study area with pointing dogs were made in August to assess hen densities and breeding success.

In 1998 and 1999, 48 poults (20 cocks and 28 hens) and 22 adults (three cocks and 19 hens) were fitted with 17-g necklace radio transmitters. The poults were pointed by dogs and flushed into nets in late August. Five adult hens were also caught using this method. At the time of capture, poults were 8-10 weeks old and were still in family groups. Capture locations were plotted on a 1:25,000 Ordnance Survey map. Adults were located at night-time roosts by a high-powered lamp and caught in a hand-held net. Adults were generally captured between November and March in each year using previously radio-tagged individuals to identify roost locations.

On average, tagged birds were located and flushed every two weeks using portable Telonics receivers and Yagi antennas. Flush positions were recorded onto 1:25,000 maps. Causes of death were ascertained by external and internal examination of the carcasses and from associated field signs. Predated individuals were as-

signed to either red fox, stoat or raptor following criteria described in Jenkins, Watson & Miller (1964), Corbet & Harris (1991), Cresswell & Whitfield (1994) and Thirgood, Redpath, Hudson & Donnelly (1998). The suite of predators within the study area is a simple one. This simplicity is partially due to the low diversity of naturally-occurring mammalian predators in northern England and importantly, also due to the virtual total removal of foxes and corvids by gamekeepers, who remove these predators to benefit red grouse. Furthermore, most of the predation incidents involved peregrines. We have never observed peregrines scavenging at corpses, nor are we aware of any references that cite this behaviour. The other chief predator was the stoat. No corpses attributed to stoats had signs of other predators such as fox, which would have been relatively obvious, to suggest that the stoat had scavenged a kill. Mortality caused by stoats was identified by bite marks to the neck, so we assume that these marks were made during the kill and would not have been present had a stoat simply scavenged a corpse. Although attributing the causes of mortality from remains is never certain, the paucity of species which are known to be scavengers allows us to assign the causes of mortality in our study area with greater than average certainty. Although our sample sizes are limited, the black grouse is an increasingly rare bird in this region so it can hardly be otherwise.

The time of autumn dispersal for each bird was taken as the last recorded presence within the natal home range, defined as the centre of the range of radio fixes from tagging prior to dispersal. The autumn dispersal distance was defined as the straight-line distance from the natal tagging location to the centre of the winter home range, defined as the centre of the range of radio fixes post dispersal if occurred and prior to the spring dispersal. Similarly, spring dispersal was timed as the last recorded presence in the winter home range, with spring dispersal distance defined as the straight-line distance from the centre of the winter home range to either the nest site for hens or the lek for cocks. The overall natal dispersal distance, a combination of autumn and spring dispersal, was measured as the straight-line distance between the natal tagging site and the nest site for hens, or the lek for cocks. The time of death was recorded as the mid-point between the last flushing occasion and the date of corpse recovery.

Survival rates were estimated by modelling individual survival histories (Lebreton, Burnham, Clobert & Anderson 1992) from two weeks after capture to death, loss of radio signal or the end of the study, whichever occurred first. To avoid bias due to capture and handling,

the first two weeks after capture were ignored, and birds found dead within two weeks of capture were excluded from the analysis. This method permitted inclusion of birds tagged at different times of the year. Survival histories were modelled as a product of weekly survival rates for each week that a bird survived, and of a weekly mortality rate (1 - survival rate) if it died. The approach was similar to a Mayfield nest survival analysis (Mayfield 1961, Hensler & Nichols 1981, Aebischer 1999). Weekly survival rates were initially assumed to differ between years, between seasons, i.e. winter (September-February) and summer (March-August), and between first-year and adult birds. The survival history of birds caught as poults and followed for more than one year involved both first-year and adult survival rates; they were considered to be adults on 1 September in the year following capture. As an example of survival history modelled in this way, a juvenile caught on 1 September 1998 that died exactly two years later gave rise to a survival probability modelled on (S^{1st} , winter 1998)²⁴ (S^{1st} , summer 1999)²⁶ (S^{adult} , winter 1999)²⁶ (S^{adult} , summer 2000)²⁵ ($1 - S^{adult}$, summer 2000), allowing 26 weeks per season and discounting the first two weeks after capture. Models were fitted using the program SURVIV (White & Garrott 1990), and involved eight different parameters: first-year weekly survival rates for winter 1998, summer 1999, winter 1999 and summer 2000, and adult weekly survival rates for the same periods; estimates of weekly survival rates were compared using likelihood-ratio tests (Lebreton et al. 1992). Survival probabilities for first-year and adult birds were calculated for both six-month periods in each year by raising weekly survival rates to the power of 26 (s^{**26}). Standard errors were calculated following Hensler (1985).

Results

Dispersal

Patterns of dispersal were similar across years and because of this, and the low sample sizes in each year, the data were combined across the two years. The mean autumn dispersal distance by first-year hens ($N = 9$) was 10.3 km (range: 3.3-17.5 km; Fig. 1A). A second period of dispersal occurred in the spring when first-year hens ($N = 6$) moved a mean distance of 5.8 km (range: 2.5-11.3 km; see Fig. 1B). The two phases of dispersal were separated by periods of relative immobility when both first-year and adult hens occupied small home ranges of < 100 ha. The mean natal dispersal distance for first-year hens ($N = 8$) was 9.3 km (range: 4.5-19.0 km). The median date of hen dispersal in autumn ($N =$

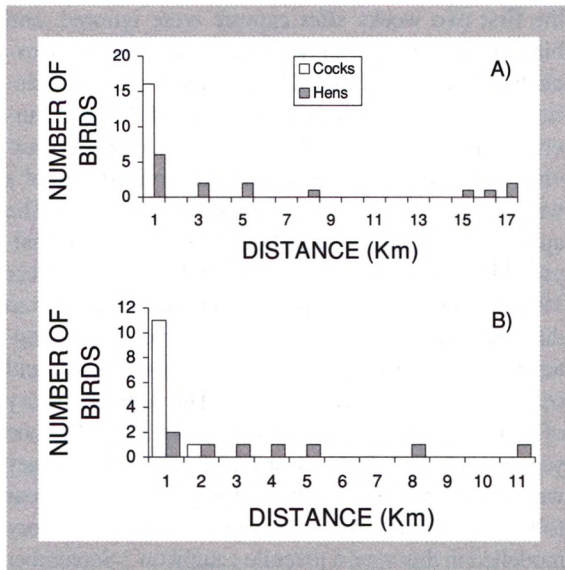


Figure 1. Distribution of distances moved by first-year black grouse of both sexes during the autumn (A) and spring (B) phase of natal dispersal.

9) was 28 October (range: 28 September - 11 November), whilst that in spring ($N = 6$) was 12 April (range: 22 March - 15 April).

No dispersal, i.e. movements longer than 1 km from the tagging location, was observed by young cocks in autumn ($N = 16$) or spring ($N = 12$) during the study. Yet during the winter of 1999, two juvenile cocks were located 11 and 8 km away from their capture locations, but these birds returned by the spring.

Natal dispersal resulted in none of the eight first-year hens remaining within the study area, whilst all of the 11 cocks remained, and all within 1 km of their natal site. If repeated flushing had caused disturbance related movements, then one would have expected similar movements from both adults and from juvenile males, but no such movements were encountered in either group. Overall, 60% of first-year hens left the study area in the autumn ($N = 15$). Of these, 67% ($N = 6$) continued their dispersal in the spring, the rest choosing to breed on their wintering grounds, whilst two hens delayed their dispersal from the natal area until spring. Despite all of the tagged first-year hens leaving the study area, August counts of hens showed a progressive increase over the study period (Table 1) suggesting compensatory immigration into the study area from outside. Our sample size is limited, but the age and sex of dispersing birds and the timing of both periods of dispersal in each year coincided almost exactly with published observations of other researchers, in particular Caizergues & Ellison (in press), giving greater confidence in the described outcome.

Table 1. Numbers of displaying male black grouse, August indices of hen abundance, and breeding success expressed as numbers of chicks reared per hen within the North Pennines study area during 1998-2000.

| | Year | | |
|----------------------------|------|------|------|
| | 1998 | 1999 | 2000 |
| Number of displaying cocks | 83 | 74 | 87 |
| August hen abundance | 34 | 47 | 58 |
| Chicks reared per hen | 1.9 | 1.7 | 0.9 |

Survival and recruitment

First-year 'winter' (September-February) survival rates differed significantly between years from 0.25 ± 0.30 (SE) in 1998 to 0.75 ± 0.27 in 1999 ($\chi^2_1 = 10.64$, $P = 0.01$). Their mean of 0.54 ± 0.14 (Table 2) was significantly less than the adult 'winter' survival rate of 0.84 ± 0.14 ($\chi^2_1 = 11.59$, $P < 0.001$). There was no evidence of a year effect on 'summer' (March-August) survival of either first-year or adult birds, and 'summer' survival rates were clearly the same for first-years and adults. Collective summer survival rates for adults and first-year birds did not differ significantly from adult winter survival rates. This allowed values to be combined to give an estimated six-monthly summer survival rate for adults and first-year birds surviving the winter of 0.85 ± 0.08 , or an annual adult survival rate of 0.72 ± 0.07 , and an annual first-year survival rate averaging 0.46 ± 0.12 .

The annual adult survival rate for both sexes combined was 0.72. Thus 0.28 recruits per adult are required to enter the adult population on 1 September to maintain a constant population. Assuming an even sex ratio, the required number of recruits would be 0.56 in year 't' per hen seen on brood counts the previous year 't-1'. Winter (September-February) juvenile survival was 0.54, and summer juvenile survival was 0.85. Hence in 1998 the number of chicks needed to produce 0.56 recruits was $0.56/(0.25 \times 0.85) = 2.64$, and in 1999 it was $0.56/(0.75 \times 0.85) = 0.88$. In 1998 the estimate of the reproductive rate required for maintenance of a constant population was higher than that measured in the study area, 1.9 chicks per hen, but in 1999 measured reproductive success was twice as high as that needed to maintain numbers. Over the two years combined reproductive success balanced adult losses.

Table 2. Winter (September-February) and summer (March-August) survival rates for first-year and adult black grouse in the North Pennines expressed as means \pm SE.

| Period | Age | Survival (\pm SE) |
|--------|------------|----------------------|
| Winter | First-year | 0.54 (\pm 0.14) |
| Winter | Adult | 0.73 (\pm 0.31) |
| Summer | First-year | 0.95 (\pm 0.37) |
| Summer | Adult | 0.84 (\pm 0.14) |

Table 3. Causes of mortality in black grouse in the North Pennines in winter (September-February) and summer (March-August) during 1998-2000.

| | Winter | | Summer | |
|----------------|---------|---------|--------|------|
| | 1998/99 | 1999/00 | 1999 | 2000 |
| Predation | | | | |
| Stoat | 6 | 2 | 0 | 0 |
| Fox | 0 | 1 | 0 | 1 |
| Raptors | 4 | 5 | 0 | 1 |
| Disease | 1 | 0 | 0 | 2 |
| Fences & wires | 3 | 0 | 0 | 0 |
| Totals | 14 | 8 | 0 | 4 |

Causes of mortality

Of the 26 corpses that allowed an assessment of cause of death, 69% were killed by either raptors or stoats (Table 3). Raptor, probably peregrine *Falco peregrinus*, and stoat kills were most frequent in the autumn and winter with 17 kills over the two years compared to one kill in spring/summer. Predation by red fox (two instances), disease (two instances) of coccidiosis and one of intestinal impaction and collision with fences and wires (three instances) were the other causes of death. There were no obvious differences in cause of death between either sexes or years.

Discussion

We found that first-year hens underwent two periods of dispersal that culminated in all radio-tagged young hens leaving the study area. Despite this, numbers of hens showed an increase over the period of the study indicating that compensatory immigration into the study area was taking place. The median natal dispersal distance for first-year hens was 9.3 km. Habitats such as improved valley bottom fields and the watershed tops of adjacent valleys which are not regularly used by black grouse (Baines 1994) did not prove a barrier to dispersal. Indeed, most hens dispersed from within their natal valley to recruit and breed in adjacent valleys. In direct contrast, no cocks dispersed more than 1 km and most recruited into the lek closest to their natal tagging site. Thus different leks within a dale and local groups of birds between dales were linked through hen dispersal in a meta-population-type structure.

The dispersal distances of first-year hens we found in our study were very similar to those described by Caizergues & Ellison (in press) in France, but there high Alpine ridges proved an obstacle to dispersal, and movements of young hens were channelled along valleys. Greater dispersal distances were encountered in Finnish forests by Marjakangas & Törmällä (1997),

where flat terrain and inter-connected habitat patches may have eased dispersal. The dispersal behaviour of black grouse differed markedly from that of red grouse within our study area, with only 25% of first-year red grouse hens moving more than 1 km and a maximum natal dispersal distance of only 3.8 km (P.K. Warren, unpubl. data). It is likely, given both the territorial breeding system of red grouse and their ten-fold higher autumn densities than peak black grouse densities, that young red grouse hens only needed to move short distances in order to cross several territories and avoid in-breeding.

Given the contraction in range and abundance of black grouse in England, perhaps more than 90% of the estimated 800 males reside within the North Pennines, an area of only 2,500 km² and only some 60 km in diameter (J. Calladine, unpubl. data). The rapid decline in numbers and range of black grouse in northern England, combined with the apparent sedentary nature of cocks, may present demographic problems. Males would appear to contribute little in terms of genetic exchange between even closely located groups of birds. This is unlikely to be a problem within the core of the range. However, at the edge, if hen dispersal is randomly directed, then hens may disperse into areas from which cocks have recently become extinct. Within northern England there have been several reported observations of hens in such circumstances.

Data on dispersal and connectivity of groups of birds within fragmented landscapes are critically important for decision-making processes within conservation programmes for black grouse (Calladine, Baines & Warren 2000). Restoration of numbers and range will rely heavily on habitat improvement and creation to unite otherwise isolated groups thus improving connectivity. Given that hens are more mobile than cocks and that lekking arenas are of a highly traditional nature, the creation of suitable habitat may have to be combined with cock translocation to ensure effective range consolidation or expansion within fragmented landscapes.

Vital rates in our and in other studies

We estimated an annual adult survival rate of 0.72 for cocks and hens combined, but a lower first-year survival rate of 0.46. Lower juvenile survival was attributable to predation by raptors and stoats. The value for adult survival is high compared to both other estimates in the United Kingdom and elsewhere in Europe. The only other estimate for the United Kingdom is for northeast Scotland, where Picozzi (1986) recorded a rate of 0.51 for hen survival. Equivalent data from Scandinavia report considerable variations in survival rate both between

years: 0.28-0.52 (Willebrand 1988) and between studies (Spidsø, Hjeljord & Dokk 1997). However, values involving several years derived from study means, e.g. 0.53 in Finland (Lindén 1981) and 0.54 in Sweden (Angelstam 1984) were more consistent. In Central Europe and the Alps, estimates of survival rates of adults were higher and thereby more similar to those found in our study, with 0.66 survival (hens only) in the Netherlands and 0.56-0.84 in the French Alps (Caizergues & Ellison 1997). Common to our study, several studies reported lower survival of first-year birds due to predation (Angelstam 1984, Willebrand 1988, Caizergues & Ellison 1997), with most describing predation by raptors as the most frequent cause of death (Angelstam 1984, Picozzi 1986, Willebrand 1988, Caizergues & Ellison 1997, Spidsø et al. 1997).

By contrast, the average reproductive rate of 1.5 chicks per hen per year was similar to estimates elsewhere in Europe, but lower than equivalent estimates in Britain. Reproductive rates from 10 previous studies in six European countries, summarised by Baines (1990) varied from 1.2 to 3.0, with a mean of 1.9 chicks per hen per year. The reproductive rate for birds in our study area was higher than the mean of 1.2 recorded for 20 sites in the same region (Calladine et al. 2000), but lower than that for six sites in Wales (1.7; RSPB, unpubl. data) and 16 sites in the Highlands of Scotland over the same period (2.1; K. Blake, unpubl. data). Causes of low breeding success are currently being investigated in a parallel study.

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References

Åberg, J., Jansson, G., Swenson, J.E. & Angelstam, P. 1995: The effect of matrix on the occurrence of Hazel Grouse (*Bonasa bonasa*) in isolated habitat fragments. - *Oecologia* 103: 265-269.

Aebischer, N.J. 1999: Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. - *Bird Study* 46: 22-31.

Angelstam, P. 1984: Sexual and seasonal differences in mortality of the Black Grouse *Tetrao tetrix* in boreal Sweden. - *Ornis Scandinavica* 15: 123-124.

Baines, D. 1990: The ecology and conservation of Black Grouse in Scotland and northern England. - In: Lumiej, J.T. & Hoogeveen, Y.R. (Eds.); *The Future of Wild Galliformes in the Netherlands*. Amersfoot, pp. 106-118.

Baines, D. 1994: Seasonal differences in habitat selection by Black Grouse *Tetrao tetrix* in the northern Pennines, England. - *Ibis* 136: 39-43.

Baines, D. 1996: Seasonal variation in lek attendance and lekking behaviour by male Black Grouse *Tetrao tetrix*. - *Ibis* 138: 177-180.

Baines, D. & Hudson, P. 1995: The decline of Black Grouse in Scotland and northern England. - *Bird Study* 42: 122-131.

Caizergues, A. & Ellison, L.N. 1997: Survival of Black Grouse *Tetrao tetrix* in the French Alps. - *Wildlife Biology* 3: 177-188.

Caizergues, A. & Ellison, L.N. in press: Natal dispersal and its consequences in Black Grouse. - *Ibis*.

Calladine, J., Baines, D. & Warren, P. 2000: Restoration of moorland habitat in northern England: A conservation initiative for Black Grouse. - *Cahiers d'Ethologie* 20: 521-532.

Corbet, G.B. & Harris, S. 1991: *The Handbook of British Mammals*. - Blackwells, Oxford, 588 pp.

Cramp, S. & Simmons, K.E.L. 1980: *The birds of the Western Palearctic*, Vol. 2. - Oxford University Press, Oxford, 695 pp.

Cresswell, W. & Whitfield, D.P. 1994: The effects of raptor predation on wintering wader populations. - *Ibis* 136: 223-232.

Gibbons, D.W., Reid, J.W. & Chapman, R.A. 1993: *The New Atlas of Breeding Birds in Britain and Ireland*. - Poyser, London, pp. 988-991.

Hancock, M., Baines, D., Gibbons, D., Etheridge, B. & Shepherd, M. 1999: Status of male Black Grouse *Tetrao tetrix* in Britain in 1995-96. - *Bird Study* 46: 1-15.

Hensler, G.L. 1985: Estimation and comparison of functions of daily nest survival probabilities using the Mayfield method. - In: Morgan, B.J.T. & North, P.M. (Eds.); *Statistics in Ornithology*. Springer-Verlag, Berlin, Lecture Notes in Statistics No. 29: 289-301.

Hensler, G.L. & Nichols, J.D. 1981: The Mayfield method of estimating nesting success: a model, estimators and simulation results. - *Wilson Bulletin* 93: 42-53.

Hines, J.E. 1986: Survival and reproduction of dispersing Blue Grouse. - *Condor* 88: 43-49.

Hudson, P.J. 1992: *Grouse in Space and Time: The Population Biology of a Managed Gamebird*. - Game Conservancy Trust, Fordingbridge, UK, 224 pp.

Hudson, P.J. & Newborn, D. 1995: *Red Grouse and Moorland Management*. - Game Conservancy Trust, Fordingbridge, UK, 169 pp.

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

Keppie, D.M. 1979: Dispersal, over-winter mortality and recruitment of Spruce Grouse. - *Journal of Wildlife Management* 43: 717-727.

Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. 1992: Modelling survival and testing biological hypotheses

- using marked animals - a unified approach with case studies. - *Ecological Monographs* 62: 67-118.
- Lindén, H. 1981: Estimation of juvenile mortality in the Capercaillie Tetrao urogallus and the Black Grouse T. tetrix from indirect evidence. - *Finnish Game Research* 39: 35-51.
- Marjakangas, A., Aspegren, H. & Kyllönen, M. 1991: Spring dispersal and subsequent movements of yearling female Black Grouse Tetrao tetrix in eastern central Finland. - *Transactions of the Congress of International Union of Game Biologists* 20: 297-301.
- Marjakangas, A. & Törmällä, L. 1997: Female age and breeding performance in a cyclic population of Black Grouse Tetrao tetrix. - *Wildlife Biology* 3: 195-203.
- Mayfield, H.F. 1961: Nesting success calculated from exposure. - *Wilson Bulletin* 73: 255-261.
- Picozzi, N. 1986: Black Grouse research in north-east Scotland. - Unpublished report, Banchory, Kincardineshire, 53 pp.
- Piertney, S.B., MacColl, A.D.C., Bacon, P.J. & Dallas, J.F. 1998: Local genetic structure in Red Grouse (*Lagopus lagopus scoticus*): evidence from microsatellite DNA markers. - *Molecular Ecology* 7: 1645-1654.
- Sharrock, J.T.R. 1976: *The Atlas of Breeding Birds in Britain and Ireland*. - Poyser, Carlton, 479 pp.
- Smith, A.A. 1997: Dispersal and movements in a Swedish Willow Grouse *Lagopus lagopus* population. - *Wildlife Biology* 3: 279.
- Spidsø, T., Hjeljord, O. & Dokk, J.D. 1997: Seasonal mortality of black grouse Tetrao tetrix during a year with little snow. - *Wildlife Biology* 3: 205-209.
- Storch, I. 1997: The role of metapopulation concept in conservation of European woodland grouse. - *Wildlife Biology* 3: 272.
- Thirgood, S.J., Redpath, S.M., Hudson, P.J. & Donnelly, E. 1998: Estimating the cause and rate of mortality in Red Grouse *Lagopus lagopus scoticus*. - *Wildlife Biology* 4: 65-71.
- Willebrand, T. 1988: Demography and ecology of Black Grouse populations. - PhD thesis, University of Uppsala, Sweden, 148 pp.
- White, G.C. & Garrott, R.A. 1990: *Analysis of wildlife radio-tracking data*. - Academic Press, London, 383 pp.