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Source: Wildlife Biology, 17(2) : 135-142

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/10-085>

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Evaluation of the distance sampling technique to survey red grouse *Lagopus lagopus scoticus* on moors in northern England

Philip Warren & David Baines

We surveyed red grouse *Lagopus lagopus scoticus* using pointing dogs in spring and again in summer from 2000 to 2010 on four moors in northern England using a line-transect distance sampling method. We compared density estimates generated with those obtained using three other methods on the same moors: counts of calling males within sample blocks of 0.5-km², absolute counts of grouse within sample blocks of 0.5-km² using a line of beaters and gamekeepers' own transect counts obtained using their dogs. We found that distance estimates were positively correlated with abundance estimates from all three sampling methods. Our distance sampling estimates of males pre-breeding were 47% higher than call count estimates, with pre-breeding distance sampling estimates 65% higher than the absolute counts. Distance sampling along transects across the whole moor provides a method for extensive surveys of red grouse, generating estimates of grouse population size at a moor level which can be directly related to management practices, particularly to harvesting and parasite control strategies.

Key words: distance sampling, drive counts, gamekeepers, *Lagopus lagopus scoticus*, pointing dogs, red grouse

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Received 5 August 2010, accepted 28 December 2010

Associate Editor: Ilse Storch

In Britain, red grouse *Lagopus lagopus scoticus* are an economically important game bird, with large tracts of heather *Calluna vulgaris* moorland managed to provide driven shooting (Hudson & Dobson 2001). Factors that determine red grouse abundance have been intensively studied and include rotational heather burning (Miller et al. 1966), predation (Jenkins et al. 1964), harvesting (Potts et al. 1984, Bunnefeld et al. 2009), spacing behaviour (MacColl et al. 2000, Moss & Watson 2001) and parasites, in particular the caecal threadworm *Trichostrongylus tenuis* (Potts et al. 1984, Hudson et al. 2002) and the louping ill virus (Laurenson et al. 2004).

Many existing grouse monitoring programmes assess pre- and post-breeding densities within 1-km² blocks using pointing dogs (Hudson & Newborn 1995, Evans et al. 2007). This method is effective for small-scale studies, providing information on an-

nual variations in density and breeding success. This makes it possible to predict cyclic changes (Moss & Watson 2001), but yields little direct information on population processes other than birth rates or on the spatial distribution of grouse across the moor. It also assumes that the 1-km² block is representative of the moor as a whole, and this may not always be the case. Grouse moors comprise large areas, typically 10–50 km² (Hudson 1992), and managers require accurate estimates of density and breeding success to plan harvesting regimes (Bunnefeld et al. 2009) and parasite control strategies (Newborn & Foster 2002). Many management decisions are taken at the whole-moor scale, or within moor at the beat scale, an area of moorland managed by one gamekeeper (5–15 km²; Hudson & Newborn 1995). Hence, spatially reliable data on grouse density and abundance at extensive moor scales are required.

Counting the whole moor using dogs would be logistically difficult; therefore, we consider a line-transect distance sampling method (Buckland et al. 2001, Thomas et al. 2010) to estimate variations in patterns of grouse density and total abundance at the moor scale. We compared density estimates generated by distance sampling with the estimates obtained from three other survey methods on the same moors: counts of calling males (Hudson 1992), absolute counts of grouse using a line of beaters within sample blocks of 0.5-km² and gamekeepers' own transect counts using their dogs.

Material and methods

Our study was conducted between 2000 and 2010 on four privately owned grouse moors in County Durham, England. Three of the grouse moors were contiguous (81 km²), and the fourth was located 8 km to the north (32 km²). Altitude ranged from 240 m to 650 m a. s. l. The moors were characterised by the predominance of heather, along with other dwarf shrubs such as bilberry *Vaccinium myrtillus*, bell heather *Erica cinerea*, cross-leaved heath *E. tetralix* and various grasses, sedges and rushes. To create harvestable surpluses of grouse for shooting, gamekeepers were employed to manage the heather by rotational strip burning to produce a mosaic of heather ages and structures (Miller et al. 1966) and to control the potential predators of grouse, mainly red fox *Vulpes vulpes*, carrion crow *Corvus corone*, magpie *Pica pica*, stoat *Mustela erminea*, weasel *M. nivalis* and brown rat *Rattus norvegicus* (Hudson & Newborn 1995). The moors were grazed by sheep *Ovis aries*, usually all year round.

Distance sampling

We used line-transect distance sampling (Buckland et al. 2001, Thomas et al. 2010) to survey grouse across the study moors. We initiated surveys on all four moors in the spring of 2000. An outbreak of Foot and Mouth Disease in 2001 prevented data collection on all moors in the spring and from two moors in the summer of that year. We collected data from two moors in the spring of 2002 and thereafter from only one moor of 19 km². Our surveys were conducted pre-breeding between 6 March and 2 April and post-breeding between 11 July and 3 August, prior to harvesting which commenced on 12 August.

We placed a grid of transect lines spaced at 500-m

intervals over the four study moors and allocated a random start point. The surveyors walked each transect whilst systematically working an English pointer dog on both sides of the transect line to search for grouse. When grouse were located, the perpendicular distance from the transect line to the grouse was measured using a GPS, with the position along the line also recorded. The sex (adults only) and the age in the summer (adult or juvenile) of the grouse were recorded when flushed, along with the individual dog used and the dog's age. We recorded only one measure of distance to each covey of birds. We took care to ensure that flushed birds were not recounted along the survey line by watching to see where the birds resettled. We only conducted survey work in good weather, with light winds and good visibility. Surveys were not undertaken in heavy rain, strong winds or low cloud. We began surveys shortly after dawn to maximise scenting conditions for the pointing dogs. Surveys were conducted on average for two to three hours in order to maintain the searching effectiveness of the dogs. The surveys were undertaken by two independent surveyors. Over the period of the study, surveyor A used six dogs, while surveyor B used three dogs, but only one at any one time.

We analysed data separately for each survey period and year using Distance 6.0 (Thomas et al. 2010). Frequency histograms of the perpendicular distance of grouse from the transect line were plotted with candidate detection probability models during the exploratory stage of the analysis. We selected the models which gave the best fit on minimum Akaike's Information Criterion (AIC) scores (Akaike 1973) and χ^2 goodness-of-fit tests. We chose a half-normal estimator for all seasons and years. To allow for variations in the ESW between individual pointing dogs, dog was included as a factor-type covariate using the multiple-covariate distance sampling (MCDS) engine in Distance 6.0.

In addition to deriving estimates of density and population size, we needed to map the spatial abundance of grouse across the moors in the spring of 2000 and 2003 in order to select sample survey squares for comparing densities from distance sampling with those obtained from counts of both calling males and total birds from drive counts in areas of predicted low, medium and high density. We mapped the pre-breeding spatial abundance of grouse on three moors in 2000 and one moor in 2003, by summing the number of birds observed on

each 500-m section of the transect lines and allocating to each a coordinate relating to the mid-point of the section. We entered these spatial abundance data into an Idrisi GIS to produce maps of spatial distribution, using kriging (Isaacs & Srivastava 1989, Stein 1999). We used a semivariogram to quantify the spatial autocorrelation in the data and to define the weightings that determined the contribution of each data point to the prediction of new values at the non-sampled locations.

Calling males

We surveyed territorial 'calling' males in April and early May 2000 in 17 sample blocks of 25-ha. The sample blocks were intersected by a distance-sampling transect line through the centre and selected at random across the study area in relation to grouse abundance from the interpolated map, with five blocks in low density (< 10 grouse km^{-1}) areas, six in medium density (10-20 grouse km^{-1}) areas and six in high density (> 20 grouse km^{-1}) areas. Call counts began at dawn with the observers positioned so that they could see and hear from all parts of the block. Surveys continued until 06:45, thus coinciding with the peak of male display activity (Hudson 1992). All calling male grouse seen or heard were recorded.

Drive counts

Absolute counts of grouse were made from four 25-ha blocks in April and early May 2000 and a further eight blocks in 2003. A line of surveyors, evenly spaced at 30-m intervals, walked waving flags through each block to flush all grouse. Surveys were undertaken during 09:00-17:00. Sample blocks were selected at random in relation to mapped grouse abundance in that spring. In 2000, two blocks were in low density (< 10 grouse km^{-1}) areas and two in medium density (10-20 grouse km^{-1}) areas, in 2003 a further two blocks were in low density (< 10 grouse km^{-1}) areas, three were in medium density (10-20 grouse km^{-1}) areas and three were in high density (> 20 grouse km^{-1}) areas.

Gamekeeper counts

Gamekeepers routinely survey their grouse in July to estimate how many birds are available for shooting in August. In July 2000, gamekeepers on two of the study moors worked their dogs along 22 pre-defined routes distributed in relation to shooting drives. All grouse flushed were counted and an index of abundance (grouse km^{-1}) derived from

total grouse seen divided by the length of transect. We compared these indices with abundance estimates derived from distance sampling for the same drive, through sub-dividing the study area into blocks relating to the known drive areas and splitting the line-transects accordingly.

Statistical analysis

To check for any differences in the hunting ranges of pointing dogs, we calculated the mean distance of grouse flushes from the transect line for each dog for every moor, season and year, as it was not feasible to calculate an Estimated Strip Width (ESW) using Distance for each period due to insufficient registrations (< 60) to accurately fit the detection function (Buckland et al. 1993). We tested differences in hunting range between dogs using a General Linear Model (GLM) in Systat Version 12. The hunting range was entered as the dependent variable (weighted by the number of values in each mean) and as each surveyor worked his own dogs, dogs were nested within surveyor as statistical model factors and entered along with moor, year, surveyor and season as the categorical independent variables.

To assess whether the hunting range of dogs differed in relation to age, the individual dog's hunting ranges were assessed using a GLM with hunting range as the dependent variable (weighted by the number of values in each mean) and dog and age as the categorical independent variables.

To establish whether the ESW modelled using Distance and the subsequent estimates of grouse density generated differed between moor, season and year, we tested both independently using GLMs. Both ESW and grouse density estimates (log-transformed to normalise) were entered into

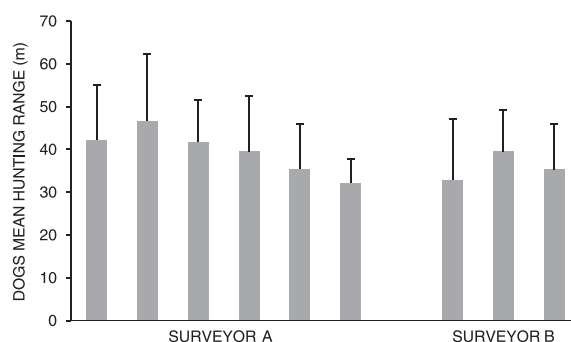


Figure 1. Mean hunting ranges (\pm SE) of the nine pointing dogs used by the two surveyors (six by surveyor A and three by surveyor B) during the study.

Table 1. Pre-breeding estimates of red grouse density and population size on four moors in northern England during 2000-2010 using distance sampling; ESW = estimated half strip width and CL = 95% confidence limits.

Moor (km ²)	Year	Total transect length (km)	Encounter rate (flush events km ⁻¹)	ESW	Density (grouse km ⁻²)	Population size (95% CL)
Moor A (19.2)	2000	37.2	6.5	51.4	101.4	1947 (1526-2485)
Moor B (20.7)	2000	40.1	6.3	60.2	93.8	1942 (1543-2443)
Moor C (32.5)	2000	46.5	7.6	49.0	131.7	4281 (3635-5043)
Moor D (41.3)	2000	78.8	8.4	53.3	146.2	6037 (5104-7141)
Moor A	2002	35.3	9.0	46.8	168.9	3243 (2759-3812)
Moor B	2002	34.7	12.1	49.6	215.7	4465 (3745-5323)
Moor A	2003	34.9	7.1	47.5	119.2	2289 (1952-2685)
Moor A	2004	34.4	6.9	49.1	124.2	2385 (2028-2804)
Moor A	2005	34.4	5.5	54.3	84.3	1619 (1299-2018)
Moor A	2007	16.6	7.3	61.3	109.5	2103 (1528-2893)
Moor A	2008	34.4	6.9	52.3	120.0	2303 (1876-2828)
Moor A	2009	34.4	8.2	52.8	133.6	2565 (2234-2943)
Moor A	2010	34.4	6.6	57.8	98.9	1899 (1622-2223)

independent models as the dependent variable, with moor, season and year as the categorical independent variables.

We compared density estimates generated from distance sampling with estimates for the equivalent block for pre-breeding calling males, absolute counts from drive counts and gamekeeper summer transect counts (all log-transformed to normalise) by ANOVA and correlation. ANOVA was used to assess whether the ratio of females to males (log-transformed to normalise) encountered on drive counts (no dogs) and distance sampling transects using dogs on the same block differed in relation to survey method and density category.

Results

The hunting ranges of dogs varied between seasons ($F_{1,70}=5.57$, $P=0.02$), dogs ($F_{7,70}=5.39$, $P<0.001$) and surveyors ($F_{1,70}=5.57$, $P=0.02$), but not between moors ($F_{3,70}=1.69$, $P=0.18$) or years ($F_{10,70}=1.55$, $P=0.14$). Hunting ranges in spring were 36.1 ± 12.2 m in comparison to 38.2 ± 5.4 m in summer. These varied between dogs from 32.2 ± 5.7 m to 46.7 ± 15.7 m (Fig. 1) and between the two surveyors (Surveyor A: 41.5 ± 6.2 m, Surveyor B: 34.7 ± 9.2 m). No effect of dog age was detected on searching ranges ($F_{10,74}=0.87$, $P=0.56$).

The ESW differed between years ($F_{10,13}=4.32$,

Table 2. Post-breeding estimates of red grouse density and population size on four moors in northern England during 2000-2010 using distance sampling; ESW = estimated half strip width and CL = 95% confidence limits.

Moor	Year	Total transect length (km)	Encounter rate (flush events km ⁻¹)	ESW	Density (grouse km ⁻²)	Population size (95% CL)
Moor A	2000	33.6	6.9	59.9	282.8	5430 (4360-6762)
Moor B	2000	36.3	7.0	66.8	333.0	6893 (5626-8446)
Moor C	2000	51.5	5.8	57.6	228.5	7426 (6126-9002)
Moor D	2000	74.9	7.5	58.2	324.5	13401 (11214-16061)
Moor A	2001	35.0	6.9	51.6	494.9	9502 (7471-12086)
Moor B	2001	38.0	7.9	52.7	429.6	8892 (6996-11302)
Moor A	2002	35.1	7.9	53.5	393.0	7549 (6130-9248)
Moor A	2003	34.4	4.9	48.9	277.5	5328 (4209-6744)
Moor A	2004	34.4	7.5	50.4	432.8	8310 (6539-10561)
Moor A	2005	34.4	1.5	61.0	45.8	880 (566-1369)
Moor A	2006	34.4	2.6	71.3	131.8	2530 (1823-3511)
Moor A	2007	34.4	7.0	55.4	560.9	10769 (8093-14330)
Moor A	2008	34.4	6.2	54.2	421.9	8101 (6386-10278)
Moor A	2009	34.4	3.6	51.6	189.4	3636 (2625-5036)
Moor A	2010	34.4	6.3	51.6	511.7	9824 (7821-12339)

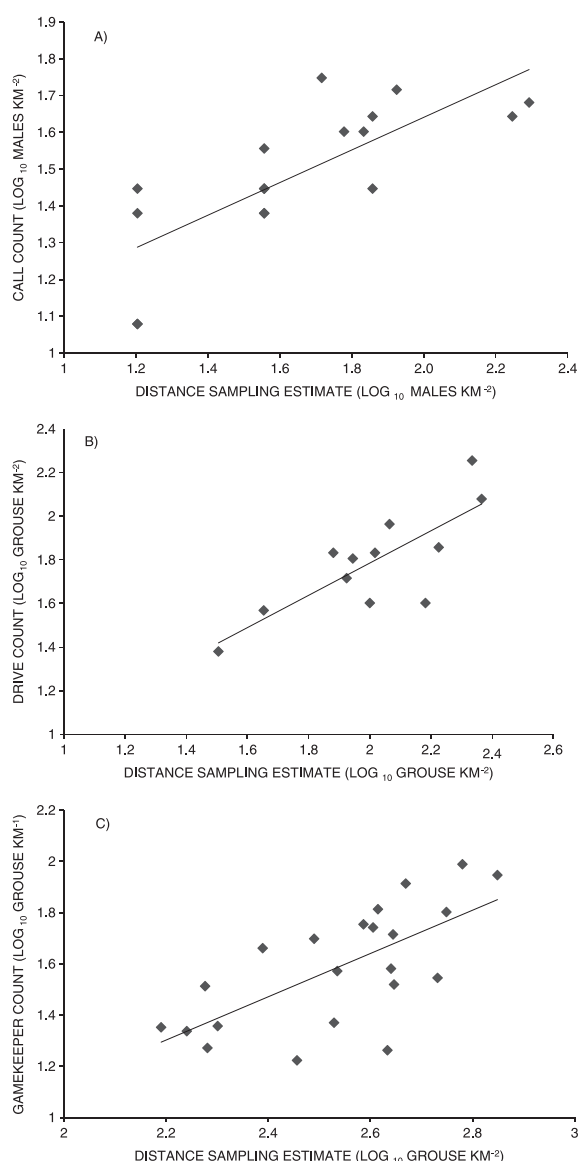


Figure 2. Comparative estimates of abundance pre-breeding from counts of calling males (A), drive counts (B) and post-breeding from gamekeepers' counts (C) with distance sampling estimates (log grouse km⁻²). A) shows calling males log males km⁻²; $y = 0.44x + 0.75$, $r = 0.77$, $P < 0.001$, $N = 17$; B) drive counts log grouse km⁻²; $y = 0.74x + 0.31$, $r = 0.79$, $P = 0.002$, $N = 12$; and C) gamekeepers' counts log grouse km⁻¹; $y = 0.84x - 0.56$, $r = 0.68$, $P = 0.001$, $N = 22$.

$P = 0.008$), but not between season ($F_{1,13} = 4.22$, $P = 0.06$) or moors ($F_{3,13} = 2.26$, $P = 0.13$; Tables 1 and 2). Grouse densities differed significantly between season ($F_{1,13} = 29.4$, $P < 0.001$) but not between years ($F_{10,13} = 2.56$, $P = 0.06$) or moors ($F_{3,13} = 0.18$, $P = 0.91$). Grouse density was three times higher in summer (mean 292 ± 53 km⁻²) than in spring (mean 123 ± 9 km⁻²).

Call count and distance sampling estimates were positively correlated ($r = 0.77$, $N = 17$; Fig. 2A). Density estimates differed between methods ($F_{1,28} = 7.76$, $P = 0.009$) and between density categories ($F_{2,28} = 29.46$, $P < 0.001$), but there was no significant interaction between method and density category ($F_{2,28} = 2.52$, $P = 0.10$). Distance sampling estimates of males pre-breeding were 47% higher than the call count estimates (Fig. 3A).

The ratio of females to males encountered on drive counts (using beaters only) did not differ from line-transect distance sampling using dogs ($F_{1,18} = 0.65$, $P = 0.43$) or between density categories ($F_{2,18} = 1.48$, $P = 0.25$). Therefore, we compared counts of both males and females. Drive count and distance sampling estimates were positively correlated ($r = 0.79$, $N = 12$; see Fig. 2B). Density estimates differed between methods ($F_{1,18} = 10.97$, $P = 0.004$) and between density categories ($F_{2,18} = 21.12$, $P < 0.001$), but there was no interaction between method and density category ($F_{2,28} = 0.36$, $P = 0.70$). Distance sampling estimates were 65% higher than the drive count estimates (see Fig. 3B).

Post-breeding counts of adults and juveniles by gamekeepers (grouse km⁻¹) were positively correlated with the distance sampling estimates (grouse km⁻²) for the same areas ($r = 0.68$, $N = 22$; see Fig. 2C). Estimates differed between methods ($F_{1,38} = 404.31$, $P < 0.001$) and between density categories ($F_{2,38} = 24.72$, $P < 0.001$), but there was no interaction between method and density category ($F_{2,38} = 0.28$, $P = 0.76$; see Fig. 3C).

Discussion

The first consideration of our study was to evaluate whether the distance sampling technique using pointing dogs met the assumptions of distance sampling theory (Thomas et al. 2010). Willow ptarmigan *Lagopus lagopus* have been surveyed using distance sampling in Norway, albeit at significantly lower densities (Pedersen et al. 1999), and willow ptarmigan, rock ptarmigan *Lagopus muta* and white-tailed ptarmigan *Lagopus leucura* have been surveyed using an aerial distance sampling technique (Pelletier & Krebs 1997). A critical assumption is accurately measuring the distance from the transect line. The open homogenous nature of moorland habitats allows good visibility and this in combination with the behavioural response of grouse to the trained pointing dogs,

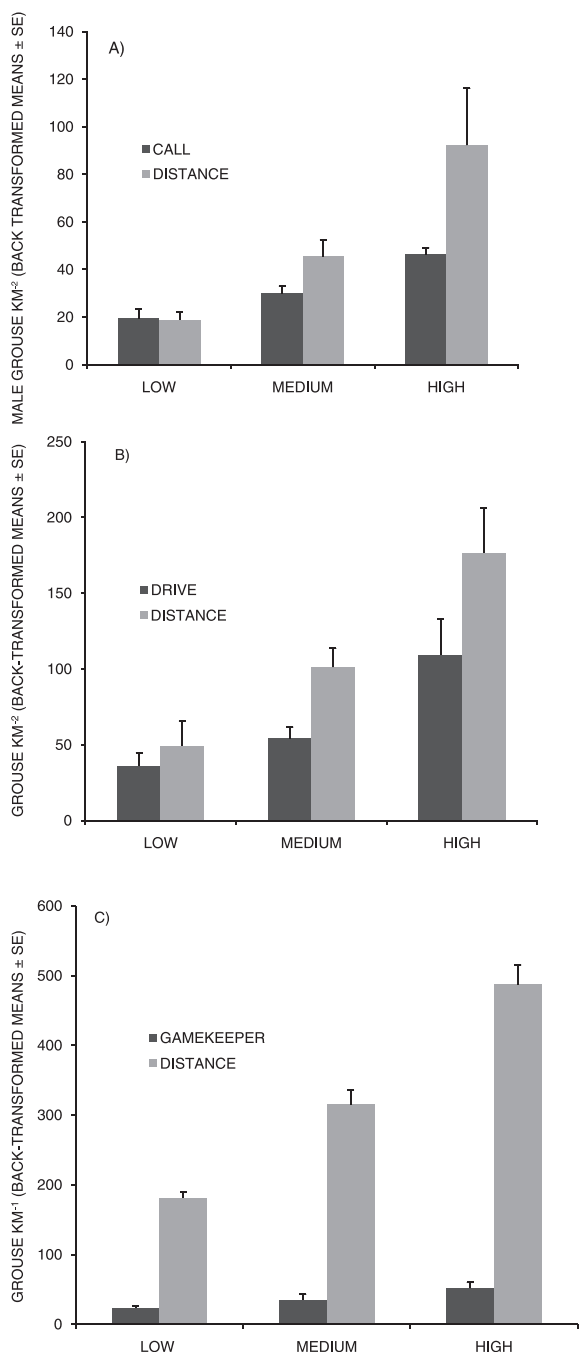


Figure 3. Comparative estimates of abundance pre-breeding from counts of calling males (A), drive counts (B) and post-breeding from gamekeepers' counts (C) with distance sampling estimates (grouse km⁻²). A) shows calling males (grouse km⁻²) within sample 25-ha blocks at low (N = 5), medium (N = 6) and high grouse densities (N = 6); B) drive counts (grouse km⁻²) within sample 25-ha blocks at low (N = 4), medium (N = 5) and high grouse densities (N = 3); and C) gamekeepers' transect counts (grouse km⁻¹) at low (0-200 grouse km⁻²), medium (201-400 grouse km⁻²) and high (> 401 grouse km⁻²) grouse density.

which is to crouch, allowed accurate measures of distance to be obtained. In spring, red grouse are highly territorial (MacColl et al. 2000) and are reluctant to leave their defended territories. Similarly post-breeding in summer, grouse are in family groups of young and adults and are reluctant to flush, allowing the dog to accurately 'point' their position. Outside these key periods, grouse are less territorial. In autumn and winter they occur in flocks (Hudson 1992) and readily flush when up to 200 m from the observer. In these conditions, accurate measures of distance were found to be impossible and the method proved impractical.

Evasive movement away from the observer, or failure to detect animals close to or on the transect line can bias density estimates (Turnock & Quinn 1991, Ruetten et al. 2003). We expect some movement by grouse prior to detection by the pointing dogs, but inspection of the distance data showed no peaks, which suggested that any movements that may have occurred appeared to be relatively small and of a random nature, which did not cause bias to the density estimates. A study using radio-tagged willow ptarmigan in Norway found that pointing dogs detected all birds on the line and that birds did not move in response to the approaching dog and handler prior to flushing (Pedersen et al. 2004).

Adequate sample sizes are also important, with sample sizes of at least 60-80 sightings required to give reliable estimates of density (Buckland et al. 2001). This was readily achievable on our study moors, where spring densities ranged from 81 to 215 grouse km⁻², but in areas where bird densities are much lower, for instance in Norway (Pedersen et al. 1999), where willow ptarmigan were found at densities of 5-8 birds km⁻², survey design needs to ensure sufficient encounters.

In our study, differences in the hunting ranges between dogs and the surveyors working their dogs were found, albeit small. This can be attributed to two main factors, the first is that surveyor A trained surveyor B to work pointing dogs, and secondly that both surveyors used the same breed and sex (males), therefore similar size of pointing dog. A decline in the hunting range for individual dogs as they aged may have been expected, but was not the case. The surveyors worked dogs less as they aged, consistently replacing them with younger, fitter dogs.

The hunting ranges and ESW calculated for the dogs in our study were considerably lower than those recorded in similar studies on willow ptarmi-

gan in Norway. Willow ptarmigan were found at low density, 2.2 -13.2 birds km⁻² in spring and 3.3-46.0 birds km⁻² in summer (Pedersen et al. 1999) with the ESW almost twice as wide as ours, being on average 102.9 m (range: 41-143 m) in spring and on average 81.7 m (range: 46-123 m) in summer. This variation is likely to be caused by differing dog handling methods used to find grouse at low densities. In our study, grouse were found at higher densities and the dogs were worked in a methodical figure of eight routine from the surveyor, turned by a whistle command when at 60-100 m distances from the transect, rather than allowed to continue to search beyond this until they encounter grouse. It is evident from comparing the results from our and other studies that there is the potential for significant variation between different hunting dogs and handlers, dependent on hunting strategies and the breed of dogs used (Guthery & Mecozzi 2008). Adopting distance sampling procedures, can take these variations and biases into account when generating density and abundance, allowing reliable comparisons to be made.

The hunting ranges calculated for the hunting dogs have interesting connotations for the monitoring of grouse population dynamics as many monitoring programmes assume that counts from 1-km² blocks surveyed along six parallel line transects are 'total' counts (Evans et al. 2007). A comparison of findings from our study with those of others (Pedersen et al. 2004, Guthery & Mecozzi 2008) shows significant variation in the ESW of hunting dogs. Therefore care has to be taken when interpreting the results from block counts, particularly when assessing density-dependent events such as strongylosis disease outbreaks and when planning harvest rates.

Density estimates generated by distance sampling were correlated with estimates from all three count methods. Pre-breeding distance sampling estimates were consistently higher than the drive counts as were the counts of calling males. The drive count method using beaters only may not have flushed all the red grouse that were present, whilst the call count method may underestimate the numbers of calling males at high density, owing to individual males not being identifiable from one another and because the observer may be distracted by displaying males nearby at the expense of males further away.

The generation of moor-scale estimates of grouse numbers are particularly important as they facili-

tate further studies that relate to the scales of management employed on grouse moors, particularly in relation to harvest rates (Bunnefeld et al. 2009). Little is known of the threshold harvesting levels required to harvest grouse populations sustainably and this method provides moor-level density estimates that can be directly related to bag data, which are collected at the moor-level. Using line-transects also facilitates the creation of maps of grouse abundance, which enables further spatial scale studies to assess dispersal (Brøseth et al. 2005, Warren & Baines 2007) and patterns of overwinter losses in relation to variations in habitat quality/extent to be considered. Adopting line-transect distance sampling allows large areas of ground to be surveyed economically and within practical periods of time (Rosenstock et al. 2002). The suitability of the method appears dependent on the species of interest, which in this case is due to the response of red grouse to the pointing dogs.

Acknowledgements - we thank the landowners and gamekeepers for access to study areas, particularly Lindsay Waddell, Robert Beadle, Peter Fawcett and Andy Walker. We are also grateful to Nicholas Aebischer for statistical advice and comments.

References

- Akaike, H. 1973: Information theory and extension of the maximum likelihood principle. - In: Petran, B.N. & Csaaki, F. (Eds.); International Symposium on Information Theory, Akademiai Kiado, Budapest, Hungary, pp. 267-281.
- Brøseth, H., Tufto, J., Pedersen, H.C., Steen, H. & Kastedalen, L. 2005: Dispersal patterns in a harvested willow ptarmigan population. - *Journal of Applied Ecology* 42: 453-459.
- Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. 1993: Distance Sampling: Estimating Abundance of Biological Populations. - Chapman & Hall, London, UK, 446 pp.
- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. 2001: Introduction to Distance Sampling. Estimating abundance of biological populations. - Oxford University Press, Oxford, UK, 432 pp.
- Bunnefeld, N., Baines, D., Newborn, D. & Milner-Gulland, E.J. 2009: Factors affecting unintentional harvesting selectivity in a monomorphic species. - *Journal of Animal Ecology* 78: 485-492.
- Evans, S.A., Mougeot, F., Redpath, S.M. & Leckie, F. 2007: Alternative methods for estimating density in an

- upland game bird: the red grouse *Lagopus lagopus scoticus*. - *Wildlife Biology* 13(2): 130-139.
- Guthery, F.S. & Mecozzi, G.E. 2008: Developing the concept of estimating bobwhite density with pointing dogs. - *Journal of Wildlife Management* 72(5): 1175-1180.
- Hudson, P.J. 1992: Grouse in Space and Time: The population Biology of a Managed Gamebird. - The Game Conservancy Trust, Fordingbridge, UK, 224 pp.
- Hudson, P.J. & Dobson, A.P. 2001: Harvesting unstable populations: red grouse *Lagopus lagopus scoticus* (Lath.) in the United Kingdom. - *Wildlife Biology* 7(3): 189-195.
- Hudson, P.J., Dobson, A.P. & Newborn, D. 2002: Parasitic worms and population cycles of red grouse. - In: *Population Cycles: The Case for Trophic Interactions*. Oxford University Press, Oxford, UK, pp. 109-130.
- Hudson, P.J. & Newborn, D. 1995: Red Grouse and Moorland Management. - Game Conservancy Trust, Fordingbridge, UK, 169 pp.
- Isaacs, E.H. & Srivastava, R.M. 1989: An introduction to Applied Geostatistics. - Oxford University Press, New York, New York, USA, 561 pp.
- Jenkins, D., Watson, A. & Miller, G.R. 1964: Predation and red grouse populations. - *Journal of Applied Ecology* 1: 183-122.
- Laurenson, M.K., Norman, R.A., Gilbert, L., Reid, H.W. & Hudson, P.J. 2004: Mountain hares, louping ill, red grouse and harvesting: complex interactions but few data. - *Journal of Animal Ecology* 73: 811-813.
- MacColl, D.C., Pieltney, S.B., Moss, R. & Lambin, X. 2000: Spatial arrangement of kin affects recruitment success in young male red grouse. - *Oikos* 90: 261-270.
- Miller, G.R., Jenkins, D. & Watson, A. 1966: Heather performance and red grouse populations. Visual estimates of heather performance. - *Journal of Applied Ecology* 3: 313-326.
- Moss, R. & Watson, A. 2001: Population cycles in birds of the grouse family (Tetraonidae). - *Advances in Ecological Research* 32: 53-111.
- Newborn, D. & Foster, R. 2002: Control of parasite burdens in wild red grouse *Lagopus lagopus scoticus* through the indirect application of anthelmintics. - *Journal of Applied Ecology* 39(6): 909-914.
- Pedersen, H.C., Steen, H., Kastdalen, L., Brøseth, H., Ims, R.A., Svendsen, W. & Yoccoz, N.G. 2004: Weak compensation of harvest despite strong density-dependent growth in willow ptarmigan. - *Proceedings of the Royal Society London* 271: 381-385.
- Pedersen, H.C., Steen, H., Kastdalen, L., Svendsen, W. & Brøseth, H. 1999: The impact of hunting on willow ptarmigan populations. Progress report 1996-1998. - NINA Oppdragsmelding 578: 1-43.
- Pelletier, L. & Krebs, C.J. 1997: Line-transect sampling for estimating ptarmigan (*Lagopus* spp.) density. - *Canadian Journal of Zoology* 75: 1185-1192.
- Potts, G.R., Tapper, S.C. & Hudson, P.J. 1984: Population fluctuations in red grouse: analysis of bag records and simulation model. - *Journal of Animal Ecology* 53: 21-36.
- Rosenstock, S.S., Anderson, D.R., Giesen, K.M., Leukering, T. & Carter, M.F. 2002: Landbird counting techniques: current practices and an alternative. - *The Auk* 119: 46-53.
- Ruette, S., Stahl, P. & Albaret, M. 2003: Applying distance sampling methods to spotlight counts of red foxes. - *Journal of Applied Ecology* 40: 32-43.
- Stein, M.L. 1999: Interpolation of Spatial Data: Some Theory for Kriging. - Springer Series in Statistics, Springer, New York, USA, 243 pp.
- Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A. & Burnham, K.P. 2010: Distance software: design and analysis of distance sampling surveys for estimating population size. - *Journal of Applied Ecology* 47: 5-14.
- Turnock, B.J. & Quinn, T.J.,II 1991: The effect of responsive movement on abundance estimation using line transect sampling. - *Biometrics* 47: 701-715.
- Warren, P. & Baines, D. 2007: Dispersal distances of juvenile radio tagged red grouse *Lagopus lagopus scoticus* on moors in northern England. - *Ibis* 149(4): 758-762.