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Alternative methods for estimating density in an upland game bird: the red grouse *Lagopus lagopus scoticus*

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For some species, reliable quantitative estimates of population size can be difficult to obtain. Density estimates of red grouse *Lagopus lagopus scoticus* are usually obtained through counts using trained pointer dogs. In this paper, we examine two alternative, and potentially easier, methods for estimating red grouse breeding density: one direct, based on counts of males responding to playbacks of territorial calls, and one indirect, based on counts of droppings along transects. We counted grouse on 14 1-km^2 areas for 1-3 years in 2002-2004 using trained dogs and compared these density estimates (range: 23-220 grouse/km^2) with density estimates derived from playback counts and dropping counts. For playback counts, we counted males responding to a playback of territorial calls at nine points spread over a given 1-km^2 area. For dropping counts, we counted the number of fibrous dropping roost piles along two 1-km transects across each 1-km^2 area. Generalised Linear Models indicated that male, female and total grouse density, measured by counts with dogs, could be predicted from playback counts of males, and that total grouse density could be predicted from dropping counts. However, playback counts provided better predictions than did dropping counts. Neither time of day nor wind affected responses to playback, but in clear weather fewer males responded than was expected. Playback counts could thus provide a useful alternative method for estimating grouse density, when or where counts with dogs are not feasible.

Key words: count, density estimate, dropping transect, game bird, Lagopus lagopus scoticus, playback, red grouse, territorial bird

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The sustainable management of game species and the study of their population ecology depend on reliable estimates of population density (Borralho et al. 1996, Harkonen & Heikkila 1999). A wide range of estimation methods is available, the suitability of which will depend on factors such as the species and habitat concerned, the management questions to be addressed, the scale of the study and logistical constraints (Overton 1971, Marques et al. 2001). For some species it may be advantageous or necessary to use different techniques in different situations, in which case it is important to compare the abundance estimates derived from different methods.

The red grouse *Lagopus lagopus scoticus* is a common game bird, typical of upland heather *Calluna vulgaris* moorland in the UK. In many upland areas, commercial grouse shooting is economically important, and much of the heather moorland in the UK is managed for this purpose (Fraser of Allander Institute for Research on the Scottish Economy 2001). Each year, grouse moor managers plan a harvesting regime based on estimates of density and breeding success. Reliable density estimates are also crucial for studying population dynamics. Red grouse exhibit cyclic fluctuations in abundance and have been the subject of long-term demographic studies since the 1950s (e.g. Jenkins et al. 1963, Hudson et al. 1992, Watson et al. 1994). Traditionally, density estimates have been based on direct counts with dogs, although retrospective analyses often involve indirect inference from harvesting data (Potts et al. 1984, Cattadori et al. 2003). Other methods that have been used for red grouse include mapping male territories from observations of territorial disputes (Jenkins et al. 1963, Moss et al. 1994), dawn counts of calling males (Watson & O'Hare 1979) and constant effort intensive searches (Stillman & Brown 1995). A 'three-man transect' distance sampling method is also commonly used for various grouse species, particularly in boreal forests (Rajala 1974, Beshkarev et al. 1993).

Counting red grouse using trained pointer dogs has been shown to produce consistent, reliable density estimates (Jenkins et al. 1963), and is used routinely by moor managers and scientists alike (e.g. Hudson & Newborn 1995, Mougeot et al. 2003a,b). However, the method requires trained dogs, experienced observers and is time consuming. Furthermore, a dog is only able to take part in one or two counts per day and counts must be conducted in good weather conditions. These limitations mean that replication is generally not practical. In this paper, we examine two alternative, potentially easier, methods for estimating red grouse density: one direct, based on counts of males observed following playback of a territorial call, and one indirect, based on counts of grouse droppings along transects (see also Nyström et al. 2005). We tested whether these methods could provide reliable and useful density estimates, comparable to those derived from counts using dogs. We expected: 1) counts of males responding to playbacks, and of droppings along transects, to differ between areas of varying density, but to be consistent within these areas, and 2) playbacks and dropping counts to be good predictors, based on confidence intervals of predictions, of grouse density, as measured using counts with dogs.

Material and methods

Study species

Red grouse populations commonly show population cycles (Potts et al. 1984). The large fluctuations in density between years, varying from a few birds up to several hundred birds per km^2, imply that managers need to census their populations before harvesting starts. In addition, knowing how many birds are present in spring is useful to broadly evaluate how many grouse might be present in late summer, as the number of grouse available for harvesting will depend both on spring density and breeding success. Red grouse are territorial for most of the year, with males establishing their territories in autumn and maintaining them through the following spring (Jenkins et al. 1963, Watson & Jenkins 1964). Males defend their territory boundaries, making frequent flight and ground calls (described in Watson & Jenkins 1964, Hudson 1992, Watson et al. 1994). Laying starts in April-May and young fledge in July-August (Cramp & Simmons 1980). Red grouse feed almost exclusively on heather (Cramp & Simmons 1980) and produce excrement consisting of about 88% fibrous pellets and 12% soft caecal droppings (Moss & Parkinson 1972). Piles of the fibrous pellets are left where a bird roosts, whether overnight or during the day (Savory 1978).

Study areas

We conducted this study on four moors, two in northern England (Catterick in North Yorkshire 54°20.9'N-1°50.9'W, and Moorhouse in Cumbria

54°43.8'N-2°27.3'W) and two in northeastern Scotland (Edinglassie 57°12.5'N-3°09.2'W and Glen Dye 56°56.7'N-2°36.4'W). We studied grouse abundance between spring 2002 and spring 2004, in a total of 14 1-km^2 study areas distributed across the four moors (Appendix I).

Counts using dogs

We counted grouse on each 1-km^2 area with the aid of trained dogs (Jenkins et al. 1963, Watson & Miller 1976). Counting red grouse using trained pointer dogs provides consistent, reliable density estimates (Jenkins et al. 1963). These counts have been shown to be repeatable (R. Moss, unpubl. data) and provide estimates of territorial male density in spring similar to those obtained from detailed field studies, in which males are individually colour-tagged, their territories mapped using instances of territorial behaviour and counted within defined areas. Because it is the most reliable, this method is routinely used by grouse managers and scientists alike (e.g. Hudson & Newborn 1995, Mougeot et al. 2003a,b).

During counts, a trained and experienced observer and a pointer dog walked six regularly spaced transects across the area, ensuring that all the ground was covered by the dog. While the observer walks along the transect lines, the dog quarters the ground, running at right angles to the line crossing back and forth over the observer's transect line. The observer ensures that the dog covers all the ground in between transects, and takes it to ground that was not checked, when necessary. Dogs locate birds by scent, and as they use scent carried on the wind, they do not need to run directly over each bird to locate it. In order to facilitate scent detection and avoid double counting, transect lines were arranged at an angle to the dominant wind direction, such that flushed birds would move outside the count area or into areas that had already been covered. The observer always tried to check if birds that were flushed came back onto ground that had not been counted yet. Recording where flushed birds landed on a map of the counted area helped avoid double counting. As each bird or group of birds was found and flushed, their sex (on the basis of call, plumage and wattle size; Cramp & Simmons 1980) and number were recorded. We counted areas with the aid of dogs in spring (late March - late April) 2002, 2003 and 2004, and in summer (early August) 2002. Counts lasted approximately 3-4 hours each and were conducted in good weather (avoiding rain, hot days and strong winds). Grouse densities in the study areas, measured using this method, ranged within 23-220 birds per km^2 (see Appendix I).

Playback counts

Each playback count consisted of playbacks at nine points evenly distributed across a 1-km^2 plot, and always at least 100 m inside the plot boundary. At each point, we played a male territorial call (flight call plus ground call), once in each of the four cardinal directions, using a portable tape player (Matsui RTR 203). The playback of each of the four calls lasted ca five seconds, and the speaker volume was set to match that of a calling male. Following the playback, we scanned the surrounding area with binoculars for five minutes and recorded males that responded by calling or showing within a 100-m radius of the survey point. We also included males flushed by the observer on approach to and within 100 m of the playback point, if they were not contacted during the playback itself. For each playback, we scored the weather conditions wind (none, light or moderate) and cloud cover (clear, patchy or overcast). Counts were not conducted during rain or strong winds. Playbacks were conducted in the morning (8:00-12:00) or in the afternoon (15:00-18:30). We did playback counts on nine 1-km^2 plots between late April and early May 2002.

Dropping counts

Each count consisted of an observer walking two 1-km transects across a 1/km^2 area. Start points were randomly selected and transects were at least 200 m apart. We counted 'roost piles' encountered within a metre on either side of each transect line (see Nyström et al. 2005). Roost piles were defined as groups of five or more fibrous pellets. Single or scattered droppings were excluded. Piles were classified as either 'fresh' or 'old', on the basis of colour, texture and desiccation. We categorised dropping as 'fresh' when they were dark green with a white tip and as 'old' when they lacked the white tip and their colour had turned to brown. Fresh droppings were most likely $<$ 1 month old. We did a total of 22 dropping counts on 13 1-km^2 areas; 18 in spring 2002, 2003 and 2004, and four in summer 2002.

Statistical analyses

We used SAS 8.0 (SAS 2001) for statistical analyses. We used Generalised Linear Models (GLM) for all analyses. These models are like general linear models, but allow non-normally distributed variables, such as count data, to be fitted to models and regression on these variables to be performed. Dependent variables (counts of grouse or roost piles) were fitted to GLMs using the Poisson error distribution with a log link function. Counts of males responding to playback were underdispersed so, whenever a count of responding males was the dependent variable, the dispersion parameter was estimated. In all other cases (including dropping counts), the response variable was overdispersed, and the dispersion parameter was fixed at 1. All tests were two-tailed. R^2 equivalents were calculated as the percentage of deviance explained by the model.

Results

Playback counts

We first examined variation in the number of males detected per playback point within areas (nine points per area) and between areas (nine areas). The number of males detected per playback point differed significantly between areas (GLM: F = 19.14, df = 8, P < 0.001), but not within areas (GLM: playback point nested within area: F = 0.05, df = 71, P = 0.99).

We then examined the relationship between the mean number of males detected per playback point and grouse density in an area. The mean number of males per point explained 92% of variation in the number of males measured by counts with dogs (GLM: $F_{1,7} = 107.68$, P < 0.001; Fig. 1A, Table 1), 94% of variation in the total number of grouse (GLM: $F_{1,7} = 241.86$, P < 0.001; see Fig. 1B and Table 1) and 92% of variation in the number of females (GLM: $F_{1,7} = 136.56$, P < 0.001; see Table 1).

Finally, we tested whether time of day or weather conditions affected the number of males detected per playback point, controlling for measured male density (from counts using dogs). The number of males per point was not significantly explained by time of day (GLM: morning vs afternoon: $F_{1,77}$ = 0.98, P = 0.324) or wind strength (GLM: $F_{2,76}$ = 0.55, P = 0.577), but was significantly explained by cloud cover (GLM: $F_{2,76} = 5.48$, P < 0.01). In clear weather conditions, fewer males were detected per

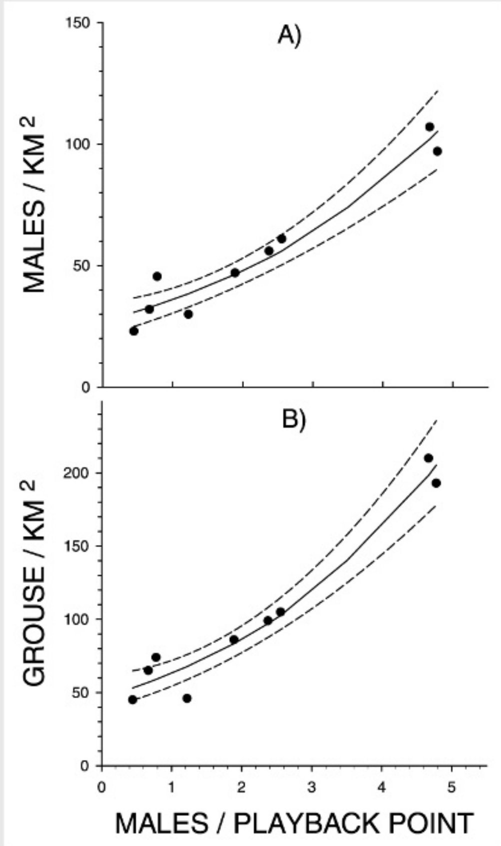

Figure 1. Relationships between the mean number of males detected per playback point and the number of male grouse (A) and the total number of grouse (B), measured by counting with dogs on 1-km^2 study plots. Dashed lines show the 95% confidence limits of the regression equation.

Table 1. Regression equations for predicting A) the total number of grouse (TG), the number of male grouse (MG) and the number of female grouse (FG) counted with dogs from the mean number of males detected per playback point (MPP); and B) total grouse density as measured using dogs (TG) from the mean total number of roost piles along two transects (TRP), the mean number of fresh piles (FRP) and the mean number of old piles (ORP). Figures given in the R^2 column are the proportion of deviance explained by the model, i.e. an R^2 equivalent.

	Response (y)	Predictor (x)	Regression equation (± standard error)	R^2	F	P	N
A)	TG	MPP	$Log_e(y) = 3.834 (\pm0.068) + 0.312 (\pm0.020)x$	0.94	241.86	<0.001	9
	MG	MPP	$Log_e(y) = 3.301 (\pm0.090) + 0.284 (\pm0.027)x$	0.92	107.68	<0.001	9
	FG	MPP	$Log_e(y) = 2.957 (\pm0.103) + 0.345 (\pm0.030)x$	0.92	136.56	<0.001	9
B)	TG	TRP	$Log_e(y) = 2.098 (\pm0.108) + 0.614 (\pm0.026)Log_e(x)$	0.79	539.86	<0.001	22
	TG	FRP	$Log_e(y) = 3.459 (\pm0.057) + 0.464 (\pm0.022)Log_e(x)$	0.66	442.16	<0.001	21
	TG	ORP	$Log_e(y) = 2.241 (\pm0.104) + 0.610 (\pm0.026)Log_e(x)$	0.77	512.18	<0.001	21

playback point than was expected from measured male density.

Dropping counts

We first examined variation in the number of roost piles per transect within areas (two transects per area) and between areas (22 areas). The total (fresh + old) number of piles differed significantly between areas (GLM: F = 89.30, df = 21, $P < 0.001$), but not within areas (GLM: transect nested within area: F = 4.25, df = 22, P = 0.99). The number of fresh piles also differed significantly between areas (GLM: F = 28.12, df = 20, $P < 0.001$), but not within (GLM: F = 2.00, df = 21, P = 0.99). Similarly, the number of old piles differed significantly between areas (GLM: F = 71.03, df = 20, $P < 0.001$), but not within (GLM: F = 4.57, df = 21, P = 0.99).

Second, we examined the relationship between the mean number of piles along the two transects and grouse density. Variation in the number of grouse measured by counts using dogs was significantly explained by the mean number of roost piles along two transects (GLM: $F_{1,20} = 539.86$, $R^2 = 0.79$, $P < 0.001$; Fig. 2, see Table 1), the mean number of fresh piles (GLM: $F_{1,19} = 442.16$, $R^2 = 0.66$, $P < 0.001$; see Table 1), and the mean number of old piles (GLM: $F_{1,19} = 512.18$, $R^2 = 0.77$, $P < 0.001$; see Table 1).

Discussion

Playback counts

The number of males detected per playback point varied significantly more between areas of differing density than within areas. Furthermore, density estimates from dog counts could be predicted from the mean number of males responding to playbacks in a given area. These results suggest that playback counts provide an alternative method to estimate red grouse density. Confidence intervals using an average playback count for a given area were small enough to make this method useful for predicting density (see Fig. 1). For instance, an average count of two males per playback gives an estimated density of 86 (77-95) grouse/km^2, and an average count of four males per playback gives an estimated density of 165 (144-186) grouse/km^2. Further work would be required to assess the method's repeatability, as well as its effectiveness at very low densities, which were not represented in our study. Nevertheless, it performed well across a range of densities that are commonly found in red grouse. At low densities, males are more likely to remain silent and undetected (Watson & Jenkins 1964, Hudson 1992), and the true population density might therefore be underestimated by a call-count survey, but birds might still respond well to a playback call in these situations. We detected a playback

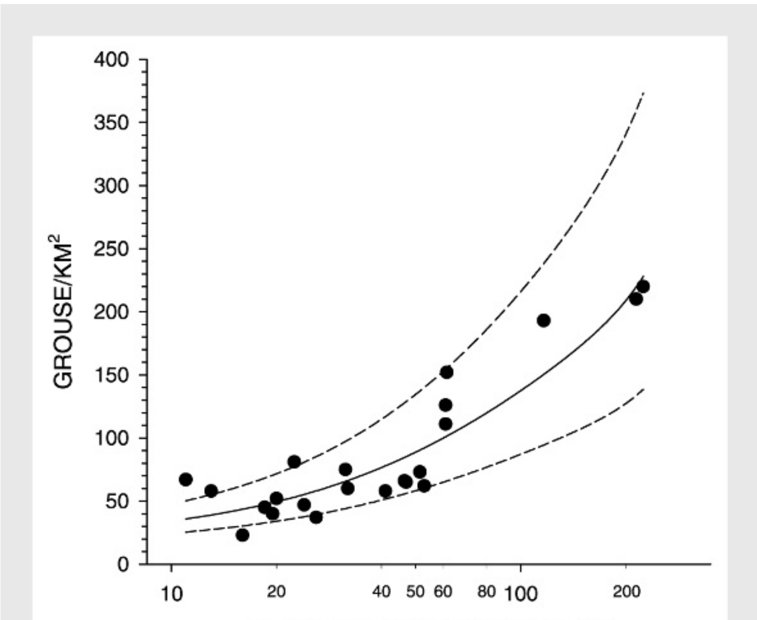

Figure 2. Relationship between the mean number of roost piles (natural logarithm) per 1-km transect and the number of grouse counted with dogs in the same 1-km^2 area. Dashed lines show the 95% confidence limits of the regression equation.

response at all our study areas, but would recommend caution in applying our regression equations (see Table 1) outside the range of grouse densities presented here (45-210 birds/km^2).

Counting male calls during the breeding season is widely used to determine the presence or abundance of game birds (e.g. Smith & Gallizioli 1965, Brown et al. 1978, Keppie 1992, Rice 2003). Some studies have used playbacks or imitation to stimulate responses (Marion et al. 1981, Schroeder & Boag 1989, Yue-Hua & Xing-Lu 1993), a common technique for other elusive bird groups (e.g. Ratcliffe et al. 1998). However, there are a number of potential biases and limitations in the use of this method. For instance, the intensity of territorial behaviour in grouse varies diurnally, seasonally and annually (Jenkins et al. 1963, Watson & Jenkins 1964, Hudson 1992, Watson et al. 1994). We conducted playbacks in spring, the seasonal peak in territorial behaviour, but the exact timing of the peak is difficult to assess and may vary between years (Jenkins et al. 1963). We avoided the peaks in territorial behaviour around dawn and dusk in order to minimise the effect of diurnal variations, and found no effect of time of day on the response of males to playbacks. Conducting call counts during the early morning peak in activity, as practised by Watson & O'Hare (1979) and recommended by Hansen & Guthery (2001), might improve density estimates. However, it reduces the number of counts that can be done in a day and could be problematic at high densities when numerous males call at the same time. By using playbacks to elicit territorial behaviour, we were able to conduct call counts outside the periods of peak activity and throughout the day, and the responses to these playback calls provided useful estimates of male and total grouse density (see Figure 1).

Several studies have found an impact of environmental variables such as wind, light intensity and temperature on the number of calls detected during counts (e.g. Robel et al. 1969, Little & Crowe 1992, Pierce & Westbrooke 2003). In our study, we found no effect of wind strength on playback counts, possibly because we avoided days with strong wind. We also avoided rain. We did, however, find a significant effect of cloud cover, with fewer males detected on clear days. A possible explanation for this finding is that males reduce their conspicuousness in clear weather conditions in order to reduce predation risk from raptors. Clear days could therefore be avoided to improve playback density estimates.

Playback censuses of red grouse have several potential advantages over counts using dogs. They do not require trained animals, represent less disturbance to the birds, and are relatively quick and cheap to carry out. They can also provide an indication of a population's distribution across an area, but index the territorial male population rather than the total population. This could be an issue in species, or in situations where sex ratios are biased. In red grouse, breeding female density is largely determined by territorial male density (Moss et al. 1996, Mougeot et al. 2003a,b). Accordingly, playback counts not only predicted male density, but also female and total density. Previously, playback call counts have been used during a population level experiment, providing important estimates of male density at a time when access to study sites was not possible with dogs (Mougeot et al. 2003a). This method could therefore provide a useful alternative for grouse moor managers or field biologists wishing to monitor breeding populations.

Dropping counts

Counts of roost piles along transects varied more between than within areas of different density, and mean counts along two transects across a given area predicted total grouse density, measured using counts with dogs. Thus, transect counts of droppings were repeatable, maybe because transects were long enough (1 km) to detect enough piles in each line, and also because the distribution of territorial grouse within the habitat was not too aggregated and the habitat relatively homogenous. Longer transects might be needed at lower density or where grouse are more aggregated, so the method could be adjusted for other situations or species. Longer transects might also allow better predictions. For instance, another study used transects of ca 13 km to estimate density of rock ptarmigan *Lagopus mutus* and willow ptarmigan *L. l. lagopus* in northern Sweden (Nyström et al. 2005). Dropping counts also represent an alternative method to estimate red grouse density. However, confidence intervals for the predictive equations were wider than for playback counts, and the error of density estimates potentially large (see Fig. 2). Separate counts of fresh or old droppings performed equally well (see Table 1), but for ease of survey, comparability between different observers and precision of the density estimate, we would recommend using the total roost piles measure. We detected roost piles even in the lowest density area (23 birds km^{-2}), but further work is required to assess the repeatability of dropping counts and their effectiveness in monitoring population changes over time.

Counts of faecal material are a common means of indirectly assessing the distribution, habitat preferences, movements and population size or density of both birds and mammals (Bennett et al. 1940, Angerbjörn 1983, Klaus 1993, Forys & Humphrey 1997, McCurdy 1997, Timmerman & Buss 1998, Vernes 1999, Fox & Hudson 2001). Fibrous dropping volume has been used previously to assess habitat use in red grouse (Savory 1978, Welch 1982) and also densities of willow and rock ptarmigan (Nyström et al. 2005). In some cases, it is also possible to infer the sex and age (chicks) of the birds that roosted from their droppings (see Nyström et al. 2005), so this method could be used in summer to assess number of young and old grouse, and to evaluate productivity.

Several authors draw attention to potential sources of error associated with counting pellet groups (e.g. Putman 1984). Strip transects, as used in our study, have a high perimeter to area ratio, which can lead to sampling bias when observers must decide whether to include marginal pellets (Harkonen & Heikkila 1999, Krebs 1999). This factor is likely to be particularly important in low density populations, where inappropriate inclusion or exclusion of even a small number of droppings may substantially affect the population estimate (Murray et al. 2002). Red grouse fibrous droppings remain intact for many months (Savory 1978), but decay rate variation in relation to habitat characteristics or environmental factors (weather) has not been investigated. This might have contributed to a relatively poor ability to predict density (i.e. large confidence intervals; see Fig. 2).

Dropping counts nevertheless have a number of advantages over counts using dogs. They do not require trained animals or particularly skilled observers, involve minimal disturbance, and can be performed more rapidly (in an hour or less), at any time of day, in a broader range of weather conditions. They also have the potential to incorporate diverse species in one survey (e.g. Jachmann 1991, Lindström et al. 1994, Nyström et al. 2005) and involve an inert form of evidence that can be subjected to field-plot sampling and statistical analysis (Neff 1968). Furthermore, dropping counts reflect average abundance over a period of time, whereas both dog and playback counts yield a potentially misleading estimate of abundance for a single day (Marques et al. 2001). However, dropping counts cannot distinguish between territorial and non-territorial birds and do not provide detailed information regarding the distribution, sex and age of individuals within the population. Dropping counts represent a very simple and cost-effective alternative means of measuring overall density, even though they provide relatively crude estimates. They therefore have potential applications in situations where disturbance is an issue, resources are limiting or where frequent estimates of abundance over broad areas are required.

We have evaluated two alternative methods and highlighted potential applications and advantages in providing indices of red grouse population density. Our results showed that playback counts could provide a useful alternative means of evaluating grouse density, whereas dropping counts provided less useful density predictions.

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Appendix I.

Sampling design and density range on the moors Catterick (CA), Edinglassie (EG), Glen Dye (GD) and Moorhouse (MH) in England (E) and Scotland (S) during 2002-2004.

Country	Moor	Area	Year	Density (grouse.km^{-2})	Dropping transect counts	Playback counts
E	CA	CA1	2002	81	1	
E	CA	CA1	2003	58	1	
E	CA	CA2	2002	152	1	
E	CA	CA2	2003	58	1	
E	CA	CA3	2002	126	1	
E	CA	CA3	2003	52	1	
E	CA	CA4	2003	60	1	
S	EG	EG1	2002	99		1
S	EG	EG1	2003	73	1	
S	EG	EG2	2002	105		1
S	EG	EG2	2004	62	1	
S	EG	EG3	2002	46		1
S	GD	GD1	2002	74		1
S	GD	GD1	2003	45	1	
S	GD	GD2	2002	45		1
S	GD	GD2	2003	47	1	
S	GD	GD3	2002	86		1
S	GD	GD3	2003	67	1	
E	MH	MH1	2002	193	1	1
E	MH	MH1	2003	40	1	
E	MH	MH1	2004	66	1	
E	MH	MH2	2002	210	1	1
E	MH	MH2	2003	75	1	
E	MH	MH2	2004	111	1	
E	MH	MH3	2002	65	1	1
E	MH	MH3	2003	23	1	
E	MH	MH4	2002	220	1	
E	MH	MH4	2003	37	1	