

Factors affecting unintentional harvesting selectivity in a monomorphic species

Nils Bunnefeld^{1*}, David Baines², David Newborn³ and E. J. Milner-Gulland^{1,4}

¹Department of Life Sciences, Imperial College London, Silwood Park, Ascot SL5 7PY, UK; ²The Game and Wildlife Conservation Trust, The Gillett, Forest-in-Teesdale, Barnard Castle DL12 0HA, UK; ³The Game and Wildlife Conservation Trust, Swale Farm, Satron, Gunnerside, Richmond DL11 6JW, UK; and ⁴Centre for Population Biology, Imperial College London, Silwood Park, Ascot SL5 7PY, UK

Summary

1. Changes in the abundance of populations have always perplexed ecologists but long-term studies are revealing new insights into population dynamic processes. Long-term data are often derived from harvest records although many wild populations face high harvesting pressures leading to overharvesting and extinction. Additionally, harvest records used to describe population processes such as fluctuations in abundance and reproductive success often assume a random off-take.

2. Selective harvesting based on phenotypic characteristics occurs in many species (e.g. trophy hunting, fisheries) and has important implications for population dynamics, conservation and management.

3. In species with no marked morphological differences between the age and sex classes, such as the red grouse *Lagopus lagopus scoticus* during the shooting season, hunters cannot consciously select for a specific sex or age class during the shooting process but harvest records could still give a biased reflection of the population structure because of differences in behaviour between age and sex classes.

4. This study compared age and sex ratios in the bag with those in the population before shooting for red grouse at different points in the shooting season and different densities, which has rarely been tested before.

5. More young than old grouse were shot at large bag sizes and vice versa for small bag sizes than would be expected from the population composition before shooting. The susceptibility of old males to shooting compared to females increased with bag size and was high at the first time the area was shot but decreased with the number of times an area was harvested.

6. These findings stress that the assumption made in many studies that harvest records reflect the age and sex ratio of the population and therefore reflect productivity can be misleading.

7. In this paper, as in the literature, it is also shown that number of grouse shot reflects grouse density and therefore that hunting selectivity might influence population dynamics in a cyclic species.

8. The study is not only relevant for red grouse but applies to systems showing interactions between selective harvesting and wider ecological processes, such as age- and sex-related parasitism and territoriality, which may drive population fluctuations.

Key-words: age-ratio, hunting susceptibility, population fluctuations, red grouse *Lagopus lagopus scoticus*, sex ratio

Introduction

Population fluctuations of animals are explained through a combination of intrinsic and extrinsic mechanisms such as the demography of the population and stochastic environmental

effects (Leirs *et al.* 1997; Coulson *et al.* 2001). Long-term population studies are often based on data from harvested populations, for example Canada lynx (*Lynx canadensis*, Kendall, Prendergast & Bjørnstad 1998; Stenseth *et al.* 1999). Harvesting is often assumed to be random, simply another source of mortality which can reduce population size. However, including the effect of harvesting in studies of population dynamics is

*Correspondence author. E-mail: nils.bunnefeld@vfm.slu.se

important if we are to understand population dynamics of exploited species, as harvesting can perturb dynamics and create population fluctuations (Jonzén, Ripa & Lundberg 2002; Jonzén *et al.* 2003; Cameron & Benton 2004). Furthermore, many populations currently face high anthropogenic off-takes leading to overharvesting and extinction (IUCN Red List 2007). Therefore including harvesting in ecological studies can foster new insight into population dynamics and can help in the management of exploited populations (Lande, Saether & Engen 1997, 2003).

Hunting often purposely targets a specific age, sex or size class (e.g. in trophy hunting, fisheries). Evidence for the short and long term effects of this practice on the phenotype and life-history of vertebrates (Coltman *et al.* 2003; Hutchings 2005; Garel *et al.* 2007), and on the demographic structure, and therefore on the growth rate, of a population can be significant (Ginsberg & Milner-Gulland 1994; Cameron & Benton 2004; Hutchings 2005; Milner, Nilsen & Andreassen 2007). Most studies on hunting selectivity compare different hunting strategies (Martinez *et al.* 2005; Mysterud, Tryjanowski & Panek 2006) or harvested and nonharvested areas (Coltman *et al.* 2003); they do not, however, compare the age and sex structure of the bag with the population before harvesting to assess susceptibility to shooting according to age, sex and density.

While the effects of selective harvesting in trophy hunting and fisheries are relatively well studied (reviews in Festa-Bianchet 2003; Coltman 2008; Hutchings & Fraser 2008), in monomorphic species it is often assumed that shooting is unselective, as hunters cannot consciously select during shooting. However, in the monomorphic Canada goose (*Branta canadensis*), young of the year are more vulnerable to harvesting than older individuals (Chapman, Henny & Wight 1969; Grieb 1970; Mowbray *et al.* 2002). Hörnell-Willebrand *et al.* (2006) and Hudson (1985, 1986) addressed unintentional harvesting selectivity in two monomorphic grouse species, the willow grouse *Lagopus lagopus* (Linnaeus, 1758) and the red grouse *L. lagopus scoticus* (Latham, 1787), respectively. Adults of both sexes and adult males were over-represented in the bag when compared with counts before the hunting season respectively. The willow grouse study made the assumption that the population consisted of equal numbers of males and females and both studies did not link selectivity to any other covariates important for the study of population dynamics and management, e.g. density or timing of the season.

Red grouse populations in the UK typically fluctuate in a cyclic manner (Haydon *et al.* 2002) but it is not yet clear what drives these cycles (Redpath *et al.* 2006). Therefore studying harvesting might reveal new ideas and hypotheses to be included in the study of population dynamics. The territorial behaviour of red grouse is well studied and it has been demonstrated that old males begin to establish territories coincident with the onset of the shooting season (Jenkins, Watson & Miller 1967). Aggressiveness and territorial activity increase with population density (Moss, Watson & Parr 1996). It is also well known that old grouse carry more parasites than young

grouse (Hudson, Newborn & Dobson 1992; Mougéot, Evans & Redpath 2005a) and that parasites reduce mobility, although this has only been demonstrated in willow grouse (Holmstad, Jensen & Skorpung 2006).

At high grouse densities, we predict that during driven shooting, old males will return to their territories rather than flying over the line of hunters. This is due to territoriality or high parasite load, both as consequences of increased density and of aggressiveness. In contrast, we expect that young grouse are more likely to cross the line of hunters at high grouse densities because they have not been able to secure a territory and do not suffer from high parasite loads (reduced mobility). Therefore, we predict that with increasing grouse numbers more young grouse are shot than expected from the counts. Conversely, old males escape being shot by returning to their territories before they reach the line of hunters. We also expect that shooting selectivity will become more biased towards females later in the season when males have invested heavily in territorial behaviour and may be more reluctant to leave their territory.

In this study, we test the above predictions by comparing the age–sex ratios of birds shot at different times during the season and at different densities, with the population composition estimated from counts made just before shooting. We analysed data on grouse shooting using hierarchical mixed effects models to be able to decompose the total variation of the data into different spatial scales (Börger *et al.* 2006a,b; Sims *et al.* 2006). Using this method, we investigate the effect of management units (moors and drives within moors) on harvesting selectivity and the correlation of number of grouse shot and grouse density.

Materials and methods

DATA COLLECTION

Data on shooting selectivity were collected in 2005 and 2006 between mid-August and the end of September on eight moors in Northern England. All data come from driven grouse shooting days where beaters drive (flush into flight) grouse in the direction of a line of stationary hunters. These are situated in stone or turf butts that offer concealment and shelter for the hunters. A day of grouse shooting usually consists of four to five separate shooting locations (drives) and the data presented here reflect drives rather than shooting days. An individual drive is usually shot several times during the season, at intervals ranging from a few hours to several weeks. For a more detailed description on shooting grouse in England see Hudson (1986) and Richards (2004).

Forty-three drives were attended, and the total number of grouse shot, broken down by age and sex, was determined for each drive (Table 1). The length and the area of the drive were calculated using GIS (MapInfo Professional v8.0, MapInfo Corporation, New York, USA). This was based on the estimated drive area drawn on a map by the head keeper of the estate, who organized the drive and located the beaters. Drive area was consistent for particular drives on different days and in both years because it is mainly determined by landscape features (e.g. rivers, valleys). The number of beaters involved in each drive was also noted.

To compare the age and sex ratios of shot birds with the age and sex ratio of the population before shooting, counts were conducted

Table 1. The nested structure of the data is shown: sample size (n = number of shooting events) is broken down by moors, drives within moors and the year when the data were collected. The area covered by the beaters and the length of the drive (distance between the start location of the beaters and the line of hunters) is given in square kilometre and kilometres respectively. Area and length are given as mean (range) for all drives sampled on the specific moor. Drives can be shot more than once a year and therefore the number of drives is not equal to the sum of the number of shooting events in both years

Moor	Drives	2005 (n)	2006 (n)	Area (km ²)	Length (km)
1	2	–	2	1.0 (0.8–1.1)	1.1 (1.0–1.3)
2	2	2	–	1.3 (0.8–1.8)	1.5 (1.1–1.9)
3	3	–	3	2.6 (1.4–3.9)	1.9 (1.3–2.3)
4	1	2	1	2.1 (1.7–3.1)	2.0 (1.4–2.8)
5	2	–	5	1.1 (1.0–1.2)	1.0 (0.96–1.2)
6	5	–	11	1.5 (1.2–2.9)	1.8 (1.3–2.8)
7	7	9	–	1.7 (0.6–2.3)	1.8 (1.0–2.2)
8	2	2	6	1.5 (1.4–1.7)	1.5 (1.48–1.53)
Total	24	15	28	1.6 (0.6–3.6)	1.6 (0.96–2.8)

in July 2005 and 2006 in the same areas where shooting data were collected. For all 43 drives visited during the shooting season, the age structure was known but only for 33 drives the sex ratio of the old birds was available. The sex ratio was only determined for old grouse because of the difficulty of sexing young grouse during counts in July. The counts were part of the long term data collection conducted by the Game and Wildlife Conservation Trust to determine the ratio of old birds to young of the year and the sex ratio of the old birds (Hudson & Newborn 1995). For a subset of 30 drives, grouse density was estimated using standard methods of 1 km² block counts (Jenkins, Watson & Miller 1963; Mougéot *et al.* 2005b; Redpath *et al.* 2006) and distance sampling (Buckland *et al.* 1993). The harvest rate (number of grouse shot divided by the number of grouse counted on the same drive) was calculated for the first shooting event only because not all areas that were visited at the second and third/fourth shooting event were also visited at all previous shooting events. Thus the cumulative off-take was not known for later shooting events. This resulted in a sample size of 13 drives for the calculation of harvest rates.

STATISTICAL ANALYSIS

All analysis was carried out using the statistical package R (R Development Core Team 2007). A mixed effects model approach was chosen in preference to a residual analysis because the residual analysis often leads to biased parameter estimates (Darlington & Smulders 2001; Freckleton 2002). Separate linear mixed effects models (lme, package nlme ver. 3.1–79, Pinheiro & Bates 2000) were fitted to the response variables 'number of grouse shot per square kilometre in a single shooting event', 'harvest rate', 'relative young-to-old ratio' and 'relative sex-ratio of old birds'. The number of grouse shot per square kilometre is also called 'bag size' and was determined as all grouse shot from a single drive rather than from the whole day of shooting. To obtain the relative ratios, the sex and age ratio of the bag was divided by the sex and age ratio of the July count. The July counts and bag data derive from the same areas. The number of grouse shot, number of grouse counted and the relative age and sex

ratios were log transformed. The harvest rate was arcsine transformed (Crawley 2007). The models were fitted with a constant intercept and nested random terms. Data were collected over two years (2005 and 2006) but only two moors were nested in both years (Table 1), therefore moor and drive within moor were inserted as random effects but year was not included in the random effects.

The explanatory variables for the number of grouse shot per square kilometre, the relative age ratio and relative sex ratio were the number of beaters per square kilometre, the length of the drive the beaters covered by walking from the start of the drive to the line where the hunters were located, the total number of grouse shot in a single shooting event per square kilometre area covered, the date of the shooting event and a code indicating whether the data came from the first, second or the third/fourth shooting event (the third and fourth events were pooled together because of small sample sizes).

Grouse shooting usually is organized for a team of an average of 8.4 (range 6–12) hunters (Hudson 1986). The number of hunters was not expected to influence the study as the variation in the number of hunters was small in the current study (average 8.5, range: 6–10 hunters) and preliminary analysis showed no effect of number of hunters on the response variable. The harvest rate was fitted with the number of grouse counted per square kilometre in July as explanatory variable.

The area of the drive was correlated with the length of the drive. The significance of correlated parameters depends on the order in which they are added to the model (Whittingham *et al.* 2006) and therefore area was not included as an additional variable in the analysis. Wald tests were used to test the significance of fixed effects (Pinheiro & Bates 2000). Significance tests of the fixed effects were limited to two-way interactions to avoid overfitted models; only significant interactions are mentioned in the results section. Orthogonal contrasts were designed to compare first, second and third category of shooting event.

As suggested by Whittingham *et al.* (2006), models with different hypotheses are compared using Akaike information criterion (AIC) instead of stepwise model selection procedures. Selecting a single best model for inference based on stepwise model selection increases the risk of neglecting possible alternative hypotheses. In line with Burnham & Anderson (2002), the authors point out that models that are equally or similarly well suited to explain the variation in the response variable should be compared in their entirety and communicated as possible explanation for the observed pattern.

The model structure, nesting drive within moor, and analysing each shooting event separately within drive, enables us to correctly represent the non-independent nature of shooting events. High and low densities coincide with low sample sizes and hence there is more error associated with these extremes. Mixed effects models were assessed with a range of graphical and formal methods to identify outliers (Pinheiro & Bates 2000). The mixed effects models were run without outliers but the same results were obtained as with the full data set.

So far studies on red grouse harvesting have been conducted at the scale of the entire moor (Hudson, Dobson & Newborn 1998). However, moors comprise large areas (20–50 km²) which are subdivided into smaller areas (drives: 1–3 km²), both by gamekeepers and for shooting (Hudson 1992). A variance components analysis of the final mixed effects models described above was carried out (Pinheiro & Bates 2000; Crawley 2007) in order to estimate the variation explained by the nesting factors moor and drive within moor. The analysis was carried out with both the significant fixed effects and random effects inserted and in a second analysis the variance components were estimated with only the random effects but

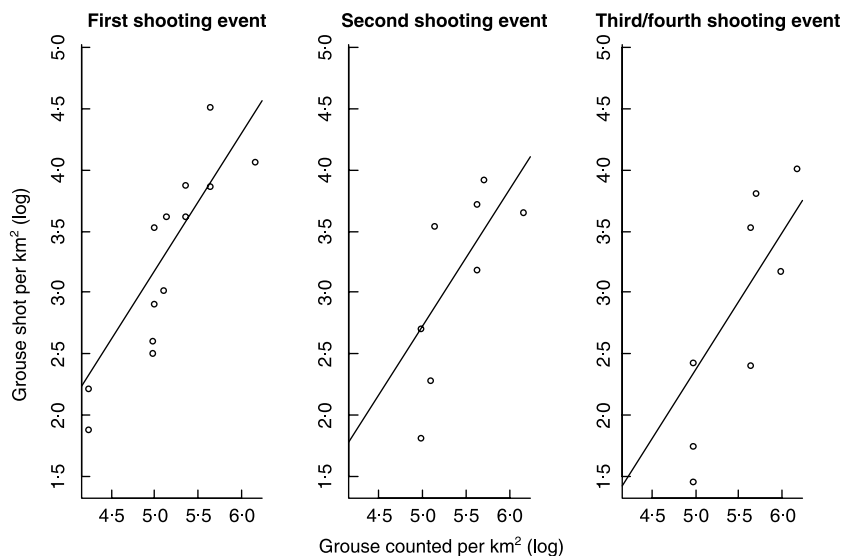


Fig. 1. The relationship between the estimated number of grouse per square kilometre counted in July and the number of grouse shot per square kilometre in a single drive for the first, second and third/fourth shooting event. The slope is the same for shooting events one, two and three/four, but the intercept is significantly lower in the second shooting event compared to the first one and the third/fourth lower than the second one (Table 2).

Table 2. Fixed effects of the mixed effects model for number of grouse shot per square kilometre (log-transformed) with drive nested within moor. The total number of grouse shot per square kilometre is explained by the shooting event (three levels) and the number of grouse counted per square kilometre in July before the shooting season. Orthogonal contrasts were built to compare first and second and second and third/fourth shooting event

Fixed effects	Estimate	SE	<i>t</i> -value (d.f. = 15)	<i>P</i> value
Intercept	-2.85	1.30	-2.19	0.045
First-second shooting event	0.43	0.11	3.97	0.001
Second-third/fourth shooting event	0.40	0.11	3.51	0.003
July count (log)	1.12	0.24	4.66	< 0.001

without fixed effects. Variance components analysis is a useful tool to decompose the total variation into different spatial scales (Börger *et al.* 2006a,b; Sims *et al.* 2006).

Results

CORRELATION OF BAG NUMBERS WITH POPULATION SIZE

The number of grouse shot per square kilometre in a single drive was positively correlated with the grouse counted per square kilometre in July (Fig. 1). The intercept depended on the shooting event, with the second shooting event having fewer grouse in the bag compared to the counts than the first shooting event and the third/fourth shooting fewer grouse than the second shooting event (Table 2). The number of beaters per square kilometre ($F_{1,11} = 3.2$, $P = 0.1$) and the length of the drive ($F_{1,11} = 0.1$, $P = 0.7$) during the shooting had no significant effect on the number of grouse shot (km^{-2}) on a single shooting event. There was no significant interaction between July counts and shooting event ($F_{1,11} = 0.5$, $P = 0.6$), which suggests that bag data provide a consistent estimate of density over the shooting season. The model including July density and shooting event as explanatory variables explained with 86% a high proportion of the variation of the number of grouse shot (km^{-2}) on a single shooting event (drive).

The harvest rate for the first shooting event was 0.16 (range 0.08–0.32). There was no effect of the number of grouse counted per square kilometre on the harvest rate at the first shooting event ($t = 1.8$, d.f. = 2, $P = 0.2$), indicating that harvest rate at a single shooting event does not depend on the number of grouse counted.

AGE RATIO

The relative age ratio increased with the number of grouse shot km^{-2} per shooting event ($t = 2.1$, d.f. = 20, $P = 0.045$), so with increasing numbers of grouse shot, relatively more young grouse were found in the bag (Fig. 2). There was no influence of shooting event ($F_{2,15} = 0.1$, $P = 0.9$), the number of beaters per square kilometre ($F_{1,15} = 0.004$, $P = 0.9$), the length of the drive ($F_{1,15} = 1.42$, $P = 0.3$) or the date ($F_{1,15} = 1.71$, $P = 0.2$) on the relative age ratio. The final model explained 27% of the variation.

SEX RATIO

The number of beaters per square kilometre ($F_{1,10} = 1.3$, $P = 0.3$), the length of the drive ($F_{1,10} = 1.8$, $P = 0.2$) and the date ($F_{1,10} = 0.002$, $P = 0.9$) had no significant effect on the relative sex ratio. Old females showed a decreasing susceptibility to shooting with increasing bag size ($t = -2.5$,

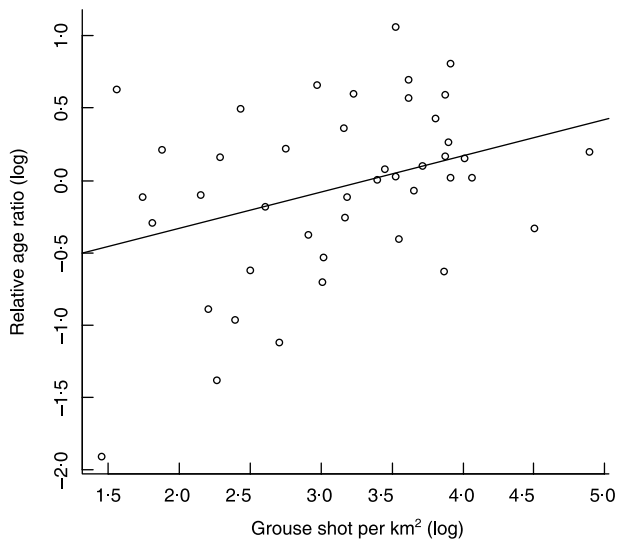


Fig. 2. The young-to-old ratio of the bag divided by the young-to-old ratio of the July count (log transformed) for the number of grouse shot km^{-2} . A log bag/count ratio > 0 for young/old means a higher proportion of young birds were shot than occurred in the population before shooting. The regression line was predicted from a mixed effect model.

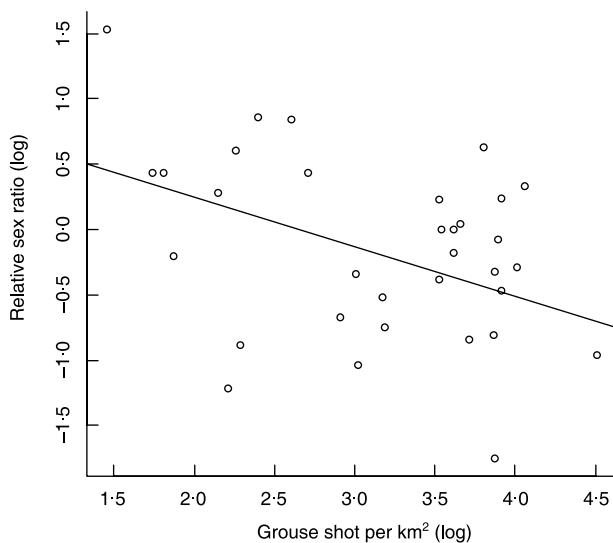


Fig. 3. The female-to-male ratio of the bag divided by the female-to-male ratio of the July count (log transformed) for different number of grouse shot per square kilometre. Only old birds were included in the sex ratio analysis because of the difficulty of sexing young grouse during counts in July. A log bag/count ratio > 0 for females/males means a higher proportion of females were shot than occurred in the population before shooting. The regression line was predicted from a mixed effect model.

d.f. = 15, $P = 0.02$; Fig. 3). A competing model substituting bag size with the number of shooting events showed that relatively more females were shot the third/fourth time an area was shot than at the first time ($t = 2.4$, d.f. = 14, $P = 0.03$). The log-transformed estimates (standard error)

Table 3. The percentage of total variance explained by the nesting factors moor and drive within moor for models with response variable total number of grouse shot per square kilometre (bag), relative age ratio (age) and relative sex ratio (sex). Model A contains only random effects, model B also fixed effects. For the sex ratio model one model with shooting event and a second one with bag size as explanatory variable is given in brackets

	Variance components (percentage)					
	Moor		Drive/moor		Residual variance	
	A	B	A	B	A	B
Bag	28	9	16	37	56	54
Age	23	12	5	—	72	88
Sex	—	— (—)	37	29 (42)	63	71 (58)

for the relative sex ratio from the mixed effect model for the first, second and third/fourth shooting event were -0.31 (0.16), -0.18 (0.22) and 0.33 (0.25) respectively. The final model with shooting event added explained 60% and with bag size added explained 69% of the variation of the relative sex ratio in the bag. The model with bag size as explanatory variable had a lower AIC (AIC = 73.7) than the shooting event model (AIC = 75.9).

VARIANCE COMPONENTS ANALYSIS

In the model explaining the number of grouse shot by the number of grouse counted, differences between moors explained between 28% (no fixed effects) and 9% (fixed effects added) of the total variance, whereas drive within moor explained between 16% (no fixed effects) and 37% (fixed effects added) of the total variance (Table 3, Model A for no fixed effects, Model B for fixed effects added).

In the analysis of relative age ratio as response variable both random effects (moor and drive) were less important; they only explained 23% and 5% of the variance respectively when no fixed effects were added (Table 3, Model A). With the number of grouse shot inserted as fixed effect, moor (12%) explained little of the variance and drive no measurable proportion in the relative age ratio (Table 3, Model B).

For the analysis of relative sex ratio, the random effect of moor had no measurable effect on the variance component and drive within moor explained 37% when no fixed effects were included in the model (Table 3, Model A). Adding the shooting event to the model as fixed effect changed the variation explained to 29% whereas adding the bag size changed the variation explained to 42% (Table 3, Model B).

Discussion

In this study, we predicted that with increasing grouse numbers more young grouse are shot than expected from the counts. We have been able to show that susceptibility of young grouse to shooting increased with bag size, which is in agreement

with our first hypothesis. At low bag numbers the relative young-old ratio was below zero indicating that more old grouse were shot than expected from the counts before shooting (Fig. 2). We found support for our second hypothesis that old males were more susceptible to shooting at early shooting events. We also showed that old males relative to old females increased in their susceptibility to shooting with bag size (Fig. 3).

Males fly over the line of hunters as singletons while females tend to fly in family groups and single birds are more likely to be shot (Hudson 1986). Old males establish territories earlier than young of the year that are still organized in family groups (Hudson 1986) and this might be more pronounced at high densities when aggressiveness and territorial behaviour is high (Moss *et al.* 1996). In addition, in low density years, red grouse nests hatch later (Jenkins *et al.* 1967) and thus young of the year have less flight ability at the start of the shooting season and are less likely to reach the line of hunters because of the exhausting effect of flying long distances. This might explain the finding that old birds are less likely to be shot at high densities (Fig. 2). High off-takes of old males and increased territorial behaviour might explain the low proportion of old males and the higher proportion of females in the bag later in the shooting season. There was no direct effect of date on the susceptibility of shooting of different age- and sex-classes, but the first shooting event was always before the second and that before the third/fourth, so there might be an interaction of timing of the season and shooting per se that affects the behaviour of red grouse during shooting. When males pass the line of hunters, they do so as singletons and are therefore more susceptible to shooting than old females particularly at high density when territorial behaviour is likely to be more important (Fig. 3). Detailed observations of marked animals during the shooting events are required to clarify behavioural mechanisms behind the observed results.

It could be hypothesized that the age composition of the bag would not be expected to reflect the composition of the population at the July count due to differential mortality rates of young and old grouse or of males and females within the old age class between the time of counting and the shooting season. However, the time period between counts (throughout July) and data collection (mid-August–end of September) was short and mortality in red grouse during this period has been shown to be low for both young and old birds (Hudson, Newborn & Robertson 1997). Also, Smith & Willebrand (1999) did not find any differences in mortality between male and female willow grouse during the period July until September. Results in this study depend on unbiased July counts of the age- and sex- ratio and density of the population. One could hypothesize that the July counts might be biased and be confounded by similar variables as the bag data. However, the grouse count methodology used in this study has been shown to deliver reliable estimates of the age and sex ratio and the density of the population (Jenkins *et al.* 1963).

This study applied mixed effects models to the data to investigate the effect of variation in spatial scale on the

shooting data. The comparison of count and bag data showed considerable variation at the moor and drive level (Table 3). These results suggest that the management units moor and drive have significant influence on the number of grouse shot per area at a given density. Variation might be added by differences in harvest targets between moors and drives set by gamekeepers and moor owners and by the hunter quality: significantly, more grouse shot at a given density with experienced hunters. Less variation due to moor and drive was found when fitting mixed effects models to the relative age and sex ratio. This indicates that the smallest scale possible (individual drives) was appropriate for the analysis.

Hudson (1985, 1986) studied the harvest rates of red grouse on the scale of the entire moor and found that the off-take was between 20% and 48% at the end of the season and that the harvest rate increased with the number of grouse counted in July. In this study, the harvest rates were calculated to have a mean of 16% (range 8–32%) for the first shooting event. There was no change in harvest rate with the number of grouse counted in July, suggesting that the increase in harvest rate observed in the study by Hudson (1985, 1986) for an entire moor depends on the number of times an area was shot and probably the overall number of areas that are shot.

The ratios of young-to-old and female-to-male birds were collected from counts in the same areas as the shooting took place and this allowed for a direct comparison of the structure of the population with the age and sex ratio of the bag. Cattadori *et al.* (2003) showed that total bag numbers for a whole moor for one season correlate well with actual population numbers estimated by the same counting method used in this study. A comparable trend was also shown in this study but on a smaller scale where the number of grouse shot in a single shooting event (drive) correlated consistently with grouse numbers obtained by counts in the same area before shooting (Fig. 1). Our study further suggests that to study shooting susceptibility, the number of grouse shot per square kilometre on a single drive is a better surrogate than the July density because it reflects density at the actual shooting event. The July density would overestimate density at the current shooting event if a considerable number of grouse were shot earlier in the season.

The ratio of juveniles to adults in the bag is a common and cost-effective method for estimating productivity in a given year. Flanders-Wanner, White & McDaniel (2004) found no trend in age ratio with time in the shooting season in a study on sharp-tailed grouse *Tympanuchus phasianellus jamesi* (Lincoln, 1917) and greater prairie chicken *Tympanuchus cupido pinnatus* (Linnaeus, 1758), which validated the use of the age-ratio method for these species. However, Hörnell-Willebrand *et al.* (2006) showed that this method is not useful for willow grouse in Sweden and Norway, because the proportion of juveniles is generally underestimated in the bag. Considerable variation in the young-to-old estimate has been observed in the same study and the proportion of juveniles seems to be higher in the bag in years with low breeding success. This study on red grouse demonstrates differences in the age-ratio and the adult sex ratio between the count and the bag, the

existence of an interaction with density, and an increase within the shooting season of the ratio of old females in the bag. Therefore, harvest data need to be treated with great caution as a proxy for the underlying population structure. Age and sex ratios obtained from harvest data need to be checked against count data collected before the harvesting season at a range of population densities before considering them as proxies for population productivity.

In a variable environment, detailed knowledge of the population size and structure are important, as uncertainty increases the chance of overexploitation and local extinction. Hauser, Pople & Possingham (2006) showed that in exceptional years (e.g. extreme weather) the monitoring effort to estimate population size has to increase, so that the management strategy can be adjusted appropriately. However, it is not just the effort put into monitoring that is important. The data that are collected determines whether the difference in population size and structure is detected by the monitoring regime. Katzner, Milner-Gulland & Bragin (2007) demonstrate that the predictive power of monitoring for population size and growth depends on the life stage that is monitored. This stresses the importance of monitoring important age and sex classes. For red grouse, the sex of old birds might be crucial to monitor because the overall assumption of equal numbers of males and females in the population might not be valid due to selective shooting as shown in this study and through the acknowledgement of the sex differences in dispersal distances (Warren & Baines 2007). A skewed sex ratio might decrease population size and harvest yield in a monogamous species where equal numbers of females and males are needed to ensure reproduction. Therefore, monitoring adult sex ratio in spring before the start of the breeding season might facilitate a first estimate of the expected number of young of the year and thus of the harvestable population.

The results of this study encourage further speculation and hypotheses regarding the effects of shooting on red grouse population fluctuations. The study showed that at high bag numbers, used as a proxy for population density, young grouse are more susceptible to shooting than old grouse. Consequently, shooting can bias the population structure towards old birds when population density is high. Given that old grouse harbour more parasites (Hudson *et al.* 1992), that parasites are accumulated at high grouse densities and that parasites reduce over winter survival (Hudson *et al.* 1992; Moss *et al.* 1993) and can generate population fluctuations (Hudson *et al.* 1998), shooting might therefore add to population crashes by leaving old, highly parasitized birds in the population at peak density. Thus shooting might be a factor in creating rather than dampening red grouse cycles. Theoretically, in a highly fluctuating species with high off-takes like red grouse, harvesting might be expected to dampen cycles. Support for the dampening effect of harvesting comes from experimental work by Watson *et al.* (1988) and Moss *et al.* (1996) who showed that experimental removal of old males prevented a population decline. In contrast, our study showed that shooting selected for young birds at high density and therefore did not remove old territorial males. Indeed, that harvesting can create cycles

has already been shown in a theoretical study on willow grouse (Jonzén *et al.* 2003) and in an empirical study on moose *Alces alces* (Linnaeus, 1758). The mean age of adult females increased because of the selective harvest of young moose. This led to an increase in productivity, which is closely related to age in moose. The mean age then decreased after years of high recruitment, and so productivity dropped, thus generating cycles (Solberg *et al.* 1999). Selective harvesting for large size can also magnify population fluctuations in fish due to changes in demographic parameters and instability of the population dynamics (Anderson *et al.* 2008). Hudson & Dobson (2001) found that harvesting apparently did not dampen red grouse cycles, and our findings may now provide an explanation for this contrast between theory and empirical data.

Acknowledgements

The authors are grateful to Estate owners for allowing us to work on their land and to the gamekeepers for their cooperation and help during and before the shooting season. Many thanks go to Nicholas Aebischer, Mick Crawley, Tom Ezard, Luca Börger for statistical advice, Tomas Willebrand, Xavier Lambin, Lynsey McInnes and one anonymous reviewer for useful comments on the manuscript. NB was funded by a John Stanley Scholarship and the field work was funded by The Game and Wildlife Conservation Trust.

References

- Anderson, C.N.K., Hsieh, C., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J., May, R.M. & Sugihara, G. (2008) Why fishing magnifies fluctuations in fish abundance. *Nature*, **452**, 835–839.
- Börger, L., Franconi, N., Ferretti, F., Meschi, F., De Michele, G., Gantz, A. & Coulson, T. (2006a) An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *American Naturalist*, **168**, 471–485.
- Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Coulson, T. (2006b) Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, **75**, 1393–1405.
- Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J.L. (1993) *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman & Hall, London.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Cameron, T.C. & Benton, T.G. (2004) Stage-structured harvesting and its effects: an empirical investigation using soil mites. *Journal of Animal Ecology*, **73**, 996–1006.
- Cattadori, I.M., Haydon, D.T., Thirgood, S.J. & Hudson, P.J. (2003) Are indirect measures of abundance a useful index of population density? The case of red grouse harvesting. *Oikos*, **100**, 439–446.
- Chapman, J.A., Henny, C.J. & Wight, H.M. (1969) The status, population dynamics, and harvest of the dusky Canada goose. *Wildlife Monographs*, **18**, 3–48.
- Coltman, D.W. (2008) Molecular ecological approaches to studying the evolutionary impact of selective harvesting in wildlife. *Molecular Ecology*, **17**, 221–235.
- Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. & Festa-Bianchet, M. (2003) Undesirable evolutionary consequences of trophy hunting. *Nature*, **426**, 655–658.
- Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B.T. (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, **292**, 1528–1531.
- Crawley, M.J. (2007) *The R Book*. Wiley & Sons, London.
- Darlington, R.B. & Smulders, T.V. (2001) Problems with residual analysis. *Animal Behaviour*, **62**, 599–602.
- Festa-Bianchet, M. (2003) Exploitative wildlife management as a selective pressure of life-history evolution of large mammals. *Animal Behavior and*

- Wildlife Conservation* (eds M. Festa-Bianchet & M. Apollonio), pp. 191–208. Island Press, Washington, DC.
- Flanders-Wanner, B.L., White, G.C. & McDaniel, L.L. (2004) Validity of prairie grouse harvest-age ratios as production indices. *Journal of Wildlife Management*, **68**, 1088–1094.
- Freckleton, R.P. (2002) On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *Journal of Animal Ecology*, **71**, 542–545.
- Garel, M., Cugnasse, J.-M., Maillard, D., Gaillard, J.-M., Hewison, M.A.J. & Dubray, D. (2007) Selective harvesting and habitat loss produce long-term life history changes in a mouflon population. *Ecological Applications*, **17**, 1607–1618.
- Ginsberg, J.R. & Milner-Gulland, E.J. (1994) Sex-biased harvesting and population dynamics in ungulates: implications for conservation and sustainable use. *Conservation Biology*, **8**, 157–166.
- Grieb, J.R. (1970) The shortgrass prairie Canada goose population. *Wildlife Monographs*, **22**, 3–49.
- Hauser, C.E., Pople, A.R. & Possingham, H.P. (2006) Should managed populations be monitored every year? *Ecological Applications*, **16**, 807–819.
- Haydon, D.T., Shaw, D.J., Cattadori, I.M., Hudson, P.J. & Thirgood, S.J. (2002) Analysing noisy time-series: describing regional variation in the cyclic dynamics of red grouse. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 1609–1617.
- Holmstad, P.R., Jensen, K.H. & Skorpung, A. (2006) Vector-borne parasites decrease host mobility: a field test of freeze or flee behaviour of willow ptarmigan. *International Journal of Parasitology*, **36**, 735–740.
- Hörnelt-Willebrand, M., Marström, V., Brittas, R. & Willebrand, T. (2006) Temporal and spatial correlation in chick production of willow grouse *Lagopus lagopus* in Sweden and Norway. *Wildlife Biology*, **12**, 347–355.
- Hudson, P.J. (1985) Harvesting red grouse in the North of England. *Game Harvest Management* (eds S.L. Beasom & S.F. Roberson), pp. 319–326. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas.
- Hudson, P.J. (1986) *The Biology and Management of a Wild Game Bird*. Game Conservancy Limited, Hampshire, UK.
- Hudson, P.J. (1992) *Grouse in Space and Time. The Population Biology of a Managed Gamebird*. Game Conservancy Limited, Hampshire, UK.
- Hudson, P.J. & Dobson, A.P. (2001) Harvesting unstable populations: red grouse *Lagopus lagopus scoticus* in the United Kingdom. *Wildlife Biology*, **7**, 189–195.
- Hudson, P.J. & Newborn, D. (1995) *A Manual of Red Grouse and Moorland Management*. Game Conservancy Limited, Hampshire, UK.
- Hudson, P.J., Dobson, A.P. & Newborn, D. (1998) Prevention of population cycles by parasite removal. *Science*, **282**, 2256–2258.
- Hudson, P.J., Newborn, N. & Dobson, A.P. (1992) Regulation and stability of a free living host-parasite system: *Trichostrongylus tenuis* in red grouse. I. Monitoring and parasite reduction experiments. *Journal of Animal Ecology*, **61**, 477–486.
- Hudson, P.J., Newborn, D.N. & Robertson, P.J. (1997) Seasonal and geographical patterns of mortality in red grouse populations. *Wildlife Biology*, **2**, 79–88.
- Hutchings, J.A. (2005) Life history consequences of overexploitation to population recovery in Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 824–832.
- Hutchings, J.A. & Fraser, D.J. (2008) The nature of fisheries- and farming-induced evolution. *Molecular Ecology*, **17**, 294–313.
- IUCN Red List (2007) <http://www.iucnredlist.org>
- Jenkins, D., Watson, A. & Miller, G.R. (1963) Population studies on red grouse, *Lagopus lagopus scoticus* (Lath.) in north-east Scotland. *Journal of Animal Ecology*, **32**, 317–376.
- Jenkins, D., Watson, A. & Miller, G.R. (1967) Population fluctuations in the red grouse (*Lagopus lagopus scoticus*). *Journal of Animal Ecology*, **36**, 97–122.
- Jonzén, N., Ranta, E., Lundberg, P., Kaitala, V. & Lindén, H. (2003) Harvesting-induced population fluctuations? *Wildlife Biology*, **9**, 59–65.
- Jonzén, N., Ripa, J. & Lundberg, P. (2002) A theory of stochastic harvesting in stochastic environments. *American Naturalist*, **159**, 427–437.
- Katzner, T.E., Milner-Gulland, E.J. & Bragin, E.A. (2007) Using modelling to assess and improve monitoring: are we collecting the right data? *Conservation Biology*, **21**, 241–252.
- Kendall, B.E., Prendergast, J. & Bjørnstad, O.N. (1998) The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles. *Ecology Letters*, **1**, 160–164.
- Lande, R., Saether, B.E. & Engen, S. (1997) Threshold harvesting for sustainability of fluctuating resources. *Ecology*, **78**, 1341–1350.
- Lande, R., Saether, B.E. & Engen, S. (2003) *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford, UK.
- Leirs, H., Stenseth, N.C., Nichols, J.D., Hines, J.E., Verhagen, R. & Verheyen, W. (1997) Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. *Nature*, **389**, 176–180.
- Martinez, M., Rodriguez-Vigal, C., Jones, O.R., Coulson, T. & Miguel, A.S. (2005) Different hunting strategies select for different weights in red deer. *Biology Letters*, **1**, 353–356.
- Milner, J., Nilsen, E.B. & Andreassen, H.P. (2007) Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology*, **21**, 36–47.
- Moss, R., Watson, A. & Parr, R. (1996) Experimental prevention of a population cycle in red grouse. *Ecology*, **77**, 1512–1530.
- Moss, R., Watson, A., Trenholm, I.B. & Parr, R. (1993) Caecal threadworms *Trichostrongylus tenuis* in red grouse *Lagopus lagopus scoticus*: effects of weather and host density upon estimated worm burdens. *Parasitology*, **107**, 199–209.
- Mougeot, F., Evans, S.A. & Redpath, S.M. (2005a). Interactions between population processes in a cyclic species: parasites reduce autumn territorial behaviour of male red grouse. *Oecologia*, **144**, 289–298.
- Mougeot, F., Piertney, S.B., Leckie, F., Evans, S., Moss, R., Redpath, S.M. & Hudson, P.J. (2005b) Experimentally increased aggressiveness reduces population kin structure and subsequent recruitment in red grouse *Lagopus lagopus scoticus*. *Journal of Animal Ecology*, **74**, 488–497.
- Mowbray, T.B., Craig, R.E., Sedinger, J.S. & Trost, R.E. (2002) Canada Goose (*Branta canadensis*). *The Birds of North America Online* (ed. A. Poole). Cornell Lab of Ornithology, Ithaca. doi: 10.2173/bna.682. <http://bna.birds.cornell.edu/bna/species/682>.
- Mysterud, A., Tryjanowski, P. & Panek, M. (2006) Selectivity of harvesting differs between local and foreign roe deer hunters: trophy stalkers have the first shot at the right place. *Biology Letters*, **2**, 632–635.
- Pinheiro, J.C. & Bates, D.M. (2000) *Mixed-effects Models in S and S-Plus*. Springer, New York.
- R Development Core Team (2007) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Redpath, S.M., Mougeot, F., Leckie, F.M., Elston, D.A. & Hudson, P.J. (2006) Testing the role of parasites in driving the cyclic population dynamics of a gamebird. *Ecology Letters*, **9**, 410–418.
- Richards, C. (2004) Grouse shooting and its landscape. The management of grouse moors in Britain. *Anthropology Today*, **20**, 10–15.
- Sims, M., Wanless, S., Harris, M.P., Mitchell, P.I. & Elston, D.A. (2006) Evaluating the power of monitoring plot designs for detecting long-term trends in the numbers of common guillemots. *Journal of Applied Ecology*, **43**, 537–546.
- Smith, A.A. & Willebrand, T. (1999) Mortality causes and survival rates of hunted and unhunted willow grouse. *Journal of Wildlife Management*, **63**, 722–730.
- Solberg, E.J., Saether, B.E., Strand, O. & Loison, A. (1999) Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology*, **68**, 186–204.
- Stenseth, N.C., Chan, K.S., Tong, H., Boonstra, R., Boutin, S., Krebs, C.J., Post, E., O'Donoghue, M., Yoccoz, N.G., Forchhammer, M.C. & Hurrell, J.W. (1999) Common dynamic structure of Canada lynx populations within three climatic regions. *Science*, **285**, 1071–1073.
- Warren, P. & Baines, D. (2007) Dispersal distances of juvenile radiotagged red grouse *Lagopus lagopus scoticus* on moors in northern England. *Ibis*, **149**, 758–762.
- Watson, A., Moss, R., Parr, R., Trenholm, I.B. & Robertson, R. (1988) Preventing a population decline of red grouse (*Lagopus lagopus scoticus*) by manipulating density. *Experientia*, **44**, 274–275.
- Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.P. (2006) Why do we still use stepwise modelling in ecology and behaviour? *Journal of Animal Ecology*, **75**, 1182–1189.

Received 10 June 2008; accepted 7 October 2008
Handling Editor: Tim Coulson