Weak compensation of harvest despite strong density-dependent growth in willow ptarmigan

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Ptarmigan and grouse species (*Lagopus* spp.) are thought to be able to compensate for a modest harvest because there is a surplus of breeding birds that are prevented from breeding by territory holders. To estimate the degree of harvest-mortality compensation reliably we experimentally harvested 0%, 15% and 30% of the willow ptarmigan (*Lagopus lagopus*) on 13 estates ranging from 20 to 54 km² in size during four hunting seasons in Norway according to a regional block design. Population overwinter growth rate was strongly negatively density dependent, but despite this, and contrary to earlier findings, only 33% of the harvest was compensated for. The lack of compensation was probably caused by long-distance juvenile dispersal that was unaffected by the harvest. The need for large-scale management experiments to detect the effects of harvest was clearly demonstrated: lack of compensation was found only when we used the whole dataset and not when the data were analysed by year or block. Our study shows that it is very difficult to demonstrate a population's lack of harvest compensation and warns against using small-scale, out-of-season or poorly replicated studies as a basis for future harvest-management decisions.

Keywords: harvest; compensation; density dependence; game; *Lagopus lagopus*

1. INTRODUCTION

Sustainable harvest requires knowledge of whether the harvest mortality is additive to natural mortality or is compensated for by increased survival or reproduction. Erroneously assuming compensation has led to over-harvest and even population extinctions (Hilborn *et al*. 1995; Lande *et al*. 1995; Myers & Cadigan 1995; Walters & Maguire 1996). During a two to three week intensive willow ptarmigan harvest in September each year, more than 100 000 Norwegian hunters shoot *ca*. 10–20% of the total population (Myrberget 1976; Steen 1989). This harvest level has been assumed to be sustainable owing to compensatory mechanisms that have been demonstrated when territory holding cocks are removed from their territories. After cock removal in high-density populations the vacant territories are immediately occupied by surplus cocks (Hannon 1983; Pedersen 1988; Ellison 1991; Moss *et al*. 1996). However, the scale and timing of such local removals in optimal willow ptarmigan habitats in the spring are not representative of hunting that covers landscape-scale estates in the autumn. Our aim was to test experimentally on an appropriate scale, and with appropriate replication, whether willow ptarmigan compensated for the harvest as suggested by removal studies.

In the only realistic harvest study on willow ptarmigan, 24% of one population was experimentally harvested during each of three harvest seasons in Sweden while two populations were left as controls (Smith & Willebrand

1999). It was found that individuals left after harvest had the same winter survival as individuals from non-hunted areas, and harvest mortality appeared to be additive to natural mortality. Despite hunting mortality being additive to natural mortality, the population size was unaffected. The authors suggested that population size was maintained by immigration from areas beyond their study area (Smith & Willebrand 1999). Immigration into a local population requires that there are individuals in the surrounding areas that for some reason decide to migrate. Because willow ptarmigan that have already bred for one season seldom move large distances between years, it is the juveniles that constitute the dispersing part of the population.

If the compensation is caused by density-dependent immigration of individuals born the previous year, the sustainability of the harvest then becomes just a matter of the size of the harvested area and whether the local population is a source or a sink (Pulliam 1988). If all compensation is driven by dispersal and the size of the harvested area is so big that it contains most dispersal movement, there would be no compensation. Following the same logic, perceived compensation would fall with increasing size of the management area.

The size of Norwegian willow ptarmigan hunting estates, and so the management area, is *ca*. 20–25 km². The interesting question is therefore how the population on a local estate responds to harvest. To account for density-dependent immigration or emigration and other sources of variability, a study must contain the essential requirements of proper experiments: controls and especially randomization and large-scale replication. This

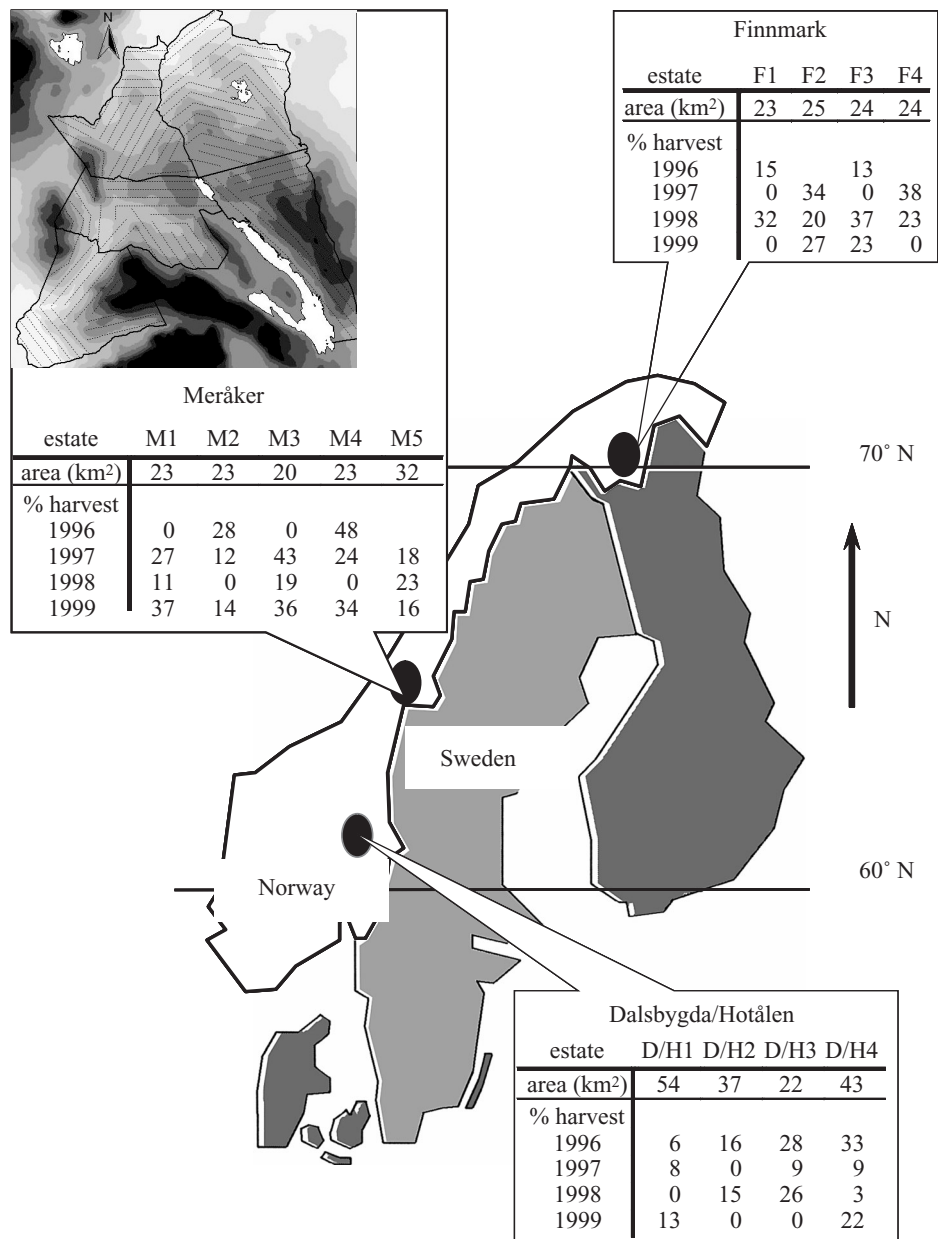[*]Author for correspondence (harald.steen@bio.uio.no).

Figure 1. The 13 estates were organized into three blocks marked by filled circles (northern, Finnmark; central, Meråker; and southern, Dalsbygda/Holtålen). In 1997, the second year of the study, a fifth estate was added to the central Norway block making 13 blocks in total. For clarity we have shown the detailed layout of the central estates. The layouts of the southern and northern estates are similar. Higher altitudes are shaded with darker grey. Black solid lines indicate estate boundaries and dotted lines are the lines used for density estimation.

means that one must experimentally harvest many estates of relevant size (i.e. the scale of game estates) with different habitat qualities and population densities.

In the 4 year study we tested whether willow ptarmigan populations compensated for harvest by experimentally assigning three approximate harvest levels (0%, 15% and 30% of the autumn population) to 13 hunting estates (figure 1). Density was estimated in early May before the onset of breeding (spring) and in mid-August before harvest (autumn) using pointing dogs and distance sampling techniques (Buckland *et al.* 1993). The harvest was conducted during the normal hunting season (10 September–1 November) with most of the harvest occurring in the first two weeks.

2. METHODS

(a) *Experimental protocol*

Thirteen hunting estates were distributed on three blocks in southeastern (four in Dalsbygda and Holtålen), central (five in Meråker) and northern Norway (four in Anarjokka, Finnmark) (figure 1). The hunting estates were already established by traditional use. By using each harvest level twice in each block each year we assured repetition of harvest level within each geographical region but were unable to repeat all harvest levels exactly in each block every year. Thus the experimental design is an incomplete randomized block design (Mead 1988). Harvest level was assigned as follows: in the initial year we assigned the three combinations of harvest levels (0 : 15%, 0 : 30% and

15% : 30%) randomly to the blocks. The two harvest levels assigned to each block were assigned randomly to two estates each, avoiding confounding between prior treatment and current treatment, and between harvest level and density. In successive years we aimed at rotating the treatment combinations (0 : 15%, 0 : 30% and 15% : 30%) northwards, giving the southernmost area the treatment combinations of the northernmost block. We achieved independence of treatment, year and hunting estate. In the last year of the treatment, the treatment combinations were randomly distributed over the three blocks. Volunteers carried out the data collection and harvest. Owing to difficulties in achieving exactly the assigned percentage harvest, the actual percentage harvests deviate somewhat from those assigned (figure 1).

(b) *Density estimation*

Density was estimated using line-transect methodology and the program DISTANCE (Buckland *et al.* 1993; Thomas *et al.* 2002). Straight transect lines were drawn on a map 400 m apart, roughly following the altitude. Only every other line was traversed on the same day ensuring that no willow ptarmigan was counted twice as a consequence of being scared from one line to another. A team of two, with a minimum of two dogs, traversed the lines. Normally one dog was running at a time. One person handled the dog and the other kept track of the transect line using a compass or global-positioning-system receiver. When the dog pointed one person stayed on the line while the other approached the dog and flushed the bird(s). Line identification and the number of adults and juveniles were recorded and the perpendicular distance from the line to where the birds were first seen was measured to the nearest metre. The dogs spend less time searching far away from the transect line than they do close to the transect line. Large clutches are easier to detect than singles or pairs and therefore large clutches are over-represented at large distances. This was corrected by estimating a cluster-size bias-correction factor. Because the same dogs and people did the fieldwork on each hunting estate throughout the study, we estimated a cluster-size bias-correction factor for each hunting estate using data from all years, but because the conditions for the autumn and spring censuses were different the correction factors differed between seasons. Encounter rates were estimated for each hunting estate, year and season without stratifying with respect to age or sex. Owing to spatial variability in habitat quality, we stratified the density estimation, both in spring and in autumn. Effective strip width (ESW) was estimated using the half-normal detection curve with the cut-off point at 5%. The detection curve was chosen using the Akaike information criterion (Thomas *et al.* 2002). Using radio-collared birds we found that we detected all birds on the line, i.e. $g(0) = 1$, and they did not move in response to the approaching dog and handler. The coefficients of variation for the density estimates averaged 21% and 24% for the spring and autumn estimates, respectively. Harvest rate was estimated from the total number present before harvest and the number shot. Chick production was taken as the number of chicks per adult estimated in the autumn. Dispersal distances in juveniles and adults were estimated based on 59 radio-tagged individuals over 4 years on estate M3 at Meråker.

(c) *Statistical analysis and model selection*

In the statistical analysis we used the overwinter rate of change ($\ln[N_{\text{spring}}/N_{\text{last autumn before harvest}}]$) in each estate as the dependent variable and the percentage harvest as the experimental variable; the natural logarithm of autumn density and chick production

(chicks per adult) were treated as continuous predictor variables. To correct for consistent regional differences in Norway and for local differences within regions, we allowed block and hunting estate as categorical independent variables in the global statistical model. To test whether the degree of compensation was dependent on population density or on the proportion of young birds in the population, we also allowed interactions between density and harvest and between harvest and chick production. Inference of effect sizes was carried out based on the model with the lowest AIC-value (Akaike 1973; Burnham & Anderson 1998). The final model was chosen using stepAIC and parameters estimated using function lm in S-PLUS4 (MathSoft 1997).

3. RESULTS

(a) *Response to harvest*

The best model for overwinter rate of change included a large effect of estate (54% of the total variance) and negative effects of population density (19% of the residual variance with estate in the model), harvest rate (17% of the residual variance with estate and density in the model) and chick production (4% of the residual variance with estate, density and harvest rate in the model) (table 1). As no interactions improved the model, the effect of harvest was independent of the large variation in quality among estates and the negative density-dependent growth rate. The coefficients of the selected model indicate that only 33% of the harvest was compensated for (figure 2). This implies that, for a given estate, a 10% harvest leads to 6.7% fewer individuals next spring. Population density was a stronger predictor of overwinter rate of change than was harvest rate and had a compensatory effect, which amounted to 66% (table 1). This means that a natural population that in the autumn is 10% smaller than another on the same estate has only 3.4% fewer individuals the next spring.

(b) *Movement*

Adults moved very short distances and the sexes did not differ. In juvenile females the median natal dispersal distance was 2817 m while the median juvenile male movement distance was 1406 m (table 2).

4. DISCUSSION

The weak compensation for hunting despite a fairly strong density-dependent growth rate was surprising, but can be explained by two attributes of willow ptarmigan biology. First, high population densities are associated with a high fraction of juvenile birds ($r^2 = 0.44$, $n = 49$, $p < 0.0001$) and, second, most juveniles disperse and settle outside their natal estate between autumn and spring (table 2). Together these impose a positive density-dependent dispersal rate at the population level, and, given a mosaic of sources and sinks, a mechanism for negative density-dependent population growth.

Harvest will not interfere with this form of density dependence because hunters harvest adults and juveniles indiscriminately and natural winter mortality does not appear to be density dependent (Smith & Willebrand 1999). That some compensation for harvest takes place can be explained by weak density-dependent immigration

Table 1. Coefficients of the focal terms in the model best describing overwinter rate of change ($=\ln[N_{spring}/N_{last\ autumn\ before\ harvest}]$).
(The full model also contained the categorical variable estate. The 12 coefficients are not shown.)

term	coefficient	s.e.	p
intercept	1.510	0.363	< 0.003
ln(autumn density)	−0.676	0.108	< 0.001
harvest rate	−0.007	0.003	< 0.05
chick production	−0.212	0.122	< 0.09

Table 2. Sex-dependent dispersal distances (m) for adults and juveniles determined from radiotelemetry for both sexes.
(Adult dispersal distances are from the territory or nest of one year to that of the next, while for juveniles they are natal dispersals.
There are seven juvenile birds where the sex was unknown; they are excluded from the sex-specific presentation but included in
the pooled data.)

	adults				juveniles			
sex	median	mean	s.e.	n	median	mean	s.e.	n
female	351	366	54	16	2817	3213	836	6
male	347	345	41	16	1406	2618	662	14
pooled	351	355	34	32	2598	3978	683	27
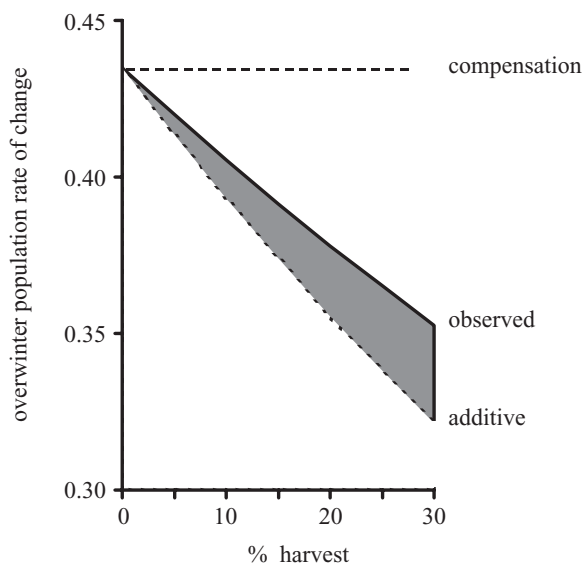
Figure 2. Overwinter rate of change in willow ptarmigan density compensated for 33% of the harvest mortality, and the compensation was density independent. The size of the shaded area indicates the true compensation at different harvest levels. The values are calculated for the D/H1 estate in southern Norway. Chick production was set to 1.5 chicks per adult and density was 20 willow ptarmigan km^{-2}.

between the time of harvest and the next spring. The effect of juvenile dispersal on the density-dependent overwinter rate of change will diminish if the management area is large enough to encompass the scale of juvenile natal dispersal. Because the willow ptarmigan present after harvest do not survive the winter better as a consequence of harvest mortality (Smith & Willebrand 1999), harvest mortality must therefore be additive to natural mortality, and harvest management must therefore be based on reproductive surplus (Steen & Erikstad 1996).

The fairly large spatial and temporal variability in the data not accounted for by density-dependent growth or hunting highlights the necessity for spatiotemporal replication of experimental treatments. For example, if there was no temporal replication in our study (i.e. each year across all blocks was analysed separately) the effect of harvest would be detected in only one out of the 4 years. Likewise, if there was no spatial replication (i.e. data from the three blocks were analysed separately), a significant effect would be detected in one out of the three blocks.

Owing to an exceptionally large-scale properly replicated harvest experiment in space and time, we have been able to document that, despite the presence of density-dependent mechanisms, compensation for harvest mortality is not guaranteed. In the future, caution should therefore be exercised when making harvest-management decisions of whether or not a species can compensate for harvest mortality based on observational or small-scale studies.

REFERENCE

Akaike, H. 1973 Information theory as an extension of the maximum likelihood principle. In *Second Int. Symp. on Information Theory* (ed. B. N. Petrov & F. Csaki), pp. 267–281. Budapest: Akademiai Kiado.

Buckland, S. T., Anderson, D. R., Burnham, K. P. & Laake, J. L. 1993 *Distance sampling: estimating abundance of biological populations*. London: Chapman & Hall.

Burnham, K. P. & Anderson, D. R. 1998 *Model selection and inference: a practical information–theoretic approach*. New York: Springer.

Ellison, L. E. 1991 Shooting and compensatory mortality in tetraonids. *Ornis Scand.* **22**, 229–239.

Hannon, S. J. 1983 Spacing and breeding density of willow ptarmigan in response to an experimental alteration of sex ratio. *J. Anim. Ecol.* **52**, 807–820.

Hilborn, R., Walters, C. J. & Ludwig, D. 1995 Sustainable exploitation of renewable resources. *A. Rev. Ecol. Syst.* **26**, 45–67.

Lande, R., Engen, S. & Sæther, B.-E. 1995 Optimal harvesting of fluctuating populations with a risk of extinction. *Am. Nat.* **145**, 728–745.

MathSoft 1997 *S-PLUS 4 guide to statistics*. Seattle, WA: MathSoft.

Mead, R. 1988 *The design of experiments*. Cambridge University Press.

Moss, R., Watson, A. & Parr, R. 1996 Experimental prevention of a population cycle in red grouse. *Ecology* **77**, 1512–1530.

Myers, R. A. & Cadigan, N. G. 1995 Was an increase in natural mortality responsible for the collapse of the northern cod? *Can. J. Fish. Aquat. Sci.* **52**, 1274–1285.

Myrberget, S. 1976 Hunting mortality, migration, and age composition of Norwegian willow grouse (*Lagopus lagopus*). *Norwegian J. Zool.* **24**, 47–52.

Pedersen, H. C. 1988 Territorial behaviour and breeding numbers in Norwegian willow ptarmigan: a removal experiment. *Ornis Scand.* **19**, 81–87.

Pulliam, H. R. 1988 Sources, sinks, and population regulation. *Am. Nat.* **132**, 652–661.

Smith, A. & Willebrand, T. 1999 Mortality causes and survival rates of hunted and unhunted willow grouse. *J. Wildl. Mngmt* **63**, 722–730.

Steen, H. & Erikstad, K. E. 1996 Sensitivity of willow grouse *Lagopus lagopus* population dynamics to variations in demographic parameters. *Wildl. Biol.* **2**, 27–35.

Steen, J. B. 1989 *Rypeliv og rypejakt*. Oslo: Gyldendal Norsk Forlag.

Thomas, L., Laake, J. L., Strindberg, S., Marques, F. F. C., Buckland, S. T., Borchers, D. L., Anderson, D. R., Burnham, K. P., Hedley, S. L. & Pollard, J. H. 2002 DISTANCE 4.0 Release 2. Research Unit for Wildlife Population Assessment, University of St Andrews, UK. See http://www.ruwpa.st-and.ac.uk/distance/.

Walters, C. & Maguire, J. J. 1996 Lessons for stock assessment from the northern cod collapse. *Rev. Fish Biol. Fish.* **6**, 125–137.