

## Grouse dynamics and harvesting in Kainuu, northeastern Finland

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We study the dynamics of the capercaillie, black grouse, hazel grouse and willow grouse in Kainuu game management district in northeastern Finland in the years 1989–2004. It appears that the 6–7 year periodicity that prevailed in this region from 1960s up to 1980s has now vanished in all species. The grouse data are modelled using a linear autoregressive model with lag terms for population dynamics including grouse harvest as annual bag and an index of winter severity (winter-time area of Baltic Sea ice cover). We use the Akaike information criterion for selecting the best model for each species; first order lag is forced to the models. It turns out that a term is needed for harvesting (with a negative coefficient) in models for all species. For the capercaillie and the hazel grouse second order lag was included, for the black grouse and the willow grouse first order lag suffices. The willow grouse is the only species where the index of winter strength (with a negative coefficient) is needed in the model.

The dynamics of populations exhibiting simultaneous cyclic fluctuations over large areas have been popular subject among population ecologists for over a century (Elton 1924, Angelstam et al. 1984). One reason for this interest (besides scientific) is that many species with economic significance show fluctuations of this kind. For example, forest grouse species (willow grouse *Lagopus lagopus*, capercaillie *Tetrao urogallus*, black grouse *T. tetrix* and hazel grouse *Bonasa bonasia*) are important game birds and their hunting has a large economic (at least in the past), cultural and recreational value. Various factors have been suggested for maintaining the cycles (Ranta et al. 1995). These include time-delayed density dependence and various types of random external perturbances, including the weather, predators, parasites and harvesting.

Recent decades have witnessed drastic grouse population declines in Finland. For example, capercaillie populations have decreased by 60% between early 1960s and late 1980s. Respective declines are 40%, 30% and 50% for the black grouse, hazel grouse and willow grouse (Helle et al. 2002, 2003, Ludwig 2006). These changes have often been attributed to anthropogenic changes in forest landscapes, i.e. habitat loss, fragmentation and degradation, and to the corollary increase in the numbers of small to medium sized mammalian predators (Åberg et al. 1995, Kurki and Lindén 1995, Kurki et al. 1997, 2000, Storch 2000, Borchtchevski et al. 2003). Also global climate change may be associated with the decline of grouse as shown by Ludwig et al. (2006) for a black grouse population. However, we still lack the final understanding about the reasons for grouse population decline (Ranta et al. 2003).

The effects of hunting on grouse population dynamics and abundance are not very well known. Hunting is often thought to be of marginal importance and some authors have considered the effects of hunting negligible with respect to the recent well-documented decline in grouse populations in northern Europe (Storch and Willebrand 1991, Helle et al. 2002, Ranta et al. 2008). The key issue in harvesting any natural population is whether the mortality caused by hunting is additional or compensatory. Ideally, ecologically sustainable harvesting should be compensatory although harvesting mortality is probably always at least partly additional. Usually compensatory mortality is associated with high density dependence on the population; harvested individuals are assumed to make way for the remaining ones. This view is not supported by Pedersen et al. (2003) who found the mortality of willow grouse to be weakly compensatory despite strong density dependence. In an experimental study, Lindén and Sorvoja (1992) found signs of partially compensatory hunting mortality. If hunting mortality is at least partially compensatory, populations should increase faster after heavy hunting mortality because reduced population density should enhance reproductive success.

There are various recommendations of how natural populations should be harvested. Lande et al. (1997) demonstrated with a modelling approach the effects of four different easily applicable harvesting strategies. They showed that the so-called proportional threshold harvest (certain proportion of the population is harvested above a threshold population size) resulted in the largest cumulative hunting bag in the long run and also in the lowest risk of extinction of harvested populations. Other hunting strategies,

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constant harvest, threshold harvest without proportionality and proportional harvest without threshold, resulted in larger risks of extinction and in reduced long-term harvest yield. Likewise, Lindén (1991) suggested, based on long-term empirical data, that cyclic grouse populations should be hunted with varying pressure depending on the state of the population: large and increasing populations could be harvested proportionately more than small and declining populations, see also (Jonzen et al. 2003). Thus, both theoretical and empirical studies suggest that for optimal sustainable yield, hunting pressure should be reduced when populations are declining and no or very little hunting is optimal at the low end of population fluctuations.

There are many ways hunting authorities may restrict grouse hunting in Finland, if population densities based on monitoring counts such suggest. Game management districts may shorten or even close hunting season which according to hunting law is between 10 September and 31 October. Local authorities and hunting clubs on private land are able to set even more strict regulations. Selling hunting licences to state-owned land also has to follow the decisions made by game management districts and number of licences are sold in relation to grouse density. Also recommendations for quota, how many birds can be hunted by a hunter, are given, but there are no data available, how well recommendations are being followed.

We model 16 year grouse census and hunting bag data from the province of Kainuu (northeastern Finland) to examine if hunting has an effect on population size. This is especially important to know because the number of hunters approximately tripled between 1960 and 2000 and thus increased hunting pressure may be one reason for the observed population declines (see also Lindén and Raijas 1986). We also examine whether hunting mortality shows signs of compensatory effects by regressing hunting mortality and the population growth rate. We further examine whether or not large and increasing grouse populations are harvested more than small and declining ones as recommended by Lindén (1991) and Lande et al. (1997).

## Material and methods

### Data

We use wildlife triangle census data in Kainuu province (appr. 65°N, 28°E), northeastern Finland, from 1989 to 2004. Wildlife triangle census routes are 12 km long and each side of the triangle is 4 km (details in Helle et al. 1996, Pellikka et al. 2007). Censuses are conducted in August, mainly by local hunters. The main belt is 60 m in breadth, covered by a three-person chain. Density estimates are calculated by multiplying the main belt area with numbers of grouse observed adjusted for total forest area. This is a fairly accurate method as the census efficiency is high (80% on average; Brittas and Karlbom 1990).

All observed grouse individuals were aged as juveniles or adults and counted. Census routes are assumed to be situated randomly in the landscape. The province of Kainuu was chosen as a study area due to the best coverage of wildlife triangle censuses in Finland. Forest land covers about 75%

of the area, peat lands 15% and lakes 10%. Practically all old-growth forests are confined to the nature conservation areas, which form ca 3% of the land area. The province borders the practically continuous 'green belt' of old-growth forests on the Russian side of the border.

Information on the grouse hunting bag was obtained from the Finnish Game and Fisheries Research Institute. These estimates are based on nation-wide questionnaires sent out to 5000 (ca 2% of all hunters in Finland) hunters annually.

### Modelling

We describe the grouse dynamics with:

$$X(t+1) = a_0 + a_1X(t) + a_2X(t-1) - hB(t) - cW(t) + \varepsilon \quad (1)$$

Where  $X$  is grouse population density (individuals  $\text{km}^{-2}$ ),  $a_0$ ,  $a_1$  (lag one) and  $a_2$  (lag 2) are model parameters related to grouse numbers, while  $B$  is the annual grouse bag (killed grouse  $\text{km}^{-2}$  in the Kainuu province);  $W$  is an index of the severity of the winter (Baltic Sea Ice coverage); normalised to mean zero and unit variance and  $\varepsilon$  is an error (or noise) term. Baltic Sea ice coverage (<[www.itameriportaali.fi/en/tietoa/jaa/jaatalvi/en\\_GB/jaatalvi/](http://www.itameriportaali.fi/en/tietoa/jaa/jaatalvi/en_GB/jaatalvi/)>) varies notably between the years and is generally a good surrogate of winter severity in the surrounding areas. It also correlates strongly with NAO (Koslowski and Loewe 1994), therefore we assume it to describe winter conditions also in our study area but possibly with better accuracy than NAO or Arctic oscillation. Severity of winter has various effects on grouse species as summarised by Lindén (2002). Effects of winter weather are not necessarily straightforward on grouse, as the mild winters may actually make the life of grouse more difficult. This is e.g. because the formation of ice to trees increases when the temperature crosses often the 0°C line. Also the typical habit of grouse spp., using of a snow roost during the night, is not possible if the snow layer is very hard and icy. Lindén (1981a) found out that on capercaillie survival was higher in southern Finland in short and mild winters, whereas in northern Finland survival was higher in long, cold and snowy winters. Winter conditions clearly have a significant effect on the life of grouse spp., but exact responses are difficult to predict. Adding such a climatic variable into our models was mainly motivated by getting some comparison to the hunting effect from a variable known to have effect on the survival and fecundity of grouse spp.

The species-specific grouse population data differentiate the adult and young birds, but the hunting bag data does not. Therefore we model changes in annual total grouse density under harvest. The Eq. 1 is referred to as the full model, and Akaike information criterion (corrected for small samples),  $AIC_C$  and  $\delta AIC_C$  (difference between AIC models) is used to check out whether a reduced model (stripping off in turn  $h$ ,  $W$  and lag 2 terms in Eq. 1) gives a better fit (Burnham and Anderson 2002, Johnson and Omland 2004). For biological reasons we retained the constant,  $a_0$ , and the first order lag term,  $a_1$ . Hence, various parameter inclusions give us eight different models (Table 1).

For each model ( $i$  goes from 1 to 8) we also calculated the Akaike weight

$$w = \frac{\exp[-0.5 \times \delta AIC_C(i)]}{\sum [\exp(-0.5 \times \delta AIC_C)]} \quad (2)$$

to see how likely each model is. With eight models the expectation is 1/8, or 0.125.

We derived a few life history characters using the August census data for grouse and annual bag for the harvest: (1) a measure of reproductive success is simply juveniles(t)/adults(t), (2) adult survival rate is adults(t + 1)/[total(t)

– harvest(t)], and (3) harvest mortality is harvest(t)/total(t). The estimates were derived from the best fitting model with  $\delta AIC_C = 0$ . Note that survival rate estimate also includes 1st-winter survival, which may be lower than older age classes.

Furthermore, we estimated how well the current harvesting pattern fits the given recommendations (Lindén 1991, Lande et al. 1997) by regressing the harvest mortality at time t against the size of the population (X(t)) and against the change in population size from year t–1 to t. We also estimated the recovering ability of grouse populations by

Table 1. Basic statistics of the eight models fitted to the grouse dynamics data ( $a_0$  = constant,  $a_1$  = term for lag one,  $a_2$  = term for lag two,  $h$  = intensity of harvest,  $c$  = role of winter climate,  $r^2$  = coefficient of determination,  $\delta AIC_C$  = Akaike information criterion corrected for small sample minus the smallest value of  $AIC_C$ ,  $w$  = weight of the model [equal weight expectation = 0.125]). The most parsimonious model ( $\delta AIC_C = 0$ ) is indicated with bold typeface. For each species we also sum up the Akaike weights for inclusion of the winter severity, harvest and second order lag to the model (expectation = 0.5).

(A) Capercaillie

Model no.	$a_0$	$a_1$	$a_2$	$h$	$c$	$r^2$	$\delta AIC_C$	$w$
(1)	8.10	0.10	–0.53	–0.25	0.12	0.50	13.76	0.000
(2)	3.60	0.36	.	–0.59	0.03	0.33	9.10	0.006
(3)	9.88	–0.05	–0.68	.	0.13	0.46	6.02	0.030
(4)	5.50	0.03	.	.	–0.02	0.01	8.24	0.010
<b>(5)</b>	<b>7.56</b>	<b>0.16</b>	<b>20.49</b>	<b>20.25</b>	.	<b>0.48</b>	<b>0.0</b>	<b>0.621</b>
(6)	3.52	0.37	.	–0.59	.	0.33	2.63	0.166
(7)	9.36	0.01	–0.65	.	.	0.45	5.54	0.038
(8)	5.57	0.02	.	.	.	0.01	3.20	0.125

Summed Akaike weights: winter = 0.048, harvest = 0.795, lag 2 = 0.692

(B) Black grouse

Model no.	$a_0$	$a_1$	$a_2$	$h$	$c$	$r^2$	$\delta AIC_C$	$w$
(1)	–0.58	1.06	0.02	–2.43	0.55	0.59	13.51	0.001
(2)	–0.12	1.04	.	–2.37	0.54	0.58	4.85	0.068
(3)	12.20	0.27	–0.51	.	0.26	0.31	12.04	0.001
(4)	7.13	0.28	.	.	0.06	0.06	9.87	0.005
(5)	–0.17	1.03	0.01	–2.19	.	0.53	6.49	0.030
<b>(6)</b>	<b>0.02</b>	<b>1.02</b>	.	<b>–2.16</b>	.	<b>0.54</b>	<b>0.00</b>	<b>0.779</b>
(7)	11.78	0.29	–0.50	.	.	0.30	5.79	0.043
(8)	7.07	0.29	.	.	.	0.06	4.83	0.069

Summed Akaike weights: winter = 0.077, harvest = 0.880, lag 2 = 0.076

(C) Hazel grouse

Model no.	$a_0$	$a_1$	$a_2$	$h$	$c$	$r^2$	$\delta AIC_C$	$w$
(1)	–1.04	1.13	0.01	–1.49	–0.48	0.33	15.74	0.001
(2)	–0.81	1.12	.	–1.46	–0.47	0.33	7.07	0.016
(3)	6.82	0.42	–0.22	.	–0.35	0.20	9.50	0.004
(4)	5.08	0.40	.	.	–0.56	0.17	3.56	0.093
<b>(5)</b>	<b>1.53</b>	<b>0.98</b>	<b>–0.15</b>	<b>–1.34</b>	.	<b>0.29</b>	<b>0.00</b>	<b>0.556</b>
(6)	–0.35	1.06	.	–1.58	.	0.27	1.85	0.220
(7)	8.16	0.36	–0.33	.	.	0.18	3.46	0.098
(8)	6.20	0.27	.	.	.	0.08	8.05	0.009

Summed Akaike weights: winter = 0.114, harvest = 0.793, lag 2 = 0.661

(D) Willow grouse

Model no.	$a_0$	$a_1$	$a_2$	$h$	$c$	$r^2$	$\delta AIC_C$	$w$
(1)	7.76	0.11	0.01	–0.60	–0.60	0.35	4.23	0.054
<b>(2)</b>	<b>7.89</b>	<b>0.11</b>	.	<b>–0.59</b>	<b>–0.60</b>	<b>0.35</b>	<b>0.00</b>	<b>0.446</b>
(3)	9.07	0.08	–0.10	.	–0.72	0.23	7.99	0.008
(4)	7.87	0.11	.	.	–0.76	0.22	1.73	0.188
(5)	9.39	–0.03	–0.02	–0.72	.	0.23	7.92	0.009
(6)	9.087	–0.02	.	–0.74	.	0.23	1.43	0.218
(7)	11.46	–0.10	–0.18	.	.	0.05	4.45	0.048
(8)	9.51	–0.07	.	.	.	0.01	5.57	0.027

Summed Akaike weights: winter = 0.697, harvest = 0.728, lag 2 = 0.119.

plotting the population change from  $t$  to  $t + 1$  against the harvest rate at  $t$ .

## Results

The results of modelling grouse dynamics, using the information criterion, under harvest suggests the following. The temporal dynamics of the capercaillie and the hazel grouse (first order process is also sufficient) populations in Kainuu obeyed the second order autoregressive process (lag 2 term needed), while that of the black grouse and the willow grouse was of the first order (Table 1). A more notable feature is that the 'best' model ( $\delta AIC_C = 0$ ) in all species included a term for harvesting (in all models with harvesting, regardless of  $\delta AIC_C$ , parameter  $h$  attained negative values – as it should). Willow grouse is the only species for which the Akaike information criterion suggests that a term for the winter severity is needed, the impact of winter severity on this species was negative. In other words, in mild winters (when the ice coverage in the Baltic Sea is smaller) the population thrived better than in harsh winters (Table 1).

In our eight models there were four with a term for winter severity, four models with harvesting as a parameter, and four models with the second order lag included. Thus, summing up their Akaike weights and using the expectation of 0.5 we can assess the substance of that particular parameter in the model. The results are straightforward. Models with a term for harvesting had heavy weights for all species (capercaillie 0.8, black grouse 0.9, hazel grouse 0.8, willow grouse 0.7), winter severity in the willow grouse also had a rather high weight (0.7), as did the second order lag in the capercaillie and the hazel grouse, being 0.7 in both species (Table 1).

The models with  $\delta AIC_C = 0$  in Table 1 performed well and mimicked the dynamics of four grouse species (Fig. 1). Of course there is deviation between the model and the data, but with only 16 years of observations such scatter is unavoidable.

It is worth noting (Fig. 2) that in the capercaillie the number of fledglings (juvenile birds observed together with adults) was below 1 in 12 out of 16 years, while for the other species it was above 1 in most years (12 in black grouse, 14 in hazel grouse and 15 in willow grouse). The capercaillie and the black grouse has similar adult survival rates (55%) though the coefficient of variation in the black grouse was 25% (15% in the capercaillie). The corresponding figures were 52% (18%) and 41% (24%) for the hazel and willow grouse, respectively (Fig. 3). That the capercaillie had the lowest figures for juveniles per adult but comparable adult survival rate with the black grouse and the hazel grouse explains part of the fact that capercaillie densities averaged 5 individuals  $\text{km}^{-2}$  while the other two species fluctuated around 10 individuals  $\text{km}^{-2}$  (Fig. 1).

Mortality due to harvesting was the highest for black grouse (average 13.3%), often being well above 10%, while the other species suffered much smaller harvest mortality (capercaillie 5.0%, hazel grouse 7.6%, willow grouse 3.5%; Fig. 4). This fact can also be seen in the coefficient values harvesting term attained. For the black grouse, it was almost an order of magnitude larger than for the capercaillie and the willow grouse, and twice the value of the hazel grouse (Table 1).

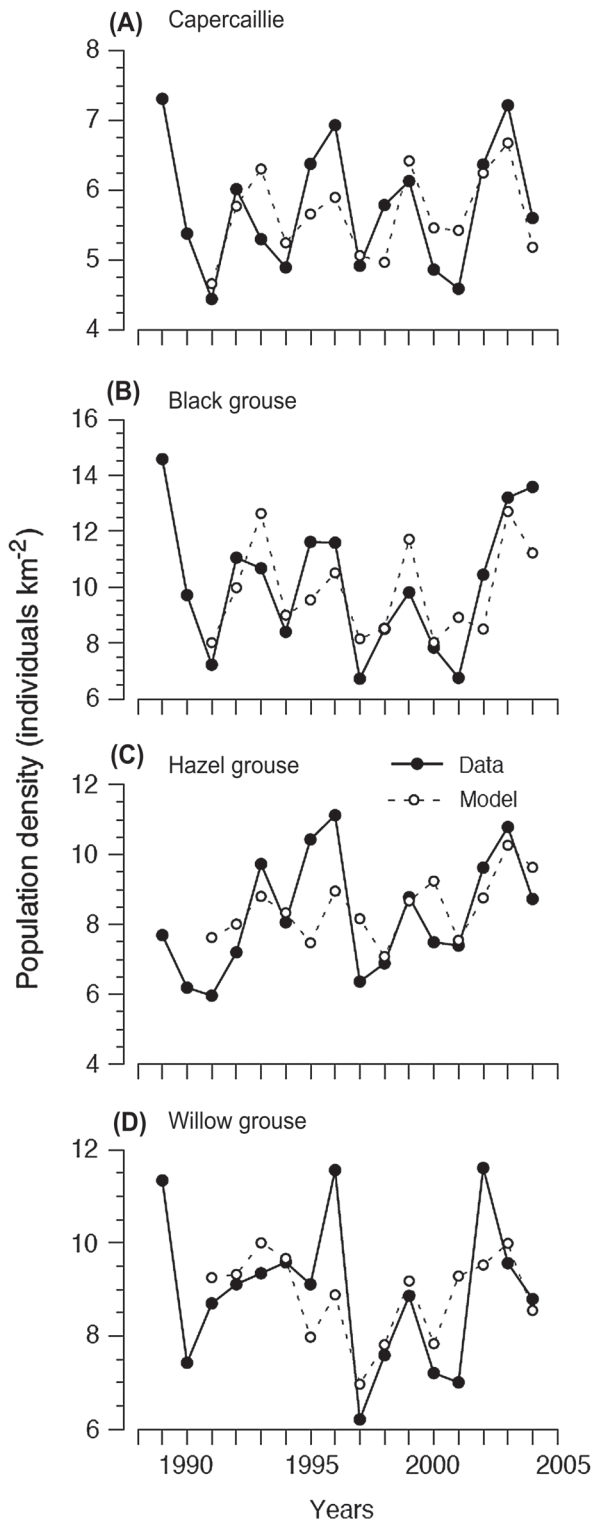


Figure 1. Population dynamics of (A) capercaillie, (B) black grouse, (C) hazel grouse and (D) willow grouse in 1989–2004 in Kainuu, northeastern Finland. Grouse densities are indicated with solid lines and closed dots, while the prediction of the best model (Table 1) is given with dashed line and open rings.

When examining the harvesting patterns (Table 2), it appeared that harvest mortality was not dependent on population size. In the willow grouse there was a slight tendency for greater harvest from small populations. In all species,

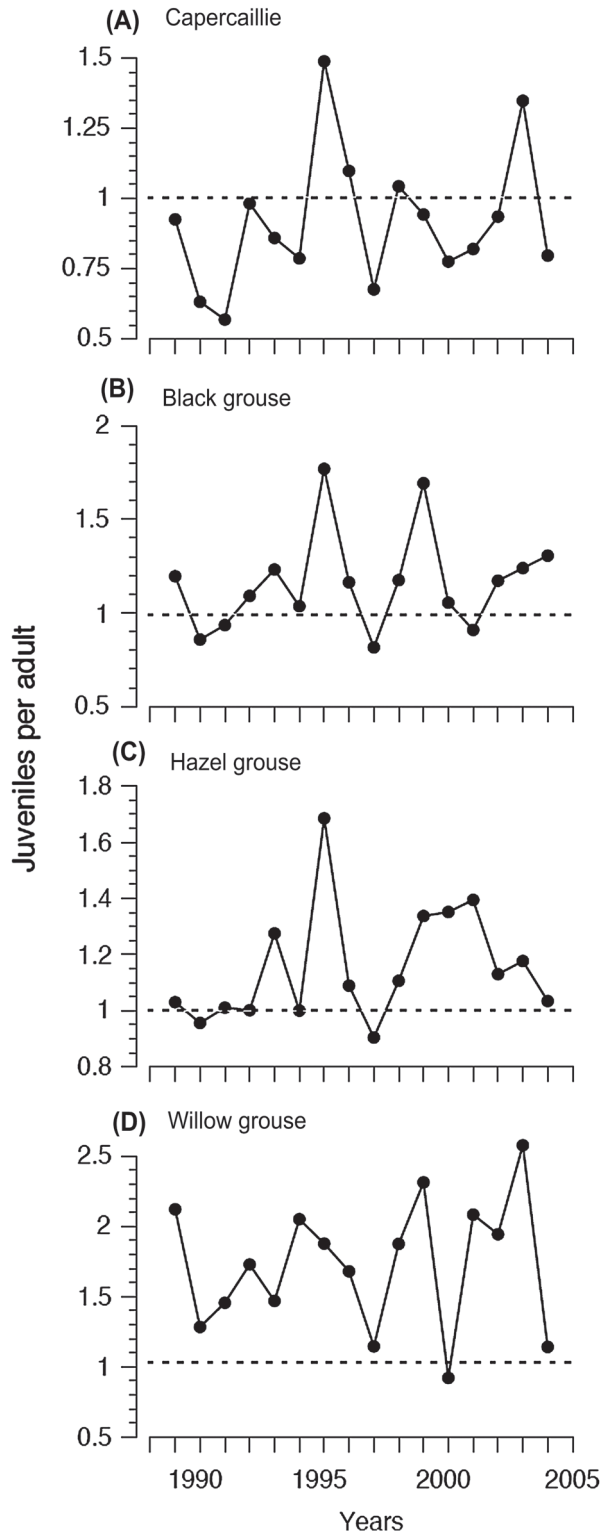


Figure 2. Number of juveniles per adult bird in 1989–2004 in the August censuses in Kainuu, northeastern Finland: (A) capercaillie, (B) black grouse, (C) hazel grouse and (D) willow grouse.

there was a tendency to harvest more declining populations than increasing ones, although the trend was significant for the willow grouse only (Table 2). Only the willow grouse populations seemed to grow faster after heavy hunting mortality.

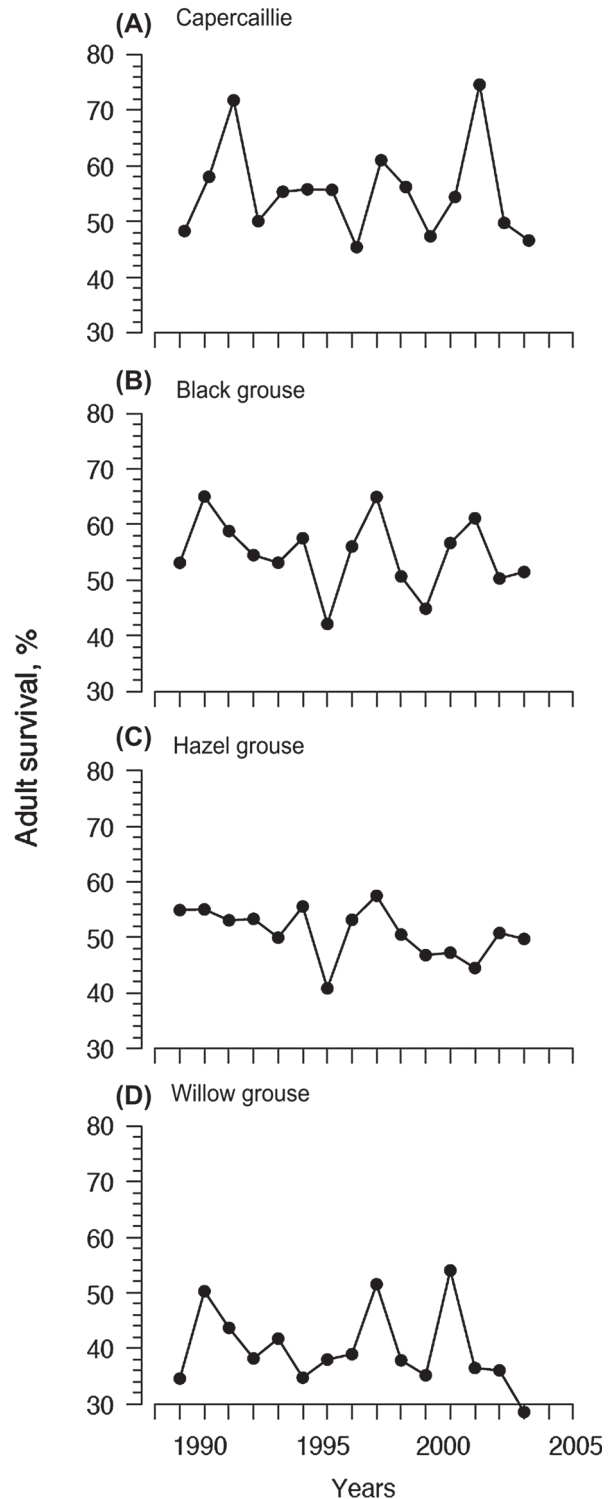


Figure 3. Adult survival in (A) capercaillie, (B) black grouse, (C) hazel grouse and (D) willow grouse in 1989–2004 in Kainuu, northeastern Finland.

## Discussion

As expected, all four species needed lag terms in their dynamics (first order for black and willow grouse, second order for capercaillie and hazel grouse). A much more important finding is that



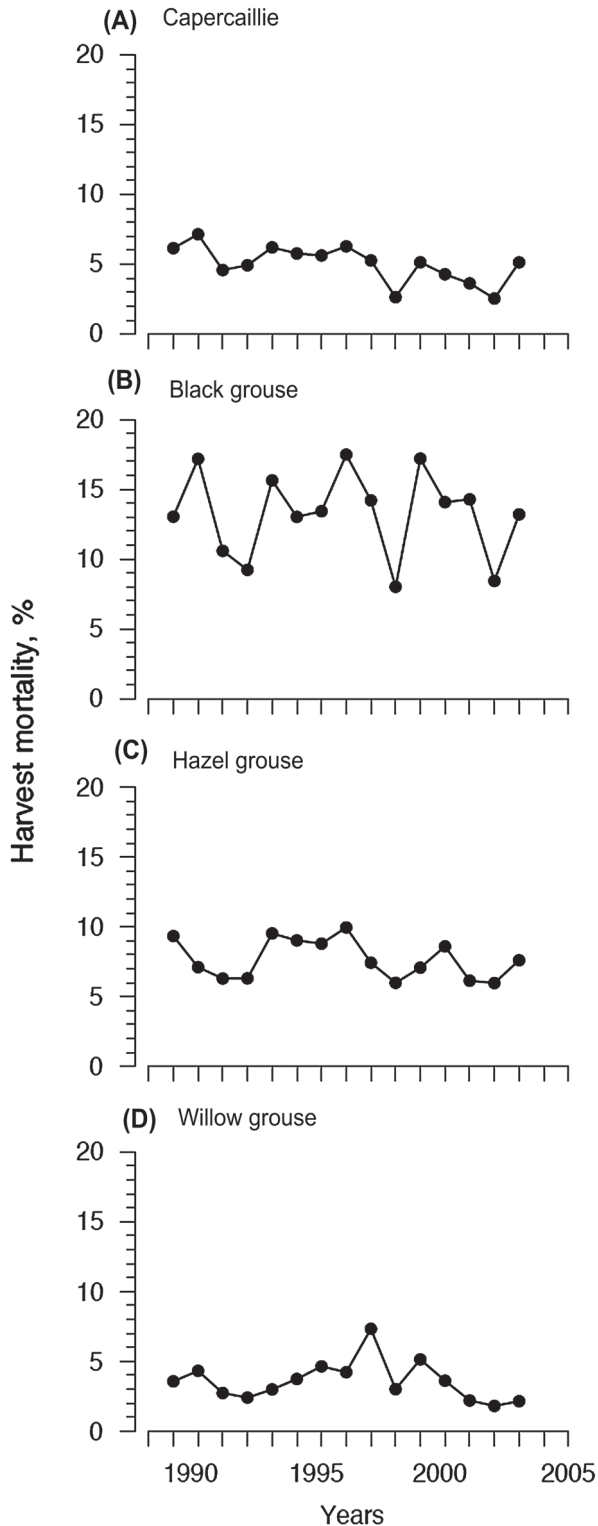


Figure 4. Harvest mortality in (A) capercaillie, (B) black grouse, (C) hazel grouse and (D) willow grouse in 1989–2003 in Kainuu, northeastern Finland.

all species also needed a negative harvesting term. Particularly for the black grouse, hunting seemed to strongly affect populations in the following year. Thus, it seems possible that harvesting plays a significant role in grouse dynamics in Kainuu. Current 3–4 year (vs 6–7 year cycles in the past) population cycles may well be at least partly harvest-induced.

Table 2. Regression coefficients to examine if large populations have been harvested more than small, if increasing populations have been harvested more than declining, and if large harvesting mortality results in more larger rate of increase in the four grouse species. Statistically significant regressions ( $p < 0.05$ ) are given in boldface.

Species	Harvest mortality $H(t)$ vs population size $X(t)$	Harvest mortality $H(t)$ vs population change $X(t-1) - X(t)$ to $t$	Harvest mortality $H(t)$ vs population change $X(t+1) - X(t)$
Black grouse	-0.220	-0.483	-0.156
Capercaillie	0.088	-0.422	-0.345
Hazel grouse	0.146	-0.374	-0.004
Willow grouse	-0.463	<b>-0.572</b>	<b>0.699</b>

Jonzen et al. (2003) and Ranta et al. (2006) demonstrated that harvesting as an external force can alter population dynamics so that stable population becomes fluctuating in a manner that we see in our study populations.

It was not totally unexpected to see that the importance of the winter severity index was fairly low for the black grouse, hazel grouse and capercaillie (Lindén 1981b), but high importance for the willow grouse was unexpected. Especially so, because based on morphological features, willow grouse could be considered to be best adapted to winter conditions (white winter plumage and feathered feet not shown by other three species). It is possible that winter severity is correlated with some other factors which, rather than cold weather per se, is limiting willow grouse survival.

The harvesting of Kainuu grouse population did not seem to follow the given guidelines and the current harvesting strategy is apparently suboptimal: the proportion of shot birds was not dependent on population size. Further, declining populations tended to have been harvested more than increasing, which could have a destabilizing effect on grouse population dynamics (Kaitala et al. 1996). The changing of harvesting strategies could result in both an increased hunting bag and small risk of population decline. This would require fast incorporation of results from August censuses into the local hunting quota and willingness to use the latest census results in the decision making.

The proportion of grouse hunted with respect to population density seems to have markedly changed during the past decades in Finland. During 1964–1972, the proportion of individuals hunted followed nicely the recommended way: increasing populations were hunted much more intensively than decreasing ones at the same density (Lindén 1981b). This pattern has since collapsed (Lindén 1991) and the present study suggests rather the opposite. Interestingly, in the past hunters behaved as ‘prudent’ predators, since they seemed to be able to adjust their hunting to prevailing grouse densities and even the phase of population cycle without a delay. This is probably because at that time populations were clearly cyclic and hunters knew beforehand what they would expect during the hunting season. Natural grouse predators, such as goshawk hunt decreasing populations more effectively than increasing ones as a result of a time delay (Lindén and Wikman 1990).

Our results suggest that in the Kainuu willow grouse population growth rate was positively associated with harvest mortality. Thus, harvest mortality in this species, but

not in other grouse, seemed to be at least partially compensatory. Two studies on willow grouse (Smith and Willebrand 1999, Pedersen et al. 2003) have suggested that in these cases the hunting mortality has been apparently mostly additive, opposite to the very basic idea of sustainable harvesting. Possible explanation for the difference in results is the lower harvest mortality rates in our case (experimental harvesting of 0%, 15% and 30% in Pedersen et al. 2003; up to 24% in Smith and Willebrand 1999 and < 8% in this study).

Even though hunting reduced grouse populations in Kainuu, it has not caused a declining trend in any of the species (Fig. 1). We therefore conclude that grouse populations in Kainuu have been exploited in a sustainable (definitions in Sutherland 2001) but not in an optimal way. However, this conclusion should be taken with caution for two reasons. First, there is possibly source–sink dynamics in Kainuu grouse populations that might be difficult to detect in census data. Thus, harvested populations in Kainuu may depend on immigration from the surrounding source areas. There is, however, no indication that grouse densities are significantly higher in the Russian Karelian forests, or in the surrounding Finnish areas (Rajasärkkä 2004). Second, potentially increased instability and variation due to hunting may cause an increased extinction risk in local grouse populations even though the current population trend is not clearly declining.

We recommend that in our study area far more care should be taken when deciding the hunting quotas for grouse species. It must be noticed that the hunting recommendations and quotas are fully voluntary except for visitors in state owned lands. Giving reliable recommendations is a challenging task, as there is only c. three weeks between the census and hunting seasons. At that point, licenses to the state owned land are already sold, therefore the only limitation methods are the recommendations to hunting clubs and individual hunters and changes to the length of hunting season. Predicting the following years' grouse population based on censuses has become more difficult since the fairly easily predictable cycles have disappeared. Therefore, a lot of responsibility goes to local hunting clubs, which need to be provided good and reliable data on population fluctuations. It is very important to stress that sometimes restrictions are for the best interest of both grouse and their hunters.

Further lesson from our study is that harvested populations may be significantly affected by hunting, even if they do not show declining pattern. Effect of harvesting may show as a modified population fluctuation pattern and can cause increased regional extinction probability.

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