

Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan

Brett K. Sandercock^{1,2*}, Erlend B. Nilsen², Henrik Brøseth² and Hans C. Pedersen²

¹Division of Biology, Kansas State University, Manhattan, KS 66506, USA; and ²Terrestrial Division, Norwegian Institute for Nature Research (NINA), Tungasletta 2, 7485 Trondheim, Norway

Summary

1. The effects of harvest on the annual and seasonal survival of willow ptarmigan *Lagopus lagopus* L. were tested in a large-scale harvest experiment. Management units were randomly assigned to one of three experimental treatments: 0%, 15% or 30% harvest. Seasonal quotas were based on the experimental treatment and estimates of bird density before the hunting season. Survival rates and hazard functions for radio-marked ptarmigan were then estimated under the competing risks of harvest and natural mortality.
2. The partially compensatory mortality hypothesis was supported: annual survival of ptarmigan was 0.54 ± 0.08 SE under 0% harvest, 0.47 ± 0.06 under 15% harvest, and was reduced to 0.30 ± 0.05 under 30% harvest. Harvest mortality increased linearly from 0.08 ± 0.05 , 0.27 ± 0.05 and 0.42 ± 0.06 from 0% to 30% harvest, whereas natural mortality was 0.38 ± 0.08 , 0.25 ± 0.05 and 0.28 ± 0.06 under the same treatments.
3. Realized risk of harvest mortality was 0.08–0.12 points higher than our set harvest treatments of 0–30% because birds were exposed to risk if they moved out of protected areas. The superadditive hypothesis was supported because birds in the 30% harvest treatment had higher natural mortality during winter after the hunting season.
4. Natural mortality was mainly because of raptor predation, with two seasonal peaks in fall and spring. Natural and harvest mortality coincided during early autumn with little potential for compensation during winter months. Peak risk of harvest mortality was 5× higher than natural mortality. Low natural mortality during winter suggests that most late season harvest would be additive mortality.
5. Environmental correlates of natural mortality of ptarmigan included seasonal changes in snow cover, onset of juvenile dispersal, and periods of territorial activity. Natural mortality of ptarmigan was highest during autumn movements and nesting by gyrfalcons *Falco rusticolus* L. Mortality was low when gyrfalcons had departed for coastal wintering sites, and during summer when ptarmigan were attending nests and broods.
6. Our experimental results have important implications for harvest management of upland gamebirds. Seasonal quotas based on proportional harvest were effective and should be set at $\leq 15\%$ of August populations for regional management plans. Under threshold harvest of a reproductive surplus, 15% harvest would be sustainable at productivity rates ≥ 2.5 young per pair. Impacts of winter harvest could be minimized by closing the hunting season in early November or by reducing late season quotas.

Key-words: grouse, hazard function, Norway, partially compensatory mortality, seasonal survival, superadditive mortality

*Correspondence author. E-mail: bsanderc@k-state.edu

Introduction

A central goal in animal ecology is to understand the interactive effects of harvest and natural mortality on exploited populations of vertebrates (Boyce, Sinclair & White 1999). A key question of theoretical and applied interest is whether harvest mortality is additive to natural mortality rates, or whether density-dependent changes in natality, age at maturity, survival or movements can compensate for losses to harvest (Burnham & Anderson 1984; Nichols *et al.* 1984; Conroy & Kremenetz 1990; Lebreton 2005). Five hypotheses have been proposed to explain the relationship between annual survival (S_a) and harvest mortality (K), and can be expressed by the equation $S_a = S_o(1 - bK)$, where S_o is the baseline survival rate in the absence of harvest, and b is a slope coefficient linking harvest mortality to annual survival (Fig. 1). The *additive mortality hypothesis* predicts that reductions in annual survival are directly related to increases in harvest mortality ($b = 1$). In contrast, the *compensatory mortality hypothesis* predicts that low rates of harvest mortality should have no effect on annual survival ($b = 0$) up to a threshold set by the natural mortality rates ($c = 1 - S_o$), above which harvest mortality should be additive. A third hypothesis, the *partially compensatory mortality hypothesis* predicts an intermediate response; harvest mortality may be additive, but the degree of compensation is greater at low levels of harvest mortality. Under sequential density dependence, carry-over effects link demographic rates in different seasonal periods and can lead to population responses outside the bounded continuum between additivity and compensation. The *superadditive (or depensatory) hypothesis* posits that harvest can cause additional natural mortality ($b > 1$, Kokko 2001; Liermann & Hilborn 2001), which may occur if social structure is disrupted (Milner, Nilsen & Andreassen 2007; Pauli & Buskirk 2007) or if crippling loss is increased (Servanty *et al.* 2010). Alternatively, the *overcompensation hypothesis* predicts that low rates of harvest can increase survival ($b < 0$, Boyce *et al.* 1999; Ratikainen *et al.* 2008), which may occur if harvest reduces the density-dependent effects of competition (Benton, Cameron & Grant 2004; Zipkin *et al.* 2008). Understanding the effects of harvest mortality on annual survival and identifying thresholds for additive mortality are critical to development of sustainable harvest strategies. A sustain-

able strategy should optimize yields but minimize risk of depletion, whether the strategy is based on take of a constant number of individuals, a fixed proportion of the population, or a surplus above a predetermined threshold of escapement (Lande, Sæther & Engen 1997; Fryxell, Smith & Lynn 2005).

Five main factors determine the response of vertebrate populations to harvest under natural conditions. First, life-history strategies are important, with additivity and compensation predicted for wildlife species with slow and fast life histories, respectively (Conroy & Kremenetz 1990). Harvest mortality is more likely to be additive to natural mortality in wildlife species with high survival and low fecundity, because they have less capacity to compensate for harvest and other forms of mortality (Hamel *et al.* 2006; Sedingner *et al.* 2007; Reese & Connelly 2011). Conversely, wildlife species with high fecundity and low survival may be more likely to produce a reproductive surplus and thus have compensatory responses to harvest (Burger *et al.* 1994; Coulson, Milner-Gulland & Clutton-Brock 2000). Second, population status is relevant because compensatory mortality is predicted to arise because of density-dependent changes in natural mortality (Nichols *et al.* 1984). Populations at or above carrying capacity should have greater ability to compensate for harvest, whereas harvest mortality is more likely to be additive in low-density or declining populations (Bartmann, White & Carpenter 1992). Third, the impacts of harvest will be mediated by seasonal timing in harvest and natural mortality (Boyce *et al.* 1999; Kokko 2001; Ratikainen *et al.* 2008). Additivity is more likely if harvest mortality overlaps or follows periods of natural mortality, but will be compensatory if harvest precedes seasonal periods of high natural mortality (Clark 1987; Pollock *et al.* 1989; Hudson, Newborn & Robertson 1997). Fourth, individual heterogeneity in survival and vulnerability to harvest is common in wildlife populations and can lead to apparent compensation, hampering detection of additive mortality (Dufour, Ankney & Weatherhead 1993; Lebreton 2005). Thus, it is important to control for sex, age and other factors affecting vulnerability to natural and harvest mortality. Last, animal movements may influence the effects of exploitation on open populations. Compensation can occur if dispersal leads to demographic rescue in spatially structured populations (Smith & Willebrand 1999; Martin,

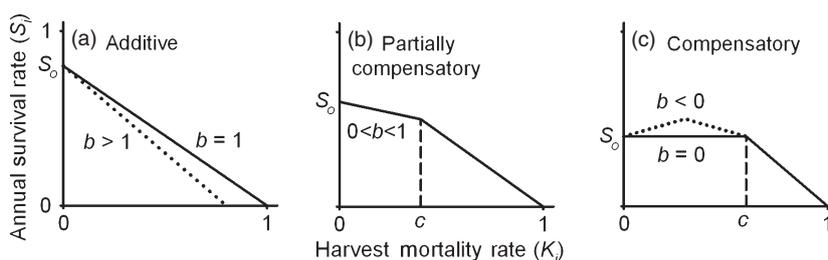


Fig. 1. Hypotheses for the effects of harvest mortality (K) on the annual survival (S) of exploited populations of animals. The (a) additive mortality hypothesis predicts that annual survival should decline with harvest ($b = 1$), the (b) partially compensatory mortality hypothesis predicts an intermediate response ($0 < b < 1$) and the (c) compensatory mortality hypothesis predicts that annual survival should be unaffected by harvest ($b = 0$), up to a threshold (c), determined by the complement of the baseline survival of an unharvested population ($c = 1 - S_o$). Models with sequential density dependence predict that the effects of harvest can be superadditive ($b > 1$) or lead to overcompensation ($b < 0$).

Stacey & Braun 2000; Cooley *et al.* 2009; Kvasnes *et al.* 2010). On the other hand, harvest may have additive effects on populations in poor-quality patches or in fragmented landscapes, or in species with weak dispersal ability (Small, Holzwardt & Rusch 1991; Guthery, Peterson & George 2000; Humberg, Devault & Rhodes 2009).

Field tests of the hypotheses for the effects of harvest on terrestrial vertebrates have generally taken one of three approaches. Population counts in areas with different levels of hunting pressure have been widely used to assess the impacts of harvest on population dynamics of gamebirds (Palmer & Bennett 1963; McGowan 1975; Bergerud 1985; Mentis & Bigalke 1985; Stoll & Culbertson 1995; Connelly *et al.* 2003; Pedersen *et al.* 2004). Population counts are less intensive than estimation of demographic parameters from marked individuals, but cannot be used to disentangle the relative contributions of natality, survival and movements to changes in population size. Analyses of counts also have several statistical pitfalls (Anderson & Burnham 1981; Sedinger & Rotella 2005; Sedinger *et al.* 2010). A second approach has been to use mark-recapture models for dead recovery data to estimate survival rates under different harvest regulations (Nichols *et al.* 1984; Pollock, Conroy & Hearn 1995; Aebischer, Potts & Rehfisch 1999; Schaub & Lebreton 2004; Lebreton 2005; Sedinger *et al.* 2010). Dead recovery data will be the best information for migratory species, but observational analyses cannot support causal inference (Nichols *et al.* 1984; Nichols & Johnson 1989; Rexstad 1992), and hypothesis testing is challenging if independent estimates of harvest are unavailable (Otis 2002), or if harvest regulations track population size (Sedinger & Rexstad 1994; Sedinger & Rotella 2005; Sedinger *et al.* 2007). Analyses of dead recovery data can be informative if combined with experimental harvest scenarios and Bayesian approaches for assessing the process correlations among recovery and cause-specific mortality rates (Sedinger *et al.* 2010; Servanty *et al.* 2010).

A third approach has been to conduct harvest experiments based on treatment and control areas with randomization and replication. Manipulations of exploitation have frequently been proposed for animal populations, but logistical, financial and political constraints have limited tests to relatively few species (Nichols & Johnson 1989; Ellison 1991; Burger *et al.* 1994). Early experiments examined survival of upland gamebirds in response to gradients of harvest risk such as distance from roads (Fischer & Keith 1974; Small *et al.* 1991) or duration of hunting season (Pack *et al.* 1999). Other field experiments have used protected and hunted areas to examine the effects of harvest on survival of radio-marked birds (Smith & Willebrand 1999; Williams, Lutz & Applegate 2004; Duriez *et al.* 2005; Buenestado *et al.* 2009), and mammals (Bartmann *et al.* 1992; Boland & Litvaitis 2008; Obbard & Howe 2008; Cooley *et al.* 2009). These studies improve on analyses of dead recoveries by use of experimental protocols, but most were unable to regulate levels of harvest in hunted areas, did not assign treatments at random and had little to no replication.

Here, we report on the results of a large-scale harvest experiment designed to examine the links among harvest, predation and patterns of seasonal and annual survival in exploited populations of willow ptarmigan *Lagopus lagopus* L. Willow ptarmigan and red grouse *L. l. scoticus* (Latham) are important birds for recreational and subsistence hunting throughout their circumpolar range (Jenkins, Watson & Miller 1963; Weeden 1963; Bergerud 1970; Myrberget 1976; Pedersen & Karlsen 2007). In previous work, we showed that hunting disturbance has no effect on ptarmigan dispersal but increases use of cover by birds in hunted areas (Brøseth & Pedersen 2000, 2010; Brøseth *et al.* 2005). Pedersen *et al.* (2004) examined the effects of experimental harvest on population counts and found evidence for the partially compensatory hypothesis, with compensation accounting for one-third of the harvest mortality at harvest rates < 30% (but see Sedinger *et al.* 2010). Similarly, Smith & Willebrand (1999) compared survival of radio-marked ptarmigan in hunted and unhunted areas and reported that harvest mortality of 0–24 was additive. Here, we examine the impacts of harvest on survival (Fig. 1) by monitoring radio-marked ptarmigan within a subset of the same experimental treatments used by Pedersen *et al.* (2004). We focus solely on the impacts of harvest on survival because clutch size, nest survival and brood survival show little evidence of density-dependence in ptarmigan (Bergerud 1970; Watson *et al.* 1984; Myrberget 1988), although compensatory natality may be important in other gamebirds (Ellison 1991; Bro *et al.* 2003). We apply new statistical models designed for staggered entry telemetry data to estimate survival rates and hazard functions under the competing risks of harvest and natural mortality (Heisey & Patterson 2006). Our three objectives were (i) to test five competing hypotheses (superadditive, additive, partially compensatory, compensatory and overcompensation) for the effects of experimental harvest on ptarmigan survival rates, (ii) to determine seasonal and annual patterns of harvest and natural mortality and (iii) to develop improved recommendations for management of willow ptarmigan and other upland gamebirds.

Materials and methods

STUDY AREA AND STUDY SPECIES

The 3-year study was conducted during August 1996–July 1999 in a 121.8-km² area in the municipalities of Meråker (Nord-Trøndelag county) and Selbu (Sør-Trøndelag county), central Norway (Fig. S1, Supporting information, 63°10′–63°20′N, 11°30′–11°45′E). The study area is a mid elevation site (600–800 m) at the boundary between the northern boreal and low alpine ecoregions. The vegetation is dominated by scattered forests of mountain birch *Betula pubescens* Ehrh. and spruce *Picea abies* (L.), shrub patches of dwarf birch *B. nana* L. and willows *Salix* spp., and a field layer of sedges, grasses, and ericaceous plants. At higher elevations, dwarf birch heath is interspersed with moraine ridges with lichens and sedges. The climatic conditions average 140 days per year with temperatures > 6 °C and annual precipitation between 100 and 150 cm. Snow cover at the study area is 1–3 m deep during winter and persists from

early October to late May. The main predators in the study area capable of killing ptarmigan were gyrfalcons *Falco rusticolus* L. and golden eagles *Aquila chrysaetos* (L.), with occasional observations of goshawks *Accipiter gentilis* (L.), red foxes *Vulpes vulpes* (L.), and ermine *Mustela erminea* L. Scavengers that might feed on carcasses of dead ptarmigan included ravens *Corvus corax* L., hooded crows *Corvus cornix* L., and pine martens *Martes martes* (L.), with rare sightings of Eurasian jays *Garrulus glandarius* (L.), magpies *Pica pica* L., and wolverines *Gulo gulo* (L.).

Ptarmigan were monitored year-round in our field study. The first week of our study year was set to be 13–19 August when juveniles were first captured for radio-marking. The hunting season was open from 10 September to 31 October in our experimental units. Juvenile ptarmigan remained close to their natal territories until the end of September, but started natal dispersal movements in early October (Brøseth *et al.* 2005; H. Brøseth & H.C. Pedersen, unpublished data). Adult ptarmigan were sedentary year-round, and males defended territories in autumn (Pedersen, Steen & Andersen 1983; Rørvik, Pedersen & Steen 1998; Brøseth *et al.* 2005). In the nonbreeding season from mid-October to mid-March, adults moved up to 2–4 km and formed small flocks of < 10 birds, especially during periods of inclement winter weather. The breeding season included a spring period of territorial activity from mid-March to mid-May (Pedersen *et al.* 1983) and a summer nesting and brood-rearing period from mid-May to mid-August (Erikstad, Pedersen & Steen 1985; Munkebye *et al.* 2003).

FIELD METHODS

Willow ptarmigan were captured for this study during two periods of the year. Incubating females were trapped at the nest during June or July, and both adults and juvenile birds aged 1–2 months old were captured in August using trained pointing dogs and large V-nets (Brøseth *et al.* 2005; Brøseth & Pedersen 2010). In late winter, ptarmigan were captured at night during March and April with handheld spotlights and long-handled dip nets from snowmobiles. At first capture, we sexed and aged ptarmigan as juveniles (< 12 months) or adults (> 12 months) by plumage coloration, wing and tail length, and patterns of pigmentation in the outer primaries (Bergerud, Peters & McGrath 1963). Each bird was marked with a uniquely numbered leg ring and a necklace radio-transmitter equipped with 3-h mortality sensors and an expected battery life of 12 or 24 months. Radio-transmitters were light-weight at 10–12 g (Lotek, Televilt) or 15–16 g (Bio-track), and in all cases, they were < 4% of the body mass of captured ptarmigan. Our survival data were based solely on radio-marked birds, which could be a concern if transmitters were a handicap that differentially affected the cause-specific risks of mortality (Besnard, Novoa & Gimenez 2010; Sedinger *et al.* 2010). The best controlled experiments with large samples and modern analytical approaches have found no evidence that necklace collars affect survival rates in upland gamebirds (Palmer & Wellendorf 2007; Terhune *et al.* 2007). Our estimates of survival should be unbiased, because four independent studies have shown that necklace radios have little to no effect on the demographic parameters or movements of ptarmigan under natural conditions (Erikstad 1979; Cotter & Gratto 1995; Thirgood *et al.* 1995; Hannon, Gruys & Schieck 2003).

Radio-marked birds were located by approaching the birds on the ground with portable receivers and by conducting radio-triangulation at distances of 50–100 m without flushing the birds. All positions were recorded in UTM coordinates with handheld GPS receivers (Pedersen *et al.* 1999; Brøseth & Pedersen 2000). Birds were checked weekly during May–October, daily during the 2-week period

following the start of the hunting season on September 10, and every 2–4 weeks during the winter months of November–April. In addition, ptarmigan were located from small aircraft with flights over the study area at the start and end of the winter.

If radios were heard to be on mortality signal, we tried to locate the bird as quickly as possible to determine cause of death. *Harvest mortality* included radios recovered from birds shot by hunters, and occasional crippling mortalities where a bird was recovered dead during the hunting season with evidence of pellet damage to the transmitter or the body. In cases of natural mortality, we tried to determine cause of death from the carcass and associated sign at the kill site, recognizing that activity of scavengers can make it difficult to make unambiguous statements about causes of mortality (Hudson *et al.* 1997; Bumann & Stauffer 2002). *Natural mortality* events were classified as *raptor predation* if bird faeces were present, if the head or breast muscles were removed, or if feathers were plucked without evidence of chewing. We considered natural mortalities to be caused by *mammalian predation* if there were bite marks on the transmitter, tracks or scat at the kill site, or the whole carcass was cached underground. We considered deaths to be caused by *unknown predators* if the carcass was dismembered without other signs, or if evidence of both raptors and mammals were found at the recovery site. Deaths of *unknown cause* included cases where radios were recovered without any other sign, and cases where the radio was heard to be on mortality signal, but the battery failed before the carcass could be retrieved from under a snowdrift or another inaccessible site.

HARVEST EXPERIMENT

The study area was subdivided into five experimental management units ranging in size from 20.5 to 32.3 km². Densities of willow ptarmigan were estimated with line-transect methods based on distance sampling, and all transects were surveyed between 13 August and 9 September, immediately before the start of the hunting season (Pedersen *et al.* 2004). Transect lines were straight, followed elevational contours, and spaced 400 m apart (Fig. S1, Supporting information). Each transect line was traversed by a team of two volunteers with trained pointing dogs, and alternate lines were surveyed on the same day to minimize double-counting of birds. When ptarmigan were encountered, observers recorded group size, composition by sex and age-class and perpendicular distance from the transect line. Tests with radio-marked birds showed that the underlying assumptions of distance sampling were met: all birds on the transect line were detected, birds did not move during approach until flushed by the dog, and detection curves were a good fit to the distributions of perpendicular distance (Pedersen *et al.* 1999). August densities of ptarmigan in the five management units ranged from 7.6 to 19.8 birds per km² during 1996 and 1997, and from 13.4 to 34.0 birds per km² in 1998 (Table S1, Supporting information). Ptarmigan populations in Norway have had cyclic dynamics in the past, but changing environmental conditions have reduced the periodicity and the amplitude of peaks in population numbers since the mid-1980s (Kausrud *et al.* 2008).

We used proportional harvesting to set seasonal bag limits (hereafter ‘unit quotas’) for each management unit based on the August densities and three experimental harvest regimes (Lande *et al.* 1997; Fryxell *et al.* 2005). Each year, the five management units were assigned to one of three treatments: 0% harvest, 15% harvest or 30% harvest. Treatments were assigned at random the first year and then units were rotated through the alternate treatments. Annual survival rates of willow ptarmigan in Scandinavia range from 40% to 60% (Myrberget 1988; Steen & Erikstad 1996; Smith & Willebrand 1999),

and the high harvest treatment was set at 30% to be half of the expected annual mortality in a year of low survival (Hickey 1955). We set the intermediate harvest rate to be 15% to test for possible thresholds in compensatory survival between 0% and 30% harvest. Taking management unit 14 in 1996 as an example, line transect sampling yielded a density estimate of 17.9 birds per km² in August, for an estimated population of 406 birds in the 22.7 km² unit (Table S1, Supporting information). A 30% harvest treatment resulted in a unit quota of 122 birds, of which 114 birds were harvested for a realized harvest rate of 28.1%.

Management units with experimental harvest were leased by teams of hunters, who usually hunted in small groups accompanied by trained pointing dogs. Access in the five management units was controlled in cooperation with the landowners, Meraker Brug AS and Selbu Fjellstyre. Boundaries of management units were marked with bamboo poles, rivers, mountain tops and other natural geographical features. Management units with no harvest were closed to hunter access. We assessed hunter compliance with unit closures by monitoring hunting teams during the hunting season and by periodic spot checks after the hunting season had closed. In 1997, a subset of hunters carried GPS units for a study of spatial patterns of hunting effort and vulnerability to harvest (Brøseth & Pedersen 2000). All monitoring indicated that trespass by hunters into closed areas was rare.

The experimental hunting season opened on 10 September, and hunting teams were given a set quota for each management unit. Units were closed to harvest once the unit quota had been filled, and all experimental units were closed by 31 October to minimize differences in the duration of harvest. Hunting seasons for ptarmigan remained open until 28 February in adjacent state lands. If hunting teams were unsuccessful in harvesting their entire quota, project personnel conducted additional harvest within the experimental season to meet quotas. We inspected all harvested ptarmigan daily, recorded band and radio information, and sexed and aged birds by plumage or by necropsy. Levels of realized harvest were close to our target unit quotas for both the 15% (overall = 17.9%, range = 11.6–24.2%) and the 30% experimental treatments (overall = 28.6%, range = 10.8–48.2%), with some spatial and temporal variation caused by differences in terrain and hunter experience (Table S1, Supporting information). The surrounding area within 30 km of our five management units was contiguous habitat similar to our study area and open for hunting of ptarmigan.

SURVIVAL ANALYSES

We analysed seasonal survival of ptarmigan on a weekly time step. We estimated the weekly survival of willow ptarmigan in response to experimental harvest in the management units with time to event models based on known fate radio telemetry data and staggered entry of marked birds (Heisey & Patterson 2006; Murray 2006). We created encounter histories for each radio-marked bird with four variables: the first week that the bird was marked and entered the study population (Ent), the last week that the bird was detected and exited the study population (Exit), the fate of the bird at last detection (where 0 = survived and 1 = died), and the cause of mortality for birds that died (harvest or natural causes). For birds that survived, the exit date was the last week that the bird was detected alive. For birds that were shot, the exit date was the week that the bird was harvested and reported by the hunter. For birds that died of natural causes, the exit date was calculated as the midpoint between the last week the bird was detected alive and the first week that the mortality signal was heard. Most birds were monitored for only a single study year, but if a radio-marked bird survived from one study year to the next, we created independent

encounter histories for each year and set the exit and entry dates in consecutive years to be weeks 52 and 0, respectively.

Our management units (> 20 km²) were larger than the average home range size of individual ptarmigan (*c.* 0.5 km², Brøseth & Pedersen 2010). Nevertheless, ptarmigan populations were not closed and birds could move freely in and out of the management units. Unit borders along water courses provided convenient boundaries for hunters but favoured movements because riparian vegetation was suitable habitat for ptarmigan on adjacent sides of unit boundaries. We assigned birds to management units by the site of capture, or in a few cases, by the majority of locations in their home range. Juveniles remained in the management unit closest to their capture site until late September and then started dispersal movements that potentially exposed them to harvest risk during movements through other management units. If a juvenile survived for more than a year and successfully recruited into our study area, we assigned them to a new management unit based on the locations of their adult home range after settlement. For birds marked as adults, capture site and adult home range were in the same management unit for more than > 90% of all birds. In a few cases where adults were captured in winter or at a unit boundary, we assigned birds to management units based on their home range during the breeding season.

We used continuous-time models to estimate survival rates and hazard functions for ptarmigan, implemented with functions in the statistical packages of Program R (ver. 2.9.2, R Foundation for Statistical Computing, Vienna, Austria). Our initial goal was to estimate survival rates separately for each management unit by year, but our samples of radio-marked birds were not sufficient for this purpose ($n < 30$ in 10 of 14 units, Table S1, Supporting information). We opted to pool across management units and years to increase sample size, and our results should be robust to temporal and spatial heterogeneity because we combined data from 3 years of study in five management units (Fig. S1, Supporting information). Some ptarmigan were monitored in multiple years, and we included individual as a random effect in the models of Cox proportional hazards to control for potential lack of independence among encounter histories in different years. Cumulative survival per harvest treatment was estimated with staggered-entry Kaplan–Meier models (survival package, Pollock *et al.* 1989). We then estimated cause-specific cumulative mortality rates because of harvest and natural causes with the non-parametric cumulative incidence function estimator (NPCIFE), a generalization of the Kaplan–Meier method for competing risks (code adapted from Appendix of Heisey & Patterson 2006). Risk factor analyses for survival and cause-specific mortality were conducted using Cox proportional hazards (Lunn & McNeil 1995; Murray 2006). In a first step, we checked whether the assumption of proportional hazards was met by our survival data with model diagnostics based on scaled Schoenfeld residuals (cox.zph function, Fox 2002). Dummy variables were used to model the effects of harvest treatment, sex (male = 0, female = 1), and age-class (juvenile = 0, adult = 1). Hazard functions were estimated separately for all mortality causes combined, harvest mortality and natural mortality with smoothing spline functions (gss package, DelGiudice *et al.* 2006). We reduced the default value for the smoothing parameter from 1.2 to 0.5 at a risk of overfitting. All tests were two-tailed and considered significant at α -levels ≤ 0.05 .

Results

In the 3-year study, we radio-marked a total of 206 willow ptarmigan, which were monitored for 297 bird-years. We

discarded information from 25 individuals and 28 bird-years: birds that died from injuries during handling, birds that could not be monitored because the radio transmitter or battery failed, and birds that could not be assigned to a harvest treatment because their home range was outside of the five management units. Thus, the sample for our survival analyses was based on 193 radio-marked ptarmigan and 269 bird-years. This sample included 105 females, 88 males and 76 juveniles, which were distributed among each of the three harvest treatments.

In our sample of 269 bird-years, 59% of birds survived and 41% died during the study period. Of birds that died ($n = 108$), 47% were shot by hunters and 53% died of natural causes. A majority of the birds shot by hunters were successfully retrieved in the field (93%, $n = 51$). Only four birds (7%) were not retrieved after hunters killed them during the hunting season. Three of four birds had pellet damage on the radio or carcass consistent with death by shooting. The last bird was recovered as an undamaged carcass during the experimental hunting season, but was considered to be a harvest mortality because deaths without apparent cause did not occur at other times of year. Of birds that died of natural causes ($n = 57$), cause of death could not be determined in 13 cases, because the radio was not retrieved after the mortality signal was heard, and in two cases because the radio was retrieved with no other sign. All remaining natural mortality events were attributed to predation ($n = 42$), with a majority of deaths caused by raptors (57%), and the remaining losses because of unknown predators (33%) and mammals (10%). Only one predator attack on a radio-marked bird was observed during the 3-year study, a ptarmigan that was killed in flight by a gyrfalcon.

We first considered the effects of sex and age on annual survival and cause-specific mortality. In a first set of analyses, we restricted our data set to adults and modelled annual survival as a function of harvest treatment and sex. Our survival data for adults met the assumption of proportional hazards for the global model ($\chi^2_4 = 2.1$, $P = 0.72$). Females and males did not differ in their overall hazard functions (hazard ratio [HR] = 0.8, 95% CI = 0.5–1.2, $z = -1.1$, $P = 0.28$). If we stratified by cause of death, females had a higher risk of harvest mortality than males (HR = 0.4, 95% CI = 0.2–0.9, $z = -2.2$, $P = 0.003$), but the sexes had the same risk of natural mortality (HR = 0.97, 95% CI = 0.5–1.8, $z = -0.1$, $P = 0.93$). We opted to pool sexes in the rest of our analyses, because we were primarily interested in the potential compensation of natural mortality for harvest mortality, and hunter selectivity should not affect our conclusions.

In a second set of analyses, we modelled annual survival of adults and juveniles as a function of harvest treatment and age-class. Our survival data met the assumption of proportional hazards for a global model with harvest treatments only ($\chi^2_2 = 3.1$, $P = 0.22$), but not if we added age-class to the model as well ($\chi^2_3 = 10.5$, $P = 0.015$). If we stratified by cause of death, the assumption of proportional hazards between juveniles and adults was met for harvest mortality

($\rho = -0.06$, $\chi^2_1 = 0.2$, $P = 0.66$), but not for natural mortality ($\rho = 0.35$, $\chi^2_1 = 6.0$, $P = 0.015$). Inspection of residual plots indicated that the risk of mortality was higher for juveniles during August and September but was then similar for the two age-classes after 2 months of monitoring. Accordingly, we retained age-class as a factor in our global model, but hazard ratios for age-class should be interpreted with caution, as model assumptions were not met.

Annual survival varied as a function of harvest treatment (analysis of deviance: $\chi^2_2 = 10.2$, $P = 0.006$) and age-class ($\chi^2_1 = 2.9$, $P = 0.09$). Differences among the experimental treatments were consistent with the partially compensatory mortality hypothesis (Fig. 1b). Annual survival of ptarmigan was 0.54 ± 0.08 SE in units closed to hunting, 0.47 ± 0.06 under 15% harvest, and was reduced to 0.30 ± 0.05 under 30% harvest (Fig. 2a). Compared to the 0% harvest treatment, mortality risk did not increase under 15% harvest (HR = 1.4, 95% CI = 0.8–2.4, $z = 1.2$, $P = 0.23$), but was significantly higher under 30% harvest (HR = 2.2, 95% CI = 1.3–3.7, $z = 2.9$, $P = 0.004$). The overall mortality risk tended to be higher among juveniles than adults, but the hazard ratio was not significantly different from one (0.70, 95% CI = 0.46–1.08, $z = -1.6$, $P = 0.11$).

We stratified by cause of death to determine if patterns of annual survival among the experimental treatments were determined by differences in harvest or natural mortality.

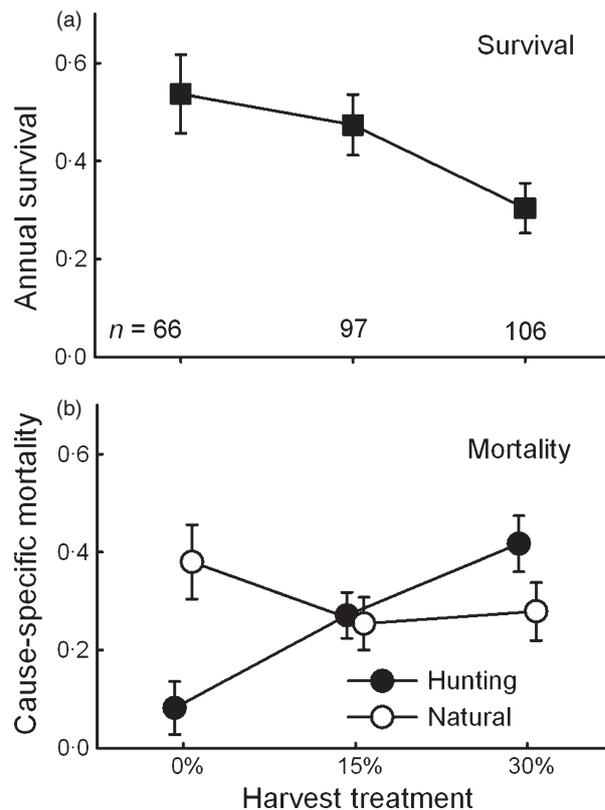


Fig. 2. (a) Annual survival rates (\pm SE) and (b) cause-specific mortality rates (\pm SE) of radio-marked willow ptarmigan exposed to three levels of experimental harvest at Meråker-Selbu, Norway, 1996–1998.

The risk of harvest mortality differed among the three experimental treatments ($\chi^2_2 = 19.3$, $P < 0.001$) and was also affected by age-class ($\chi^2_1 = 4.5$, $P = 0.034$). Harvest mortality risk was 8–12% higher than our set harvest treatments and increased linearly from 0.08 ± 0.05 in units with no hunting, 0.27 ± 0.05 under 15% harvest and 0.42 ± 0.06 under 30% harvest (Fig. 2b). Compared to the 0% harvest treatment, the risk of harvest mortality increased four-fold under 15% harvest (HR = 4.0, 95% CI = 1.3–12.0, $z = 2.4$, $P = 0.014$) and more than six-fold under the 30% harvest treatment (HR = 6.6, 95% CI = 2.4–18.1, $z = 3.7$, $P < 0.001$). Adults had a lower risk of harvest than juveniles (HR = 0.5, 95% CI = 0.3–0.9, $z = -2.2$, $P = 0.034$).

In contrast to the results for harvest mortality, the risk of natural mortality did not differ among the experimental treatments ($\chi^2_2 = 1.2$, $P = 0.55$) and were unaffected by age-class ($\chi^2_1 = 0.01$, $P = 0.92$). Natural mortality risk was 0.25 ± 0.05 and 0.28 ± 0.06 in units with 15% and 30% harvest, but was somewhat higher in units closed to hunting (0.38 ± 0.08 , Fig. 2b). Compared to the 0% harvest treatment, the overall risk of natural mortality was similar in both the 15% (HR = 0.8, 95% CI = 0.4–1.6, $z = -0.6$, $P = 0.54$) and 30% harvest treatments (HR = 1.1, 95% CI = 0.6–2.1, $z = 0.4$, $P = 0.72$). Adults and juveniles had the same risk of natural mortality (HR = 1.0, 95% CI = 0.6–1.9, $z = 0.1$, $P = 0.93$).

We examined seasonal survival rates and hazard functions to determine the potential for compensatory mortality as a response to autumn harvest. Our experimental hunting season lasted from 10 September to 31 October, but continued in the surrounding areas until 28 February. The steepest drops in cumulative survival occurred during the first 2–3 weeks of the hunting season (Fig. 3a–c), and weekly hazard functions were higher during the hunting season than at any other time of the year (Fig. 4a). Unexpectedly, reductions in cumulative survival also occurred in the 0% harvest treatment and were comparable to losses in the 15% harvest treatment (Fig. 3a,b). Cause-specific hazard functions confirmed that the risk of harvest was limited to the hunting season, and maximum hazard risk closely followed our three experimental treatments (Fig. 4b). Seasonal peaks in hazard functions for harvest were similar between the two harvest treatments, but were 1–2 weeks later in the 0% harvest when dispersing birds were exposed to risk of harvest. Overall differences between the maximum hazard for harvest mortality (c. 0.25, Fig. 4b) and natural mortality in three harvest treatments (c. 0.05, Fig. 4c) suggested that the mortality risk from teams of Norwegian hunters with trained dogs was roughly 5× greater than the risk of natural predators.

One seasonal period of natural mortality occurred in fall and overlapped with the fall hunting season, and a second period of similar magnitude occurred during the spring (Fig. 4c). To test for seasonal interactions between harvest and natural mortality, we used the 0% treatment as a baseline and tested the effects of harvest treatment on natural mortality of birds during the experimental hunting season from 10 September to 31 October ($n = 136$). Consistent with

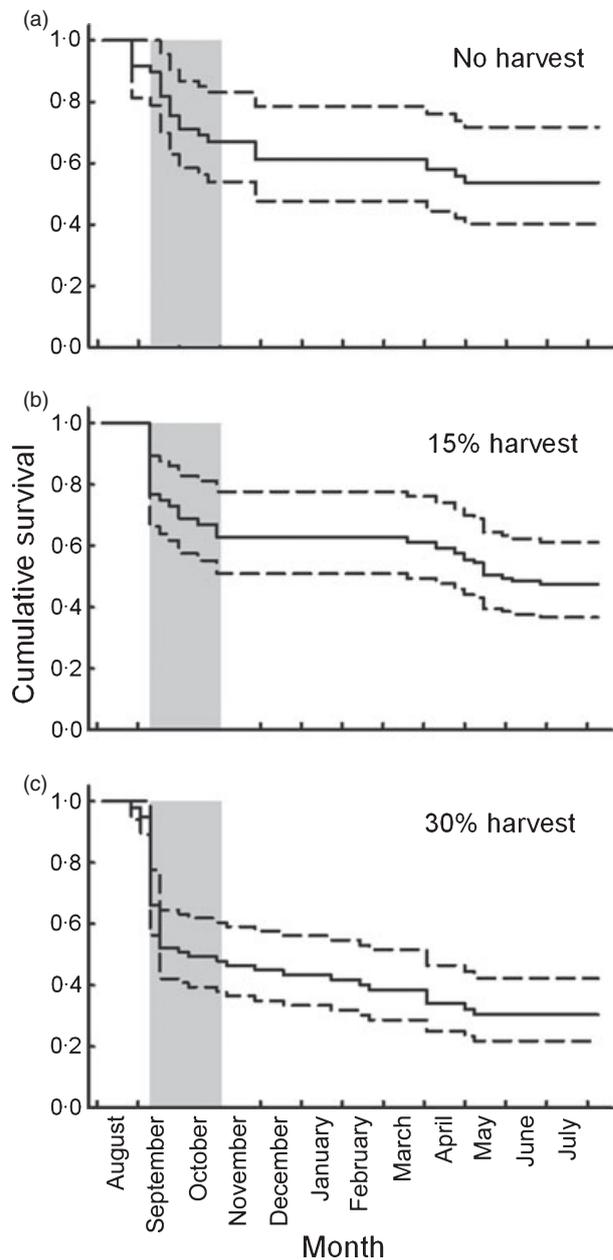


Fig. 3. Kaplan–Meier estimates of cumulative weekly survival ($\pm 95\%$ CI) under (a) 0% harvest, (b) 15% harvest or (c) 30% harvest for radio-marked willow ptarmigan at Meråker-Selbu, Norway, 1996–1998. Grey bars denote the duration of the experimental hunting season from 10 September to 31 October.

the partially compensatory hypothesis, the risk of natural mortality during the hunting season tended to be lower in the 15% treatment (HR = 0.4, 95% CI = 0.1–1.4) and also the 30% harvest treatment (HR = 0.2, 95% CI = 0.05–1.1). Overall, the risk of natural mortality of ptarmigan was > 3 times lower if a management unit was harvested (HR = 0.3, 95% CI = 0.1–0.9, $z = -2.1$, $P = 0.036$). Thus, cumulative survival rates of birds in the 0% harvest treatment dropped during fall because the risk of natural mortality was highest for this experimental treatment.

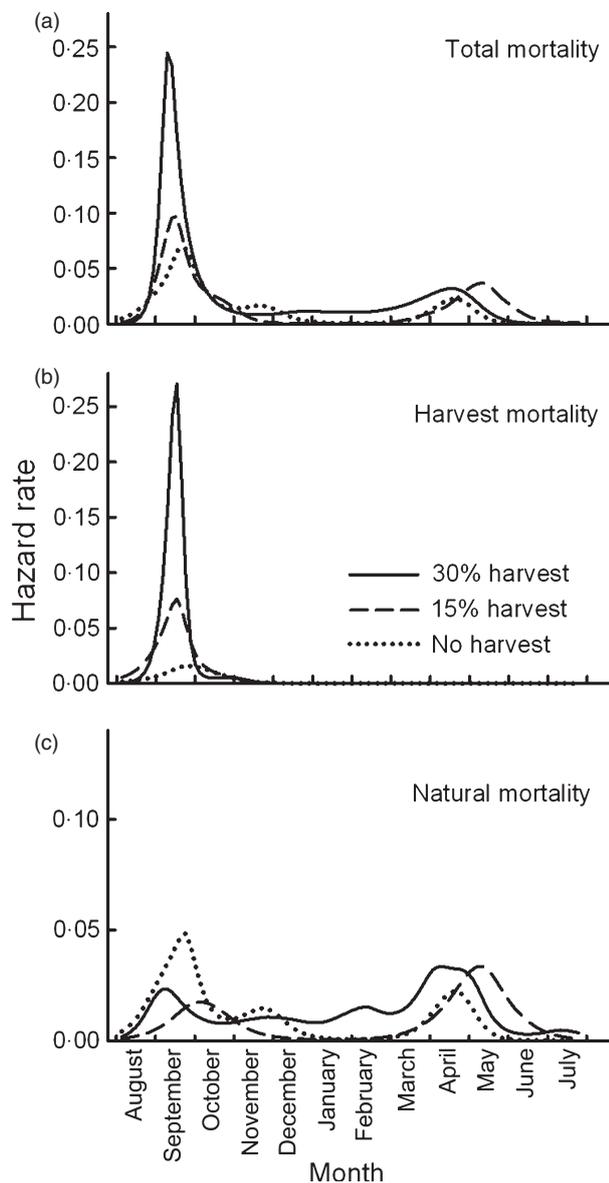


Fig. 4. Smoothed instantaneous hazard functions for (a) all mortality factors combined, (b) harvest mortality only and (c) natural mortality only, for the weekly mortality risk of radio-marked willow ptarmigan at Meråker-Selbu, Norway, 1996–1998.

Mortality was negligible among ptarmigan in units that had 0–15% harvest after conclusion of the experimental hunting season. Surprisingly, winter losses continued among birds that had been exposed to the 30% harvest treatment during the 4-month winter period from 1 November to 28 February (Fig. 3c). Weekly hazard functions for natural mortality were near zero at harvest rates $\leq 15\%$, but were *c.* 0.01–0.02 following 30% harvest (Fig. 4c). Numbers of radio-marked birds in our sample were lowest in the period between the end of the hunting season and the start of winter captures, and we opted to pool the 0% and 15% harvest treatments to examine lag effects of harvest on winter mortality during the 4-month winter period after the experimental harvest season ($n = 148$). Consistent with the superadditive

mortality hypothesis, the risk of natural mortality during winter was > 4 times higher among birds in the 30% harvest treatment than the 0–15% treatments (HR = 4.6, 95% CI = 1.4–15.0, $z = 2.5$, $P = 0.011$).

A second period of high natural mortality occurred during the 3-month spring period of mid-March to late May, with additional drops in cumulative survival (Fig. 3) that led to another seasonal peak in the hazard function for natural mortality (Fig. 4c). Hazard functions for natural mortality were similar among the three experimental treatments during spring. Little natural mortality occurred during nesting and brood-rearing activities in June to August, and hazard functions remained low during the summer months (Figs 3 and 4c).

To examine environmental correlates of seasonal variation in natural mortality, we pooled all harvest treatments and estimated hazard functions for natural mortality for ptarmigan at our mountain study site in central Norway. Weekly hazard values were > 0.01 during September–October, and again during late March–May (Fig. 5a). The two seasonal periods of mortality risk coincided with snowfall in autumn and snowmelt in spring (Fig. 5b), when birds were completing feather moult between the dark brown alternate plumage and the white basic plumage. With respect to the annual cycle of willow ptarmigan (Fig. 5c), the fall peak in natural mortality coincided with brood break-up and the onset of juvenile dispersal, and the start of fall territoriality among males. Hazard functions were low during winter when birds were moving about in small flocks, and also during summer when ptarmigan were attending nests and broods. Compared to the annual cycle of the gyrfalcon (Fig. 5d), peaks in the natural mortality of ptarmigan occurred during the juvenile dispersal of young falcons and during the early stages of the gyrfalcon breeding cycle. Hazard functions of ptarmigan were low when gyrfalcons would be caring for dependent young, and during winter when gyrfalcons had departed mountain territories for wintering sites at the coast.

Discussion

The effects of experimental harvest on the annual and seasonal survival rates of radio-marked willow ptarmigan provided strong support for the partially compensatory mortality hypothesis and confirmed our earlier conclusions based on analyses of population counts (Pedersen *et al.* 2004). Compared to areas protected from hunting, harvest mortality was partially compensated under 15% harvest but was additive under 30% harvest. We were unable to test the effects of radios on cause-specific mortality rates, and full compensation may occur at higher harvest rates if radios are a handicap (Sedinger *et al.* 2010). Overall, evidence for partial compensation was consistent with four of the main five factors that determine population responses of vertebrates to harvest: willow ptarmigan are a relatively short-lived gamebird with high fecundity, densities of birds were typical of mountain habitats in central Norway, sex and age-class created heterogeneity in mortality risk and movements linked

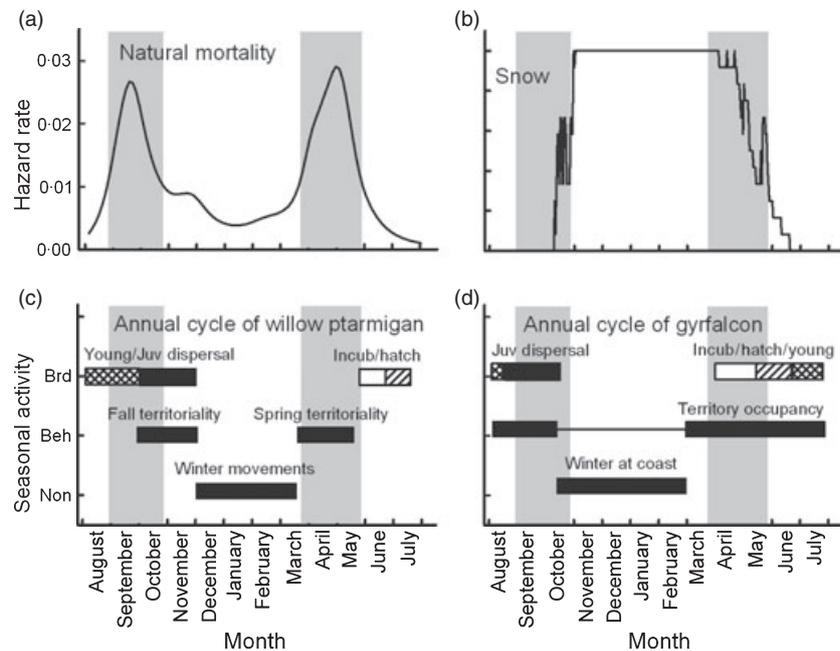


Fig. 5. Environmental correlates of seasonal variation in natural mortality, estimated by (a) smoothed hazard functions for all harvest treatments combined. (b) Average snow cover at Stuggusjøen Lake (730 m.a.s.l., 35 km south of Meråker-Selbu), 1996–1999. Seasonal timing of breeding, territorial behaviour, and nonbreeding activity of (c) willow ptarmigan (Pedersen *et al.* 1983; Erikstad *et al.* 1985; Munkebye *et al.* 2003) and (d) gyrfalcons in central Norway (Langvatn & Moksnes 1979; Tømmeraas 1989; Potapov & Sale 2005). Grey bars denote seasonal periods where the weekly hazard function was > 0.01 .

our experimental units to a larger contiguous region of suitable habitat. A prevailing view in wildlife management is that harvest mortality should precede periods of high natural mortality. Here, peaks in the cause-specific hazard functions unexpectedly coincided during the experimental hunting season and thus limited the seasonal potential for compensatory responses to harvest for Norwegian ptarmigan.

Densities, survival rates and social behaviour of ptarmigan at our study site were representative of conditions in mountain areas of Fennoscandia. Ptarmigan densities varied between 7 and 32 birds per km² at our study site in central Norway, which were comparable to densities of 10–33 birds per km² in similar habitat in Sweden (Aanes *et al.* 2002). The potential for compensatory and additive mortality may differ among populations of willow ptarmigan because densities are lower in arctic Canada (< 8 birds per km², Weeden 1963), but higher at coastal islands of Norway (40–110 pairs per km², Myrberget 1988), alpine sites in northern Canada (40–80 birds per km², Martin, Hannon & Rockwell 1989), and managed shooting estates in northern England and Scotland (40–200 birds per km², Jenkins *et al.* 1963; Hudson 1985).

Annual survival rates of willow ptarmigan in our 0–15% harvest treatments (0.47–0.54) were comparable to unhunted populations of willow ptarmigan (0.43, Sandercock, Martin & Hannon 2005; 0.44, Pedersen 1984; 0.52, Steen & Erikstad 1996; 0.53, Smith & Willebrand 1999), whereas annual survival rates of ptarmigan in the 30% harvest treatment (0.30) were comparable to other hunted populations (0.28, Smith & Willebrand 1999). Differences in annual survival among the experimental treatments were consistent with the hypothesis of partially compensatory mortality, with full to partial compensation at low harvest and additive mortality at high harvest. Our study population was nonmigratory and relatively sedentary over the year (Brøseth *et al.* 2005), and annual survival and impacts of harvest will likely differ for northern

populations of ptarmigan which migrate between separate breeding and nonbreeding areas (Irving *et al.* 1967; Myrberget 1976). Collection of ptarmigan into migratory flocks could increase regional harvest rates, whereas sexual segregation into different areas or habitats may expose sex and age-classes to different predator assemblages (Weeden 1964; Gruys 1993; Hannon *et al.* 2003; Schwab, Simon & Nash 2005).

HARVEST MORTALITY

Our experimental results for willow ptarmigan provided evidence for partial compensation under a 15% harvest rate and a harvest mortality of 0.27, and additive mortality under a 30% harvest rate and harvest mortality of 0.42. Previous studies have reported similar thresholds: harvest rates $> 10\%$ were partially compensated in red grouse (Hudson 1985), whereas harvest mortality of 0.24 was additive in willow ptarmigan (Smith & Willebrand 1999). Harvest mortality may have been additive to natural mortality in our experiment because realized harvest mortality rates were 0.08–0.12 points higher than our set harvest treatments of 0–30%. Our management units were considerably larger than the average home range of willow ptarmigan, but movements of birds out of protected areas exposed birds to higher risk of harvest. Movements out of reserves have been implicated in elevated mortality rates and population declines of wide-ranging species of animals (Woodroffe & Ginsberg 1998; Novaro, Redford & Bodmer 2000; Powell & Bjork 2004), and our results demonstrate that the same issue can apply to sedentary gamebirds. On the other hand, protected areas without harvest can be source populations that reduce extinction risk (Fryxell, Lynn & Chris 2006; Casas *et al.* 2009; Cooley *et al.* 2009) and have been proposed for sustainable management of willow ptarmigan (Willebrand & Hörnell 2001). Low levels

of harvest mortality for ptarmigan in 0% harvest treatments < 35 km² suggest that protected areas may need to be larger. Effective reserve design will need a better understanding of the effects of dispersal and migratory movements on spatial dynamics (Rørvik *et al.* 1998; Brøseth *et al.* 2005; Kvasnes *et al.* 2010).

Given a potential threshold for effects of harvest > 15% in willow ptarmigan, what harvest rates are likely to be sustainable for management? Recommended harvest rates covary with the life-history strategies of upland gamebirds and range from 50% to 70% for northern bobwhites *Colinus virginianus* (Guthery *et al.* 2000), 30–50% for white-tailed ptarmigan *L. leucura* and forest grouse (Braun & Rogers 1971; DeStefano & Rusch 1986; Ellison, Léonard & Menoni 1988), and 10–15% for large-bodied species including capercaillie *Tetrao urogallus* (Moss, Weir & Jones 1979), greater sage-grouse *Centrocercus urophasianus* (Sedinger *et al.* 2010), and wild turkeys *Meleagris gallopavo* (Pack *et al.* 1999). Comparative data from telemetry studies of upland gamebirds support our experimental results for ptarmigan by indicating that harvest may be additive at harvest rates > 20%. Harvest rates or harvest mortality < 20% are compensatory in chukars *Alectoris chukar* (2–14%, Robinson *et al.* 2009), greater sage-grouse (< 11%, Sedinger *et al.* 2010), ruffed grouse *Bonasa umbellus* (12%, Devers *et al.* 2007), and grey partridge *Perdix perdix* (≤ 20%, Watson *et al.* 2007). Conversely, harvest rates > 30% are additive in white-tailed ptarmigan (15–48%, Braun 1969 in Bergerund 1985), grey partridge (30%, Besnard *et al.* 2010), ruffed grouse (60%, Small *et al.* 1991), and northern bobwhite (60%, Williams *et al.* 2004). Lower harvest rates of 10–12% are additive in wild turkeys (Pack *et al.* 1999; Alpizar-Jara *et al.* 2001), which might be expected for a large-bodied gamebird.

Our results provided evidence for the superadditive hypothesis because the 30% harvest treatment had lag effects on winter survival not observed in units with lower rates of harvest. Two nonexclusive mechanisms may explain this result. First, lag effects could be a direct effect of sublethal wounding (Servanty *et al.* 2010). Holmstad (1998) collected ptarmigan by snaring in Øvre Dividal, a national park in northern Norway with high harvest pressure, and found that 14% of birds contained an average of 2.7 pellets per bird. This explanation seems unlikely in our project, because few of the ptarmigan killed by hunters were not retrieved (5–7%, Smith & Willebrand 1999; this study), but could be an issue if retrieval of downed birds is more difficult for gamebirds in forest or shrubland habitats (5–19%, DeStefano & Rusch 1986; Small *et al.* 1991; Burger *et al.* 1995). Second, lag effects could be an indirect effect of harvest disturbance. Raptors and other predators could have been attracted to management units with 30% harvest by the activity of pointing dogs and flushing birds (Ellis *et al.* 1993). Alternatively, the effects of harvest on habitat use by ptarmigan (Olsson, Willebrand & Smith 1996; Brøseth & Pedersen 2010) could have reduced survival through negative impacts on behaviour, physiology or body condition (Madsen & Fox 1995; Thiel *et al.* 2007).

NATURAL MORTALITY

A majority of natural mortality in our field study was because of predation by raptors, which is consistent with previous field studies of seasonal mortality in willow ptarmigan (Hudson *et al.* 1997; Smith & Willebrand 1999; Hannon *et al.* 2003), and annual mortality of upland gamebirds (Thirgood *et al.* 2000; Valkama *et al.* 2005; Watson *et al.* 2007). At least three species of raptors were observed in our study area, but gyrfalcons were likely the most important species as a specialist predator of ptarmigan in Scandinavia (Langvatn & Moksnes 1979; Nyström *et al.* 2005). Seasonal patterns of natural mortality for our study population at an inland site in Norway included a spring peak during mid-March to May and also an autumn peak during September to October. Smith & Willebrand (1999) also found that mortality rates of willow ptarmigan in Sweden were highest during autumn and low during the winter. Hannon *et al.* (2003) observed the highest rates of mortality during autumn for ptarmigan in northern Canada, with lower peaks in mortality during the breeding season for females, and during spring territoriality for males. Last, Hudson *et al.* (1997) collected carcasses of red grouse in northern England and Scotland and reported that seasonal mortality from predator and parasites was greatest during early spring.

A seasonal peak in autumn mortality might be expected if fall territoriality regulates population numbers (Jenkins *et al.* 1963). Fall territoriality is a feature of nonmigratory populations of willow ptarmigan and red grouse in the southern extent of their range, including central Norway, Scotland and Newfoundland (Pedersen *et al.* 1983), and has been implicated as a density-dependent mechanism capable of inducing population cycles (Mougeot *et al.* 2003; New *et al.* 2009). In this study, we found weak evidence that fall territoriality was associated with mortality risk, because hazard functions for natural mortality were declining during the onset of fall territoriality. Watson (1985) studied a high-density population of red grouse where predators were controlled and showed that autumn social status had a major effect on fitness of marked birds, with overwinter losses of 97% and 2% among nonterritorial and territorial individuals. In contrast, Park, Hurley & Hudson (2002) reported overwinter survival rates of 66% and 70% among nonterritorial and territorial birds in a population without predator control. Our experimental results are consistent with Park *et al.* (2002) in suggesting that territorial status may confer less of an advantage for ptarmigan in populations with high predation pressure.

The two seasonal peaks in the hazard functions for natural mortality were associated with environmental conditions and the timing of events in the annual cycles of ptarmigan and gyrfalcons. The first seasonal peak was associated with snowfall, the timing of brood break-up and the onset of juvenile dispersal in ptarmigan and movements of juvenile raptors. A second seasonal peak was associated with snowmelt, spring territoriality of ptarmigan and early stages of breeding in gyrfalcons. High mortality rates were associated with changing snow conditions and the timing of feather moult. It is unlikely

that environmental conditions and plumage determined predation risk alone because ptarmigan have behavioural adaptations to avoid detection. Females select habitat patches where their mottled plumage improves concealment (Steen, Erikstad & Høidal 1992), and male rock ptarmigan *L. muta* facultatively preen or neglect their plumage to adjust how conspicuous they appear (Montgomerie, Lyon & Holder 2001). In both periods of high natural mortality, ptarmigan were conspicuous in territorial defense and courtship display behaviours (spring only), and also had higher rates of vocalizations (Pedersen *et al.* 1983). Territorial activity may have increased the risk of predation for ptarmigan while gyrfalcons were beginning to nest and also later in the season during juvenile dispersal (Langvatn & Moksnes 1979; Tømmeraas 1989).

The lowest periods of natural mortality included the winter and breeding periods, which was consistent with gyrfalcons as the main predator in our study area. Adult gyrfalcons sometimes overwinter at mountain territories, but most of the inland population in Scandinavia migrates to wintering sites at coastal areas (Bakken, Runde & Tjørve 2003; Potapov & Sale 2005). Winter survival was high in our mountain population after gyrfalcons had departed the study site, and ptarmigan are well adapted for extreme climatic conditions (Martin & Wiebe 2004; Sandercock *et al.* 2005). Willow ptarmigan are also found on coastal islands in Norway (Myrberget 1988), and winter mortality may be higher among coastal populations exposed to winter predation by gyrfalcons. Mortality rates of ptarmigan were low during the late stages of the gyrfalcon breeding cycle in June to July (Langvatn & Moksnes 1979), which was surprising, because the energy demands for breeding gyrfalcons should be highest while parents are feeding fully grown young in the nest and for up to six weeks after fledging (Potapov & Sale 2005). Hazard functions for natural mortality of ptarmigan could have been low because birds are secretive during incubation and brood-rearing and difficult for gyrfalcons to locate and kill, or because gyrfalcons switch to alternative avian prey during late summer (Nielsen & Cade 1990). On the other hand, predation risk from mammalian predators is usually highest during nesting and brood-rearing because grouse rely on camouflage for concealment (Angelstam 1984; Wiebe & Martin 1998; Hagen *et al.* 2007). Low rates of seasonal mortality for ptarmigan during the breeding season suggest that mammalian predation was less important than raptor predation during our 3-year study. A regional outbreak of sarcoptic mange in 1976–1986 decimated red fox numbers throughout Scandinavia (Smedshaug *et al.* 1999), and our field project was conducted during the 1990s when fox numbers were still recovering. Seasonal mortality rates of ptarmigan could be higher during the breeding season now, following recovery and expansion of red foxes into alpine areas (Tannerfeldt, Elmhagen & Angerbjörn 2002).

HARVEST STRATEGIES FOR PTARMIGAN

Three general strategies have been proposed for sustainable harvest of exploited populations of vertebrates: constant,

proportional and threshold harvesting (Lande *et al.* 1997; Fryxell *et al.* 2005). Under the three harvest strategies, annual quotas for harvest are based on a fixed number of individuals, a fixed proportion of the population size or a fixed escapement where harvest is restricted to surplus individuals above a threshold population size or level of productivity. Constant harvest is a poor strategy for managing fluctuating populations because high harvest rates at low population numbers increases extinction risk (Lande *et al.* 1997). Thus, terrestrial vertebrates are usually managed with either proportional or threshold harvest strategies (Fryxell *et al.* 2001; Bradshaw *et al.* 2006; Boland & Litvaitis 2008).

Proportional harvest strategies have been widely applied to upland gamebirds. Harvest quotas of 30–50% have been recommended for red grouse on managed shooting estates where densities reach 40–200 birds per km² (Jenkins *et al.* 1963; Hudson 1985). Based on simulation models, Aanes *et al.* (2002) recommended restricted proportional harvesting at 50% for a fluctuating population of willow ptarmigan at densities of 10–33 birds per km² in Sweden. Our experimental field data suggest that the harvest quotas of Aanes *et al.* (2002) would be unsustainable, because harvest rates > 15% caused additive mortality in ptarmigan populations at densities of 8–34 birds per km² in central Norway. High harvest quotas of 30–50% might be sustainable for red grouse, but only if greater compensation occurs at higher densities or because predators are controlled. Interactions may be difficult to predict if harvest is directly density-dependent (Cattadori *et al.* 2003), whereas raptor predation is usually inversely density-dependent (Nielsen 1999; Thirgood *et al.* 2000; Tornberg 2001). Nevertheless, if proportional harvesting is used to manage willow ptarmigan in Norway, harvest quotas should be set at ≤15% of August population numbers, with the caveat that movements out of protected areas will increase realized harvest mortality rates above the set harvest treatments.

Threshold harvest strategies are effective at minimizing extinction risk (Lande *et al.* 1997) but face two practical problems with implementation: population size must be estimated with respect to the desired threshold, and hunters must forego harvest opportunities in years closed to hunting. A modified threshold harvest strategy could be to set quotas based on reproductive surpluses (Moss *et al.* 1979; Myrberget 1985; Ellison *et al.* 1988; Kastdalen 1992; Pedersen & Karlsen 2007). Willow ptarmigan breed as yearlings and show little age structure in fecundity or survival rates (Erikstad *et al.* 1985; Smith & Willebrand 1999; Munkebye *et al.* 2003; this study). Hence, the finite rate of population growth (λ) can be written as: $\lambda = (F/2) S_j + S_a$, where $F/2$ is the number of female young per pair under a 1 : 1 sex ratio, and S_j and S_a are juvenile and adult survival. If 1-month old juveniles have similar overwinter survival rates as adults ($S_j = S_a^{11/12}$), then the average brood size needed for a stationary population ($\lambda = 1$) is $F = 2(1 - S)/S^{11/12}$. Given annual survival rates of 0.54, 0.47, and 0.30, productivity would have to be 1.6 young per pair under 0% harvest, and 2.1 and 4.2 young per pair under 15% and 30% harvest. Past

estimates of the productivity needed to sustain unhunted ptarmigan populations range from 1.8 to 2.5 chicks per pair (Steen & Erikstad 1996; Smith & Willebrand 1999). Productivity of ptarmigan tends to be variable in Scandinavia (CV = 40–50%), but averages 2.4–3.1 young per pair for brood counts (2.8–3.1, Steen *et al.* 1988; 2.4–3.1, Steen & Haugvold 2009), and 2.8–3.0 young per pair from juvenile : adult ratios in harvest data (2.9, Myrberget 1974; 2.8–3.0, Hörnell-Willebrand *et al.* 2006). Estimates of young per pair could be biased if females with broods use different habitats than failed breeders, or if hunter selectivity favours harvest of one age-class. Nevertheless, production rates of >2.1 young per pair should sustain 15% harvest in most years, whereas production >4.1 young per pair would sustain a 30% harvest rate only in years of exceptionally good production. Thus, a conservative threshold harvesting strategy for ptarmigan could be to set harvest quotas based on reproductive surpluses >2.5 young per pair (Kastdalen 1992).

Both proportional and threshold harvest strategies assume that harvest is conducted as a pulse within a short period. Most of our experimental harvest was conducted within the first 2–3 weeks of the hunting season, similar to harvest of other populations of grouse (Palmer & Bennett 1963; Bergerud 1972; Smith & Willebrand 1999). Our results join models of sequential density dependence in showing that an understanding of seasonal timing of harvest and natural mortality is critical for management (Kokko 2001; Ratikainen *et al.* 2008). In Fennoscandia, ptarmigan can be harvested until late February or March by either hunting or traditional methods of snaring (Myrberget 1976; Holmstad 1998; Pedersen & Karlsen 2007). Potential for compensation may be limited in our population because harvest mortality coincided with autumn peaks in natural mortality. Compensation for harvest after 1 November was limited in our study because natural mortality rates were low over winter, and experimental harvest did not affect hazard functions for natural mortality during the second peak of spring mortality. Thus, shooting or snaring of ptarmigan during the winter months could be additive mortality that would impact population numbers at the start of the spring breeding season. Late season harvest is often additive in gamebirds (Pollock *et al.* 1989; Stoll & Culbertson 1995; Connelly *et al.* 2000; Reese & Connelly 2011), but compensation might be possible if seasonal mortality increases in late winter or spring (Small *et al.* 1991; Hudson *et al.* 1997; this study). To minimize additive effects of winter mortality on ptarmigan, managers could close hunting seasons in November instead of February, or alternatively, reduce quotas for late season harvest discounted by seasonal mortality rates.

Our field experiment provided key insights for the applied management of upland gamebirds. We experimentally manipulated exploitation across three levels of harvest, used large treatment areas that were replicated in a crossover design and estimated cause-specific mortality rates and hazard functions for radio-marked birds. Our project results are among the first experimental evidence for the partially compensatory and superadditive hypotheses and illustrate

the importance of considering seasonal patterns when investigating interactions between harvest and natural mortality. The impacts of harvest on seasonal and annual variation in survival likely differ among populations and animal species exposed to different sets of environmental conditions. General conclusions await additional harvest experiments for a broader range of exploited populations of terrestrial vertebrates, but our experimental protocols and quantitative methods will provide a useful model for future work.

Acknowledgements

We thank the many field assistants who helped us to capture and monitor radio-marked ptarmigan for this project. G.E. Frilund and N.G. Yoccoz assisted with project coordination, data management and earlier analyses. B.R. Patterson kindly shared examples of R code which were a starting point for our statistical analyses. E.A. Rexstad and J.S. Sedinger provided constructive reviews of previous versions of the manuscript. Financial support for the field project was provided by the Norwegian Directorate for Nature Management, the Norwegian Research Council through the program 'Use and management of outlying fields', and the Norwegian Institute for Nature Research. B.K. Sandercock was supported by the Division of Biology at Kansas State University and the Norwegian Institute for Nature Research in Trondheim, Norway.

References

- Aanes, S., Engen, S., Sæther, B.-E., Willebrand, T. & Marcström, V. (2002) Sustainable harvesting strategies of willow ptarmigan in a fluctuating environment. *Ecological Applications*, **12**, 281–290.
- Aebischer, N.J., Potts, G.R. & Rehfish, M. (1999) Using ringing data to study the effect of hunting on bird populations. *Ringing and Migration*, **19**(Suppl.), S67–S81.
- Alpizar-Jara, R., Brooks, E.N., Pollock, K.H., Steffen, D.E., Pack, J.C. & Norman, G.W. (2001) An eastern wild turkey population dynamics model for Virginia and West Virginia. *Journal of Wildlife Management*, **65**, 415–424.
- Anderson, D.R. & Burnham, K.P. (1981) Bobwhite population responses to exploitation: two problems. *Journal of Wildlife Management*, **45**, 1052–1054.
- Angelstam, P. (1984) Sexual and seasonal differences in mortality of the black grouse *Tetrao tetrix* in boreal Sweden. *Ornis Scandinavica*, **15**, 123–134.
- Bakken, V., Runde, O. & Tjørvæ, E. (2003) *Norwegian Bird Ringing Atlas Vol. 1: Divers – Auks*. Stavanger Museum, Stavanger, Norway.
- Bartmann, R.M., White, G.C. & Carpenter, L.H. (1992) Compensatory mortality in a Colorado mule deer population. *Wildlife Monographs*, **121**, 3–39.
- Benton, T.G., Cameron, T.C. & Grant, A. (2004) Population responses to perturbations: predictions and responses from laboratory mite populations. *Journal of Animal Ecology*, **73**, 983–995.
- Bergerud, A.T. (1970) Population dynamics of the willow ptarmigan *Lagopus lagopus alleni* L. in Newfoundland 1955 to 1965. *Oikos*, **21**, 299–325.
- Bergerud, A.T. (1972) Changes in the vulnerability of ptarmigan to hunting in Newfoundland. *Journal of Wildlife Management*, **36**, 104–109.
- Bergerud, A.T. (1985) The additive effect of hunting mortality on the natural mortality rates of grouse. *Game Harvest Management* (eds S.L. Beasom & S.F. Roberson), pp. 345–366. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas.
- Bergerud, A.T., Peters, S.S. & McGrath, R. (1963) Determining sex and age of willow ptarmigan in Newfoundland. *Journal of Wildlife Management*, **27**, 700–711.
- Besnard, A., Novoa, C. & Gimenez, O. (2010) Hunting impact on the population dynamics of Pyrenean grey partridge *Perdix perdix hispaniensis*. *Wildlife Biology*, **16**, 135–143.
- Boland, K.M. & Litvaitis, J.A. (2008) Role of predation and hunting on eastern cottontail mortality at Cape Cod National Seashore, Massachusetts. *Canadian Journal of Zoology*, **86**, 918–927.
- Boyce, M.S., Sinclair, A.R.E. & White, G.C. (1999) Seasonal compensation of predation and harvesting. *Oikos*, **87**, 419–426.
- Bradshaw, C.J.A., Fukuda, Y., Letnic, M. & Brook, B.W. (2006) Incorporating known sources of uncertainty to determine precautionary harvests of saltwater crocodiles. *Ecological Applications*, **16**, 1436–1448.

- Braun, C.E. & Rogers, G.E. (1971) *The White-Tailed Ptarmigan in Colorado*, Technical Publication No. 27. Colorado Division of Game, Fish and Parks, Ft. Collins, Colorado.
- Bro, E., Deldalle, B., Massot, M., Reitz, F. & Selmi, S. (2003) Density dependence of reproductive success in grey partridge *Perdix perdix* populations in France: management implications. *Wildlife Biology*, **9**, 93–102.
- Brøseth, H. & Pedersen, H.C. (2000) Hunting effort and game vulnerability studies on a small scale: a new technique combining radio-telemetry, GPS and GIS. *Journal of Applied Ecology*, **37**, 182–190.
- Brøseth, H. & Pedersen, H.C. (2010) Disturbance effects of hunting activity in a willow ptarmigan population. *Wildlife Biology*, **16**, 241–248.
- Brøseth, H., Tufto, J., Pedersen, H.C., Steen, H. & Kastdalen, L. (2005) Dispersal patterns in a harvested willow ptarmigan population. *Journal of Applied Ecology*, **42**, 453–459.
- Buenestado, F., Ferreras, P., Blanco-Aguilar, J.A., Tortosa, F.S. & Villafuerte, R. (2009) Survival and causes of mortality among wild red-legged partridges *Alectoris rufa* in southern Spain: implications for conservation. *Ibis*, **151**, 720–730.
- Bumann, G.B. & Stauffer, D.F. (2002) Scavenging of ruffed grouse in the Appalachians: influence and implications. *Wildlife Society Bulletin*, **30**, 853–860.
- Burger Jr, L.W., Kurzejeski, E.W., Vangilder, L.D., Dailey, T.V. & Schulz, J.H. (1994) Effects of harvest on population dynamics of upland gamebirds: are bobwhite the model? *Transactions of the North American Wildlife and Natural Resources Conference*, **59**, 466–476.
- Burger Jr, L.W., Dailey, T.V., Kurzejeski, E.W. & Ryan, M.R. (1995) Survival and cause-specific mortality of northern bobwhite in Missouri. *Journal of Wildlife Management*, **59**, 401–410.
- Burnham, K.P. & Anderson, D.R. (1984) Tests of compensatory vs. additive hypotheses of mortality in mallards. *Ecology*, **63**, 105–112.
- Casas, F., Mougeot, F., Vinuela, J. & Bretagnolle, V. (2009) Effects of hunting on the behaviour and spatial distribution of farmland birds: importance of hunting-free refuges in agricultural areas. *Animal Conservation*, **12**, 346–354.
- 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.
- Clark, W.M. (1987) Effects of harvest on annual survival of muskrats. *Journal of Wildlife Management*, **51**, 265–272.
- Connelly, J.W., Apa, A.D., Smith, R.B. & Reese, K.P. (2000) Effects of predation and hunting on adult sage grouse *Centrocercus urophasianus* in Idaho. *Wildlife Biology*, **6**, 227–232.
- Connelly, J.W., Reese, K.P., Garton, E.O. & Commons-Kemner, M.L. (2003) Response of greater sage-grouse *Centrocercus urophasianus* populations to different levels of exploitation in Idaho, USA. *Wildlife Biology*, **9**, 335–340.
- Conroy, M.J. & Krementz, D.G. (1990) A review of the evidence for the effects of hunting on American black duck populations. *Transactions of the North American Wildlife and Natural Resources Conference*, **55**, 501–517.
- Cooley, H.S., Wielgus, R.B., Koehler, G.M., Robinson, H.S. & Maletzke, B.T. (2009) Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. *Ecology*, **90**, 2913–2921.
- Cotter, R.C. & Gratto, C.J. (1995) Effects of nest and brood visits and radio transmitters on rock ptarmigan. *Journal of Wildlife Management*, **59**, 93–98.
- Coulson, T., Milner-Gulland, E.J. & Clutton-Brock, T. (2000) The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. *Proceedings of the Royal Society of London, Series B*, **267**, 1771–1779.
- DelGiudice, G.D., Fieberg, J., Riggs, M.R., Powell, M.C. & Pan, W. (2006) A long-term age-specific survival analysis of female white-tailed deer. *Journal of Wildlife Management*, **70**, 1556–1568.
- DeStefano, S. & Rusch, D.H. (1986) Harvest rates of ruffed grouse in north-eastern Wisconsin. *Journal of Wildlife Management*, **50**, 361–367.
- Devers, P.K., Stauffer, D.F., Norman, G.W., Steffen, D.E., Whitaker, D.M., Sole, J.D., Allen, T.J., Bittner, S.L., Buehler, D.A., Edwards, J.W., Figert, D.E., Friedhoff, S.T., Giuliano, W.W., Harper, C.A., Igo, W.K., Kirkpatrick, R.L., Seamster, M.H., Spiker Jr, H.A., Swanson, D.A. & Tefft, B.C. (2007) Ruffed grouse population ecology in the Appalachian Region. *Wildlife Monographs*, **169**, 1–35.
- Dufour, K.W., Ankney, C.D. & Weatherhead, P.J. (1993) Condition and vulnerability to hunting among mallards staging at Lake St. Clair, Ontario. *Journal of Wildlife Management*, **57**, 209–215.
- Duriez, O., Eraud, C., Barbraud, C. & Ferrand, Y. (2005) Factors affecting population dynamics of the Eurasian woodcocks wintering in France: assessing the efficiency of a hunting-free reserve. *Biological Conservation*, **122**, 89–97.
- Ellis, D.H., Bednarz, J.C., Smith, D.G. & Flemming, S.P. (1993) Social foraging classes in raptorial birds. *BioScience*, **43**, 14–20.
- Ellison, L.N. (1991) Shooting and compensatory mortality in tetraonids. *Ornis Scandinavica*, **22**, 229–240.
- Ellison, L.N., Léonard, P. & Menoni, E. (1988) Évolution des effectifs de tétraonyles sur un territoire de chasse. *Gibier Faune Sauvage*, **5**, 309–320.
- Erikstad, K.E. (1979) Effects of radio packages on reproductive success of willow grouse. *Journal of Wildlife Management*, **43**, 170–175.
- Erikstad, K.E., Pedersen, H.C. & Steen, J.B. (1985) Clutch size and egg size variation in willow grouse *Lagopus l. lagopus*. *Ornis Scandinavica*, **16**, 88–94.
- Fischer, C.A. & Keith, L.B. (1974) Population responses of central Alberta ruffed grouse to hunting. *Journal of Wildlife Management*, **38**, 585–600.
- Fox, J. (2002) Cox proportional-hazards regression for survival data. *An R and S-Plus Companion to Applied Regression*. (ed J. Fox), pp. 1–18 (Appendix). Sage Publications, Inc, Thousand Oaks, California.
- Fryxell, J.M., Lynn, D.H. & Chris, P.J. (2006) Harvest reserves reduce extinction risk in an experimental microcosm. *Ecology Letters*, **9**, 1025–1031.
- Fryxell, J.M., Smith, I.M. & Lynn, D.H. (2005) Evaluation of alternate harvesting strategies using experimental microcosms. *Oikos*, **111**, 143–149.
- Fryxell, J., Falls, J.B., Falls, E.A., Brooks, R.J., Dix, L. & Strickland, M. (2001) Harvest dynamics of mustelid carnivores in Ontario, Canada. *Wildlife Biology*, **7**, 151–159.
- Gruys, R.C. (1993) Autumn and winter movements and sexual segregation of willow ptarmigan. *Arctic*, **46**, 228–239.
- Guthery, F.S., Peterson, M.J. & George, R.R. (2000) Viability of northern bobwhite populations. *Journal of Wildlife Management*, **64**, 646–662.
- Hagen, C.A., Pitman, J.C., Sandercock, B.K., Robel, R.J. & Applegate, R.D. (2007) Age-specific survival and probable causes of mortality in female lesser prairie-chickens. *Journal of Wildlife Management*, **71**, 518–525.
- Hamel, S., Côté, S.D., Smith, K.G. & Festa-Bianchet, M. (2006) Population dynamics and harvest potential of mountain goat herds in Alberta. *Journal of Wildlife Management*, **70**, 1044–1053.
- Hannon, S.J., Gruys, R.C. & Schieck, J.O. (2003) Differential seasonal mortality of the sexes in willow ptarmigan *Lagopus lagopus* in northern British Columbia, Canada. *Wildlife Biology*, **9**, 317–326.
- Heisey, D.M. & Patterson, B.R. (2006) A review of methods to estimate cause-specific mortality in presence of competing risks. *Journal of Wildlife Management*, **70**, 1544–1555.
- Hickey, J.J. (1955) Some American population research on gallinaceous birds. *Recent Studies in Avian Biology* (ed A. Wolfson), pp. 326–396. University of Illinois Press, Urbana, Illinois.
- Holmstad, P.R. (1998) Do bag records of willow ptarmigan underestimate hunting mortality? *Fauna (Oslo)*, **51**, 94–96.
- Hörnelt-Willebrand, M., Marcström, 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., Newborn, D. & Robertson, P.A. (1997) Geographical and seasonal patterns of mortality in red grouse *Lagopus lagopus scoticus* populations. *Wildlife Biology*, **3**, 79–87.
- Humberg, L.A., Devault, T.L. & Rhodes Jr, O.E. (2009) Survival and cause-specific mortality of wild turkeys in northern Indiana. *American Midland Naturalist*, **161**, 313–322.
- Irving, L., West, G.C., Peyton, L.J. & Paneak, S. (1967) Migration of willow ptarmigan in arctic Alaska. *Arctic*, **20**, 77–85.
- 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.
- Kastdalen, L. (1992) *Skogshøns og jakt*. Norges Bondelag, Norsk skogsbruksforening, Norges Skogeierforbund, and Norges Jeger og Fiskerforbund, Oslo, Norway.
- Kausrud, K.L., Mysterud, A., Steen, H., Vik, J.O., Østbye, E., Cazelles, B., Framstad, E., Eikeset, A.M., Mysterud, I., Solhøy, T. & Stenseth, N.C. (2008) Linking climate change to lemming cycles. *Nature*, **456**, 93–98.
- Kokko, H. (2001) Optimal and suboptimal use of compensatory responses to harvesting: timing of hunting as an example. *Wildlife Biology*, **7**, 141–150.
- Kvasnes, M.A.J., Storaas, T., Pedersen, H.C., Bjørk, S. & Nilsen, E.B. (2010) Spatial dynamics of Norwegian tetraonid populations. *Ecological Research*, **25**, 367–374.
- Lande, R., Sæther, B.E. & Engen, S. (1997) Threshold harvesting for sustainability of fluctuating resources. *Ecology*, **78**, 1341–1350.
- Langvatn, R. & Moksnes, A. (1979) On the breeding ecology of the gyrfalcon *Falco rusticolus* in central Norway 1968–1974. *Fauna norvegica Series C, Cinclus*, **2**, 27–39.

- Lebreton, J.-D. (2005) Dynamical and statistical models for exploited populations. *Australian and New Zealand Journal of Statistics*, **47**, 49–63.
- Liermann, M. & Hilborn, R. (2001) Depensation: evidence, models and implications. *Fish and Fisheries*, **2**, 33–58.
- Lunn, M. & McNeil, D. (1995) Applying Cox regression to competing risks. *Biometrics*, **51**, 524–532.
- Madsen, J. & Fox, A.D. (1995) Impacts of hunting disturbance on waterbirds – a review. *Wildlife Biology*, **1**, 193–207.
- Martin, K., Hannon, S.J. & Rockwell, R.F. (1989) Clutch size variation and patterns of attrition in fecundity of willow ptarmigan. *Ecology*, **70**, 1788–1799.
- Martin, K., Stacey, P.B. & Braun, C.E. (2000) Recruitment, dispersal, and demographic rescue in spatially-structured white-tailed ptarmigan populations. *Condor*, **102**, 503–516.
- Martin, K. & Wiebe, K.L. (2004) Coping mechanisms of alpine and arctic breeding birds: extreme weather and limitations to reproductive resilience. *Integrative and Comparative Biology*, **44**, 97–105.
- McGowan, J.D. (1975) Effect of autumn and spring hunting on ptarmigan population trends. *Journal of Wildlife Management*, **39**, 491–495.
- Mentis, M.T. & Bigalke, R.C. (1985) Experimental hunting of grassland francolins in the Natal Drakensberg. *South African Journal of Wildlife Research*, **15**, 12–16.
- Milner, J.M., Nilsen, E.B. & Andreassen, H.P. (2007) Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology*, **21**, 36–47.
- Montgomerie, R., Lyon, B. & Holder, K. (2001) Dirty ptarmigan: behavioral modification of conspicuous male plumage. *Behavioral Ecology*, **12**, 429–438.
- Moss, R., Weir, D. & Jones, A. (1979) Capercaillie management in Scotland. *Woodland Grouse Symposium* (ed T.W.I. Lovel), pp. 140–155. World Pheasant Association, Sudbury, Suffolk, UK.
- Mougeot, F., Redpath, S.M., Moss, R., Matthiopoulos, J. & Hudson, P.J. (2003) Territorial behavior and population dynamics in red grouse *Lagopus lagopus scoticus*. I. Population experiments. *Journal of Animal Ecology*, **72**, 1073–1082.
- Munkebye, E., Pedersen, H.C., Steen, J.B. & Brøseth, H. (2003) Predation of eggs and incubating females in willow ptarmigan *Lagopus l. lagopus*. *Fauna norvegica Series C, Cinclus*, **23**, 1–8.
- Murray, D.L. (2006) On improving telemetry-based survival estimation. *Journal of Wildlife Management*, **70**, 1530–1543.
- Myrberget, S. (1974) Variations in the production of the willow grouse *Lagopus lagopus* (L.) in Norway, 1963–1972. *Ornis Scandinavica*, **5**, 163–172.
- Myrberget, S. (1976) Hunting mortality, migration, and age composition of Norwegian willow grouse (*Lagopus lagopus*). *Norwegian Journal of Zoology*, **24**, 47–52.
- Myrberget, S. (1985) Is hunting mortality compensated for in grouse populations, with special reference to willow grouse? *Transactions of the International Union of Game Biologists*, **17**, 329–336.
- Myrberget, S. (1988) Demography of an island population of willow ptarmigan in northern Norway. *Adaptive Strategies and Population Ecology of Northern Grouse* (eds A.T. Bergerud & M.W. Gratson), pp. 379–419. University of Minnesota Press, Minneapolis, Minnesota.
- New, L.F., Matthiopoulos, J., Redpath, S. & Buckland, S.T. (2009) Fitting models of multiple hypotheses to partial population data: investigating the causes of cycles in red grouse. *American Naturalist*, **174**, 399–412.
- Nichols, J.D. & Johnson, F.A. (1989) Evaluation and experimentation with duck management strategies. *Transactions of the North American Wildlife and Natural Resources Conference*, **54**, 566–593.
- Nichols, J.D., Conroy, M.J., Anderson, D.R. & Burnham, K.P. (1984) Compensatory mortality in waterfowl populations: a review of the evidence and implications for research and management. *Transactions of the North American Wildlife Conference*, **49**, 535–554.
- Nielsen, Ø.K. (1999) Gyrfalcon predation on ptarmigan: numerical and functional responses. *Journal of Animal Ecology*, **68**, 1034–1050.
- Nielsen, Ø.K. & Cade, T.J. (1990) Seasonal changes in food habits of gyrfalcons in NE-Iceland. *Ornis Scandinavica*, **21**, 202–211.
- Novaro, A.T., Redford, K.H. & Bodmer, R.E. (2000) Effect of hunting in source-sink systems in the neotropics. *Conservation Biology*, **14**, 713–721.
- Nyström, J., Ekenstedt, J., Engström, J. & Angerbjörn, A. (2005) Gyr falcons, ptarmigan and microtine rodents in northern Sweden. *Ibis*, **147**, 587–597.
- Obbard, M.E. & Howe, E.J. (2008) Demography of black bears in hunted and unhunted areas of the boreal forest of Ontario. *Journal of Wildlife Management*, **72**, 869–880.
- Olsson, G.E., Willebrand, T. & Smith, A.A. (1996) The effects of hunting on willow grouse *Lagopus lagopus* movements. *Wildlife Biology*, **2**, 11–15.
- Otis, D.L. (2002) Survival models for harvest management of mourning dove populations. *Journal of Wildlife Management*, **66**, 1052–1063.
- Pack, J.C., Norman, G.W., Taylor, C.I., Steffen, D.E., Swanson, D.A., Pollock, K.H. & Alpijar-Jara, R. (1999) Effects of fall hunting on wild turkey populations in Virginia and West Virginia. *Journal of Wildlife Management*, **63**, 964–975.
- Palmer, W.L. & Bennett Jr, C.L. (1963) Relation of season length to hunting harvest of ruffed grouse. *Journal of Wildlife Management*, **27**, 634–639.
- Palmer, W.E. & Wellendorf, S.D. (2007) Effect of radiotransmitters on northern bobwhite annual survival. *Journal of Wildlife Management*, **71**, 1281–1287.
- Park, K.J., Hurley, M.M. & Hudson, P.J. (2002) Territorial status and survival in red grouse *Lagopus lagopus scoticus*: hope for the doomed surplus? *Journal of Avian Biology*, **33**, 56–62.
- Pauli, J.N. & Buskirk, S.W. (2007) Risk-disturbance overrides density dependence in a hunted colonial rodent, the black-tailed prairie dog *Cynomys ludovicianus*. *Journal of Animal Ecology*, **44**, 1219–1230.
- Pedersen, H.C. (1984) Territory size, mating status, and individual survival of males in a fluctuating population of willow ptarmigan. *Ornis Scandinavica*, **15**, 197–203.
- Pedersen, H.C. & Karlsen, D.H. (2007) *Alt om Rypa: Biologi, Jak, og Forvaltning*. Tun forlag AS, Grønland, Oslo, Norway.
- Pedersen, H.C., Steen, J.B. & Andersen, R. (1983) Social organization and territorial behaviour in a willow ptarmigan population. *Ornis Scandinavica*, **14**, 263–272.
- Pedersen, H.C., Steen, H., Kastdalen, L., Svendsen, W. & Brøseth, H. (1999) Betydningen av jakt på lirypebestander. Framdriftsrapport 1996–1998. *NINA Oppdragsmelding*, **578**, 1–43.
- Pedersen, H.C., Steen, H., Kastdalen, L., Brøseth, H., Ims, R.A., Svendsen, W. & Yoccoz, N.G. (2004) Weak compensation of harvest despite strong density-dependent growth in willow ptarmigan. *Proceedings of the Royal Society of London, Series B*, **271**, 381–385.
- Pollock, K.H., Conroy, M.J. & Hearn, W.S. (1995) Separation of hunting and natural mortality using ring-return models: an overview. *Journal of Applied Statistics*, **22**, 557–565.
- Pollock, K.H., Moore, C.T., Davidson, W.R., Kellogg, F.E. & Doster, G.L. (1989) Survival rates of bobwhite quail based on band recovery analyses. *Journal of Wildlife Management*, **53**, 1–6.
- Potapov, E. & Sale, R. (2005) *The Gyrfalcon*. T & AD Poyser, London, UK.
- Powell, G.V.N. & Bjork, R.D. (2004) Habitat linkages and the conservation of tropical biodiversity as indicated by seasonal migrations of three-wattled bellbirds. *Conservation Biology*, **18**, 500–509.
- Ratikainen, I.I., Gill, J.A., Gunnarsson, T.G., Sutherland, W.J. & Kokko, H. (2008) When density dependence is not instantaneous: theoretical developments and management implications. *Ecology Letters*, **11**, 184–198.
- Reese, K.P. & Connelly, J.W. (2011) Harvest management for greater sage-grouse: a changing paradigm for game bird management. *Studies in Avian Biology*, in press.
- Rexstad, E.A. (1992) Effect of hunting on annual survival of Canada geese in Utah. *Journal of Wildlife Management*, **56**, 297–305.
- Robinson, A.C., Larsen, R.T., Flinders, J.T. & Mitchell, D.L. (2009) Chukar seasonal survival and probable causes of mortality. *Journal of Wildlife Management*, **73**, 89–97.
- Rorvik, K.-A., Pedersen, H.C. & Steen, J.B. (1998) Dispersal in willow ptarmigan *Lagopus lagopus* – who is dispersing and why? *Wildlife Biology*, **4**, 91–96.
- Sandercock, B.K., Martin, K. & Hannon, S.J. (2005) Life history strategies in extreme environments: comparative demography of arctic and alpine ptarmigan. *Ecology*, **86**, 2176–2186.
- Schaub, M. & Lebreton, J.-D. (2004) Testing the additive versus the compensatory hypothesis of mortality from ring recovery data using a random effects model. *Animal Biodiversity and Conservation*, **27**, 73–85.
- Schwab, F.E., Simon, N.P.P. & Nash, S. (2005) Age and sex segregation of wintering willow ptarmigan in Labrador. *Northwestern Naturalist*, **12**, 113–118.
- Sedinger, J.S. & Rexstad, E.A. (1994) Do restrictive harvest regulations result in higher survival rates in mallards? A comment. *Journal of Wildlife Management*, **58**, 571–577.
- Sedinger, J.S. & Rotella, J.J. (2005) Effect of harvest on sage-grouse *Centrocercus urophasianus* populations: what can we learn from the current data? *Wildlife Biology*, **11**, 371–375.
- Sedinger, J.S., Nicolai, C.A., Lensink, C.J., Wentworth, C. & Conant, B. (2007) Black brant harvest, density dependence, and survival: a record of population dynamics. *Journal of Wildlife Management*, **71**, 496–506.
- Sedinger, J.S., White, G.C., Espinosa, S., Partee, E.T. & Braun, C.E. (2010) Assessing compensatory versus additive harvest mortality: an example using greater sage-grouse. *Journal of Wildlife Management*, **74**, 326–332.

- Servanty, S., Choquet, R., Baubet, É., Brandt, S., Gaillard, J.-M., Schaub, M., Toigo, C., Lebreton, J.-D., Buoro, M. & Gimenez, O. (2010) Assessing whether mortality is additive using marked animals: a Bayesian state-space modeling approach. *Ecology*, **91**, 1916–1923.
- Small, R.J., Holzward, J.C. & Rusch, D.H. (1991) Predation and hunting mortality of ruffed grouse in central Wisconsin. *Journal of Wildlife Management*, **55**, 512–520.
- Smedshaug, C.A., Selås, V., Lund, S.E. & Sonerud, G.A. (1999) The effect of a natural reduction of red fox *Vulpes vulpes* on small game bags in Norway. *Wildlife Biology*, **5**, 157–166.
- Smith, A. & Willebrand, T. (1999) Mortality causes and survival rates of hunted and unhunted willow grouse. *Journal of Wildlife Management*, **63**, 722–730.
- Steen, H. & Erikstad, K.E. (1996) Sensitivity of willow grouse *Lagopus lagopus* population dynamics to variations in demographic parameters. *Wildlife Biology*, **2**, 27–35.
- Steen, J.B., Erikstad, K.E. & Høidal, K. (1992) Cryptic behaviour in moulting hen willow ptarmigan *Lagopus l. lagopus* during snow melt. *Ornis Scandinavica*, **23**, 101–104.
- Steen, J.B. & Haugvold, O.A. (2009) Cause of death in willow ptarmigan *Lagopus l. lagopus* chicks and the effect of intensive, local predator control on chick production. *Wildlife Biology*, **15**, 53–59.
- Steen, J.B., Steen, H., Stenseth, N.C., Myrberget, S. & Marcström, V. (1988) Microtine density and weather as predictors of chick production in willow ptarmigan, *Lagopus l. lagopus*. *Oikos*, **51**, 367–373.
- Stoll Jr, R.J. & Culbertson, W.L. (1995) Ruffed grouse hunting pressure and harvest on an Ohio public hunting area. *Ohio Fish and Wildlife Report*, **12**, 1–15.
- Tannerfeldt, M., Elmhagen, B. & Angerbjörn, A. (2002) Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia*, **132**, 213–220.
- Terhune, T.M., Sisson, D.C., Grand, J.B. & Stribling, H.L. (2007) Factors influencing survival of radiotagged and banded northern bobwhites in Georgia. *Journal of Wildlife Management*, **71**, 1288–1297.
- Thiel, D., Ménoni, E., Brenot, J.-F. & Jenni, L. (2007) Effects of recreation and hunting on flushing distance of capercaillie. *Journal of Wildlife Management*, **71**, 1784–1792.
- Thirgood, S.J., Redpath, S.M., Hudson, P.J., Hurley, M.M. & Aebischer, N.J. (1995) Effects of necklace radio transmitters on survival and breeding success of red grouse *Lagopus lagopus scoticus*. *Wildlife Biology*, **1**, 121–126.
- Thirgood, S.J., Redpath, S.M., Rothery, P. & Aebischer, N.J. (2000) Raptor predation and population limitation in red grouse. *Journal of Animal Ecology*, **69**, 504–516.
- Tømmeraaas, P.J. (1989) A time-lapse nest study of a pair of gyrfalcons *Falco rusticolus* from their arrival at the nesting ledge to the completion of egg-laying. *Fauna norvegica Series C, Cinclus*, **12**, 52–63.
- Tornberg, R. (2001) Pattern of goshawk *Accipiter gentilis* predation on four forest grouse species in northern Finland. *Wildlife Biology*, **7**, 245–256.
- Valkama, J., Korpimäki, E., Arroyo, B., Beja, P., Bretagnolle, V., Bro, E., Kenward, R., Manosa, S., Redpath, S.M., Thirgood, S. & Vineula, J. (2005) Birds of prey as limiting factors of gamebird populations in Europe: a review. *Biological Reviews*, **80**, 171–203.
- Watson, A. (1985) Social class, socially-induced loss, recruitment and breeding of red grouse. *Oecologia*, **67**, 493–498.
- Watson, A., Moss, R., Rothery, P. & Parr, R. (1984) Demographic causes and predictive models of population fluctuations in red grouse. *Journal of Animal Ecology*, **53**, 639–662.
- Watson, M., Aebischer, N.J., Potts, G.R. & Ewald, J.A. (2007) The relative effects of raptor predation and shooting on overwinter mortality of grey partridges in the United Kingdom. *Journal of Applied Ecology*, **44**, 972–982.
- Weeden, R.B. (1963) Management of ptarmigan in North America. *Journal of Wildlife Management*, **27**, 673–683.
- Weeden, R.B. (1964) Spatial separation of sexes in rock and willow ptarmigan in winter. *Auk*, **81**, 534–541.
- Wiebe, K.L. & Martin, K. (1998) Costs and benefits of nest cover for ptarmigan: changes within and between years. *Animal Behaviour*, **56**, 1137–1144.
- Willebrand, T. & Hörnell, M. (2001) Understanding the effects of harvesting willow ptarmigan *Lagopus lagopus* in Sweden. *Wildlife Biology*, **7**, 205–212.
- Williams, C.K., Lutz, R.S. & Applegate, R.D. (2004) Winter survival and additive harvest in northern bobwhite coveys in Kansas. *Journal of Wildlife Management*, **68**, 94–100.
- Woodroffe, R. & Ginsberg, J.R. (1998) Edge effects and the extinction of populations inside protected areas. *Science*, **280**, 2126–2128.
- Zipkin, E.F., Sullivan, P.J., Cooch, E.G., Kraft, C.E., Shuter, B.J. & Weidel, B.C. (2008) Overcompensatory response of a smallmouth bass (*Micropterus dolomieu*) population to harvest: release from competition? *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 2279–2292.

Received 6 July 2010; accepted 4 October 2010
Handling Editor: John Fryxell

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Fall densities of willow ptarmigan, harvest treatments, realized harvest, and number of radio-marked birds monitored in five experimental management units at the Meråker-Selbu study area, central Norway, 1996–1998.

Fig. S1. (a) Map of the study area in the municipalities of Meråker (Nord-Trøndelag county) and Selbu (Sør-Trøndelag county) in central Norway (inset), with reference numbers for the five experimental units (12–17) and locations of transect lines used to estimate population size in August. (b–d) Management units were randomly assigned to one of three experimental harvest treatments in 1996–1998.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.