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Original article

Survival of female capercaillie *Tetrao urogallus* in northern Sweden

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We studied survival and cause-specific mortality of radio-marked capercaillie *Tetrao urogallus* females relative to habitat type in northern Sweden during 2000-2004. Our high-mountain area (1,600 km^2) consisted of the alpine transition zone from Norway spruce *Picea abies*-dominated forest, mountain birch *Betula pubescens* and alpine heath. Our low-mountain areas consisted of two forest areas (300 and 160 km^2) dominated by Scots pine *Pinus sylvestris* and characterised by more intensive forestry than the first-mentioned area. Predation was the most common cause of mortality in both the high-mountain (70%) and low-mountain (90%) areas. We attributed 10% of mortality in both areas to hunting. Collisions with cars and power lines were only documented in the high-mountain area. A Cox-proportional regression model stratified by year suggested that hazard was lower for yearlings and birds using low-mountain areas, but these estimates were associated with large uncertainties. Pooling all individuals showed an average annual survival probability of 0.68 (0.62-0.75; 95% CI), with no tendency for hazard to vary among seasons. Because survival of females was comparable to those reported in other studies and the harvest mortality was low, we suggest that the capercaillie population in the Swedish high-mountain region does not need any changes in the present management strategy.

Key words: capercaillie, habitat, harvest, predation, survival, Tetrao urogallus

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Declines in capercaillie *Tetrao urogallus* populations in Scandinavia have been associated with the development of industrial forestry because intensive forestry often results in increased habitat fragmentation and reduction in age structure of stands (Rolstad & Wegge 1987, Helle et al. 1989, Kurki et al. 2000, Wegge & Kastdalen 2007). Recent studies have suggested that the proportion of forest > 50 years old is less important than previously believed, and that the extent of conifer forest in the landscape is more important (Miettinen et al. 2008, Sirkiä et al. 2010). Swedish bag statistics indicate that the general decline of capercaillie began in the 1930s. The decline was so dramatic that a 7-year hunting ban was imposed in 1949, and the ban also included black grouse *Tetrao tetrix* and hazel grouse *Bonasia bonasia*. However, bags have not been restored to previous levels after hunting was resumed (Winquist 1988). Yet, the decline seems to have ceased in recent decades, because Ottvall et al. (2009), who systematically reviewed bird-breeding census during 1977-2006 in Sweden, found that the capercaillie population had remained stable and was widely distributed.

In the Swedish high-mountain region, capercaillie have become less common as the boreal conifer forest is replaced by mountain birch *Betula pubescens czerepanovii* at higher altitudes. However, capercaillie females nest in mountain birch stands close to the

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open alpine heath habitats, and capercaillie females in the high-mountain area often migrate to lower-altitude forests with higher densities of Scots pine *Pinus sylvestris* (K. Sjöberg, unpubl. data), probably because Scots pine is their preferred food. If Scots pine forests are optimal for capercaillie, theory predicts that populations at the edge of optimal habitats will exhibit lower densities and show greater temporal variation in their vital rates (Williams et al. 2003), and therefore, they may be more sensitive to harvest mortality (Lande et al. 2003). Consequently, the wildlife management agency of the county of Västerbotten in northern Sweden has suggested that capercaillie could be vulnerable to harvest in edge habitats. In this paper, we estimate survival rates and cause-specific mortality of radio-marked capercaillie females in perceived optimal and peripheral habitats in this region.

Study area

We had three study areas that represented two different landscapes. Our main study area (a high-mountain area of 1,600 km^2) is located in northwestern Sweden near Tärnaby (65°42'N; 15°17'E) and encompasses an altitudinal gradient towards the Norwegian border. In this area, there were four major cover types: 1) alpine, above tree line (800 m a.s.l.); 2) mountain birch forest with scattered Norway spruce *Picea abies* between 600 and 800 m a.s.l.; 3) Norway spruce forest between 450 and 600 m a.s.l.; and 4) mixed stands of Norway spruce and Scots pine below 450 m a.s.l. Open bogs dominated by *Carex* spp. were present in all forest types. There was a low impact from forestry in this area because the tree harvest primarily happened by high grade-selective cutting.

Our secondary study areas are near Åsele (64°9'N; 17°20'E) of approximately 300 km^2 and Storuman (65°5'N; 17°7'E) of approximately 160 km^2. These areas are 80 km apart but have similar forest characteristics. The high-mountain area is 130 km and 200 km west of Storuman and Åsele, respectively. In the following, we refer to these areas as low-mountain areas and our large study area as the high-mountain area. Forest management is more intense in low-mountain forest areas than in the high-mountain area because clear-cut harvest management was the dominant silviculture in the forest areas. Also older forest mixed stands of Norway spruce and Scots pine occurred in the low-mountain areas. Wavy-hair grass *Deschampsia flexuosa* dominated the herbaceous layer in the young forest plantations, whereas bilberry *Vaccinium myrtillus* was the most common understory plant in older forest.

Material and methods

Capturing and monitoring of capercaillie

We captured capercaillie females from late April until early June during 2000-2004. We drove smaller roads in early morning and late evening, searching for females foraging on emerging spring vegetation along roadsides. Upon seeing a female, we drove toward her at a slow but steady speed and placed a collapsible net over her. On average, we caught one capercaillie/30.8 km of road driven. Captured females were fitted with a necklace radio-transmitter (Holohill 18 g or Televilt 23 or 32 g) and a metal leg band with a unique serial number. All transmitters had a mortality switch. We reused transmitters from recovered females if the transmitting time for a transmitter had been < 6 months. Age (yearling or old) was determined by primary feather pigmentation pattern (Helminen 1963). We recorded body weight to the nearest 10 g and wing length to the nearest millimetre.

Upon finding a dead grouse, we used carcass remains, tracks from predators, bite marks on feathers and the transmitter to determine the cause of death. Predator identification was similar to those used in other studies (Smith & Willebrand 1999); we only classified predator to general class, i.e. mammal or bird (raptor). We interpreted fading pulse rates and weakened signal during the first month after tagging as an indicator of transmitter failure. We compared the hunter kills of capercaillie with only a leg band with those having both a leg band and a radio-collar to estimate the potential effect of transmitters.

Survival analysis

We attempted to locate grouse once a week, but this was not always possible. In autumn, many females migrated to a separate winter home range that could be > 60 km away from their summer area (K. Sjöberg, unpubl. data). Therefore, winter conditions and closed roads made it impossible to reach areas of some females on a regular basis. We set the start of a year in the analysis to week 18 of the year, which was typically the second week in May. One of our aims was to estimate annual survival rates, and therefore, we divided data into annual subsets which we later

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pooled to get an average annual survival rate. This meant that some individuals were present in subsequent annual subsets; thus 55 females were present in two subsequent years in the high-mountain area and five were present in three subsequent years. This increased the number of individuals when years were pooled (Table 1).

We used a non-parametric approach to estimate survival rates (Kaplan-Meier), annual survival and graphically investigate the survival pattern in different seasons. We used Cox-Proportional hazard (CPH) regression model to evaluate the effects of area and age (adult or yearling) on survivorship when data were available for both high-mountain and low-mountain areas (i.e. during 2002-2004); 170 individuals in the high-mountain area and 65 individuals in low-mountain areas (see Table 1). The semi-parametric CPH regression model is often used in survival analysis, and it is a linear model for log-hazard that leaves the baseline hazard (intercept) unspecified. This is possible by using the hazard ratio of different sets of observations, a proportional hazard model (Cox 1972). We plotted Kaplan-Meier survival curves for area, age at death and year to investigate deviations from the proportional hazard assumption. We found that the survival curves crossed for different years, and we chose to include year as a stratification factor and evaluated four models with none, one (area or age) or two independent variables. We used scaled Schoenfeld residuals for the model diagnostics and tested the assumption of the proportional hazard assumption for each covariate by correlating the scaled Schoenfeld residuals with time (Fox 2002). The residuals for each variable were further inspected for systematic departures by plotting them against time. We used the function Coxph (regression model) and Cox.zph (residual diagnostics) in the library survival in R (R Core Team 2012). We used the function aictab to obtain ΔAIC_c, and the function modavg to average parameter values when ΔAIC_c between models was < 6. The functions were available in R library AICc modavg.

We used the Andersen-Gill modification of the CPH regression (Andersen & Gill 1982) to account for females that went unchecked for > 3 weeks. Johnson et al. (2004) used this approach when modelling survival of grizzly bears *Ursus arctos*. We constructed a data set in which each individual was represented by many rows; each row was a week of known fate for the individual. We excluded the weeks in which an individual went missing for > 3 weeks, and we changed the age of the yearling females to adults at about 20 months of age (i.e. in January).

Table 1. Number of female capercaillie radio-marked in one high-mountain and two low-mountain areas of northern Sweden. New = number of birds newly radio-marked in the year. Reentered = number of birds that was used in annual estimates and was captured the previous year. Note that five of 21 females reentering into 2003 were captured in 2001.

	High mountain			Low mountain		
Year	New	Reentered	Total	New	Reentered	Total
2000	19	-	19	-	-	-
2001	47	4	51	-	-	-
2002	35	19	54	14	-	14
2003	47	21(5)	68	16	5	21
2004	22	16	38	19	11	30
Total	170	60	230	49	16	65

Results

We caught 244 females in the high-mountain area of which we marked 206 with radio-transmitters and 56 with leg bands only. We excluded an additional 36 females because of transmitter failure (22) and early mortality or disappearance (14) from the analysis. We used the 170 remaining females in the subsequent analysis of mortality causes and survivorship. Of the 170 females, 24 were 'lost' for > 3 weeks but were later rediscovered. The average period of absence for these females was 24 weeks (minimum: 11 weeks, maximum: 39 weeks). In most cases, the 'loss' was due to seasonal migration into areas that we could not easily access in winter. Age (yearling or adult), wing length and body weight were known for 151 (102 adults and 49 yearlings) birds captured between 2001 and 2004. In low-mountain areas, we captured 49 females and age was known for 45 individuals (33 adults and 12 yearlings; see Table 1). Adults were heavier than yearlings, 2.29 kg and 1.99 kg, respectively ($t = 12.5$, $df = 132.6$, $P < 0.001$), and adults had longer wings than yearlings, 31.8 cm compared to 30.7 cm, respectively ($t = 4.5$, $df = 181.6$, $P < 0.001$).

Predation dominated mortality in the high-mountain (70%) and low-mountain (90%) areas with both mammalian (34%) and raptor (29%) predation being common. The proportion of deaths attributed to hunting was the same in both high-mountain and low-mountain areas (10%). However, it should be

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Table 2. Model selection results for the Cox proportional regression using age at death and area (high mountain vs low mountain) as covariates. The abbreviations in the headers are: K = number of parameters; AIC_c = Akaike information critera for small sample size; ΔAIC_c = the difference between the AIC_c of most parsimonious model AIC_c and the candidate model; w = Akaike weight for a candidate model relative to all candidate models; LL = log-likelihood.

Model	K	AIC_c	ΔAIC_c	w	LL
Age at death	1	430.25	0.00	0.54	-214.13
Age at death + area	2	430.55	0.30	0.46	-213.27
Null model	0	446.71	16.46	0.00	-223.35
Area	1	448.22	17.97	0.00	-223.11

noted that only one hunting mortality was recorded of a total of 11 mortalities in the low-mountain area. In the autumn following the initial capture, seven of the 168 (4%) radio-collared and two of the 56 (4%) leg-banded capercaillie were killed by hunters (Fisher's exact test: P = 1). None of the deaths in low-mountain areas were caused by collision with vehicles or power lines, whereas collisions with vehicles and power lines accounted for 9 and 11% of the deaths in the high-mountain area, respectively.

Cox regression model depicting age and age and area were our top models (Table 2) with lower hazards for yearlings and capercaillie in the low-mountain areas. The uncertainties of both models were high since both the 95% CI hazard estimates contained the hazard ratio of one. The hazard was 0.81 (0.37-1.75; 95% CI) for yearlings relative to adults (averaged for both models) and 0.63 (0.31-1.31; 95% CI) in low-mountain areas relative to the high-mountain area. The models with age at death and area or only age at death had similar model probabilities (ΔAIC_c between the models was 0.30). Model diagnostics using the scaled Schoenfeld residuals showed no violation of the proportional hazard assumptions for the model with both age at death and area ($\chi^2 = 0.10$, P = 0.95) or the model with only age at death ($\chi^2 = 0.09$, P = 0.77).

The overall annual Kaplan-Meier survival probability was 0.68 (0.62-0.75; 95% CI) when all data were pooled. We plotted the smoothed line of instantaneous hazard from the pooled data against time but did not see any pattern in seasonal hazard. In the high-mountain area, the survival rate appeared lower in the first two years than in subsequent years when data also were available for low-mountain areas (Fig. 1 and Table 3). In 2003-2004, the survival was higher in low-mountain areas compared to the high-mountain area, but the hazard estimate from the regression model was associated with large

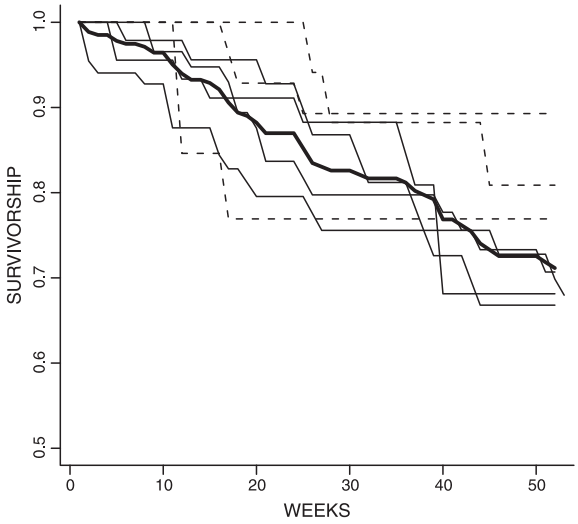


Figure 1. Annual (May-April) Kaplan-Meier survival of female capercaillies in northern Sweden. The thick solid line shows the survival of all females and years pooled. Thin solid (high mountain) and dashed (low mountain) lines show the different annual estimates of survival for birds in different habitat types.

uncertainty (see above). When we censored individuals that were killed by hunters to estimate the increase in annual survival excluding harvest mortality, the increase in average annual survival was 2% (0-4%).

Discussion

Few studies have been able to identify causes of mortality of capercaillie females. A study of capercaillie females in southern Norway (Wegge et al. 1987) reported that predation of capercaillie females was the most important source (97%) of 35 mortalities, and that goshawk *Accipites gentilis* was a common predator (60%). Similarly, in our study, predation was the most important cause of mortality but to a lesser extent (70%) than Wegge et al. (1987) reported, and neither raptors nor mammalian pred-

Table 3. Annual Kaplan-Meier survival estimates of capercaillie females in the high-mountain, low-mountain and all areas combined. Standard error and number of mortalities are shown in parentheses.

Year	High-mountain area	Low-mountain area	Combined areas
2000	0.52 (0.150; 6)	–	–
2001	0.61 (0.077; 16)	–	–
2002	0.71 (0.065; 15)	0.71 (0.121; 4)	0.71 (0.058; 19)
2003	0.68 (0.064; 19)	0.77 (0.103; 4)	0.69 (0.058; 23)
2004	0.69 (0.086; 10)	0.89 (0.058; 3)	0.72 (0.078; 13)

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ators dominated. An important mortality cause in the high-mountain area was collisions with either power lines or vehicles. Capercaillie females used dirt roads to replenish grit and feed on roadside vegetation, and all but one of the collisions with a car occurred in the snow-free season. We could not exclude that the large proportion of females killed by cars was biased in our study because we selectively captured birds using roads in spring. We believed collisions with power lines to be a consequence of seasonal migration and these collisions were mostly recorded in autumn and winter. The lack of collisions in low-mountain areas was probably due to the low number of mortalities recorded, and we did not believe that collisions were unique to the high-mountain area. In Scotland, Moss et al. (2000) found that predators caused 50% of the adult female capercaillie deaths (N = 12). It was interesting to note that the annual survival rates in the studies by Wegge et al. (1987) and Moss et al. (2000) were similar despite differences in the causes of mortality; Wegge et al. (1987) estimated monthly survival rates for different seasons which corresponded to an annual survival of 0.61, and Moss et al. (2000) estimated the annual survival rate to be 0.63. The annual estimates for the declining populations in the two studies were somewhat lower than our estimate of 0.68.

We found that our explanatory variables of age at death and area were important in the model ranking using AIC_c, but the hazard estimates for both variables were associated with large uncertainty. We expected that the relative hazard should be markedly lower in low-mountain areas compared to the high-mountain area, because the high-mountain area was a suboptimal habitat for these birds, but this was not the case. The low-mountain areas have been exposed to more intensive forestry than the high-mountain area, and the large uncertainty in the parameter estimate for area indicated that the difference in habitat was not important. Furthermore, we did not expect yearling females to survive better than adults, and we could not find any studies showing lower survival of adult compared to yearling grouse. It should be noted that the proportion of yearlings recruited varied among years; for example the proportion of yearlings captured dropped from 45% in 2003 to 5% in 2004. We captured capercaillie females over large areas, and we suspect that this could mask important local differences in survival estimates and mortality causes among years.

Few capercaillie were killed by hunters, and harvest mortality decreased the annual survival by about 0.02 in the high-mountain area. This was lower than the estimated 0.09-0.30 harvest rates reported for willow grouse *Lagopus lagopus* which were also managed by the county Wildlife Management Agency (Hörnell-Willebrand 2005). Harvest rates of capercaillie and black grouse were previously reported to also be substantially lower than willow grouse harvest rates in Norway (Kastdalen 1992). We only studied female capercaillie, so males could be exposed to higher harvest mortality because they are considered a trophy animal and the hunting season for males lasts for five months compared to three months for females.

Management implications

Our estimates of harvest mortality were low, so there was little evidence to support a revision of the present management for the capercaillie population in the high-mountain area we studied. There are only a few areas where long-term monitoring of capercaillie has been conducted in Sweden, and none were in the high-mountain region. Because our estimates of annual survival were low, we suggest that monitoring of capercaillie should be implemented in some high-mountain areas and management units that have consistently large bag sizes of capercaillie to determine if our results are typical of these areas.

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