Ann. Zool. Fennici 44: 141–151 ISSN 0003-455X
Helsinki 25 April 2007

Pattern and causes of natural mortality of capercaille, *Tetrao urogallus*, chicks in a fragmented boreal forest

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Received 21 Sep. 2006, revised version received 23 Feb. 2007, accepted 21 Jan. 2007

Wegge, P. & Kastdalen, L. 2007: Pattern and causes of natural mortality of capercaille, *Tetrao urogallus*, chicks in a fragmented boreal forest. — *Ann. Zool. Fennici* 44: 141–151.

Over a 3-year period, we equipped 115 newly hatched capercaillie chicks in 29 broods with small radio transmitters in southeast Norway. Besides monitoring the fate of the chicks, we measured the abundance of microtine rodents and insect food and, together with weather records, we examined the observed mortality in relation to these factors. On average, 57% of the chicks died within the first month of life. Mortality was highest during the first 3 weeks, coinciding with the period when chicks feed almost exclusively on insects, depend heavily on their mother for maintaining body warmth, and cannot fly well. Predation was by far the most important proximate cause of mortality, accounting for 90% of all observed losses. Only 7% of the losses could be ascribed to direct effects of cold and wet weather, all recorded during the first 8 days of life. However, because predation losses were also quite high during and immediately after heavy rainfalls, adverse weather probably predisposed the chicks to mammalian predation. Most chicks were killed by mustelids, mainly pine martens; low numbers of red fox due to sarcoptic mange probably explains the low proportion taken by this predator. Among known predation losses ($N = 40$), goshawks accounted for a minimum of 25%. Chick mortality during the first month varied markedly (29%–83%) among the three years. It was highest in the year when June weather was exceptionally wet and cold; the same year when the density of microtine rodents and food abundance in terms of insect larvae were highest. Net production in late August was poorly related to chick loss during the first month posthatch.

Introduction

Capercaille (*Tetrao urogallus*), the largest species of grouse (*Tetraonidae*), is declining in numbers throughout its wide geographical range in the Palaearctic (Storch 2001). Highly valued culturally as well as a game bird, the decline has triggered much research on its life history and habitat ecology in recent years. Evidence is accumulating that the decline is mainly caused by poor reproduction due to elevated egg and chick losses (Storaas & Wegge 1987, Wegge *et al*. 1990, Storch 1994, Moss 1994, Kurki *et al*. 1997, Kurki *et al*. 2000) as indirect effects of fragmentation of habitat (Wegge *et al.* 1992, Kurki *et al.* 2000, Storch 2000), and/or higher rainfall due to climatic change (Moss *et al.* 2001). Because most studies measured breeding success as the net production of chicks in the autumn, little is known about the proportional losses during the nesting and brood stage (Storch & Willebrand 1991). An exception is a telemetry study in the Bavarian Alps, where Storch (1994) showed that chick loss was higher than the loss of eggs. In fragmented boreal forests, however, nest predation is much higher than in Storch's study (Storaas & Wegge 1987), suggesting that the rate of chick loss may also be different.

Like other teraonids, the capercaillie is ground dwelling. Shortly after hatching, 6–8 precocial chicks leave the nest with their mother and move extensively in search for food (Wegge *et al.* 2007). During the first few days, the chicks rely on yolk food, and for 10–11 days they are not able to maintain body heat, but have to be brooded by the mother (Marcström 1960). Due to a remarkably fast growth rate (Lindén 1981), the chicks are dependent on highly nutritious and easily digestible invertebrate foods during their first weeks of life (Rajala 1959, Kastdalen & Wegge 1985, Spidsø & Stuen 1988, Picozzi *et al.* 1999, Summers *et al.* 2004). As their intestinal ceaca develop to enable efficient utilization of vegetative matter, their diets become progressively dominated by high quality plant foods (Moss & Hanssen 1980, Savory 1989). Flying ability is a priority ontogenetic development (Lindén 1981), and at the age of 10–12 days, the chicks are able to escape ground predators by flying short distances and perch in trees.

Due to poor thermoregulation in early life (Marcström 1960), the chicks are vulnerable to cold and rainy weather, and poor reproduction has been linked to such factors (Slagsvold & Grasaas 1979, Schröder & Scherzinger 1982, Moss 1986, Storch 1994, but *see* also Wegge & Grasaas 1977). Other studies have shown that chick mortality, particularly in early life, may be closely related to chick nutrition (Picozzi *et al.* 1999). Weather and food may act in concert; access to high quality insect foods may be hampered when it is cold and wet, because the chicks need to be warmed by the mother and because insects are found less easily during feeding bouts.

The development of radio telemetry as a research tool made it possible to investigate mortality during the brood phase separately from losses during the nesting phase. As the first study of its kind, in 1986–1988 we equipped newly hatched chicks with small radio transmitters and monitored their fate until 8 weeks of age. We measured the abundance of insects in the habitats of the broods to see if mortality was related to this category of chick food. In Scandinavia, the reproductive success among grouse tends to follow the vole cycle (Myrberget 1988, Marcström *et al.* 1988, Henttonen 1989) due to variations in predation pressure as explained by the alternative prey hypothesis (Hagen 1952, Angelstam *et al.* 1984). We therefore also measured the abundance of microtine rodents.

Study area and methods

Fieldwork was carried out in southeast Norway at Varaldskogen in 1986–1988 and at Fjella in 1986. Both areas are dominated by mixed coniferous forest of Norway spruce (*Picea abies*) and Scots pine (*Pinus silvestris*), with ericaceous shrubs in the field layer. Since the early 1950s, between 30% and 50% of the forests had been clearfelled and replanted into patchily distributed stands of different ages. The spring density of capercaillie was 1.5–2.0/km^2 at Varaldskogen and about 3 times higher at Fjella. Main predators on grouse in both areas were red fox (*Vulpes vulpes*), pine marten (*Martes martes*) and stoat (*Mustela erminea*), and with goshawk (*Accipiter gentilis*) more important at Varaldskogen. For more description of study areas *see* Wegge and Rolstad (1986).

Telemetry

Within a few days of hatching, 115 chicks in 29 broods were equipped with transmitters (142 MHz). Because of the small size of the newborns and their fast growth rate, we used transmitters of different sizes and replaced them at intervals

(Table 1). The transmitters were attached as backpacks with loose elastic thread. To prevent the transmitter package from becoming entangeled in the vegetation, we fastened it with instant glue to the feathers at the base of the neck. When the chicks were ca. 4 weeks old, we replaced the backpacks with necklace transmitters and encased the necklace in thin silicon rubber to prevent skin abrasion. To assess whether carrying radio transmitters affected survival, we compared the sizes of the broods with radiocollared chicks with those of broods of same age with no radioed chicks (*N* = 35) flushed during fieldwork. We also compared the mortality of chicks in two broods in which only the mothers carried radio transmitters.

We monitored the fate of the chicks by first locating the radiotagged mother. After approaching to within a distance of ca. 100 m from the brood, we usually received signal contact with the chicks. If a chick was missing, we searched thoroughly backwards towards the previous location of the brood. Because the broods were tracked 2–3 times/24 hours, determining their approximate routes of travel was not difficult. Most dead chicks were found by this backtracking method. Signs on the chicks and bite marks on the transmitter and harness were used to determine the cause of death. Often only the transmitter package was found on the ground, and occasionally fresh tracks and/or excrements from a predator were present to facilitate diagnosis. In several broods where only some of the chicks were radiomarked, we were able to also monitor the fate of unmarked individuals.

Insect abundance

At Varaldskogen, insect abundance was measured by sweep-netting at fixed locations in 3 different vegetation types known to be important brood habitats (Kastdalen & Wegge 1985). At each station (*N* = 3), insects were sampled once per week during the first 5 weeks after hatching, each sample consisting of 15 sweeps. Total area sampled at each station was ca. 500 m^2 in size, within which different parts were sweep-netted on each occasion to prevent bias from re-sampling same microsites. Insects > 2 mm in length were stored in 70% alcohol and later measured volumetrically.

Vole abundance

Also at Varaldskogen, the relative abundance of microtine rodents (mainly *Clethrionomys glareolus* and *Microtus agrestis*) was estimated by snap-trapping with ca. 600 trap-nights in spring and autumn each year at fixed transects in different habitats (Wegge & Storaas 1990).

Net chick production

Breeding success was estimated by censusing the bird population with pointing dogs in August. It is expressed as the number of chicks/hen and is based on a minimum of 20 hens recorded during the census.

Analyses

Survival rates

Following Kaplan and Meier (1958), we used Mayfield's method (Mayfield 1975) and the program MICRO-MORT (Heisey & Fuller 1985) to calculate survival rates. Daily survival is estimated as the number of radiodays within a time interval minus number of dead chicks in that interval divided by the number of radiodays in the interval (Trent and Rongstad 1974). To estimate the survival rate within a particular time

Table 1. Technical data of radio transmitters used on capercaillie chicks of different ages.

Chick age (weeks)	1	2	3–4
Chick weight (g)	35–60	60–120	120–250
Battery weight (g)	0.4	0.6	2.0
Antenna length (cm)	4.0	10.5	15.0
Total weight (g)	1.7–1.8	2.5–2.8	3.5–4.5
Percentage of bird weight	3.6–4.8	2.3–4.2	2.0–2.9
Range (m)	50–150	100–400	200–800
Life expectancy (days)	7–14	14–21	28–35

period, daily survival is raised to the number of days in the specified time interval, and this is then subtracted from 1:

$$S_n = 1 - [(x - y)/x]$$

where x is number of radiodays and y is number of dead chicks observed during n days. This method assumes that (1) the probability of survival of a chick is independent of other chicks in the brood, and (2) the probability of survival is constant during the time interval in question. Because the fate of individual chicks is not independent of that of siblings, assumption 1 is not fulfilled: when a predator finds a brood and kills one of the chicks, the probability that other chicks will also be killed is increased. This does not affect the estimated mortality rates, but confidence intervals will be underestimated. Assumption 2 was met, as observation intervals were short and nearly constant (Manly & Schmutz 2001).

Because the number of radiodays and number of chicks were large (> 30 and 10, respectively), survival rates were compared with a z-test:

$$z = (R_1 - R_2)/[\mathrm{var}(R_1) + \mathrm{var}(R_2)]^{1/2},$$
$$\text{where } P < 0.05 \text{ when } z > 1.96.$$

Weather and insect abundance

The influence of weather on the abundance of insects was analyzed based on the following data from the nearest meteorological station (Vinger):

- Sum of daily maximum temperatures (T_{max}),
- Sum of nightly minimum temperatures (T_{min}),
- Sum of diel mean temperatures (T_{ave}),
- Sum of diel precipitation (mm) (RM),
- Number of days with > 1 mm rain (RD).

These weather factors were calculated for a 30-day period before the first birds hatched (9 May–7 June) and for a 15-day period following first hatch (7–21 June). We included the data collected during 1981–1984 and 1986–1989 (8 years) in this analysis.

Results

The mortality rates of chicks in two broods where only the mothers were radiomarked were similar to those broods in which the chicks were also radiomarked (mean weekly rates during first month: 20.7% ± 10.1% (mean ± SE) in controls and 12.9% ± 7.5% (mean ± SE) in the radiomarked broods. Also, the sizes of unmarked broods (N = 35) were not larger than those of similar age where the chicks were radiomarked (Table 2). Moreover, when we compared chick losses in broods before and after radio-tagging within the first 15 days posthatch, there were no significant differences (1987: $t_{10} = 1.64$, $P = 0.20$; 1988: $t_{12} = 0.09$, $P > 0.40$). Hence, we concluded that radio-tagging, tracking and replacing transmitters had little or no effect on the natural mortality pattern of the broods.

In 1986, the mortality of radioed chicks was similar at Varaldskogen and in Fjella; hence the data were pooled.

Table 2. Mean number of capercaillie chicks in unmarked and radiomarked broods during 10-day age intervals at the study areas in southeastern Norway, 1986–1988.

	Unmarked broods			Radiomarked broods			
	Age[1]	N	Brood size	Age[1]	N	Brood size	Significance[2]
1986	21	5	3.40	20	9	4.89	ns
1987	11	5	2.60	9	7	4.14	$P < 0.14$
	22	7	3.71	23	2	3.50	ns
1988	13	4	4.25	13	9	3.89	ns
	27	14	3.14	26	7	3.71	ns

[1] Mean age (days) of unmarked and radiomarked broods in paired comparisons. [2] t-tests or Wilcoxon.

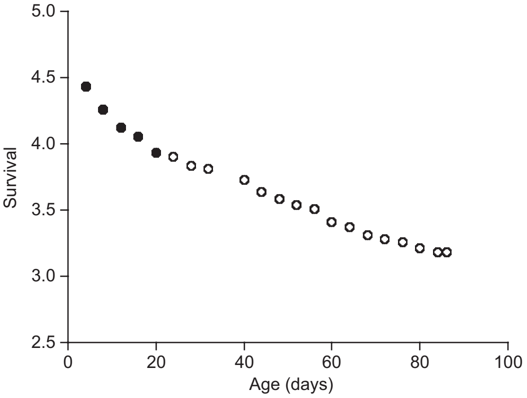

Fig. 1. Cumulative survival (ln-transformed) of radiomarked capercaillie chicks during successive 4-day intervals after hatching in southeastern Norway, 1986–1988. Filled circles: age 1–20 days. Open circles: age 20–86 days. Cumulative survival (ln-transformed) = 4.50 – 0.028 days, and 4.26 – 0.014 days, for the two age periods, respectively.

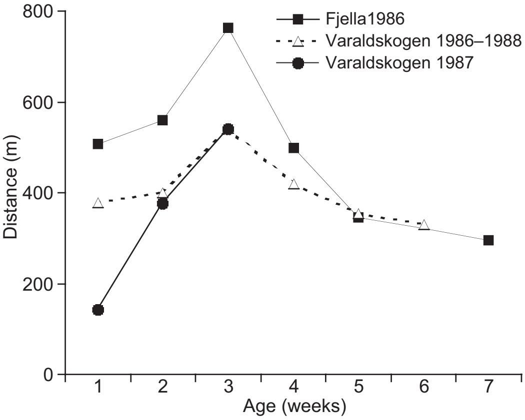

Fig. 2. Mean distance moved (m/24 hours) by capercaillie broods during their first 7 weeks after hatching in southeastern Norway, 1986–1988.

Pattern

The chicks died at a faster rate during the first 3 weeks than during the following 10 weeks ($z = 3.38$, $P < 0.01$; Fig. 1). The temporal change in mortality rate coincided with a change in the rate of brood movement. Brood diel movement distance, based on two widely spaced radiofixes/24 hours, increased during the first few weeks to > 500 m/24 hours in the their third week of life, for thereafter to decrease to ca. 300 m/24 hours. In 1987, the posthatch weather was extremely wet, and that year the broods' daily movements during the first two weeks were shorter than in the two drier years ($t_{59} = 3.76$, $P < 0.01$, Fig. 2).

Diel movement distance did not change the day following a successful predation attack or disturbance by us for replacing radio tags ($t = 0.24$ and 0.77 in age intervals 1–15 days and 16–30 days, respectively, $P > 0.28$, both periods). There was a clear tendency, although not significant, of shorter time intervals between predatory attacks and a higher proportion of chicks lost per attack during the first 15 days of chick age than during the following 15 days. Similarly, there was a tendency for more chicks to be killed during a predatory event in the first 15 days after hatching than in the following 15 days (Table 3). One or more chicks died in all

Table 3. Brood movements (m/24 hours ± SE), frequency of predatory events and proportion of capercaillie chicks killed/attack during first 15 days and the following 15 days of brood age at the study areas in southeastern Norway, 1986–1988.

	N[1]	1–15 days		*N*[1]	16–30 days
Movement after disturbance[2]	32	350 ± 35.0		23	563 ± 79.3
Movement undisturbed[3]	58	337 ± 39.8		71	496 ± 38.3
Significance		$P = 0.44$			$P = 0.38$
	N[1]	1–15 days	Significance	*N*[1]	16–30 days
Days between predatory events	17	13.1	$P = 0.18$	9	24.3
Chicks within broods killed per predatory event (%)	56	55.4	$P = 0.44$	43	32.6

[1] Number of events. [2] Mean distance moved (m) between 2 radiolocations spaced 15–30 hours apart the day following predation or disturbance by us for changing transmitters. [3] Undisturbed movement distance (m).

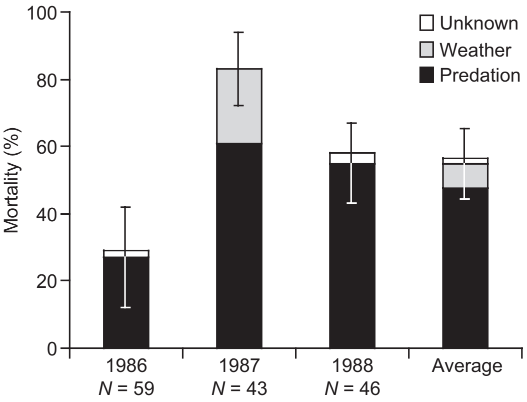

Fig. 3. Natural mortality (± 95% c.i.) of capercaillie chicks during first month of life in southeastern Norway, 1986–1988. *N* = number of monitored chicks.

radiomarked broods; all chicks were lost in 24% of the broods.

On average, 56.7% of the chicks died within the first month of life, but losses varied significantly among years ($z > 2.00$, $P < 0.05$), from 29% in 1986 to as high as 83% in the wet summer of 1987 (Fig. 3).

In 1988, losses from broods were monitored until the end of the year. During the summer (6 June to 20 August) chick loss averaged 14.4% per week; thereafter it averaged 4.0% per week ($z = 3.26$, $P < 0.01$). Only 11% of the chicks were alive at the end of the year.

Causes of mortality

Predation was by far the most important proximate mortality factor (Fig. 3 and Table 4). Of 88 deaths, only 6 died as a direct cause of rainy, cold weather, all within the first 2 weeks after hatching. No cause of death could be ascribed for three dead chicks.

Among 40 depredated chicks where the predator group could be identified, mammals killed 2/3 and raptors 1/3. However, many chicks disappeared from the broods and were not found because they were transported far from the site (mainly raptors), burried or placed inside rocky ground or dens (mammals), or the transmitter was damaged (both groups). Mustelids, mainly pine marten, and goshawk killed most of the chicks (Table 5).

The summer of 1987 was exceptionally cold and rainy. It rained 17 days from the first recorded hatching date (June 8) to the end of the month (23 days); total rain for the month was 275% of the last 11-year monthly average. That was the year with the highest chick loss (83%) and the only year when the loss due to the direct effect of weather was recorded (Fig. 3). Still, also that year predation accounted for most of the mortality (60%) during the chicks' first month of life.

Mortality and environmental factors

The abundance of insect larvae was correlated with low temperatures in May ($r = -0.73$, $P < 0.05$) and to a lesser extent with rain in June ($r = 0.58$, $P < 0.10$). The following equation explained 83% of the variation in the abundance of larvae: Larvae volume = $4.8 - 0.03(T_{\min})_{\text{May}} + 0.37(\text{rain days})_{\text{June}}$.

When comparing the 3 years, there were no clear relationships between early chick mortality and net chick production and between any of these and weather factors, vole abundance, or insect abundance (Table 6). Highest mortality occurred in the rainy and cold June of 1987 when the abundance of insects was highest and voles were also quite abundant. The only year when

Table 4. Distribution of dead capercaillie chicks (*N* = 88) of different ages according to mortality factors at the study areas in southeastern Norway, 1986–1988.

	1–15 days number (%)	16–30 days number (%)	1–3 months number (%)	3–6 months number (%)	Total number (%)
Weather	6 (15)	0 (0)	0 (0)	0 (0)	6 (7)
Predation	31 (79)	13 (100)	25 (96)	10 (100)	79 (90)
Unknown	2 (5)	0 (0)	1 (4)	0 (0)	3 (3)
Total	39 (100)	13 (100)	26 (100)	10 (100)	88 (100)

low chick mortality also coincided with a year of high net production in the autumn was 1986, a June when conditions were most "average". The year 1988 was characterized with conditions presumably quite favourable for chick production, but early chick mortality was rather high and net production the lowest among the 3 years.

Discussion

Methodology

Initially, we feared that our field methods might increase the mortality rate due to the extra burden of carrying a transmitter and due to frequent tracking at close distances. However, equipping < 50-g chicks with 1.8-g backpack transmitters and locating them 2–3 times per 24 hrs did not appear to affect them negatively, as the recorded mortality rates were not higher among the radioed broods than among unmarked controls. Furthermore, we detected no difference in subsequent movement distance between broods that had been flushed by us for replacing radio tags or had been attacked by predators, and undisturbed broods.

Manzer and Hannon (2007), in a similar study of sharp-tailed grouse *Tympanucus phasianellus*, also concluded that equipping small chicks with radio transmitters had negligible effects on behaviour and survival. However, they pointed out that because some chicks may not flush when disturbed, brood counts tend to underestimate brood sizes. That is probably also the case in most other species of grouse. In our study, however, we used well-trained pointing dogs and searched the sites of unmarked broods

Table 5. Distribution (%) of depredated capercaillie chicks (*N* = 79) of different ages according to predator species, southeastern Norway, 1986–1988.

Predator group	1–15 days *N* = 31	16–30 days *N* = 13	1–3 months *N* = 25	3–6 months *N* = 10	Total *N* = 79
Avian[1]	12.9	0	16.0	10.0	11.6
Mammalian					
Mustelids[2]	41.9	23.0	8.0	20.0	25.3
Red fox	3.3	23.0	0	0	5.1
Unknown[3]	0	0	4.0	30.0	5.1
Total mammalian	45.2	46.1	12.0	50.0	35.4
Unknown[4]	41.9	53.8	72.0	40.0	53.2
Total	100	100	100	100	100

[1] Mainly goshawk, [2] mainly pine marten, but also stoat and possibly mink (*Mustela vison*), [3] unknown mammal, [4] dead chicks not found.

Table 6. Capercaillie chick mortality during the first month after hatching, net chick production and environmental factors, southeastern Norway, 1986–1988.

Environmental factors	1986	1987	1988
Temperature	high (111)[1]	low (75)[1]	very high (122)[1]
Rain	low (57)[2]	enormous (207)[2]	very low (12)[2]
Insect abundance	high (2.2)[3]	very high (5.1)[3]	medium/low (1.0)[3]
Vole abundance	increasing (6)[4]	peak (24)[4]	peak (21)[4]
Chick mortality (%)	29	83	58
Net chick production[5]	1.3	1.0	0.9

[1] Percentage of mean diel temperature 5–24 June during last 11 years. [2] Percentage of mean diel precipitation 5–24 June during last 11 years. [3] Volume of insects (ml/15 sweeps) in June. [4] Number of voles/100 trap nights in early autumn; last peak year: 1984. [5] Number of chicks/hen in August census with pointing dogs.

thoroughly to make sure that virtually all chicks were found. Hence, we believe our observation of similar brood sizes among radioed and unmarked broods was unbiased.

Pattern

Although quite variable, an average of 57% of the radiomarked chicks died within the first month of life. This rate of loss is almost identical to that reported from a similar study on greater sage grouse *Centrocercus urophasianus* (Gregg 2006), the largest tetraonid in North America, but lower than the rates recently found in the smaller sharp-tailed (Manzer & Hannon 2007), ruffed grouse *Bonasa umbellus* (Larson *et al*. 2001) and red grouse *Lagopus lagopus scoticus* (Park *et al*. 2002). With clutch sizes also varying inversely with body size, this allometric relationship probably reflects adapted demographies of their breeding cycles.

As expected, chick mortality was highest during the first few weeks after hatching. However, in our calculations of time-specific mortality rates, we did not correct for autocorrelation caused by studying chicks within broods. Correcting for this would increase the variances of the two estimated rates and thus reduce the probability of detecting a significant difference between them. Because the two mortality rates (between < 1 and 3 weeks and between 3 and 12 weeks of age) were different at < 1% level of probability, and the proportional losses of chicks during predatory attacks were similar in the two time periods, we believe that the observed difference reflects a real difference in age-specific mortality between the two age groups.

The higher early posthatch mortality ocurred during the age period when the chicks depend on their mother for maintaining body warmth and when they are feeding almost exclusively on insects. It also coincided with the period when their speed of movement was highest; after about three weeks of age their daily movement distance decreased sharply. Shorter movements and somewhat lower mortality ocurred when proportion of ground insect food is still high (Rajala 1959, Kastdalen & Wegge 1985), but at an age when the chicks can fly well. Sonerud (1985) suggested that extensive ground movements by young broods of grouse and waders could be an adaptation against raptor predation, e.g. the probability of a brood being rededected by a returning goshawk is reduced by moving away after the initial attack. However, when able to fly, chicks may instead fly and hide in nearby trees. This may explain why diel movement distances were shorter at older age.

Presumably, owing to their rapid growth rate and large size, capercaillie chicks represent an increasingly attractive prey as they grow older. Hence, predation pressure is expected to increase, rather than decrease with brood age. The opposite results of a lower mortality rate is probably due to a combination of better anti-predator behavior (like flying and perching in trees) and fully developed thermoregulation. Also, the generally low density of broods, with chicks only constituting a small part of their diets, probably does not induce searching behavior for this food source among the predators.

Causes of mortality

Each year, predation was by far the most important proximate cause of mortality. Only in the extremely wet June in 1987 did some chicks die from exposure to wet and cold weather. Mammalian predators were more important than raptors, with pine marten probably being the most important species. Telemetry studies on young grouse chicks in North America also recorded predation as the main proximate mortality factor, with mammals being most important for prairie-dwelling species (greater sage grouse: Gregg 2006, sharptailed grouse: Manzer & Hannon 2007) and raptors most important for forest grouse (ruffed grouse: Larson *et al*. 2001).

Less than 20% of the losses could be ascribed with certainty to predation by raptors. The common buzzard (*Buteo buteo*) may have taken a few of the smallest chicks, as this predator also occurs in the study area and has been reported to take young capercaillie chicks (Spidsø & Selås 1988). However, the majority of losses to raptors could be ascribed with certainty to goshawk. The proportion killed by this raptor might have been even higher than our classified proportion; most of the disappearing chicks assumed to have been killed by predators (unknown category) were probably taken by goshawks and moved outside detection range. Because the proportion killed by "unknown predator" was highest among the older chicks, we suspect that goshawk predation may have been an important cause of mortality among the oldest chicks. If so, this agrees well with other studies, as forest grouse of this size category has been found to constitute a major part of its diet (Tornberg 2001).

Most chicks were killed by mustelids, particularly the pine marten. From other studies (Marcström *et al*. 1988, Lindström *et al*. 1994), we expected red fox to be more important. The relatively low proportion taken by red fox may be explained by an outbreak of sarcoptic mange; during the middle and last part of the 1980s this disease reduced the fox population to very low levels throughout the region, including our study area (Smedshaug *et al*. 1999). This probably led to increasing numbers of pine marten, as was reported elsewhere during the outbreak of this disease (Lindström *et al*. 1994).

Because predators usually remove all eggs, a large proportion of broodless hens in August might reflect high egg predation, rather than posthatch losses of chicks. Kurki and Lindén (1995) made this assumption in their analysis of reproduction of black grouse *Tetrao tetrix* in Finland, and Baines *et al*. (2004) inferred this on the basis of a recent predator control study in Scotland. However, in our study ~25% of the hens lost all their chicks. Similarly, of 9 successful clutches in a mountain forest in Germany, 3 lost all chicks before August (Storch 1994). Most of our total losses occurred in the very wet and cold 1987, and Storch (1994) also ascribed her total losses to adverse weather. Thus, the frequency of broodless hens in August does not necessarily reflect nest predation, as it is supplemented by total brood losses, which may be higher in years of heavy rainfall.

Few chicks died due to exposure, and such mortality was only recorded in the very wet and cold spring of 1987, all within the first 8 days of hatching. In 1987, total loss during the first month was 83%, by far the highest among the 3 years. The prevailing weather conditions may have predisposed the chicks to mammalian predation, as predatory losses were quite high during and immediately after heavy rainfalls. Distress calls emitted by chilled chicks may have attracted predators, as has been observed elsewhere (J. Galby pers. comm). Lepidoptera larvae reached exceptionally high densities in the rainy spring of 1987; that year a person could pick 50 larvae in 4 minutes within a 0.25 m^2 square! Thus, this super-abundance of nutritious food may have buffered against death from starvation and prevented early chick mortality from reaching an even higher level in 1987.

Combination of environmental factors

The three years differed markedly in environmental conditions (Table 5). Our prediction that a combination of favourable June weather, high abundance of preferred larvae food, and high density of voles would lead to high chick survival was only partly fulfilled. The high chick loss in early life in 1987, presumably due to both direct and indirect effects of very wet and cold weather, appeared to be compensated for by higher survival later in the summer, resulting in a similar net production of autumn chicks as in 1988, a year when the recorded brooding conditions appeared to be rather optimal. However, different rates of egg loss in those two years may have obscured real differences.

Insect food is considered to be very important for grouse chick survival (Savory 1989), although its role was not well demonstrated in this study. Interestingly, among the various weather variables tested, we found that the abundance of larvae during 2 weeks posthatch in June was most strongly correlated with low temperatures during the 30-day prehatch period. We have no explanation for this, but speculate that maybe in cold springs, the phenology of bilberry, which is the main host plant of *Lepidoptera* larvae (Atlegrim & Sjöberg 1995), is delayed, thereby offering more nutritious foods for an extended period for foraging larvae in June.

In spite of seemingly optimal conditions both in 1986 and 1988, early chick loss was twice as high in 1988, possibly because of higher predation due to reduced cover for the chicks; the very high abundance of *Lepidoptera* larvae the preceeding two years had severely defoliated the bilberry shrubs in preferred brood habitats. The lack of clearer relationships between the measured environmental variables and chick survival could have been due to an abnormally low fox population and that the 3-year study period included two successive peak years and no crash year of microtine rodents.

Acknowledgements

Several people assisted during fieldwork, and we thank Per Kristiansen, Roar Jacobsen, Trond Øvstaas and Terje Øvsthus in particular. Robert Moss gave helpful advice during data analysis and earlier reporting, and Jørund Rolstad gave constructive comments on the manuscript. We are grateful to Oslo Hunting and Fishing Association for funding the study through the T. Gotaas Fund.

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