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Original article

Cause of death in willow ptarmigan *Lagopus l. lagopus* chicks and the effect of intensive, local predator control on chick production

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Population dynamics of willow ptarmigan *Lagopus l. lagopus* are dominated by varying numbers of successful recruits to the population. One important component that determines this number is the survival of chicks from hatching to fledging at about two weeks of age. We studied the causes of death of chicks and the effects of intensive, local predator control on chick production in two areas of south-central Norway from 1997-2004. During 1997-2000, 253 chicks were captured and radio-tagged in a 2,000 ha area in Dalsbygda, Norway. Average survival for all years from hatching to two weeks of age was 33%. Predation accounted potentially for up to 73% of all deaths. Research-related deaths accounted for 17% of deaths, while 10% died of other natural causes than predation. In no case did disease or lack of food appear to be the ultimate cause of death. The localisation of broods could not be predicted from brood position the previous day and there was no correlation between brood behaviour and chick death.

Intensive local predator control was conducted in a 2,000 ha area in Numedal, Norway during 1998-2004. Red fox *Vulpes vulpes*, marten *Martes martes*, mink *Mustela erminea*, raven *Corvus c. corax* and hooded crow *Corvus c. cornix* were trapped or shot. Chick production was calculated based on pigmentation of wing feathers from all birds harvested in September. Mean chick production for all years was 3.1 chicks per two adults in the treatment area and 2.4 in an adjacent area without predator control, but the differences were not significant. In our study, therefore, predator control had no measurable effect on chick production or survival.

Key words: chick mortality, Lagopus lagopus, population dynamics, predation, willow ptarmigan

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Willow ptarmigan is the most popular game bird in Norway. Approximately 100,000 people hunt them in the autumn and kill about five birds each at a considerable cost. Understanding the mechanisms governing annual variation in the harvestable population is therefore of paramount interest to the hunters as well as to the game management administration. A central question is: what can we do to increase the autumn population? In the UK highlands, management of red grouse *Lagopus l. scoticus* has long traditions. Rotational heather burning combined with parasite and predator control have yielded satisfactory results (Hudson 1992). Similar management aimed at small game has no tradition in Norway. Scattered experiments with breeding and release, heather burning, protection and predator control have been tested, but with limited success (Phillips et al. 1992). Willow ptarmigan population dynamics are dominated by varying numbers of recruits to the population (Myrberget 1984, Steen et al. 1988b). Hens lay 10-12 eggs in May/June. On average, 25% are destroyed, often by predators like hooded crows *Corvus c. cornix*, stoat *Mustela erminea* and red foxes *Vulpes vulpes* (Myrberget 1985). More than 95% of the remaining eggs hatch, but rarely >50% of the chicks survive until September (Myrberget 1986). Each pair, therefore, produces three young per year on average.

Some studies have suggested that environmental factors, others than predation, is the main cause of deaths. The physiology and behaviour of willow ptarmigan chicks, like that of other galliform birds, would suggest that environmental factors are all important. These birds are precocious, i.e. the chicks leave the nest once they have dried following hatching. During their first two weeks of life, they are totally dependent upon being brooded by the hen, in rare cases, also by the cock. Chicks are brooded until their body temperature reaches normal values (39-41°C). Only then do they leave the hen to feed (Boggs et al. 1977, Pedersen & Steen 1979). During feeding, their body temperature declines and at a certain level, it prompts the chicks to return to the hen. The colder the weather, the sooner will the chicks cool off and the shorter the time available for feeding (Boggs et al. 1977). The larger the brood, the longer the chicks have to be brooded and less time will be available for feeding. In line with this strategy, Erikstad (1985) found that most chick deaths occurred during their first weeks of life. Slagsvold (1975) found a positive correlation between mean daily temperature in June (when the hens incubate) and chick survival, suggesting that the condition of the hen, and thus the quality of her eggs as well as her condition during chick brooding were of importance for the survival of chicks (Steen et al. 1988a). Erikstad & Andersen (1983) found that during summers with bad weather, survival was higher in small than in large broods presumably because small broods will have more time for feeding.

Several studies have suggested that predation is the dominant mortality factor in galliform birds as in most other small game (Steen 1995). Steen et al. (1988b) correlated annual willow ptarmigan chick production in two areas during a total of 42 years with indexes of weather and predation. There was a strong correlation between predator index and chick mortality, while significant correlations between indexes combining air temperature and precipitation during the first week of the chicks life could not be found. Similar results were obtained for willow ptarmigan by Holt (1952), Myrberget (1974), Hannon & Martin (2006) and Hik et al. 1986, for red grouse (Jenkins et al. 1963, Redpath 1991), capercaille *Tetrao urogallus* (Wegge & Kastdalen 2007, Kauhala & Helle 2002) and pheasant *Phasianus colchcus* (Erlinge et al. 1984).

The primary objectives of our study are to identify the major causes of death of willow ptarmigan chicks, and to identify brood behaviour that may predict brood localisation and thus affect predation of chicks. In conjunction with this study, we also examined the effects of local predator control on chick production through a game management experiment. We predict predation to be the main cause of death, that the daily localisation of broods is unpredictable, and that predator control should lead to increased annual chick production.

Material and methods

Both studies were carried out in rugged mountain areas with a density of willow ptarmigan broods seldom >1 per 10 ha. Chick mortality was studied in a 2,000 ha area in Dalsbygda, Mid-Norway, (62°35'N, 10°58'E) at an altitude between 1,000 and 1,300 m a.s.l. in June/July during 1997-2002. The predator control study was undertaken in a 2,000 ha area in Numedal (60°24'N, 9°00'E) in southern Norway between 1,000 and 1,200 m a.s.l. during 1998-2004.

Chick mortality

Newly hatched willow ptarmigan chicks were located either by following radio-tagged (12 g Lotek transmitters) hens to their nests, or by using well-disciplined gordon setter bird dogs to find broods. Permission to use radio-tags was obtained from the Norwegian Animal Research Authority 5 February 2002. The transmitters used on hens had a detection range between 2 and 10 km depending on the topography. Chicks <7 days of age, weighing 12-22 g, were equipped with 0.7 g radio-transmitters (Mod. BD-2A, Holohil systems). We tried to equip 40-50 chicks with transmitters every year. During 1997-2000, the transmitters were glued to the down coat between the shoulders with Super glue. However, as transmitters had a tendency to fall off after a few days, transmitters were secured to the skin by a minute stitch in 2001 and 2002.

Since not all chicks were tagged at the same age, different broods were not followed for the same length of time. The shortest time broods were followed was three days and the longest 19 days, while the average number of days broods were followed was 10.3 days. The transmitters lasted 3-4 weeks and had a detection distance of 100-500 m depending on the topography. A few days after fledging, we recaptured the radio-tagged chicks and removed the transmitters for use the following year.

Brood movement

To study whether brood localisation was predictable, broods were located at least once a day. During 1998-2002, their position was recorded on GPS. Daily brood movements were determined based on the recorded brood positions. During brood localisation, we started where the brood had last been located and worked carefully from there until we localised the brood. Thus, we could determine brood movements much longer than the detection range of the transmitters. We analysed statistically whether the distance and direction of brood movement could be predicted from brood localisation the previous day as an indication of predictability of brood position.

Identification of predators

In some cases, we found missing transmitters together with remnants of a chick in dens of fox, stoat or mink *Mustela vison*. In such cases, we assumed that chicks had been killed by the den owner. We also found lost transmitters in fox faeces. In other cases, we either saw the actual killing or found species-specific feathers or faeces together with the transmitters. We assume that in these cases, the chicks were killed by predators.

Some transmitters could not be localised despite very intensive searching. In these cases, we assumed that they had been destroyed or removed out of range possibly by predators. This assumption is supported by the fact that we never recaptured chicks with 'dead' transmitters and never recorded transmitters to stop emitting. Chicks that were killed by our research activities or other natural causes than predation (see Results) were often left where they were found and checked the next days. In no case had the carcass been removed. After about a week, they had been devoured by insects. Similar results were obtained for small rodents (Steen 1995). Transmitters found without remnants of chicks were assumed to have fallen off.

Effect of transmitters on survival

During 1997-1999, we checked if radio-tagging influenced the survival of the chicks. This was done by tagging about half the chicks in each brood. At fledging, we flushed the brood and compared the number of chicks with the number of tagged chicks known to be in that brood.

Predator control and willow ptarmigan chick production

We were granted permission from the appropriate authorities to control predators on a year-round basis, including the breeding season when all game in Norway is normally protected. (Thus the term intensive predator control). Hooded crows, raven and red fox were shot on bait during winter. Stoat, mink and marten were killed in Fenn traps, mark 4, 5 or 6. A total of 200 traps were put up in 1995. Birds of prey are totally protected and were therefore not killed. Traps were usually inspected once a week from May until October. We estimated that we spent 10-20 days, equivalent to 60-120 hours on the predator control field work annually.

The control area where no game management was conducted was of similar size and had common border with the experimental area. Both areas were surrounded by large mountain areas with the same type of ptarmigan habitat as in our areas.

Annual chick production was calculated from the number of birds in the hunting bags from the two areas and presented as young per two adults. Age was determined by inspection of pigmentation on the three outermost wing feathers according to the method of Bergerud et al. (1963).

Statistical analyses

A possible negative effect of the radio transmitters on survival was analysed using mixed models implemented in R (R Development Core Team 2005). We chose to use mixed models to account for the possible clutch specific probabilities to disappear. Whether a chick had a transmitter or not was entered as a fixed factor. Clutch was modelled as random factor and was nested in year. The significance of the fixed factor was tested using analysis of variance (Crawley 2003).

To test the hypothesis that brood movement is random in order to avoid predators and that consecutive brood movements are therefore independent, we modelled the dependencies of two consecutive moved distances and angles of movement with generalised linear models (GLM) implemented in R (R Development Core Team 2005). The data were overdispersed and we have therefore chosen to use quasi error term with a log link in the analysis.

Table 1. Survival of radio-tagged willow ptarmigan chicks from hatching to 2-3 weeks of age.

	Number of chicks		Survival of chicks	
Year	Tagged	Untagged	Tagged	Untagged
1997	42	22	9 (21%)	4 (18%)
1998	34	31	17 (50%)	18 (58%)
1999	19	19	5 (26%)	3 (16%)
All years	95	72	31 (33%)	25 (35%)

The effects of predator control on chick production were estimated using Wilcoxen matched pair signed rank test.

Results

Chick mortality

The difference in survival of tagged and untagged chicks (Table 1) was not significant ($P > 0.05$).

A total of 253 chicks were radio-tagged. Of these, 97 survived the experimental period while 156 (67%) disappeared during the test period (Table 2). Of these, 52 (34%) were killed by predators. In addition, 62 (39%) of the tags were lost, and these losses could be due to predation, destroyed tags or the inability to locate and find the tags (especially when broods can move up to 2 km in a day). Overall, predation might thus account for 34-73% of chick loss. Our research activity caused the death of another 17% while 10% died from other natural causes than predation.

Of the 52 chicks that we know were killed by predators, 11 were taken by fox, 16 by stoat, five by mink, four by long-tailed skua *Stercorarius longicaudus*, two by hen harrier *Circus c. cyaneus,* three by kestrel *Falco t. tinnunculus*, one by a raven, while 10 were taken by unidentified predators.

Of the 26 chicks that were killed by our activity, seven were accidentally trampled to death by the investigators, three had gotten their wing tag caught by a branch, one was killed by one of our dogs and the rest froze to death, because we disturbed the hen with newly hatched chicks too long during cold weather.

Of the 16 killed by other natural causes than predation, eight were trampled to death by domestic sheep, one drowned, two were found dead and a post-mortem indicated ruptured atrium, while five drowned during an unusually violent rainstorm in the summer of 2001. Therefore, only the last mentioned eight died from causes not related to other animals (man included). We had no case where disease or poor nutrition appeared to be the ultimate cause of death.

Brood movements

Willow ptarmigan chicks weighed 10-13 g at hatching. At this stage, they cannot reach a height >5-7 cm above the ground, but are still able to move up to 200 m during their first day of life. Some broods were found in almost the same place for several days, others moved considerable distances. The longest one day travel was >2,000 m. The mean daily movement varied from 14 to 514 m.

Table 3 shows mean total brood movement during the first 2-3 weeks of life, mean daily movement and the mean distance between first and final localisation for each year. Linear regression analysis showed no significant correlations between these parameters and chick survival.

The distance moved by each brood in consecutive days was independent ($P > 0.5$), and so was the angle of displacement on consecutive days ($P > 0.15$).

In 2001, we observed some unusual and interesting chick behaviour that, to our knowledge, has not been described earlier. In three instances, groups of chicks between 1 and 3 weeks old left their brood, possibly tempted by mild weather, and wandered off

Table 2. Fate of 253 radio-tagged willow ptarmigan chicks from hatching to 2-3 weeks of age.

			Cause of death		
Year	Chicks tagged	Total deaths	Predation N+disappeared	Research	Other natural causes
1997	46	37	4+21	4	8
1998	34	17	6+6	4	1
1999	39	22	6+7	9	0
2000	38	11	2+8	1	0
2001	46	35	20+6	4	5
2002	50	34	14+14	4	2
Total	253	156 (67% of total)	52+62 (73% of deaths)	26 (17% of deaths)	16 (10% of deaths)

Table 3. Mean total brood movement from hatching to 2-3 weeks of age, mean daily movement and distance from where the brood was first observed to where it was last located and chicks per two adults based on birds harvested in September, 1998-2002.

Year	Broods	Mean brood displacement, m (SD)			Chicks/ brood
		Total	Daily	From first location	
1998	8	1078 (696)	112 (54)	323 (219)	5.1
1999	5	2000 (966)	352 (135)	144 (1124)	3.5
2000	7	1568 (1224)	143 (106)	784 (866)	5.3
2001	7	2135 (1280)	164 (64)	620 (769)	2.9
2002	9	2704 (1467)	266 (171)	1506 (1323)	3.3

Table 4. Number of predators killed annually in the experimental area. Years with abundant small rodents are marked with*.

Year	Red fox	Mink	Marten	Stoat	Crow	Raven
1995*	4	8	5	114	7	2
1996	7	10	3	29	5	5
1997	8	0	2	15	7	2
1998*	9	4	4	61	12	0
1999	4	5	4	28	7	1
2000	5	6	2	19	4	2
2001*	4	4	0	12	8	4
2002	13	5	1	27	7	5
2003	8	11	4	48	7	3
2004	6	8	3	57	5	6

on their own. Three chicks eventually joined other broods while the rest, two in one group and three in another continued on their own. The excursion went well for a week and the chicks moved for several 100 m a day and appeared to thrive. However, following a violent thunderstorm, all five orphaned chicks drowned. No chick that was part of a brood died that night.

Predator control

Table 4 summarises the number of predators killed annually in the experimental area during our study. Table 5 lists annual chick production. Mean chick production during 1998-2004 was 3.1 for the experimental area and 2.4 for the control area. This is equivalent to an improvement in chick production of only about 30% or 0.6 chicks per brood. The difference was not statistically significant (signed ranks test). A total of 348 birds were shot in the experimental area and 354 in the control area.

Discussion

The finding that predation is the dominant cause of death in willow ptarmigan followed our main prediction. This does not imply, however, that factors like weather, disease and food quality or availability is without importance. Such factors may be proximal causes of death by rendering the chicks more susceptible to predation. Thus, Moss et al. (1990) found that parasitism increases predation on red grouse, and Hudson et al. (1992) showed that red grouse heavily infested by parasites were more easily located by pointing dogs than birds which were not infested. Most likely, they would also be an easier prey to predators. Erikstad & Andersen (1983) found that willow ptarmigan chicks grew slower in summers with low temperatures and a shortage of insects than in normal summer weather. This too may indirectly influence mortality.

Willow ptarmigan chicks are exposed to a wide range of predators, some hunting mainly by sight, others by scent and some also by sound. One well known avoidance strategy in pre-fledged chicks is to freeze and rely on their excellent camouflage once an intruder/predator is spotted. However, since the chicks must find all their food by moving about in the terrain, they leave a scent track, and at the same time, reduce the benefit from the camouflage. Further, when willow ptarmigan broods forage, both hen and chicks continuously emit contact calls that can be heard up to 50 m away (Wike et al. 1987).

The study of brood movements indicated that these movements are largely unpredictable, which might be a strategy that serves also to reduce predation. Other aspects of unpredictable behaviour are revealed by the placement by the hen of her nest and by the behaviour of the broods. Nests can be found in almost any type of vegetation and the behaviour of the parents holds little relationship with the number, location or age of chicks.

Table 5. Chick production (number of chicks per two adults) in the annual hunting bags. Years with abundant small rodent populations marked with*. Numbers of birds shot are given in parenthesis.

Year	1998*	1999	2000	2001*	2002	2003	2004
Experimental	4.3 (19)	2.7 (47)	3.4 (12)	5.0 (95)	3.0 (110)	0.6 (12)	2.2 (53)
Control area	4.0 (54)	2.4 (64)	1.1 (62)	3.0 (50)	3.6 (104)	0 (0)	1.6 (20)

If predation is the dominant cause of death of willow ptarmigan chicks, one would expect predator control to be an efficient strategy to increase the ptarmigan population. This expectation has indeed received support. Marcstrøm et al. (1989) carried out an experiment on the effect of intensive predator control on the population of black grouse *Lyrurus tetrix* and capercaille. On one of two islands where predators were removed, chick production was about twice as high as on the island that was left untouched. Predator control in two areas in Finland gave similar results (Kauhala et al. 2000).

In the present experiment, we failed to detect a significant effect, despite the fact that we practised intensive and year-round predator control. We suggest that this equivocal result is due to the nature of the experiment. The areas used for predator control were relatively small, which most likely allowed immigration of predators from nearby control areas, predator abundance was not directly measured and the experiment was not replicated. Also, when we kill a predator, we most likely kill territorial individuals first, thus leaving the area open for immigrants to establish themselves. In fact, in the extreme case, predation may increase in an area where predators are controlled since the removal of one territorial individual may give room for more than one immigrant.

Predator control is efficient when carried out in areas that are isolated, either as islands or geographically. This is supported by the findings of Marcstrøm et al. (1989) that predator control on islands is quite effective in increasing the population of galliform birds. However, Parker (1984) found only a slight effect on chick production of corvid control practised on one half of an island compared to that on the other half. Hudson (1992) showed that predator control on the UK grouse moors is more efficient when practised in larger areas.

Thus, based on a cost benefit analysis, predator control would hardly be chosen as the appropriate management tool to achieve the desired population. It seems more appropriate to regulate the hunting pressure by bag limit, length of hunting season, and other regulatory means.

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References

Bergerud, A.T., Peters, S.S. & McGrath, R. 1963: Determining sex and age of willow ptarmigan in New Foundland. - Journal of Wildlife Management 27: 700-711.

Boggs, C., Norris, E. & Steen, J.B. 1977: Behavioral and physiological temperature regulation in young chicks of the willow grouse. - Comparative Physiology Biochemistry 58A: 371-372.

Crawley, M.J. 2003: Statistical computing. - Wiley, England, pp. 669-708.

Erikstad, K.E. 1985: Growth and survival of willow grouse chicks in relation to home range size, brood movements and habitat selection. - Ornis scandinavica 16: 181-190.

Erikstad, K.E. & Andersen, R. 1983: The effect of weather on survival, growth rate and feeding time on willow grouse broods of different sizes. - Ornis scandinavica 14: 249-252.

Erlinge, S., Frylestam, B., Gøranson, G., Høstedt, G., Liberg, O., Loman, J., Nilsson, I.N., von Schantz, T. & Sylven, M. 1984: Predation on brown hare and ringneck pheasant populations in southern Sweden. - Holarctic Ecology 7: 300-304.

Hannon, S. & Martin, K. 2006: Ecology of juvenile grouse during the transition to adulthood. - Journal of Zoology 269(4): 422-433.

Hik, D.S., Hannon, S.J. & Martin, K. 1986: Northern harrier predation on willow ptarmigan. - Wilson Bulletin 98: 597-600.

Holt, E. 1952: Rypeproduksjon - værforhold. - Jeger og Fisker, Oslo, pp. 120-126. (In Norwegian).

Hudson, P.J. 1992: Grouse in space and time. - The game conservancy, Fordingbridge, UK, 225 pp.

Hudson, P.J., Dobson, A.P. & Newborn, D.N. 1992: Do parasites make prey vulnerable to predation? Red grouse and parasites. - Journal of Animal Ecology 61: 487-492.

Jenkins, D., Watson, A. & Miller, G.R. 1963: Population studies on the red grouse *Lagopus l. lagopus* in north east Scotland. - Journal of Animal Ecology 32: 317-376.

Kauhala, K. & Helle, P. 2002: The impact of predator abundance on grouse populations in Finland - a study based on wildlife monitoring counts. - Ornis Fennica 79(1): 14-25.

Kauhala, K., Helle, P. & Helle, E. 2000: Predator control and the density and reproductive success of grouse populations in Finland. - Ecography 23: 161-168.

Marcstrøm, V., Kenward, R.E. & Engren, E. 1989: The impact of predation on boreal tetranoids during vole cycles: an experimental study. - Journal of Animal Ecology 57: 859-872.

Moss, R., Trenholm, I.B. & Park, R. 1990: Parasitism, predation and survival of hen red grouse in spring. - Journal of Animal Ecology 59: 631-642.

Myrberget, S. 1974: Variations in the production of the willow grouse *Lagopus lagopus* in Norway, 1963-1972. - Ornis Scandinavica 5: 163-173.

Myrberget, S. 1984: Population dynamics of willow grouse, on an island in Northern Norway. - Fauna norvegicus Series C, Cinclus 7: 95-105.

Myrberget, S. 1985: Egg predation on an island population of willow grouse. - Fauna norvegicus Series C, Cinclus 8: 82-87.

Myrberget, S. 1986: Annual variation in clutch size of a population of willow grouse. - Fauna norvegicus Series C, Cinclus 9: 74-81.

Parker, H. 1984: Effect of corvid removal on reproduction of willow ptarmigan and black grouse. - Journal of Wildlife Management 48: 1197-1205.

Pedersen, H.C. & Steen, J.B. 1979: Behavioral thermoregulation in Willow Ptarmigan chicks. - Ornis Scandinavica 10: 17-21.

Phillips, J., Steen, J.B., Raen, S.G. & Aalerud, F. 1992: Effects of burning and cutting on the vegetation and on the population of Willow grouse *Lagopus L. lagopus* in Norway. - Fauna norvegicus Series C, Cinclus 15: 37-42.

R Development Core Team 2005: R: A language and environment for statistical computing. - R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org/.

Redpath, S.M. 1991: The impact of hen harriers on red grouse breeding success. - Journal of Applied Ecology 28: 659-671.

Slagsvold, T. 1975: Production of young of the willow grouse in Norway in relation to temperature. - Norwegian Journal of Zoology 23: 269-275.

Steen, H. 1995: Untangling the causes of disappearance from a local population of root voles: a test of the regional synchrony hypothesis. - Oikos 73: 65-72.

Steen, J.B., Andersen, Ø., Sæbø, A., Pedersen, H.C. & Erikstad, K.E. 1988a: Viability of newly hatched chicks of Willow Ptarmigan. - Ornis Scandinavica 19: 93-96.

Steen, J.B., Steen, H., Stenseth, N.C., Myrberget, S. & Marcstrøm, V. 1988b: Microtine density and weather as predictors of chick production in willow ptarmigan. - Oikos 51: 138-373.

Wike, R. & Steen, J.B. 1987: Intra-family communication in Willow Grouse *Lagopus lagopus*. - Fauna norvegicus Series C, Cinclus 10: 81-87.

Wegge, P. & Kastdalen, L. 2007: Pattern and causes of natural mortality of capercaille, *Tetrao urogallus,* chicks in a fragmented boreal forest. - Annales Zoologici Fennici 44(2): 141-151.