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An impact of genetic variation and predation on chick survival in willow ptarmigan *Lagopus l. lagopus*

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The present study investigates the determinants of chick survival in willow ptarmigan *Lagopus l. lagopus*. Chick survival was negatively associated with genetic relatedness of mates. This may imply that more chicks die when genetic relatedness of mates is high, i.e. low chick heterozygosity at hatching. Hence, newly hatched chicks with low heterozygosity may have reduced viability and, therefore, might suffer higher mortality due to biotic/abiotic conditions. However, there was no association between the proportion of chicks with low heterozygosity and ambient temperature, but a highly significant association with predation pressure was found. Because newly hatched chicks are unable to maintain their body temperature even at normal ambient temperatures and because willow ptarmigan chicks start chirping when they get cold, it is suggested that chicks with low genetic variation may become more exposed to predation. It is proposed that genetic variation significantly affects viability of ptarmigan chicks, but that predation is the proximate cause of death. Consistent with several earlier studies, predation was related both to nesting females and to survival of the chicks. However, the present study extends these findings by suggesting a relationship between predation on one side and genetic constitution on the other, and that predation on nesting females, by reducing genetic variation among chicks at hatching, enhance chick mortality.

Key words: chick survival, genetics, Lagopus lagopus, predation, temperature, willow ptarmigan

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In Norway, the willow ptarmigan *Lagopus l. lagopus* breeds in mountainous areas throughout the country, often enduring hostile climatic conditions during the breeding season. Females incubate clutches of about 10 eggs for 21 days. The chicks hatch in late June or early July and leave the nest without parental assistance to feed within a few hours. Feeding is interrupted by periods of brooding since newly hatched chicks are unable to maintain normal body temperature even at ambient temperatures around 20°C (Aulie 1976). As in other tetraonids, long periods of brooding are required in cold and wet weather, which reduces the time available for feeding (Zwickel 1967, Theberge & West 1973, Pedersen & Steen 1979, Erikstad & Spidsø 1982, Erikstad & Andersen 1983). At the age of 10 days, ptarmigan chicks are able to maintain their body temperature under normal weather conditions (Aulie 1976, Pedersen & Steen 1979).

Contrasting views exist concerning what affects survival of willow ptarmigan chicks. In several long-term studies of *Lagopus lagopus* subspecies, no association has been found between the survival of the chicks and weather conditions during the post-hatch period (red grouse *L. l. scoticus* (Jenkins, Watson & Miller 1963), Newfoundland willow ptarmigan *L. l. alleni* (Bergerud 1970) and Scandinavian willow ptarmigan *L. l. lagopus* (Myrberget 1972, Steen, Stenseth, Myrberget & Marcström 1988a)). However, Erikstad & Spidsø (1982) found that extremely cold and wet weather is critical in preventing sufficient food intake. Slagsvold (1975), Steen (1989) and Marcström & Höglund (1980) demonstrated the importance of 'good' weather in the weeks prior to hatching indicating that the spring weather prior to hatching may be essential for the survival of chicks. They suggest that warm weather diminishes the energy demand of the female and accelerates phenological development of the plants and insects that are important food for the chicks. Several studies of willow ptarmigan have shown that predation strongly affects chick production, and that chick production is one of the key factors causing year-to-year changes in numbers (e.g. Myrberget 1972, 1983, Steen, Andersen, Sæbø, Pedersen & Erikstad 1988b). Finally, chick viability may also be influenced by annual variation in egg quality; for example, Moss, Watson, Rothery & Glennie (1981) found that chick survival in red grouse was positively related to both egg size and chick weight at hatching. Nevertheless, an earlier study of external conditions affecting chick viability in our study area did not show any such relation (Steen et al. 1988b).

The present study of survival in willow ptarmigan chicks evaluates the impact of ambient temperature, predation and genetic variation of the chicks.

Methods

Our study was carried out in Dovrefjell National Park in central Norway (62°17'N, 09°39'E) during 1981-1985. The study area was described in detail by Pedersen, Steen & Andersen (1983).

During April and May, adult males were live-trapped in their territories during morning and evening display periods (for methods see: Pedersen et al. 1983); in June, adult females were mostly caught on their nests with a hand net. The proportion of females suffering egg predation was recorded in all years. One- to four-week-old chicks were captured alive from late June to mid-July. To observe any annual differences in age distribution, the age of chicks was determined at the day of sampling based on the development of plumage and body weight. In several cases, the chicks had been marked with small tape tags under the wing shortly after hatching, making accurate ageing possible. In order to minimise sampling error, a large proportion of broods in the study area were sampled each year. Blood samples were taken from a wing vein. Genotypes were identified by means of electrophoretic separation of serum esterases (EST) in polyacrylamide gels using isoelectric focusing with carrier ampholyte (PAGE-IEF) (Rørvik 1987). Family studies have shown that eight polymorphic genes (Rørvik 1989) encode the various forms of the enzyme. Electromorph patterns are consistent with a model of six independent genes, each with two alleles and two genes, each of which has four alleles (duplicated genes).

The mean number of eggs per nest and chick production (number of chicks per two adults) observed about 2-3 weeks after mean hatching date were calculated from field observations by Steen et al. (1988b), whereas the number of unmated territorial males and females suffering egg predation were registered in the present study (see Table 1). The ambient temperature in the chick-rearing season was registered annually as mean daily maximum temperature from 20 June to 15 July (Table 1). Percent surviving from eggs to chicks at least one week of age was estimated as the mean number of chicks per mean clutch size for breeding females (see Table 1).

The degree of genetic relatedness between any two

Table 1. Percent unmated males and females suffering egg predation, number of eggs per nest, mean daily maximum temperature from 20 June to 15 July, chick production and survival of chicks during 1981-1985. Sample sizes are given in parentheses.

Year	♂♂ unmated (%)	♀♀ suffering egg predation (%)	Number of eggs per nest	Maximum temperature (°C)	Chick production	Chick survival (%)
1981	28.6 (14)	0.0 (8)	10.1	12.9	3.8	45.1
1982	9.5 (21)	37.5 (16)	9.7	14.0	1.2	20.8
1983	14.3 (14)	27.3 (11)	9.1	15.6	3.2	52.5
1984	13.3 (15)	18.2 (11)	10.3	13.0	3.1	39.6
1985	25.0 (16)	0.0 (14)	10.9	15.2	5.8	62.1
Average:	18.1	16.6	10.1	14.1	3.4	44.0
±SD	± 8.2	±16.6	± 1.2	± 1.2	± 1.6	± 15.5

individuals is the probability that two homologous genes drawn at random, one from each, carry identical alleles. In our study, genes were regarded identical if their gene products were inseparable by electrophoresis, which Falconer (1981) called functionally identical. An earlier study of the same willow ptarmigan population as the one we studied, showed that mating among territorial birds in the spring was random with regard to serum esterases (Rørvik, Pedersen & Steen 1990). The degree of allelic identity between potentially and successfully reproducing territorial birds, therefore, was estimated annually from the single gene frequencies in males and females, separately, and averaged over all eight marker genes. When estimating the genetic relatedness of potentially reproducing territorial birds, unmated males were excluded. When estimating the genetic relatedness of successfully reproducing territorial birds, both unmated males and females suffering egg predation/desertion were excluded. Furthermore, because the genetic relatedness between two individuals also is the same as the probability that two genes in a progeny produced by these two individuals are identical (i.e. being a homozygote), the yearly average heterozygosity expected among chicks at hatching was estimated as 1.0 minus the mean genetic relatedness among adults in the successfully reproducing parental population.

The effect of predation on chick survival may be studied on a per breeding pair basis or on a mean breeding pair basis based on annual mean. In years with low predation, a study on a per breeding pair basis in the present willow ptarmigan population found a significant relationship between ptarmigan brood size 8-12 days after hatching and genetic relatedness of the respective parents (Rørvik et al. 1990). However, to evaluate the effect of predation also years with high predation pressure must be included. Since the number of pairs with known destinies were restricted in years with high predation and because most chicks in a brood may be killed at high predator pressure, the effect of predation at the population level was best evaluated on a mean breeding pair basis.

The reason for genotyping chicks was to investigate whether differences between expected chick heterozygosity at hatching and the heterozygosity of surviving chicks could be related to either predation pressure or ambient temperature. The number of heterozygous genes was counted for each chick. Genetic structure was expressed annually as: 1) the average percent heterozygosity for all chicks, and 2) a frequency distribution showing in percent the proportion of chicks within a certain group having 0, 1, 2,..., 8 heterozygous genes.

Although information about predation on chicks is scarce, it is reasonable to assume that the predators involved in egg and chick predation are food generalists, e.g. foxes *Vulpes vulpes*, mustelids and corvids (Storch & Willebrand 1991). Hence, the proportion of females suffering egg predation in June is used as a measure of predation pressure on chicks in late June to mid-July. When registering the proportion of unmated males and females suffering egg predation or desertion, only birds with known destinies were used. Therefore, the same or a somewhat higher number of birds was used to estimate genetic relatedness (see Table 2) than in the registration of unmated males and females suffering egg predation or desertion (see Table 1), except in the three first years where not all males were blood sampled. All statistics were performed using the SAS software package (SAS 1989), either as χ^2-tests, or as single regression analyses (F). In the regression analyses, the percentage of the total variation explained by the model is expressed by R^2.

Table 2. Gene frequency distribution during 1981-1985 at eight polymorphic Esterase genes in successfully reproducing willow ptarmigan, estimated mean annual degree of allelic identity between successfully reproducing male and female adults and average heterozygosity expected in chicks at hatching. p_i is the frequency of the most frequent allele from six single genes, whereas p_{ii} and q_{ii} are the homozygous frequencies in the Est-4 and Est-5 duplicated genes.

			Genes											
			Est-1	Est-2	Est-3	Est-4		Est-5		Est-6	Est-7	Est-8	Mean allelic identity of successfully repr. mates	Average expected heterozygosity in chicks (%)
Year	Sex	Number of genes investigated	p_i	p_i	p_i	p_{ii}	q_{ii}	p_{ii}	q_{ii}	p_i	p_i	p_i		
1981	♂	88	0.955	0.955	0.955	0.477	0.068	0.318	0.182	0.591	0.909	0.773		
1981	♀	64	0.813	1.000	0.938	0.438	0.031	0.125	0.375	0.750	0.750	0.813	0.610	39.0
1982	♂	136	0.941	0.912	0.912	0.397	0.132	0.309	0.191	0.441	0.912	1.000		
1982	♀	160	0.900	0.975	0.975	0.425	0.075	0.088	0.413	0.525	0.800	0.850	0.627	37.3
1983	♂	104	0.962	0.923	0.654	0.385	0.115	0.365	0.173	0.462	0.846	0.962		
1983	♀	88	1.000	0.955	0.955	0.455	0.045	0.136	0.364	0.545	0.909	0.773	0.610	39.0
1984	♂	128	0.938	0.875	0.844	0.422	0.109	0.344	0.156	0.531	0.875	1.000		
1984	♀	112	0.929	0.857	0.857	0.446	0.054	0.179	0.321	0.786	0.929	0.857	0.611	38.9
1985	♂	144	0.833	0.889	0.806	0.417	0.111	0.278	0.222	0.667	0.833	0.944		
1985	♀	144	0.861	0.889	0.944	0.389	0.139	0.208	0.292	0.722	0.806	0.861	0.589	41.1

Results

During 1981-1985, the mean genetic relatedness of successfully reproducing mates was estimated from a total of 146 adult territorial birds, with no less than 19 birds and 152 polymorphic marker genes in any one year. Mean genetic relatedness of successfully reproducing birds ranged from 0.589 to 0.627 (Table 2). Accordingly, the average heterozygosity expected in chicks at the time of hatching ranged from 37.3 to 41.1% (Table 3). A total of 342 chicks from 104 broods were captured alive, bled and genotyped (see Table 3). On average, 50% of the chicks were ≤12 days old at the time of sampling, with no different age distribution during 1981-1985 (χ^2 = 5.403, df = 4, P = 0.25). Chicks with two, three or four heterozygous genes constituted almost 90% of all sampled chicks. Individuals with one or six heterozygous genes were observed only in some years, whereas chicks with zero, seven or eight heterozygous genes were never observed (Table 4).

Table 3. Average heterozygosity observed in surviving chicks and deviation between observed and expected heterozygosity in chicks during 1981-1985. Number of chicks/brood investigated are given in parentheses.

Year	Average heterozygosity observed (%)	Deviation (%)
1981	37.2 (143/41)	-1.8
1982	44.6 (28/9)	7.3
1983	41.1 (51/14)	2.1
1984	39.5 (33/9)	0.6
1985	38.5 (87/31)	-2.6
Average:	40.2	1.1
±SD	± 2.9	± 3.9

Single regression analyses between chick survival and ambient temperature (F = 1.02, P = 0.39, R^2 = 25%) as well as predation pressure (F = 2.87, P = 0.19, R^2 = 49%) could not significantly explain annual variations in chick survival. However, there was a significant positive association between chick survival and heterozygosity expected (H_{EXP}) among chicks at hatching (Fig. 1).

Because dead chicks were never found in the study area, the main cause of death could not be determined directly. However, there was no association between the deviation in observed and expected heterozygosity (H_{OBS} - H_{EXP}) and annual ambient temperatures (F = 0.01, P = 0.95, R^2 < 1%), but a significant association with predation pressure was found (F = 29.75, P = 0.01, R^2 = 91%). In addition, there was a significant relationship between predation pressure and observed heterozygosity of surviving chicks (F = 23.28, P = 0.02, R^2 = 89%). This may imply that the annual differences between the observed average heterozygosity in surviving chicks and the expected average heterozygosity in chicks at hatching may be explained by year-to-year variations in predation pressure.

Of 58 incubating females with known genotype and destiny, five out of 28 females (17.9%) with three or fewer heterozygous genes and 10 out of 30 females (33.3%) with four or more heterozygous genes suffered egg predation or deserted their nest. As none had more than six heterozygous genes (H6) or less than one (H1), and only three females belonged to either H1 or H6, H1 was pooled with H2 (H1,2) and H6 was pooled with H5 (H5,6). By dividing these 58 females into four categories, a signifi-

Table 4. Annual frequency distribution of observed number of heterozygous marker genes in surviving chicks during 1981-1985.

Year	Sample size	Number of heterozygous genes								
		0	1	2	3	4	5	6	7	8
1981	143	0	0.028	0.322	0.350	0.245	0.055	0.000	0	0
1982	28	0	0.000	0.143	0.321	0.393	0.107	0.036	0	0
1983	51	0	0.000	0.235	0.333	0.333	0.078	0.020	0	0
1984	33	0	0.000	0.273	0.364	0.303	0.061	0.000	0	0
1985	87	0	0.023	0.299	0.356	0.218	0.103	0.000	0	0

cant positive association was observed between the proportion of predated females and their number of heterozygous (H) genes (H1,2 = 14.3%, H3 = 19.0%, H4 = 30.0% and H5,6 = 40.0%; F = 80.12, P = 0.01, R^2 = 98%). Further, of 31 juvenile nesting females, two females with four or more heterozygous genes failed to reproduce (6.5%); the corresponding rate for adults was eight of 27 (29.6%). Thus, there was a significantly higher proportion of adult than juvenile territorial females with high heterozygosity that failed to reproduce (χ^2 = 5.433, df = 1, P = 0.02). The annual survival of chicks older than one week was negatively associated with the estimated genetic relatedness of successfully breeding mates (F = 19.68, P = 0.02, R^2 = 87%).

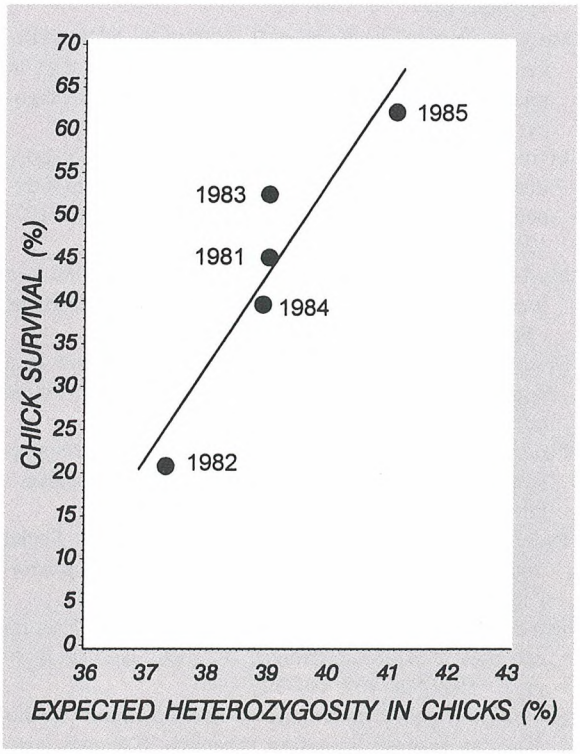

Figure 1. Association between chick survival (%) and heterozygosity (%) expected in ptarmigan chicks at hatching.

Discussion

The mean ambient temperature during the chick-rearing period showed no association with chick survival. This is consistent with several studies showing a lack of effect of post-hatching weather conditions on chick survival in Scandinavian willow ptarmigan (Holt 1953, Myrberget 1986, Steen et al. 1988b) and other *Lagopus lagopus* subspecies (Jenkins et al. 1963, Bergerud 1970).

In 1982, low chick survival (22.1%) generated significantly higher heterozygosity in surviving chicks (H_{OBS} = 44.6%) than that expected in chicks at hatching (H_{EXP} = 37.3%). This is consistent with the observation of higher chick survival in years with high heterozygosity expected among chicks at hatching than in years with low heterozygosity (see Fig. 1). The significant negative association between genetic relatedness of mates and chick survival may imply that more chicks die during their first week of life when genetic relatedness of mates is high (i.e. low chick heterozygosity at hatching). Hence, newly hatched chicks with low heterozygosity may have reduced viability and, therefore, might suffer higher mortality due to biotic/abiotic conditions. This agrees with the general view that inbred individuals with low genetic variation generate reduced fitness (Falconer 1981). The overall consequence is that ptarmigan chicks with reduced genetic variation contribute relatively less when recruited.

The cause of death could not be determined instantly because dead chicks were never found in the study area. But, as chicks are unable to maintain normal body temperature even at ambient temperatures around 20°C until the age of about 10 days (Aulie 1976, Pedersen & Steen 1979), lack of thermoregulation could be an important factor. However, there was no association between the deviation in observed and expected heterozygosity and ambient temperature, suggesting that ambient temperature probably is not the direct cause of death. Chicks with low genetic variation may, however, expose themselves more

to predation. At normal ambient temperatures it may be possible that feeding chicks with low heterozygosity lose body temperature at a higher rate than chicks with high heterozygosity. As ptarmigan chicks start chirping when they get cold (Wike & Steen 1987), chicks with low heterozygosity may start to chirp more often than chicks with higher heterozygosity. This may attract predators and expose chirping chicks to predation. In agreement with this and as the annual variations in average heterozygosity observed in chicks older than one week could be explained by year-to-year changes in the proportion of chicks with low heterozygosity, chicks with one heterozygous gene were observed only in years with no predation among nesting females (1981 and 1985, see Table 4). Chicks with two heterozygous genes were also most frequent in these years. In addition, there was a significant association between heterozygosity of surviving chicks and predation pressure, suggesting that in our study predation was the main cause of death.

In our study, predation was related both to the genetics of nesting females suffering egg predation and to the genetics of surviving chicks. In the recruitment of willow ptarmigan, therefore, the biological consequences may be as follows: More predation among nesting females with high than low heterozygosity reduces genetic variation. Reduced genetic variation among females increases the mean genetic relatedness among birds in the successfully breeding population. In years with high predation among nesting females, therefore, the heterozygosity of chicks at hatching is expected to be lower than in years with low predation, relatively. Finally, according to our study, chicks with low heterozygosity may have reduced viability and may be more exposed to predation than chicks with high heterozygosity. Several earlier studies of willow ptarmigan have shown that predation strongly affects chick production (e.g. Myrberget 1972, 1983, Steen et al. 1988a). Our investigation, however, extends these findings by suggesting a relationship between predation on one side and genetic constitution on the other, and that predation among nesting females, by reducing genetic variation among chicks at hatching, enhance chick mortality.

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