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Source: Wildlife Biology, 4(2) : 91-96

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.1998.005>

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Dispersal in willow ptarmigan *Lagopus lagopus* - who is dispersing and why?

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Rørvik, K.-A., Pedersen, H.C. & Steen, J.B. 1998: Dispersal in willow ptarmigan *Lagopus lagopus* - who is dispersing and why? - Wildl. Biol. 4: 91-96.

The present study evaluates dispersal among breeding willow ptarmigan *Lagopus lagopus* in five closely located subareas in central Norway. During a six-year period, breeding territorial ptarmigan were live-trapped, aged, sexed and genotyped. Since it is believed that female willow ptarmigan are the dispersing sex, and foreign intruders are expected to be more genetically different than birds from the natal subarea, it is predicted that the genetic similarity between breeding birds of a given year (t) and the breeders in the same territories the next year ($t+1$) would be greater for males than for females. The extent of dispersal is believed to be positively correlated with the intruder pressure. Thus, the genetic similarity outlined above is predicted to be greatest in comparisons where chick production in year t was lowest. Analysis of genetic similarity among territorial birds in two consecutive breeding seasons revealed no significant difference between males and females. However, males showed greater genetic variability between years than females. For both yearling and adult males, the increased variation coincided with changes in the population density. Hence, a significant relationship between genetic similarity and chick production for both yearling and adult males was observed. This may suggest density-dependent dispersal for males, but not for females. The fact that there was a stronger relationship between genetic similarity and natal chick production, than between genetic similarity and mean chick production on all subareas, for both adult sexes, suggests that breeding adults are more often challenged by yearlings from their own subarea than by foreign intruders from neighbouring areas.

Key words: dispersal, genetics, *Lagopus lagopus*, willow ptarmigan

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Received 13 June 1997, accepted 4 February 1998

Associate Editor: Peter J. Hudson

Although many species are philopatric, not all individuals are believed to be faithful to only one locality. The movements of those dispersing may be voluntary or enforced, environmental or innate (Howard 1960). Dispersal may play a major role in both population regulation (Lidicker 1975) and spatial distribution (Taylor & Taylor 1977). The ultimate causes of dispersal are thought to include inbreeding avoidance, competition for mates and competition for resources (Dobson & Jones 1985).

Recoveries of marked chicks and adult willow ptarmigan *Lagopus l. lagopus* in Norway from 1914 to 1971 showed that only birds marked as chicks were recovered more than 50 km from their marking sites (Myrberget 1976). This may suggest somewhat more remote movements for juveniles than for adults. However, only short-range movement was observed by Pedersen, Steen & Andersen (1983) using wing-tagging of chicks. The median distance from the tagging site to the recovery site was <1 km for chicks recovered in the autumn of tagging and three km for those recovered within the first year. Since broods with chicks not yet fledged in some years show greater daily movements than when fledged, Sonerud (1985) postulated age-dependant movements in ptarmigan. This may reduce the impact of predators using previously successful hunting areas. However, movements of broods may not be due to antipredator behaviour alone, but could also be explained by foraging activities. Thus, Erikstad (1985) and Andersen (1986) found that broods moved to higher altitudes or to other habitats tracking the progress in insects and vegetation phenology. Observations by Olsson, Willebrand & Smith (1996) did not, however, suggest a decrease in movement in relation to increased age in radio-marked broods. Neither did they observe any consistent difference in movement patterns among broods, broodless pairs or single birds. During the hunting season, the ptarmigan did not move out of the hunted area and no significant differences in movement between ptarmigan in hunted and unhunted areas were found. During winter, different populations of willow ptarmigan show great variation in movements. In some areas, regular migration from wintering areas occur (Weeden 1959, Irving, West, Peyton & Paneak 1967), whereas in others more short-range movements are seen (Gruys 1993). Finally, in many willow ptarmigan populations in Norway the birds stay in the same area more or less throughout the whole year, and only

local daily movements are observed (H.C. Pedersen, unpubl. data)

In most avian species, dispersal seems to be greater in females than in males (Greenwood 1980) and high or increasing population density may be associated with high levels of dispersal (Myers & Krebs 1971). The present study evaluates dispersal among breeding willow ptarmigan in central Norway. Only the genetic effects of dispersal are evaluated, not the proportion of foreign male and female intruders.

Methods

The study was carried out in Kongsvoll, Dovrefjell National Park, in the central part of Norway during 1981-1986. The Kongsvoll area is divided into five closely located subareas, each measuring about 10 km²: Gåvålia, Hjerkinnhø, Kolla, Knutshø and Ny-stuguhø.

Territorial breeding birds were only studied in the Gåvålia subarea. Through April and May, males were live-trapped in their territories during morning and evening display periods (for methods see Pedersen et al. 1983). Females were caught in June, mostly on the nest, using a hand net. Birds were aged as yearlings or adults based on the pigmentation of the primaries (Bergerud, Peters & McCraft 1963). Chick production in the autumn (15-20 August) was recorded in all subareas by pointing dog censuses and expressed as observed number of chicks per two adults. 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 the various forms of the enzyme are inherited by eight polymorphic genes (Rørvik 1989).

When the allele or genotype frequencies of polymorphic genes are known, two populations may be compared in a general manner for each gene to ascertain whether they share the same alleles or genotypes, and whether they have similar frequencies. As the allele frequencies in diploid organisms are usually estimated from the observed genotype frequencies, and as selection normally operates on the organisms in diploid state, it may seem more appropriate to compare genotype frequencies rather than allele frequencies (Hedrick 1971). According to Hedrick

Table 1. Genetic similarity (±SE) between two consecutive breeding seasons for sexed breeding yearling and adult willow ptarmigan during 1981-1986 in Gåvålia, central Norway. Number of investigated genotypes is given in parentheses.

Years	Yearling males	Adult males	Yearling females	Adult females
1981/82	0.938 ± 0.028 (152)	0.928 ± 0.029 (136)	0.891 ± 0.041 (144)	0.867 ± 0.055 (128)
1982/83	0.790 ± 0.078 (120)	0.976 ± 0.014 (168)	0.914 ± 0.043 (112)	0.957 ± 0.020 (192)
1983/84	0.744 ± 0.097 (56)	0.946 ± 0.028 (208)	0.945 ± 0.016 (96)	0.916 ± 0.040 (136)
1984/85	0.870 ± 0.041 (128)	0.864 ± 0.065 (200)	0.939 ± 0.024 (176)	0.874 ± 0.055 (120)
1985/86	0.955 ± 0.020 (176)	0.841 ± 0.059 (160)	0.901 ± 0.038 (168)	0.895 ± 0.030 (88)
Mean:	0.859 ± 0.041	0.911 ± 0.025	0.918 ± 0.010	0.902 ± 0.016

(1971) the genetic similarity (IH) within the same gene of two different populations (x, y) is:

$$IH = \frac{\sum^n P_{JX} - P_{JY}}{0.5(\sum^n P^2_{JX} + \sum^n P^2_{JY})} \quad (1)$$

where P_{JX} and P_{JY} are the frequencies of the J_{th} genotype in population X and Y, respectively, and n is the number of different genotypes. Therefore, the similarity value is 1.0 if the genotype frequencies in two different populations are equal, and 0.0 if they do not have any genotypes in common. Since each ptarmigan in the present study was characterised regarding eight polymorphic genes, the mean similarity of all these genes was used.

Since the genetic difference between Scandinavian willow ptarmigan populations is positively correlated with geographic distance (Rørvik & Steen 1989), dispersal would cause the genetic similarity between breeding birds of a given year (t) and the breeders in the same territories the next year (t+1) to decrease. As in most bird species (Greenwood 1980), female willow ptarmigan are believed to be the dispersing sex. Therefore, the genetic similarity between the territorial birds in the two consecutive years is predicted to be greater for males than for females. When population density and intruder pressure increase, territories contract (Huxley 1934). In tetraonids, breeding density is set mainly by recruitment (Bendell 1972). Accordingly, willow ptarmigan studies have shown a positive association between chick production and breeding density the following spring and a negative association with territory size (Myrberger 1972, Pedersen 1984). Thus, in the present study, annual variation in chick production is expected to alter the foreign intruder pressure, which is positively correlated with the extent of dispersal. Therefore, the genetic similarity outlined above is predicted to be greatest in comparisons where chick production in year t was lowest.

All statistics were performed using the SAS software package (SAS 1989), either as analyses of variance (ANOVA) or as single regression analyses. In the multiple analyses, the marginal effect (SAS type III SS) of each variable is presented. The percentage of the total variation explained by the model is expressed by R^2 .

Results

Genetic similarity values between two consecutive breeding seasons for adult and yearling territorial males and nesting females are presented in Table 1. Males tended to have somewhat higher variation between consecutive years than females (males: 0.033 vs females: 0.013), but no significant difference in mean genetic similarity between the sexes was observed (males: 0.885 vs females: 0.910). A model of genetic similarity in relation to age, chick production in Gåvålia (CpG), chick production in Kongsvoll (CpK), and the full range of interactions was constructed. Among males this produced a model ($F = 59.07$, $P = 0.0002$, $R^2 = 98\%$, d.f. = 4, 5) with four significant elements; age ($P = 0.0001$), CpK ($P = 0.002$), the age*CpK interaction ($P = 0.0001$) and the CpK*CpG interaction ($P = 0.0004$). Among females this produced a model ($F = 7.75$, $P = 0.03$, $R^2 = 91\%$, d.f. = 5, 4) also with four significant elements; CpK ($P = 0.05$), the age*CpK interaction ($P = 0.04$), the

Table 2. Mean chick production in the natal subarea Gåvålia and grand mean of all Kongsvoll subareas, central Norway, during 1981-1985.

	Gåvålia	Kongsvoll
1981	4.3	4.9
1982	0.7	2.1
1983	1.6	1.9
1984	5.3	4.4
1985	6.3	7.0
Mean:	3.6	4.1

Table 3. Single regression statistics showing to which extent mean chick production in the Gåvålia subarea and the grand mean of all Kongsvoll subareas may explain variations in estimated genetic similarity of aged and sexed breeding willow ptarmigan in Gåvålia, central Norway.

Sex	Age	Chick production in Gåvålia and genetic similarity	Chick production in all Kongsvoll areas and genetic similarity
♂	Yearling	P = 0.06 R ² = 75%	P = 0.01 R ² = 90%
♂	Adult	P = 0.01 R ² = 90%	P = 0.07 R ² = 73%
♀	Yearling	P = 0.60 R ² = 10%	P = 0.30 R ² = 34%
♀	Adult	P = 0.11 R ² = 64%	P = 0.24 R ² = 41%

age*CpG interaction (P = 0.04) and the CpK*CpG interaction (P = 0.05).

Single regression analyses between the genetic similarity of territorial birds in the Gåvålia subarea (see Table 1) and chick production in the previous year (Table 2), showed no significant relationship for either female yearling or female adult willow ptarmigan (Table 3). However, the genetic similarity of male adults was negatively related to mean chick production in the Gåvålia subarea, and the genetic similarity of male yearlings was positively related to the grand mean of chick production in all of the

Kongsvoll subareas (see Table 3, Fig. 1). In addition, observed changes in genetic similarity between two consecutive breeding seasons for adult birds in Gåvålia were more strongly associated with chick production in the Gåvålia subarea, whereas changes in genetic similarity among yearlings were best explained by changes in the mean chick production on the entire Kongsvoll area (see Table 3).

Discussion

The significant multiple models imply that chick production on both the natal subarea (Gåvålia) and all the Kongsvoll areas significantly affected genetic similarity in both age classes of males and females, and that the effects significantly differed between the age classes of males. In addition, the significant interaction in both sexes between chick production on the natal subarea and on all the Kongsvoll areas may suggest that chick production on the different areas have different effects.

The genetic similarity between territorial birds in two consecutive breeding seasons was not significantly higher for breeding males than for females. However, males had about 2.5 times higher variation in genetic similarity between years than females. For both yearling and adult males, the increased variation coincided with changes in the population density. Hence, a significant relationship between genetic similarity and chick production for both yearling and adult males was observed (see Table 3). This may suggest density-dependent dispersal for males but not for females. This is in accordance with observations of the great tit *Parus major* (Greenwood, Harvey & Perrins 1979). For great tits, increased breeding density is related to increased dispersal of males. Females have a similar pattern of dispersal, but with no comparable density effect. It is also consistent with observations in the lesser snow goose *Anser caerulescens* (Cooke, Macinnes & Prevett 1975). However, in most avian species, dispersal seems to

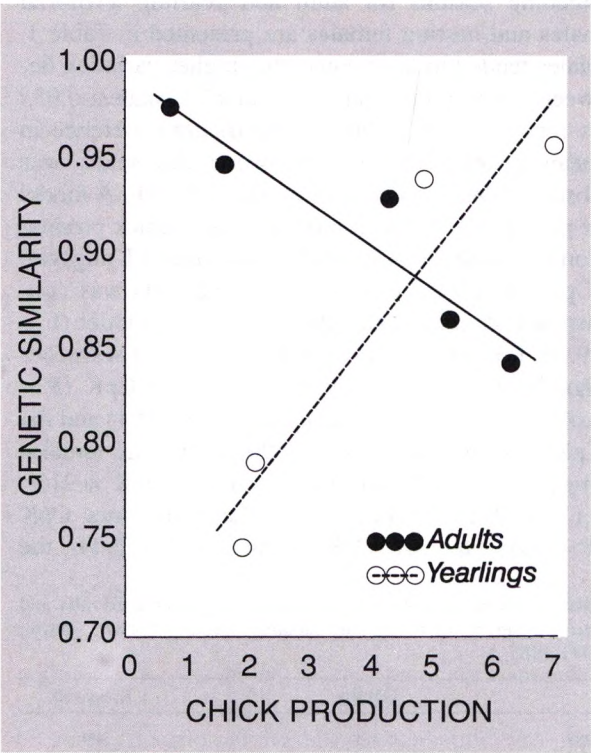


Figure 1. Relationship between chick production and genetic similarity for adult and yearling territorial males in the breeding seasons. The genetic similarity is plotted against mean chick production in the Gåvålia subarea for adult males and against the grand mean of chick production in all of the Kongsvoll areas for yearling males.

be greater in females than in males (Greenwood 1980), as observed in the North American *Lagopus l. alexandrae* (Martin & Hannon 1987).

The significant relationship between genetic similarity and chick production was positive for male yearlings and negative for male adults (see Fig. 1). For yearlings, the positive relationship may be due to high chick production reducing the possibility of foreign intruders getting access to territories. Inversely, when chick production is low, foreign intruders may have easier access to territories in the Gåvålia sub-area. As foreign intruders are expected to be more genetically different than birds from the natal sub-area, they may have caused the genetic changes in the yearling breeding population. An opposite argument may be valid for adult males. According to Pedersen et al. (1983), 41% of all territorial males in Gåvålia were retrapped in two or more breeding seasons during 1980-1983. Hence, territorial males may occupy the same territory for more than one breeding season, causing increased genetic similarity between consecutive years. As low chick production reduces breeding density the following spring (Myrberget 1972, Pedersen 1984) and as low breeding density, due to low intruder pressure, may favour reproduction among native adult territorial males, a negative relationship may be expected between genetic similarity and chick production for adult males.

It is well documented that red grouse *Lagopus l. scoticus* and Newfoundland willow ptarmigan *Lagopus l. alleni* establish territories in the autumn (Jenkins, Watson & Miller 1963, 1967, Bergerud & Mercer 1966, Mercer 1969). Since it is a general belief that the same holds true for male Norwegian willow ptarmigan (Haftorn 1971, Pedersen et al. 1983), the present data suggest that yearling males who fail to establish a territory in the autumn may move to another area during the winter. The stronger relationship between genetic similarity in both sexes of adults in Gåvålia and chick production in Gåvålia, compared to the mean chick production on the entire Kongsvoll area (see Table 3), may suggest that territorial adults more often are challenged by yearlings from their own natal subarea than by foreign intruders from neighbouring areas. This is in accordance with findings in red grouse (Lance 1978, Watson, Moss, Parr, Mountford & Rothery 1994).

Acknowledgements - we are grateful to O. Schjetne and L. Schirmer for assistance in the field, and to M. Øverland and two anonymous referees for comments on the manu-

script. The project has been supported by the Norwegian Research Council of Science and Humanities, and by the Nordic Council for Wildlife Research.

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