Dispersal in Spruce Grouse: Is Inheritance Involved?

Research on great tits, *Parus major*, has suggested that dispersal distances of offspring resemble those of their parents (Greenwood et al. 1979). Dispersal tendencies may also be similar among related offspring (Hilborn 1975 for four species of *Microtus;* Keppie 1980 for spruce grouse, *Dendragapus canadensis*). Although dispersal in vertebrates is frequently attributed to genotypic factors, evidence illustrating inheritance of dispersal tendencies and/or differences between genotypic and environmental components of phenotypic variance is uncommon.

This paper reports on dispersal tendencies of marked female spruce grouse, and their offspring, in a population studied from 1965 to 1985 in southwestern Alberta (50° 39′ N, 114° 39′ W). Dispersal of spruce grouse from their brood range to the range where they breed or attempt to breed, can be divided into discrete autumn and spring phases of movement separated by a winter period when relatively little movement occurs (Keppie 1975). The spring phase of dispersal appears to be caused by a variety of proximal factors, of which the inheritance of dispersal and non-dispersal tendencies is but one (Schroeder 1985a).

Grouse were captured with noosing poles (Zwickel & Bendell 1967; Schroeder 1986) and individually marked with colour-coded leg bands. Locations of birds encountered on the study area were plotted using grid coordinates superimposed over air photos. Designation of season was based on aspects of spruce grouse behaviour, such as dispersion (Herzog & Boag 1978) and timing of migration and dispersal (Herzog & Keppie 1980; Schroeder 1985a), and were as follows: winter (16 October–31 March) and summer (16 May–15 August). These designations, with 6–8 weeks between them, enabled us to separate normal daily movements within summer or winter ranges from dispersal or migration movements.

The migratory status of adults was used as an indication of spring dispersal; previous research suggests that migratory movements between winter and summer ranges retrace the first spring dispersal movement (Herzog & Keppie 1980; Schroeder 1985a). Brood hens and offspring having both winter and summer ranges on the study area were classed as non-dispersers, whereas those crossing

the boundaries of the study area were classed as dispersers. Since virtually all birds residing on the study area were found with a line-transect census technique (Boag & McKinnon 1982), offspring disappearing before or during their first period of spring dispersal, and not seen again, were assumed to have died and were not classed in terms of dispersal status. Comparison of dispersal status with actual spring dispersal distances (when the actual locations of an individual's winter and summer ranges were known) showed that dispersers moved longer distances (median of 2·4 km; $N=30$) than non-dispersers (median of 0·3 km; $N=221$; $P<0·001$; Mann–Whitney U-test).

Of 68 brood hens examined, 35 were classed as dispersers and 33 were classed as non-dispersers. These female spruce grouse produced 91 broods with 83 male and 35 female offspring of known dispersal status. If data for more than one chick of a sex were available for a brood, one chick was randomly selected and used in the analysis (reduced sample of 65 males and 31 females).

Fewer male offspring of non-dispersing brood hens dispersed in the spring than did the male offspring of dispersing females ($G=9·17$, $P<0·005$; Table I). The dispersal status of adult females did not appear to influence the dispersal status of their female offspring ($G=0·11$, $P>0·5$).

Like most other species of birds (Greenwood & Harvey 1982), spruce grouse females disperse more frequently than males (Keppie 1979; Herzog & Keppie 1980; Schroeder 1985a, b). Movements recorded for radio-marked birds suggest that 7% of males and 32% of females in this population disperse further than 2 km (Schroeder 1985a). One possible explanation for differences between dispersal tendencies of males and females is that maternal effects (differences in the environment and/or behaviour of individual brood hens) may influence one sex more than the other. However, the spring phase of dispersal occurs approximately 6 months after the brood break-up of juvenile spruce grouse (Schroeder 1985a, b). While males generally leave the brood about 2 weeks before females, neither sex appears to be influenced by their brood hen after brood break-up (Schroeder 1985b). Although nepotism cannot be entirely discounted, the general movement of all birds away from their natal habitat during the autumn phase of dispersal suggests that maternal effects probably cannot explain differences in spring dispersal between male and female offspring.

Another possible explanation for differences in the dispersal tendencies between males and females is that the dispersal trait may be genotypic in origin. Although numerous polygenic models could explain a similar outcome, it is possible that a recessive dispersal trait (sex-linked) could frequently appear as a phenotype in females (the heterozygous sex), while in males this trait could be masked by a dominant 'non-dispersal' allele.

The measurement and analysis of actual dispersal distances might help to estimate heritability accurately (Greenwood et al. 1979; also see van Noordwijk 1984). However, behavioural differences relating to social interactions and timing of movement between long-distance (more than 2 km) and short-distance (less than 2 km) dispersers/migrants in spruce grouse, suggest that a tendency to disperse may exist as a dimorphic trait in the population (Schroeder 1985a). Even if there are heritable components to spring dispersal movements, other factors such as agonistic interactions, territoriality, and/or social behaviour may influence movement as well (discussion in Schroeder 1985a). Explanations of dispersal movements are not necessarily exclusive (Dobson & Jones 1985).

The observations from this study suggest that inheritance may influence the dispersal status of spruce grouse. If inheritance of dispersal tendencies is more important for females than males, reasons for the increased rate of dispersal in females may be related to ultimate consequences of their movement (see discussions in Gaines & McClenaghan 1980; Greenwood & Harvey 1982). More long-term research on animal populations of known lineage is necessary before the relative importance of various proximate and ultimate reasons for patterns of dispersal can be understood.

Table I. Spring dispersal status of spruce grouse offspring in relation to the dispersal status of their brood hen

	Brood hen	
Offspring status	Disperser	Non-disperser
Male		
Disperser	11	1
Non-disperser	25	28
Female		
Disperser	8	10
Non-disperser	5	8

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