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**Ecological *versus* genetic dispersal: inconsistencies as revealed by
the assessment of sex-related spatial genetic structure in two
grouse species?**

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Abstract.

Population genetics theory predicts a sex-difference in genetic structure in species displaying extensive sex-biased dispersal. As a result, the use of molecular methods for inferring patterns of sex-biased dispersal in animals has been increasing in recent years. However, the relationship between movements of genes (or genetic dispersal) and movement of individuals between their birth site and the place where they reproduce (ecological dispersal) might not be straightforward.

We compared pattern of genetic structure between males and females in two bird species displaying female biased dispersal. As expected, we detected a more marked isolation-by-distance effect in males than in female in the monogamous rock ptarmigan. However, the reverse trend was found in the lekking black grouse even though female-biased dispersal is probably stronger than in rock ptarmigan. We hypothesize that mating behaviour of both, males and females, is responsive for this situation.

We conclude that in species displaying complex mating behaviour, a more or less complete uncoupling between genetic and ecological dispersal could occur. If evidence for such a situation could be gathered in other taxa, the importance of inbreeding in promoting the evolution of sex-biased dispersal would be seriously questionable.

Dispersal is a central parameter of demographic and evolutionary processes. Because, dispersal can affect social structure it has also attracted much of the attention of behavioural ecologists. Mainly two approaches are currently employed to investigate dispersal: i) the demographic approach, which consists in monitoring movements of individually marked animals and ii) the genetic approach based on the analysis of the spatial distribution of genes. However, the two approaches do not deal with the same parameters. The demographic approach is very efficient for quantifying movements of individuals (ecological dispersal), but estimating the genetic consequences of these movements (and therefore their evolutionary significance) is virtually impossible. The genetic approach measure gene flow (genetic dispersal), but translating these estimates in terms of dispersal distances is not straightforward.

Advances to bridge the gap between demography and population genetics are being made. For example, methods using information from the spatial and/or temporal distribution of genes have been developed to detect population bottlenecks or to estimate some dispersal parameters e.g., the number of migrant m or the second moment of dispersal distances σ^2 (Cornuet & Luikart 1996, Rousset 1997, 2000b). Information gathered with hyper-polymorphic markers such as microsatellites would allow detecting sex-biased dispersal (e.g., Favre *et al.* 1997, Richardson *et al.* 2002, Vitalis 2002). However, the underlying assumptions of these methods/models often make their range of applicability narrow, and their robustness to violations of these assumptions has not yet been thoroughly investigated. As an example, many authors assume that the detection of sex-related differences in genetic structure directly reflect differences in dispersal distances between the sexes. This would be true in monogamous species, but one can imagine that in polygynous species and/or in species without pair bond, the relationship between ecological and genetic dispersal no more exist.

Beside the specific problem of estimating dispersal and measuring its consequences, population geneticists recognize that studies combining the demographic/ecological and the genetic/evolutionary approaches are badly needed for improving our knowledge about the influence of social structure and demographic traits on the distribution of genetic variability (Chesser 1991; Sugg *et al.* 1996).

As part of an ongoing study on population genetics and demography, we assessed sex-differences in genetic structure in two galliformes: the black grouse (*Tetrao tetrix*) and the rock ptarmigan (*Lagopus mutus*). These two birds, which belong to the sub-family of grouse (*Tetraoninae*), display similar survivorship and productivity. With a generation time of 3-4 years they would be more sensitive to variations in survival than to changes in reproductive success (see Caizergues & Ellison 1997). Moreover, breeding densities of these birds are of the same order of magnitude and usually display moderate variations other years (Observatoire des Galliformes de Montagne *unpublished data*). In the black grouse, juvenile females disperse on average almost seven times farther than males (Caizergues & Ellison 2002). Dispersal data are currently not available for the rock ptarmigan but, in Alaska, females migrate farther than males between breeding and wintering ranges (Weeden 1964) indirectly suggesting that natal dispersal distance of females might be also longer. Evidence for female biased dispersal has been gathered in the white tailed ptarmigan *Lagopus leucurus*, which has the same ecology as the rock ptarmigan in the Rocky mountains (Giesen & Braun 1993; Martin *et al.* 2000).

Mating is the main aspect in which the two species differ. While the rock ptarmigan is strictly monogamous, the black grouse is a typical polygynous lekking bird. Consequently, the variance in male breeding success would be much higher in the black grouse than in the rock ptarmigan.

In both species, individuals sampled were genetically characterized using microsatellites (12 loci for the black grouse and 6 loci for the rock ptarmigan)(Caizergues *et al.* 2001a; Caizergues *et al.* 2001b, Caizergues *unpublished data*). Black grouse samples were collected along a *ca* 300 km transect in Finland (min distance between individuals males = 1 km, females = 1 km; max distance between individuals males = 298 km, females = 302 km) and rock ptarmigans were collected in the Alps along a *ca* 300 km transect (min distance between individuals males = 1 km females = 1 km, max distance between individuals males = 286 km, females = 288 km). Sex-related differences in genetic structure were assessed by computing the isolation-by-distance model of Rousset (2000a). We opted for this method because it was designed for situations in which populations are continuously distributed (Rousset 1997, 2000a), which was the case for both species in the context and at the spatial scale where samples were collected. Confidence intervals of regressions' slopes were computed using the ABC method implemented in the 3.3 version of GENEPOP (see Leblois *et al.* 2000).

Because, dispersal is biased toward females in both species, we initially predicted a stronger genetic structure in males (the philopatric sex) than in females (the dispersing sex) in both the black grouse and the rock ptarmigan. In other words, a steeper slope in males than in females was expected for the isolation-by-distance effect. We also expected that the between-sex difference in genetic structure should be more prominent in the polygynous species than in the monogamous one. We formulated this prediction because in lekking species and more particularly in the black grouse, clusters of kin males are expected due to the joint effects of the leptokurtic distribution in male reproductive success and their very strong philopatry (see Höglund *et al.* 1999, Caizergues & Ellison 2002).

In agreement with our prediction, we detected a significant isolation-by-distance effect for rock ptarmigan males (Mantel test, $P = 0.003$, intercept = -0.028, slope = 0.012,

confidence interval = +0.017, +0.006, N=50) but not for females ($P = 0.15$, intercept = -0.036, slope = 0.0066, confidence interval = +0.021, -0.0061, N = 50). Surprisingly, the reverse trend was detected in the black grouse i.e., the isolation-by-distance was significant for females ($P = 0.013$, intercept = regression slope = 0.008, confidence interval = N = 55,) but not for males ($P = 0.29$, intercept =, regression slope = -0.0016, confidence interval =, N = 55). Moreover, contrary to expectations the genetic structure was apparently weaker in black grouse males than in rock ptarmigan males.

Because the analyses were based on small samples sizes, we cannot totally rule out our results reflect a sampling artefact rather than a “biological reality”. However, the data presented here are based on exactly the same number of males and females in each distance class. Moreover, similar samples size could be obtained for both species.

Assuming our results somewhat reflects a “biological reality”, now the question is: could any peculiarity of the lekking mating system explain the unexpected reverse trend observed in the black grouse? Addressing this question requires a good knowledge of the behaviour of males and females during the mating season. Fortunately, thanks to radio-telemetry, we gathered evidence that some black grouse females mate on leks up to 7 km from their nest site (Caizergues 1997). Additionally, some migratory females might mate in the vicinity of their wintering ground before departing for their nesting site sometimes up to 14 km distant from their wintering area (Caizergues & Ellison 2002). Therefore, thanks to the mating behaviour of their mother the genes of juvenile males would be carried away from those of their father over long distances (of the same order of magnitude than those accomplished by juvenile female during dispersal), even though they display a strong philopatry. Moreover, part of the weaker than expected genetic structure found in black grouse males might be due to their own mating behaviour. It is commonly, assumed that only dominant males aged of 2 years or older can perform copulations (Höglung & Alatalo 1995).

However, one cannot totally exclude that some wandering yearling males contribute to mating. During our radio-tracking study, we had the opportunity to monitor yearling males, some of which visited leks up to 14 km distant from the lek where they later secured a territory. Thus even though these males will settle on a lek nearby their birth site, their gene could potentially be dispersed much more farther when, in their first year of life, they visit leks often very distant from their birth site.

To conclude, even if they need to be confirmed, our results emphasize the danger of using genetics methods alone for inferring patterns of sex-biased dispersal in animals. For the first time, a tangible example of why and how genetic and ecological dispersal can be unconnected in an animal is given. However, mathematical modelling is badly needed for exploring the conditions leading to such a situation and further empirical studies combining the genetic and ecological approaches are absolutely necessary for assessing its occurrence in animals. Would inbreeding avoidance be still considered as a major evolutionary force of sex-biased dispersal if genetic and ecological dispersal happened to be more often unconnected than previously thought?

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