

# Sex-biased dispersal in a northern ungulate population

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*Abstract.* In most mammals dispersal is male-biased and in many polygynous ungulates female philopatry and matrilineal grouping involve small-scale genetic structure. We have through sex-related differences in microsatellite allele distribution addressed sex-biased dispersal in a spatially expanding northern ungulate population. The Norwegian red deer population (*Cervus elaphus atlanticus*) has the last hundred years grown substantially and expanded spatially after a major decline from 300 to 100 years ago. Previous Bayesian analyses suggest a present division of genetic variation into five geographically separated subpopulations. Among these subpopulations the overall  $F_{st}$  values were 0.067 (SE=0.014) for males and 0.094 (SE=0.017) for females. Pairwise  $F_{st}$  values were significantly higher for females than males, demonstrating a stronger genetic structure among females, and that dispersal has been lower in females than males. Accordingly, a higher number of male than female first generation dispersers were identified among the five subpopulations using Bayesian assignment with prior population information, but significantly so only with relaxed stringency levels of assignment. The identified male-biased dispersal distances varied from 30 to 300 kilometers suggesting male biased dispersal on a large scale in red deer.

**Key words:** Bayesian assignment; *Cervus elaphus*; Norwegian deer; range expansion; sex-biased dispersal.

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## Introduction

Dispersal is sex-biased when the members of one sex are faithful to their natal range and / or matrilineal group (philopatric), while members of the other sex are more likely to disperse (Prugnolle & de Meeus, 2002). Most mammalian species exhibit male-biased dispersal and female philopatry (Greenwood, 1980; Clutton-Brock, 1989; Prugnolle & de Meeus, 2002), but recent applications of genetic tools suggest wide variation in the direction, magnitude and timing of sex-biased dispersal (Handley & Perrin, 2007). Theoretical studies show that philopatry in concert with polygony may involve small scale genetic differentiation

among social groups (Chesser, 1991b; Chesser, 1991a), which may have important evolutionary consequences for kin and localized selection (Coltman *et al.*, 2003). In many ungulate species polygony and philopatry thus involves a pronounced fine-scale genetic structure (Mathews & Porter, 1993; Petit *et al.* 1997; Purdue *et al.*, 2000; Coltman *et al.*, 2003; Nussey *et al.*, 2005). Sex-biased dispersal at the subpopulation and meta-population levels has however been poorly documented (Prugnolle & de Meeus, 2002), but has recently been reported for turtles (Bowen & Karl, 2007) and bats (Chen *et al.*, 2008).

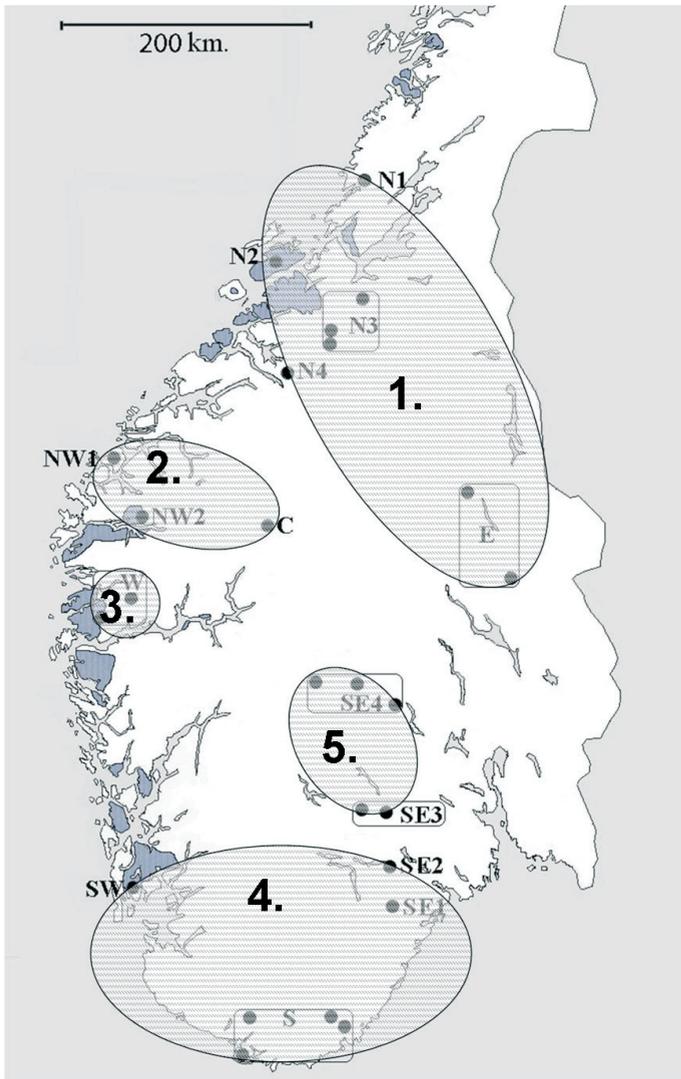


Fig. 1. Sampling localities of Norwegian red deer divided according to five clusters identified by Bayesian assignment (from Haanes *et al.*, 2010). Solid grey shading indicates the approximate distribution of the population around 1900 (Collett, 1909; Langvatn, 1998), rectangles show combinations of locations to obtain at least 15 individuals per locality and the Bayesian clusters are indicated by transparently shaded ovals.

The red deer (*Cervus elaphus*) is a highly polygynous (Pemberton *et al.*, 1992) and philopatric species (Clutton-Brock *et al.*, 1982b; Clutton-Brock *et al.*, 2002) with many populations genetically structured at the subpopulation level (Hartl *et al.*, 1990; Herzog & Gehle, 2001;

Kuehn *et al.*, 2004). On the small Scottish island of Rhum, philopatry and male-biased dispersal may explain the observed extreme fine-scale genetic structure, which has declined with time as population density has increased (Nussey *et al.*, 2005), but may also account for genetic structure on a larger scale among management blocks (Nussey *et al.*, 2006). In the large northern population in Norway, a genetic structure of five subpopulations has been suggested, which may be explained by previous strong genetic drift and subsequent limitations to gene flow during population growth and spatial expansion (Haanes *et al.*, 2010). These limitations to gene flow include both isolation by distance and geographical barriers like fiords and steep mountains. A drastic decline from 300 to 100 years ago limited the population to a few hundred individuals along the west coast (Collett, 1909; Ingebrigtsen, 1924), but after one century of growth and spatial expansion the population is today distributed throughout southern

Norway, counting between 100 000 and 130 000 individuals (Langvatn, 1988; Forchhammer *et al.*, 1998; Langvatn, 1998). We have investigated whether dispersal is sex-biased on a large scale within the spatially expanding Norwegian red deer population. Specifically we have assessed sex-biased dispersal through sex-related differences in genetic structure between subpopulations and by identifying first generation dispersers through Bayesian assignment analyses.

**Material and methods**

Among 419 individuals from 15 localities (Fig.1) sampled for genetic analysis of the Norwegian red deer population, the sex of 279 adults were recorded as 112 females and 167 males. To increase the power and resolution of our analyses, all 419 samples were used in the individual-based identification of genetic structure and dispersers (STRUCTURE), while only adults with a known sex were used to identify sex-specific structure (*Fst*). Samples were sent in by hunters, who provided estimates of age and weight (slaughtered). All individuals were genotyped in 14 polymorphic microsatellite loci that show Mendelian heredity in Norwegian red deer (Haanes *et al.*, 2005; cf. Haanes *et al.*, 2010). These were CSSM03 (Moore *et al.*, 1994), OarCP26 (Ede *et al.*, 1995), RT5 (Wilson *et al.* 1997), SRCRSP10 (Bhebhe *et al.*, 1994), NVHRT73 and NVHRT48 (Røed & Midthjell, 1998), McM58 (Hulme *et al.*, 1994), OarFCB193 and OarFCB304 (Buchanan & Crawford, 1993), BM5004, BM888, BMC1009, BM4208 and BM4107 (Bishop *et al.*, 1994).

Bayesian assignment (STRUCTURE 2, Pritchard *et al.*, 2000) *without prior information about population structure* has previously been used to show that the 15 sampled Norwegian red deer localities can be divided into five subpopulations (Haanes *et al.*, 2010). For each of a different number of genetic clusters ( $K \in [1,7]$ ),

Fig. 2. Individual posterior probabilities of Bayesian assignment to each of two to five clusters (STRUCTURE with  $K \in [2,5]$ ), different colours) among 419 red deer in each of 15 sampled localities (from Haanes *et al.*, 2010).

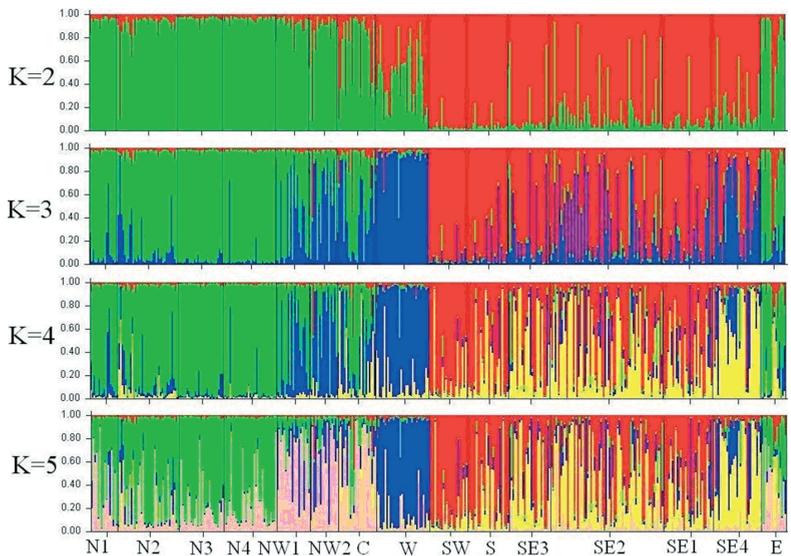


Table 1 Mean posterior probability ( $\ln \Pr(D|K)$ ), standard deviation (SD) and delta K across n runs with STRUCTURE given different numbers of subpopulations ( $K \in [1,7]$ ) for 419 Norwegian red deer genotyped in 14 microsatellite loci (from Haanes *et al.*, 2010). The most likely number of clusters according to Baye's theorem ( $K=5$ ;  $P > 0.99$ ) and delta K, are marked in boldface.

K	n	$\ln \Pr(D K)$	SD	$\Delta K$
1	10	-14034.7	0.4	
2	10	-13223.8	1.8	332.3
3	10	-13013.9	2.5	65.1
4	10	-12926.6	3.4	28.8
5	10	<b>-12868.5</b>	2.6	<b>156.1</b>
6	10	-13175.6	147.3	2.8
7	10	-13244.1	215.6	4.1

an admixture model ( $\alpha=1$ ,  $\alpha_{\max}=50$ ) with uniform priors, correlated allele frequencies (Falush *et al.*, 2003), 100 000 burnins cycles and 500 000 MCMC iterations was run 10 times. The log likelihood of the data ( $\ln \Pr(X|K)$ ) was highest for  $K = 5$  and the statistic *delta K* (Evanno *et al.*, 2005) was pronounced higher for  $K = 2$  and  $K = 5$  (Table 1). Since *delta K* is negatively related to the increasing variance among repeated runs and often increasing posterior probabilities with higher  $K$  values, it reflects the main genetic structure of the data set

(Evanno *et al.*, 2005), and the genetic structure of Norwegian red deer was interpreted as a main dichotomy with a lower hierarchical level of five subpopulations (Haanes *et al.*, 2010). The proportionate cluster membership was for most individuals and localities much higher in one of the clusters (Fig. 2, Appendix Table S1), and the data was divided into five well geographically separated clusters separated by tens to hundreds of kilometers (Fig 1).

As summary genetics not have been published for the five identified Norwegian subpopulations, each of the five identified subpopulations was assessed through exact tests of Hardy-Weinberg equilibrium (HW) across the 14 loci using GENEPOP 3.4 with the default settings (Raymond & Rousset, 1995). Sequential Bonferroni correction was used to adjust for all repeated tests (Rice, 1989). To assess genetic variation we used FSTAT 2.9.3 (Goudet, 2001) to calculate the allelic richness (El Mousadik & Petit, 1996) and the gene diversity (Nei, 1987) for each subpopulation across loci. Summary statistics from the 15 locations can be found in Appendix Table S2 and Appendix Table S3 shows details on allelic frequencies among the five subpopulations.

To assess sex-biased dispersal we used FSTAT 2.9.3 (Goudet, 2001) to calculate pairwise  $F_{st}$  values for males and females separately (Weir & Cockerham, 1984) between these five subpopulations (assuming HW when no significant deviations were detected). The numbers of adult individuals per sex per subpopulation are given in Table 2. To assess whether dispersal between the subpopulations was higher for males than females we used one Student's paired  $t$ -test to assess for differences in  $F_{st}$  values (JMP 7.0.1., 2007).

Table 2. The numbers of adult Norwegian red deer with known sex which were sampled in each of five identified subpopulations.

Subpopulation	females	males
1	28	31
2	17	27
3	16	9
4	38	68
5	13	32

Sex-biased dispersal may be detected through individual Bayesian assignment (Prugnolle & de Meeus, 2002; Freeland, 2005; Handley & Perrin, 2007). To identify first generation dispersers ( $n=419$ ), we used Bayesian assignment *with the five subpopulations predefined according to prior information on where each individual was sampled* (POPINFO=1, GENSBACK=0, Pritchard *et al.*, 2000). Model settings included admixture ( $\alpha=1$ ,  $\alpha_{max}=50$ ), only moderate migration ( $\nu=0.05$ ), 100 000 burnins and 500 000 iterations. Among individuals assigned to other subpopulations than where they were sampled, STRUCTURE identifies significant first-generation dispersers. Mark-and recapture has shown that STRUCTURE can detect most natal dispersers with moderate genetic structure (e.g.  $F_{st} \geq 0.06$ ) and that almost 100% accuracy may be obtained with less structure using high stringency levels of assignment (Berry *et al.*, 2004). The numbers of significant first-generation dispersers identified by STRUCTURE that were adult and where

Table 3. Genetic variation in the five identified Norwegian red deer subpopulations ( $n = 419$ , the involved locations also given, see Fig 1), each represented by estimates of allelic richness ( $A_R$ ), unbiased gene diversity (H) and inbreeding ( $F_{is}$ ) averaged across loci. Standard errors in brackets (SE).

Subpopulation	n	$A_R$	(SE)	H	(SE)	$F_{is}$	(SE)
1: N 1-4, E	127	4.12	(.39)	0.60	(.04)	0.04	(.02)
2: NW 1-2, C	60	4.18	(.37)	0.63	(.04)	0.04	(.02)
3: W	32	4.18	(.35)	0.61	(.04)	-0.05	(.02)
4: SW, SE 1-2	145	4.02	(.29)	0.62	(.03)	0.03	(.02)
5: SE 3-4	54	3.90	(.29)	0.61	(.04)	0.08	(.02)

Table 4. Pairwise  $F_{st}$  values for females and males separately between five geographic subpopulations of Norwegian red deer identified by Bayesian assignment and the difference between pairs ( $\Delta-F_{st}$ ). Probabilities that  $F_{st}$  values differ from zero ( $P$ ) and significance after sequential Bonferroni correction *in italic*.

Subpopulation	Female $F_{st}$	$P$	Male $F_{st}$	$P$	$\Delta-F_{st}$
1 and 2	0.030	.0001	0.018	<i>.0001</i>	0.012
1 and 3	0.088	.0001	0.088	<i>.0001</i>	0
1 and 4	0.122	.0001	0.118	<i>.0001</i>	0.005
1 and 5	0.123	.0001	0.090	<i>.0001</i>	0.034
2 and 3	0.079	.0006	0.036	<i>.0035</i>	0.043
2 and 4	0.138	.0001	0.076	<i>.0001</i>	0.063
2 and 5	0.140	.0001	0.052	<i>.0001</i>	0.084
3 and 4	0.088	.0001	0.093	<i>.0001</i>	-0.005
3 and 5	0.059	.0035	0.065	<i>.0003</i>	-0.006
4 and 5	0.013	.067	0.014	<i>.0004</i>	-0.002
Average (SE)	0.094 (0.017)		0.067 (0.014)		0.023 (0.010)

the sex was known were assessed according to different stringency levels of assignment, the one with the highest  $q$  value or values higher than 0.5, 0.7, or 0.9. In addition, an alternative Bayesian assignment algorithm (Rannala & Mountain, 1997), implemented in GENECLASS 2 (Piry *et al.*, 2004), was also used to detect first-generation migrants, using the same data set ( $n=419$ ) and 10 000 simulations to account for Type I errors with two different

Table 5. Number of male and female first-generation dispersers among the five identified subpopulations according to STRUCTURE with different stringency levels as criterion for assignment (CA) and according to GENECLASS with different alpha ( $\alpha$ ) levels. Whether the number of dispersers is higher for males than females is tested through Fishers exact tests, for which probabilities ( $P$ ) are given (significant differences in bold\*\*).

CA	STRUCTURE			GENECLASS			
	♂	♀	$P$	♂	♀	$P$	$\alpha$
Highest $q$	13	1	<b>0.009**</b>	19	2	<b>0.002**</b>	0.05
$q>0.5$	11	1	<b>0.022**</b>	10	1	<b>0.027**</b>	0.01
$q>0.6$	7	1	0.110				
$q>0.7$	7	1	0.110				
$q>0.8$	3	0	0.218				
$q>0.9$	2	0	0.361				

alpha levels (0.05 and 0.01; Paetkau *et al.*, 2004). Only adult first-generation dispersers where the sex was known were considered. To test if the number of dispersers was higher for males than for females we used Fisher Exact tests (one-tailed) because of low and zero table values (Bhattacharyya & Johnsen, 1977).

## Results

With the original data set divided according to the five identified subpopulations, only one locus (OarF-

CB193) was found to be deviating from HW in one subpopulation (nr. 5,  $P<0.002$ ). The level of genetic variation estimated through allelic richness and gene diversity was equal among the five subpopulations, but relatively low (Table 3).

For adults with a known sex, across the 14 genotyped loci the proportion of missing alleles was two percent for both females and males. Only one locus (BMC1009) was for females in

one subpopulation (nr. 4) found to be deviating from HW ( $P<0.004$ ). HW was therefore assumed for the remainder of analyses. Among the five Norwegian red deer subpopulations overall  $F_{st}$  values were 0.067 (SE=0.014) for the 167 males and 0.094 (SE=0.017) for the 112 females. Pairwise  $F_{st}$  values among subpopulations separate for each sex varied from 0.01 to 0.14 and all were significantly different from zero except one, which involved a very low  $F_{st}$  value (Table 4). In a pairwise  $t$ -test the  $F_{st}$  values among subpopulations

were significantly higher for females than for males ( $t=2.24$ ,  $P=0.03$ ,  $df=9$ ), with an average difference of 0.023 (SE=0.010).

Individual-based Bayesian assignment identified more males than females as first-generation dispersers among the five subpopulations. For the STRUCTURE analysis the difference was significant only with relaxed levels of assignment while for both alpha levels significantly more males were detected through the GENECLASS analysis (Table 5). In the STRUCTURE analysis, some individuals were assigned with coefficients varying between 0.4 (highest  $q$ ) to 0.6 because of partial assignment to more than one subpopulation, and statistical tests were not significant when these individuals were omitted at the higher stringency levels. Among males identified as dispersers between subpopulations (lowest stringency level in STRUCTURE but lowest alpha and highest stringency in GENECLASS), the distance in kilometers between sampling location and the outer edge of the assigned cluster (Fig. 1) varied from 30 ( $n=2$ ), to 100-150 ( $n=5$ ) and 200-300 ( $n=6$ ). These were adult stags ( $n=8$ ) weighing from 107 to 143 kg ( $n=5$ ), and sub-adults ( $n=5$ ) weighing from 61 to 88 kg ( $n=4$ ), respectively.

## Discussion

The differences between the sexes in genetic structure estimated from microsatellite markers suggest that dispersal is more limited in females than males and thus that dispersal is male-biased between the subpopulations of the Norwegian red deer population. The high and significant  $F_{st}$  values indicate that the sample sizes were adequate for each sex, as the only non-significant  $F_{st}$  value was relatively low. The subpopulations are separated by tens to hundreds of kilometers (Fig. 1) and the differences in genetic structure therefore reflect limitations to dispersal on an intermediate to large scale in this expanding ungulate population.

Sex-specific  $F_{st}$  values between the 15 sampled localities indicate a similar bias also for short-distance dispersal but sample sizes were too low to achieve significant  $F_{st}$  values (data not presented). Bayesian analyses offer a powerful alternative for quantitative estimates of sex-biased dispersal (Handley & Perrin, 2007), and the higher number of identified male than female first generation dispersers between subpopulations provide strong support for a male-biased dispersal on a large scale. Most of these originated in subpopulations four and five in the south-east (Fig S1 in supplementary), which lies in relatively flat and low-lying areas compared to the western shore where steeper topography and fiords like the Sognefjorden lying to the south of subpopulation 3 act as major barriers against dispersal (Haanes *et al.*, 2010). Moreover, the majority of detected dispersers dispersed to more distant subpopulations rather than to the closest possible subpopulation (Fig S1). However, the efficiency of the STRUCTURE algorithm is reduced with low levels of genetic differentiation (Berry *et al.*, 2004; Latch *et al.*, 2006) and since our  $F_{st}$  values indicate mostly moderate to weak genetic structure (Wright, 1978; Hartl & Clark, 1997), the number of dispersers may have been underestimated. This is reflected by the higher number of first-generation dispersers identified through the GENECLASS analysis, which provides good support for the results and conclusions.

In red deer, male-biased dispersal has been well documented through field studies (Clutton-Brock *et al.*, 1982b). However, genetic methods may give additional insights into how sex-biased dispersal translates into gene flow (Handley & Perrin, 2007). As dispersed individuals successfully reproduce, their genetic contribution will translate into gene flow. The higher male than female dispersal suggested by differences in genetic structure and numbers of dispersers within the Norwegian population

will therefore, depending on the mating success of the dispersers, in the next generation translate to gene flow between the subpopulations. Genetic differentiation from polygony and limitations to gene flow by philopatry among social groups (Chesser, 1991b; Chesser, 1991a) have been reported as fine-scale genetic structure in several ungulates like Soay sheep (*Ovis aries*; Coltman *et al.*, 2003), Mediterranean mouflon (*Ovis gmelini*; Petit *et al.*, 1997) and White-tailed deer (*Odocoileus virginianus*; Mathews & Porter, 1993; Purdue *et al.*, 2000), and red deer (Nussey *et al.*, 2005; Frantz *et al.*, 2008). On a scale of a few kilometers, male-biased gene flow has been suggested from a much weaker genetic structure in nuclear microsatellite markers than in maternally inherited mitochondrial DNA among red deer management blocks on the Scottish island of Rhum (Nussey *et al.*, 2006). Within the relatively small study area of Rhum, a maximum distance of 22 kilometers for male dispersal has been recorded (Clutton-Brock *et al.*, 1982b). By comparison, our Bayesian analyses identified mainly long-distance male dispersal on a scale of 10 to 100 kilometers, of which most were large adults that probably contribute to reproduction and thus gene flow. Such long-distance dispersal distances have also previously been reported both from the Norwegian population (Collett, 1912; Ahlén, 1965) and other spatially expanding ungulate populations with sex-related differences in genetic structure such as elk (Petersburg *et al.*, 2000) and white-tailed deer (Long *et al.*, 2005).

Many ungulate species with fine-scale genetic structure from philopatry and polygony have a recent history of demographic growth (Mathews & Porter, 1993; Purdue *et al.*, 2000; Coltman *et al.*, 2003), even though increasing dispersal with population growth and increased density would be expected to break down such structure. On the northern management block of Rhum, red deer were released from the an-

nual cull from 1972 and population density was allowed to increase. Here the fine-scale genetic structure actually declined as population density increased until the year 2001, but observed dispersal between population subdivisions did not increase in either sex and the decline was instead explained by an increased female breeding population size and a reduced level of polygony (Nussey *et al.*, 2005). However, during this period overall male emigration increased (Clutton-Brock *et al.*, 1997; Clutton-Brock *et al.*, 2002) and the spatial association between female relatives increased (Albon *et al.*, 1992). By comparison, the growing Norwegian population has during the last century expanded spatially (Langvatn, 1988; Forchhammer *et al.*, 1998; Langvatn, 1998), involving dispersal of both males and females into new areas. In red deer hinds, increases in the density of matrilineal groups may involve increased competition and reduced reproductive success (Clutton-Brock *et al.*, 1982a), and experiments have shown that aggression increases with density (Blanc & Thériez, 1998). We suggest that as the Norwegian red deer population grew (Langvatn, 1988; Forchhammer *et al.*, 1998; Langvatn, 1998), in addition to increased male emigration, hinds started to disperse from core areas as density increased and competition intensified.

Several hypotheses proposed to explain sex-biased dispersal have been classified into three main hypotheses (Prugnolle & de Meeus, 2002; Freeland, 2005); the resource-competition hypothesis (Greenwood, 1980), the local mate-competition hypothesis (Dobson, 1982; Perrin & Mazalov, 1999), and the inbreeding avoidance hypothesis (Pusey, 1987). More recently, cooperative behaviour of kin and enhanced use of local resources have been added as a fourth hypothesis (Perrin & Lehmann, 2001; Le Galliard *et al.*, 2006; Handley & Perrin, 2007). From its limited distribution one century ago (Collett, 1909; Ingebrigtsen, 1924),

the Norwegian population has expanded considerably (Langvatn, 1988; Forchhammer *et al.*, 1998; Langvatn, 1998) and competition for local resources in newly established areas can probably be excluded. Due to a strongly male-biased harvest of Norwegian red deer the sex-ratio of the population is skewed towards females (Langvatn & Loison, 1999). Increased bias of the sex-ratio towards females has been shown to decrease male harem holding periods and increase the proportion of males that hold harems (Clutton-Brock *et al.*, 1997), and any pronounced local male competition for female mates seems therefore unlikely in the Norwegian population. Finally, with the social grouping of philopatric females in red deer (Clutton-Brock *et al.*, 1982b; Clutton-Brock *et al.*, 2002), the hypothesis of cooperation among female relatives can not be excluded, but may rather be complementary to inbreeding avoidance. In social mammals, inbreeding avoidance probably has played an important role in the evolution of dispersal, as shown among polygynous sciurid species where the degree of male-biased dispersal increases with sociality (Devillard *et al.*, 2004). Natal faithfulness towards mobile social units may involve similar genetic differentiation as philopatry (Prugnolle & de Meeus, 2002), especially with polygynous mating systems (Chesser, 1991a), and we suggest that hinds during spatial population expansion dispersed in matrilineal groups to maintain the benefits of cooperation and that the long male dispersal distances are related to inbreeding avoidance. A possible management implication of this may apply to particularly small and genetically structured populations where the male proportion in the population should be maintained to avoid inbreeding. This suggests that rather than just considering the five identified genetically differentiated subpopulations as separate management units one should probably rather manage the whole population as one meta-population.

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Ulik spredning mellom kjønnene i en nordlig populasjon klovdyr (hjort)

*Abstract in Norwegian / Sammendrag:* Hos de fleste arter pattedyr skjer spredning oftest hyppigere og over lengre avstander blant hanndyra enn blant hunndyra, og i mange polygame arter klovdyr vil hjemmekjærhet og matrilinéære grupperinger blant hunndyra medføre en småskala genetisk strukturering. Ved å undersøke for kjønnsrelaterte forskjeller i fordelingen av allelfrekvensene til mikrosatellitter i arvestoffet har vi belyst hvorvidt dette er tilfellet hos en geografisk ekspanderende nordlig klovdyrpopulasjon. Den norske hjortepopulasjonen (*Cervus elaphus atlanticus*) har det siste århundret vokst betraktelig i antall og geografisk utbredelse etter at bestanden ble drastisk redusert for 300 til 100 år siden. Tidligere Bayesiske analyser tyder på en nåværende oppdeling av genetisk variasjon i fem geografisk adskilte underbestander. Blant disse underbestandene av hjort var de sammenlagte  $F_{st}$ -verdiene 0,067 (SE=0,014) for hanndyr

og 0,094 (SE=0,017) for hunndyr. Parvise  $F_{st}$ -verdier var signifikant høyere for hunndyr enn for hanndyr, noe som demonstrerer en sterkere genetisk struktur mellom hunndyr, samt en lavere grad av spredning blant hunndyr enn blant hanndyr. I samsvar med dette ble et høyere antall hanndyr enn hunndyr identifisert som førstegenerasjons spredere mellom de fem underbestandene ved bruk av Bayesiske analyser med forhåndsinformasjon om hvor prøvene ble samlet inn, men antallet var bare signifikant høyere når analysens grenser for tilskrivning var avslappet. Den identifiserte og hovedsakelig hannlige spredningen innebar avstander som varierte fra 30 til 300 kilometer, noe som tyder på at denne typen bias forekommer på en stor geografisk skala hos hjort.

## Appendix

Table S1. Proportion of membership for the 15 sampled localities of Norwegian red deer to each of five clusters in a Bayesian assignment test (average across individuals) using uniform priors and an admixture model (from Haanes *et al.*, 2010).

Locality	Cluster 1	Cluster 2	Cluster 3	Cluster 4	Cluster 5
N1	<u>0.502</u>	0.384	0.078	0.018	0.019
N2	<u>0.646</u>	0.194	0.081	0.023	0.056
N3	<u>0.755</u>	0.195	0.024	0.013	0.013
N4	<u>0.703</u>	0.249	0.018	0.013	0.018
NW1	0.162	<u>0.633</u>	0.170	0.015	0.021
NW2	0.079	<u>0.572</u>	0.287	0.033	0.029
C	0.136	<u>0.525</u>	0.118	0.056	0.165
W	0.030	0.053	<u>0.801</u>	0.024	0.093
SW	0.015	0.015	0.046	<u>0.773</u>	0.151
S	0.018	0.021	0.062	<u>0.645</u>	0.255
SE1	0.016	0.029	0.131	<u>0.567</u>	0.257
SE2	0.044	0.077	0.104	<u>0.396</u>	0.380
SE3	0.038	0.040	0.127	0.390	<u>0.405</u>
SE4	0.039	0.036	0.237	0.102	<u>0.587</u>
E	<u>0.355</u>	0.289	0.073	0.088	0.196

Table S2. Sample size (n), locality name, allelic richness ( $A_R$ ), unbiased gene diversity (H) and inbreeding coefficient ( $F_{IS}$ ) for each of the 15 sampled Norwegian red deer localities (modified from Haanes *et al.*, 2010). Standard errors (SE) in brackets.

Locality	Name	n	$A_R$	H	$F_{IS}$
N1	Åfjord	16	4.1 (.4)	0.62 (.04)	0.014
N2	Hitra	37	3.7 (.4)	0.56 (.05)	0.017
N3	Skaun / Meldal / Rennebu	27	3.5 (.3)	0.58 (.05)	-0.032
N4	Sunndal	32	3.6 (.3)	0.58 (.05)	0.031
NW1	Hareid	20	3.8 (.4)	0.59 (.05)	0.052
NW2	Eid	17	3.9 (.4)	0.63 (.04)	0.030
C	Skjåk	23	4.0 (.3)	0.64 (.03)	0.007
W	Fjalar / Gaular	32	3.8 (.3)	0.61 (.04)	-0.039
SW	Tysvær	23	3.6 (.4)	0.59 (.04)	0.012
S	Farsund / Hægebo- stad / Birkenes / Evje	25	3.7 (.3)	0.61 (.03)	0.071
SE1	Drangedal	30	3.7 (.2)	0.62 (.03)	-0.042
SE2	Nome	68	3.6 (.2)	0.61 (.03)	0.027
SE3	Hjartdal / Notodden	25	3.6 (.2)	0.60 (.04)	0.073
SE4	Flå / Hol / Gol	29	3.6 (.2)	0.61 (.04)	0.065
E	Rendal / Elverum	15	3.8 (.3)	0.65 (.03)	0.006

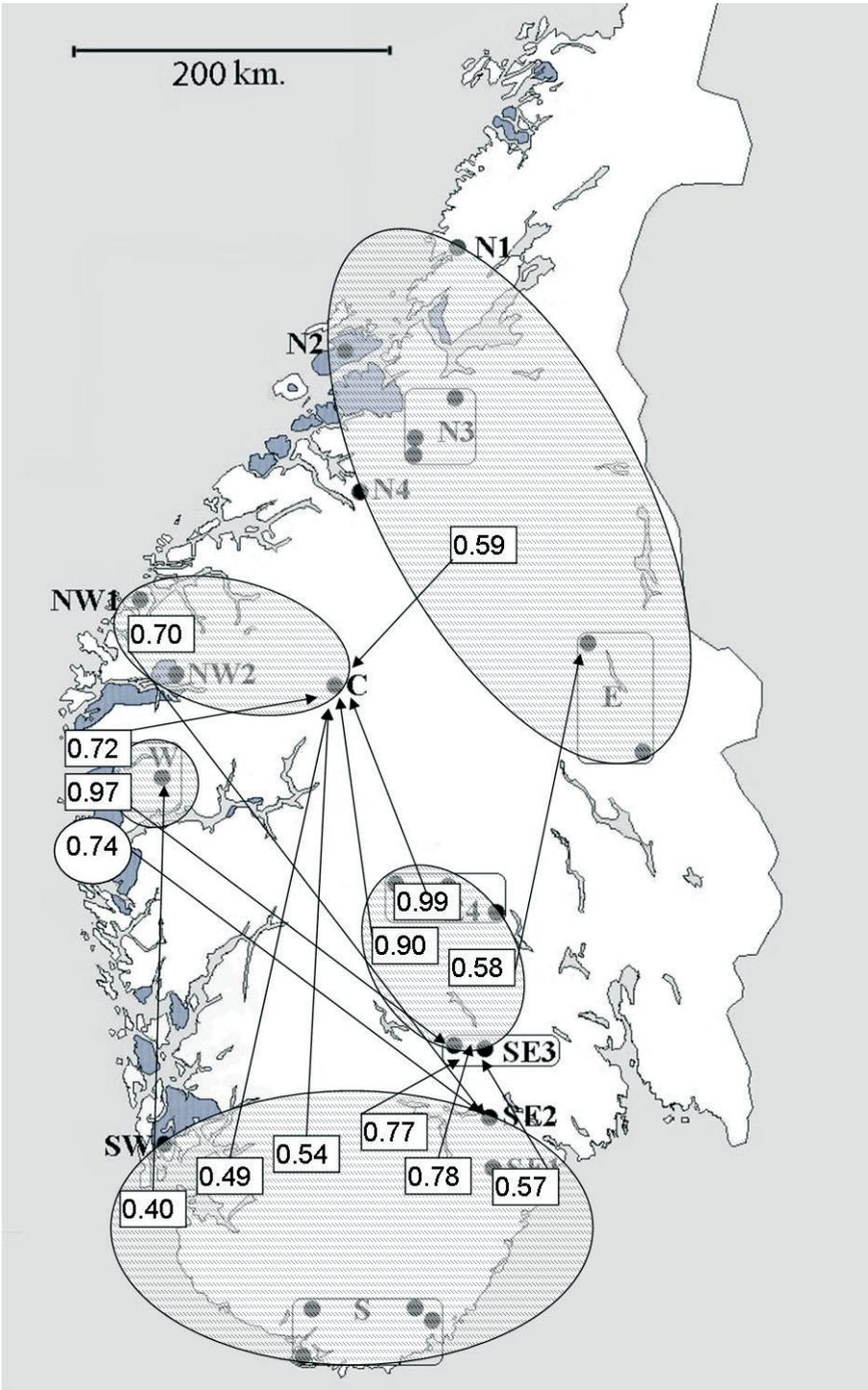


Fig. S1. Norwegian red deer long-distance dispersers identified through STRUCTURE with priors on which subpopulation each individual was sampled, their sex (rectangle=male, circle=female), sampling location (arrow points to, indicating the direction of dispersal, and the likelihood of assignment (coefficient  $q$ ).

Table S3. Allele frequencies (p:) for 14 microsatellite loci in five Norwegian red deer subpopulations.

	pop1	pop2	pop3	pop4	pop5
Locus 1					
N	120	59	32	144	53
p: 1	0.104	0.076	0.047	0.035	0.075
p: 2	0.463	0.492	0.5	0.174	0.264
p: 3	0.425	0.381	0.281	0.691	0.547
p: 4	0	0	0.016	0	0
p: 5	0.008	0.051	0.156	0.101	0.113
Locus 2					
N	121	59	30	141	53
p: 1	0.508	0.39	0.067	0.113	0.075
p: 2	0.004	0	0	0	0
p: 3	0.339	0.254	0.65	0.429	0.538
p: 4	0.149	0.356	0.283	0.457	0.387
Locus 3					
N	124	54	26	126	48
p: 1	0.403	0.269	0.385	0.115	0.125
p: 2	0.585	0.583	0.481	0.702	0.75
p: 3	0.012	0.148	0.135	0.183	0.125
Locus 4					
N	120	56	29	127	54
p: 1	0.046	0.196	0.121	0.213	0.157
p: 2	0.638	0.679	0.603	0.559	0.556
p: 3	0.233	0.045	0.259	0.209	0.278
p: 4	0	0	0	0.008	0
p: 5	0.083	0.08	0.017	0.012	0.009
Locus 5					
N	127	60	32	145	50
p: 1	0.11	0.308	0.328	0.314	0.19
p: 2	0.425	0.425	0.266	0.334	0.43
p: 3	0.339	0.142	0.031	0.01	0.02
p: 4	0.031	0.1	0.313	0.09	0.16
p: 5	0.091	0.017	0	0.224	0.15
p: 6	0.004	0.008	0.063	0.028	0.05

	pop1	pop2	pop3	pop4	pop5
Locus 6					
N	120	58	32	133	46
p: 1	0.275	0.241	0.547	0.267	0.359
p: 2	0.238	0.147	0.016	0.162	0.043
p: 3	0.479	0.612	0.438	0.571	0.598
p: 4	0.008	0	0	0	0

	pop1	pop2	pop3	pop4	pop5
Locus 7					
N	126	60	31	145	51
p: 1	0.012	0.1	0.21	0.038	0.039
p: 2	0.119	0.142	0.016	0.003	0.01
p: 3	0.004	0	0	0	0
p: 4	0.194	0.158	0.21	0.266	0.196
p: 5	0.167	0.283	0.355	0.31	0.412
p: 6	0.063	0	0	0.003	0
p: 7	0.44	0.317	0.21	0.379	0.343

	pop1	pop2	pop3	pop4	pop5
Locus 8					
N	123	60	31	145	54
p: 1	0.203	0.383	0.532	0.214	0.287
p: 2	0.317	0.183	0.21	0.3	0.269
p: 3	0.004	0	0	0.003	0
p: 4	0.252	0.267	0.194	0.097	0.139
p: 5	0.093	0.067	0.016	0.045	0.083
p: 6	0.13	0.1	0.048	0.341	0.222

	pop1	pop2	pop3	pop4	pop5
Locus 9					
N	121	60	31	142	53
p: 1	0.004	0	0	0	0
p: 2	0.012	0.117	0.129	0.081	0.085
p: 3	0.165	0.217	0.226	0.32	0.33
p: 4	0.157	0.242	0.161	0.025	0
p: 5	0.025	0	0	0	0
p: 6	0.103	0.083	0.016	0	0
p: 7	0.074	0.117	0	0.046	0.16
p: 8	0.004	0	0	0.011	0.009
p: 9	0.285	0.125	0.242	0.391	0.368
p: 10	0.165	0.05	0.145	0.113	0.028
p: 11	0.004	0.05	0.081	0.014	0.019

	pop1	pop2	pop3	pop4	pop5
Locus 10					
N	125	55	30	144	53
p: 1	0.096	0.182	0.133	0.003	0
p: 2	0.54	0.536	0.2	0.201	0.255
p: 3	0.144	0.082	0.167	0.028	0.047
p: 4	0.008	0.082	0.367	0.243	0.33
p: 5	0	0	0.017	0	0
p: 6	0.212	0.118	0.117	0.524	0.368

Locus 11					
N	122	60	32	141	52
p: 1	0.152	0.192	0.016	0.021	0
p: 2	0.48	0.483	0.438	0.106	0.135
p: 3	0.008	0	0	0	0
p: 4	0.357	0.308	0.547	0.649	0.827
p: 5	0.004	0.017	0	0.223	0.038

Locus 12					
N	124	58	32	144	52
p: 1	0.181	0.198	0.125	0.215	0.308
p: 2	0.476	0.388	0.297	0.326	0.433
p: 3	0.238	0.241	0.031	0.156	0.077
p: 4	0.105	0.172	0.516	0.285	0.183
p: 5	0	0	0.031	0.017	0

Locus 13					
N	120	57	28	142	54
p: 1	0.154	0.158	0.339	0.57	0.407
p: 2	0.008	0.035	0.018	0.148	0.231
p: 3	0.833	0.807	0.643	0.282	0.361
p: 4	0.004	0	0	0	0

Locus 14					
N	118	53	29	140	54
p: 1	0.025	0.047	0.052	0.093	0.148
p: 2	0.148	0.274	0.155	0.364	0.287
p: 3	0.826	0.679	0.793	0.543	0.565

