

Rapidly declining fine-scale spatial genetic structure in female red deer

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Abstract

A growing literature now documents the presence of fine-scale genetic structure in wild vertebrate populations. Breeding population size, levels of dispersal and polygyny — all hypothesized to affect population genetic structure — are known to be influenced by ecological conditions experienced by populations. However the possibility of temporal or spatial variation in fine-scale genetic structure as a result of ecological change is rarely considered or explored. Here we investigate temporal variation in fine-scale genetic structure in a red deer population on the Isle of Rum, Scotland. We document extremely fine-scale spatial genetic structure (< 100 m) amongst females but not males across a 24-year study period during which resource competition has intensified and the population has reached habitat carrying capacity. Based on census data, adult deer were allocated to one of three subpopulations in each year of the study. Global F_{ST} estimates for females generated using these subpopulations decreased over the study period, indicating a rapid decline in fine-scale genetic structure of the population. Global F_{ST} estimates for males were not different from zero across the study period. Using census and genetic data, we illustrate that, as a consequence of a release from culling early in the study period, the number of breeding females has increased while levels of polygyny have decreased in this population. We found little evidence for increasing dispersal between subpopulations over time in either sex. We argue that both increasing female population size and decreasing polygyny could explain the decline in female population genetic structure.

Keywords: *Cervus elaphus*, density dependence, dispersal, polygyny, population structure

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Introduction

An understanding of the processes underlying population structure at fine spatial scales is central to evolutionary biology. Fine-scale population structure may facilitate kin or localized selection processes, as well as potentially confounding population and quantitative genetic research (Coltman *et al.* 2003). Recently, studies have shown such fine-scale spatial structure within populations of a variety

of vertebrate taxa using genetic techniques (Shorey *et al.* 2000; Taylor *et al.* 2001; Lampert *et al.* 2003). Theoretical and empirical studies have explained such genetic structuring in terms of mating systems and dispersal patterns (Chesser 1991; Sugg *et al.* 1996; Dobson 1998). Where limited dispersal results in close spatial associations between relatives, fine-scale structure will arise (Chesser 1998). Highly polygynous breeding systems, where only a handful of unrelated males father offspring, enhance structure, as many offspring receive paternal genes from the same source and local co-ancestry will be increased (Chesser 1991).

In mammals, male-biased dispersal and female philopatry are the norm (Greenwood 1980; Clutton-Brock 1989). Females tend to remain close to their maternal relatives

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throughout their lives, often forming matrilineal social groups (Greenwood 1980). Male-biased dispersal may have evolved in concert with female philopatry and polygyny to avoid costs of inbreeding associated with bisexual philopatry (Chesser 1991). Studies of mammalian social structure through population genetics have utilized F -statistics (Wright 1965) to examine partitioning of genetic variance and levels of inbreeding in species showing discrete social groups. Using the social group as the subpopulation unit, numerous studies have documented F_{ST} values significantly different from zero, indicating genetic structuring between groups, as well as negative F_{IS} values, indicating less inbreeding than expected under complete breeding within groups (see Storz 1999 for review). In mammal species with fission-fusion societies showing less discrete group structure, examination of the correlation of genetic relatedness estimates with distances between pairs of individuals has also revealed structure at fine spatial scales (Coltman *et al.* 2003; Hazlitt *et al.* 2004).

The presence and implications of temporal and spatial variation in mammalian population structure have been largely ignored. However, recent research has shown that population genetic parameters may vary spatially within species or populations, specifically where habitat fragmentation differs (Peacock & Smith 1997; Stow *et al.* 2001). There is also evidence of temporal instability in such parameters (Viard *et al.* 1997; Piertney *et al.* 1999; Garant *et al.* 2000), which could itself represent an important intrinsic factor in population dynamic patterns (Lambin & Krebs 1991). Changes in the number of breeding individuals, dispersal patterns, and levels of inbreeding and polygyny would be expected to influence population genetic parameters such as fixation indices (Chesser 1991, 1998; Balloux 2004). There is evidence that variation in resource competition can alter group composition, ranging and spacing behaviour in mammals (Albon *et al.* 1992; Kilpatrick *et al.* 2001), and ultimately influence population genetic structure (Pope 1998; Aars & Ims 2000), as well as influencing male emigration and the distribution of male mating success (Clutton-Brock *et al.* 1997; Pemberton *et al.* 1999). Here, we explore temporal variation in fine-scale genetic structure in a wild red deer population and relate this specifically to variation in population size, dispersal patterns and polygyny associated with the population's recent release from culling.

Previous research on the study population

The red deer (*Cervus elaphus* L.) in the North Block study area of the Isle of Rum, Scotland, have been the subject of intensive individual-based study since 1973 (Clutton-Brock *et al.* 1982b). The feeding habitat within the North Block consists of areas of high quality *Agrostis-Festuca* grassland and poorer quality regions of heath and *Molinia* grassland

(Clutton-Brock *et al.* 1982b). The population's mating system is polygynous, with males competing to dominate harems of oestrous females between September and November each year (Clutton-Brock *et al.* 1997). Male emigration is common between the ages of 2 and 5 years and is density dependent, with many males returning to the North Block later in life to rut (Clutton-Brock *et al.* 1997, 2002; Catchpole *et al.* 2004). Female emigration is rare and depends mainly on the distance between their natal area and the study area's boundaries (Catchpole *et al.* 2004). Females are loosely matrilineal, and several studies have observed close spatial and social associations between maternal relatives (Clutton-Brock *et al.* 1982a; Coulson *et al.* 1997).

Following release from culling in 1973, the number of resident adult females in the population increased throughout the 1970s and early 1980s (Clutton-Brock *et al.* 1982b). The population has been at or close to carrying capacity since the mid-1980s (Albon *et al.* 2000). Previous studies have shown rising density to be associated with reductions in female fecundity, reproductive success, and overwinter calf survival (Clutton-Brock *et al.* 1987; Kruuk *et al.* 1999; Albon *et al.* 2000), as well as increased spacing between female maternal relatives (Albon *et al.* 1992). Rising female density has also been associated with increased male juvenile mortality and early emigration, and with decreased permanent male immigration into the North Block (Clutton-Brock *et al.* 1997). The ratio of adult resident females to males in the North Block has increased sharply, resulting in an almost complete absence of males from high quality grazing areas in the recent years (Coulson *et al.* 2004). Clutton-Brock *et al.* (1997) showed that the number of males obtaining successful matings increased with adult sex ratio, and argued that rising female population density and resource competition have led to decreased competition for mates amongst males.

The present study

Given the general pattern of female philopatry and male dispersal evident in this population, we expected to find fine-scale structuring of genotypes only amongst female red deer. However, as a consequence of the population's release from culling, changes in population size and mating system have occurred that would be expected to alter such fine-scale structure. The increase in the number of reproductive females, increasing dispersal of both sexes, and decreasing levels of polygyny might be expected to lead to a decrease in genetic structure amongst females over time. Here, we examined overall fine-scale genetic structure in males and females, changes in population structure over time, and we related any observed changes to analyses of temporal variation in breeding population size, dispersal and polygyny using the long-term census and genetic data collected from the North Block red deer population.

Materials and methods

Field data

All individual red deer in the North Block study area are recognizable as a result of either artificial marks (collars, ear tags or ear punches attached as calves or following immobilization) or natural markings. Since 1973, censuses of the North Block study area have been conducted at least five times a month between January and May (Coulson *et al.* 1997). On each census all individuals observed were identified and their position, to the nearest 100-m² ordnance survey (OS) grid square, was noted. Individuals were included in the analyses that follow if they were seen in at least 10% of censuses between January and May (termed 'resident' animals; see Coulson *et al.* 1997 for further discussion and justification) and were of reproductive age (≥ 3 years). Only census data from between 1978 and 2001 were analysed, unless specifically stated, to complement the available genetic data set.

We used the following parameters in our analyses.

Mean annual position. Average x and y coordinates from January to May census positions for an individual in a given year. Averages were truncated to allocate each individual to the nearest 100-m² OS grid square.

Between-year movement. For individuals resident in consecutive years, the distance between current and previous years' mean annual positions was calculated.

Population subdivisions. Many studies of the North Block red deer have treated the study area as a single unit, but there is evidence that fitness and behaviour vary spatially within the North Block (Clutton-Brock *et al.* 1982b). Subdivision of the study area based on habitat types and ranging behaviour has improved explanatory power in models of overwinter calf survival (Coulson *et al.* 1997), spacing behaviour (Albon *et al.* 1992), and other aspects of fitness (Guinness *et al.* 1978; Conradt *et al.* 1999). Following these studies, we split the study area into three subdivisions (Fig. 1): Shamhnan Insir (SI), North Kilmory Glen (NKG) and South Kilmory Glen (SKG). Individuals were assigned to one of the three subdivisions in each year they were resident to the population, according to their mean annual position.

Natal subdivision. An individual's natal subdivision was defined as the subdivision of his or her mother in the year following that individual's birth. Subdivisions were allocated based on January–May census data but calving takes place from May onwards, so this would represent maternal subdivision in the first year of life. Where natal subdivision could not be allocated in this fashion — typically

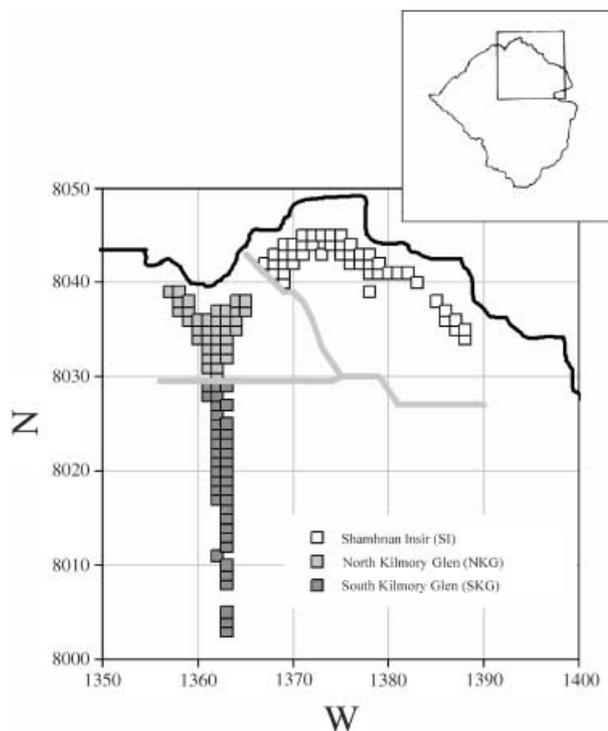


Fig. 1 Plot showing North Block study area, Isle of Rum (boxed in inset map of Rum), split into three subdivisions based on previous research. The grey lines indicate boundaries between the subdivisions. Squares indicate the regions most intensely used by adult female red deer, defined as 100-m² OS grid squares in which 9 or more females' mean annual positions were located across the study period (1978–2001).

because the individual was born before the regular censusing began — the modal subdivision across a mother's lifetime was used. This allowed natal subdivisions to be assigned to 92% of females and 87% of males resident to the study area at some point in their lifetimes.

Genetic data

Since 1982, approximately 85% of calves born in the study area have been caught shortly after birth and tissue and blood samples were taken for genotyping. Additionally, almost 300 animals born prior to this date were sampled by chemical immobilization or post-mortem. The analyses that follow include genetic data for resident adult deer that were alive between 1978 and 2001; however, restriction of the data set to 1982 onwards does not affect the nature of the findings presented here.

Individuals were genotyped at up to eight microsatellite loci: JP15, JP27, JP38, CP26, FCB193, FCB304, MAF109, TGLA94 (see Marshall *et al.* 1998 for further details). Not all individuals were genotyped at all loci, but individuals

with genotypes at fewer than four loci were excluded from the analysis. These loci have been previously shown to assort randomly and not to show evidence of deviance from Hardy–Weinberg equilibrium (Marshall *et al.* 1998).

Analysis of population structure

Analysis was conducted on individuals aged 3 years and older to exclude pre-reproductive juveniles and calves from the analyses. To assess differences between the sexes in fine-scale population genetic structure, geographical distances between the mean annual positions of pairs of individuals were compared to an index of genetic relatedness. Genetic relatedness coefficients (R ; Lynch & Ritland 1999) and geographical distances between pairs of resident individuals were examined using SPAGED1 (Hardy & Vekemans 2002). Average R estimates were taken for pairs of individuals separated by distance intervals of 100 m (from < 100 m to > 2 km), in each year of the study. The analysis was conducted separately for pairs of females and pairs of males. R coefficients for each distance interval were averaged across years for pairs of males and females to examine overall fine-scale population genetic structure. The significance of spatial genetic structuring within each sex was assessed using linear regression of mean R estimates over all years on geographical distance (Hardy & Vekemans 2002). In addition to this genetic analysis of differences between the sexes in population structure, we examined the differences between males and females in movement behaviour. We compared average between-year movement for males and females at different ages (2–10 years).

Changes in spatial partitioning of genetic variance and inbreeding were assessed using F -statistics (Wright 1965) in which the three population subdivisions were treated as subpopulations. In each year, all resident deer were assigned to a subdivision based on their mean annual position. Separate estimates of global F_{ST} and F_{IS} , as well as pairwise F_{ST} values, were generated for females and males in each year of the study period using FSTAT (Goudet 1995). Temporal trends in these estimates were assessed using a linear regression of the F -statistic on year.

Global F_{ST} values significantly greater than zero indicate greater partitioning of genetic variance between groups than within groups, while pairwise F_{ST} values represent estimates of genetic differentiation between subdivisions. Negative F_{IS} values, typical of mammalian systems, imply lower than expected inbreeding within subpopulations relative to random mating. The significance of these terms was assessed using permutation tests. FSTAT assesses global F_{ST} significance by randomizing genotypes among subdivisions and global F_{IS} by permuting alleles among individuals (Goudet 1995).

Analysis of breeding population size and mating system

Using genotypic and census data, we investigated the possibility of temporal trends in the breeding population size, dispersal between population subdivisions and levels of polygyny. In all cases, changes in indices over time were assessed by linear regression on year. The following parameters were investigated.

Female breeding population size. The number of resident females giving birth to a calf in each year of the study period was taken as an index of the breeding population size. Since the main increase in both female population size and the number of breeding females occurred in the decade following release from culling, and data were available from 1974 on female breeding behaviour and population size; this index was examined from 1974 to 2001. Note that even for females, these figures are substantially lower than the absolute count of breeding age deer alive in any one year, since not all individuals breed each year.

Dispersal. Dispersal between population subdivisions was assessed by comparing adults' natal subdivision with their assigned subdivision in a given year. If individuals had moved from their natal subdivision then the direction of dispersal was classified by their natal subdivision followed by their current subdivision (i.e. a female natal to SI, but assigned to NKG in 1980 would be classified as 'SI–NKG' for 1980). Females and males of each dispersing category were counted for each year of the study.

Male breeding population size and levels of polygyny. Estimates of these parameters were based on paternity assignment of individuals born in the North Block between 1978 and 2001, using all available microsatellite data, with CERVUS (Marshall *et al.* 1998). All males observed holding harems during a rut year were considered as potential candidate fathers. Genetic paternities were assigned where the confidence score given by CERVUS was 80% or greater. Of the calves born in the period 1978–2001, 35.4% were successfully assigned genetic paternities. If possible, males were assigned behavioural paternity where genetic paternity could not be determined. Behavioural paternities were assigned to males if they held the calf's mother in their harem for more days during the 11-day window around estimated conception than any other male (see Clutton-Brock *et al.* 1997; Kruuk *et al.* 2000; Slate *et al.* 2000 for further details and discussion of these genetic and behavioural approaches to paternity assignment). Using combined methods, 62.8% of calves were assigned paternities.

For all males observed holding harems in a given year, we calculated annual breeding success (ABS). For each study year we used this information to calculate the number of breeding males (i.e. the number of males with

one or more assigned paternities) as well as the maximum and variance in ABS in each year. Variance in male ABS was used as an index of polygyny. A previous study of this population highlighted the large number of progeny produced by a single male, named MAXI (Slate *et al.* 2002). To assess the dependence of temporal trends in polygyny on the handful of such males, we identified four males that had been assigned the most paternities across their lifetimes and investigated the effect of removing them from our data set. The identity codes of these four males, the number of offspring they sired and the years in which they bred, respectively, are as follow: RED77, 48 offspring, 1983–1991; MAXI, 36 offspring, 1978–1982; BRF76, 30 offspring, 1982–1989; BASIL, 29 offspring, 1997–2001. These individuals represented the top 0.5% of breeding males.

Temporal trends in the variance of male ABS could reflect improvements in the quality of the genetic data set in this population: the proportion of calves born that were assigned paternities each year increased over the study period ($F_{1,22} = 26.27$, $P < 0.001$). To ensure any change in polygyny was independent of this improvement, we ran a multiple regression of variance in male ABS including both year and the proportion of paternities successfully assigned in that year.

Results

Differences between the sexes in population structure

Field and genotypic data analysis across the study period both imply that male deer are highly dispersive, while females are generally philopatric and remain in close spatial proximity to relatives of the same sex (Figs 2, 3 and 4). Females tend to move relatively little across their lifetimes,

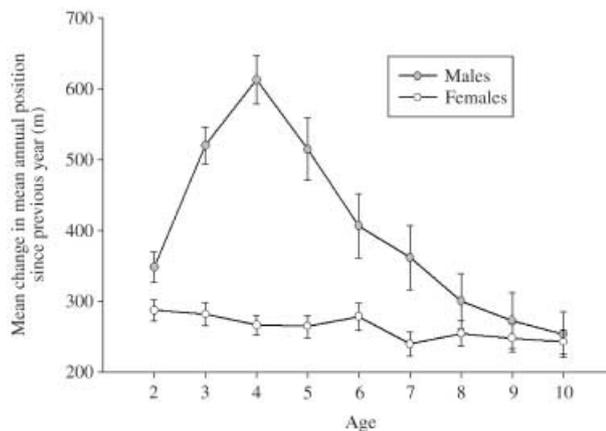


Fig. 2 Between-year movements of resident deer plotted against age of individual (at second mean annual position measured). Circles represent means for each age with standard error bars. Separate averages are shown for females (white circles) and males (grey circles). Males disperse considerably more between years than females between the ages of 3 and 5 years.

and in general had lower means and standard errors for between-year movements than males age 2 to 10 years (Fig. 2). Males born in the North Block moved increasing distances between years from ages 2 to 4 years (Fig. 2). Both these data and previous work on the population show that males are more dispersive than females, and many surviving males have dispersed from the study area by the time they reach sexual maturity (Clutton-Brock *et al.* 1982b; Catchpole *et al.* 2004).

As expected from these general differences in dispersal between the sexes, the genetic relatedness between a pair of females decreased as the distance between them became greater, but pairs of males were unrelated across the dis-

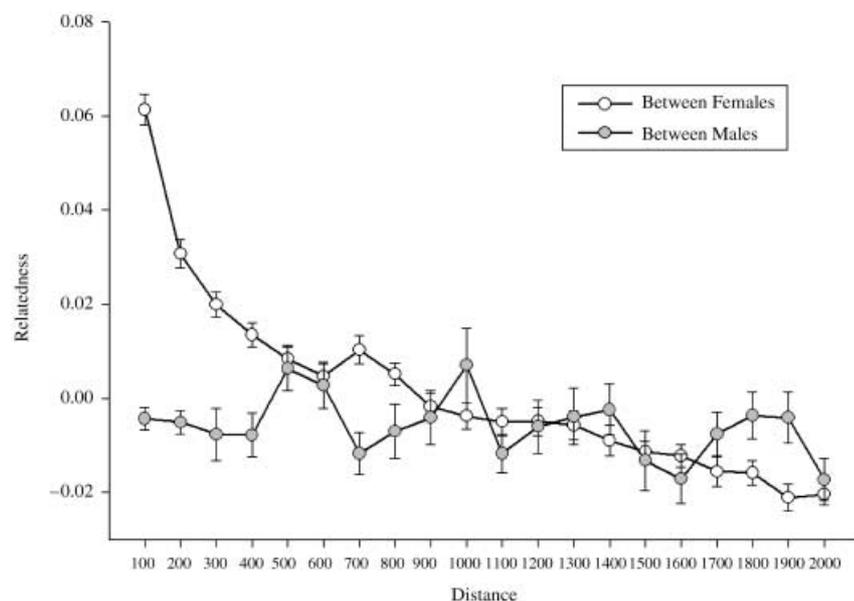


Fig. 3 Line and scatter plot showing the relationship between genetic relatedness and geographical distance amongst pairs of females (white circles) and males (grey circles). Circles represent pairwise relatedness comparisons at each distance averaged across years (1978–2001), with standard error bars. Relatedness between pairs of females is high at short distances and decreases with distance, but between pairs of males relatedness does not deviate from zero.

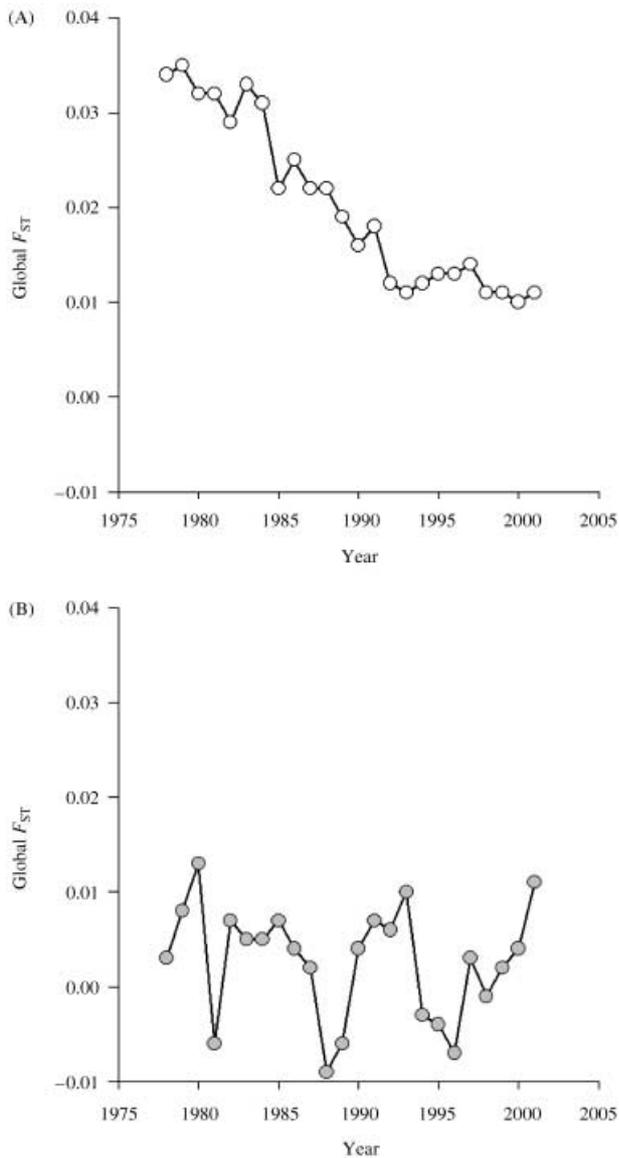


Fig. 4 Changes in global F_{ST} estimates over time, based on adult deer only with population subdivisions (see Fig. 1) treated as subpopulations. (A) Females; global F_{ST} declines significantly over the study period ($b = -0.0012 \pm 0.0001$ SE, $P < 0.001$) showing partitioning of genetic variance between the subdivisions has decreased. (B) Males; global F_{ST} shows no significant relationship with year ($b = -0.0001 \pm 0.0002$ SE, $P = 0.46$) and was only significantly greater than zero in 1980, illustrating an absence of population structure amongst males.

tance range examined (Fig. 3). Females with mean annual positions 100 m or less from one another were related, on average, at $R = +0.06$, and this decreased to a relatedness of zero at around 900 m (Fig. 3). This decline in relatedness with distance was significant (linear regression of mean R on distance amongst pairs of females: intercept = 0.053 ± 0.004 SE, slope = -0.025 ± 0.002 SE, $r^2 = 0.93$, $P < 0.001$). For

pairs of males, there was no evidence of any change or difference from zero in relatedness across the distance range examined (intercept = 0.002 ± 0.03 SE, slope = -0.006 ± 0.005 SE, $r^2 = 0.06$, $P = 0.51$).

Temporal variation in fine-scale genetic structure

Fixation indices for the North Block adult females revealed strong partitioning of genetic variation between subdivisions; however, there was no evidence of such structure amongst males. Global F_{ST} values for females were significantly greater than zero in all years of the study period for females (female mean annual $F_{ST} = 0.021$), while F_{IS} values were significantly less than zero in all years except 2000 (mean annual $F_{IS} = -0.058$). Amongst males, F_{ST} estimates were not significantly greater than zero, except in 1980 (male mean annual $F_{ST} = 0.002$), and F_{IS} estimates were not different from zero except in 2000 and 2001 (mean annual $F_{IS} = -0.022$). F_{ST} estimates significantly greater than zero suggest that there is structuring of allelic variance between the three subdivisions. Negative F_{IS} values imply an excess of heterozygosity relative to random mating.

There was a significant decline in global F_{ST} estimates for females from around 0.03–0.01 across the study period ($F_{1,22} = 201.6$, $P < 0.001$, Fig. 4A). There was no temporal trend in male F_{ST} estimates ($F_{1,22} = 0.58$, $P > 0.05$; Fig. 4B). This indicates a decline in fine-scale genetic structure amongst females, but not males, over the course of the study period. Female F_{IS} estimates increased significantly over the study period from approximately -0.08 to -0.03 ($F_{1,22} = 17.45$, $P < 0.001$), while estimates for males showed no temporal trend ($F_{1,22} = 2.19$, $P > 0.05$).

Pairwise F_{ST} estimates comparing female genotypes from SI and NKG, and SI and SKG, both show significant negative trends with time (SI–NKG: $F_{1,22} = 68.70$, SI–SKG: $F_{1,22} = 224.0$, both $P < 0.001$; Fig. 5A). In the early stages of the study, genetic distances between females in SI and SKG were around 0.06 but had declined to just over 0.01 by the mid-1990s. F_{ST} estimates between SI and NKG declined from around 0.03–0.01 over a similar period (Fig. 5A). The pairwise F_{ST} comparison of NKG and SKG females showed no significant temporal trend ($F_{1,22} = 0.31$, $P > 0.05$); it fluctuated between 0.015 and zero throughout the study period (Fig. 5A). None of the pairwise F_{ST} estimates for males showed a significant relationship with year (all regressions: $F_{1,22} < 2.3$, $P > 0.05$, Fig. 5B).

Temporal variation in breeding population size and mating system

Breeding population size. Since the population's release from culling in 1973, the number of females breeding in a given year has increased from around 55 in 1974 to fluctuate between 70 and 100 from the mid-1980s onwards ($F_{1,25} =$

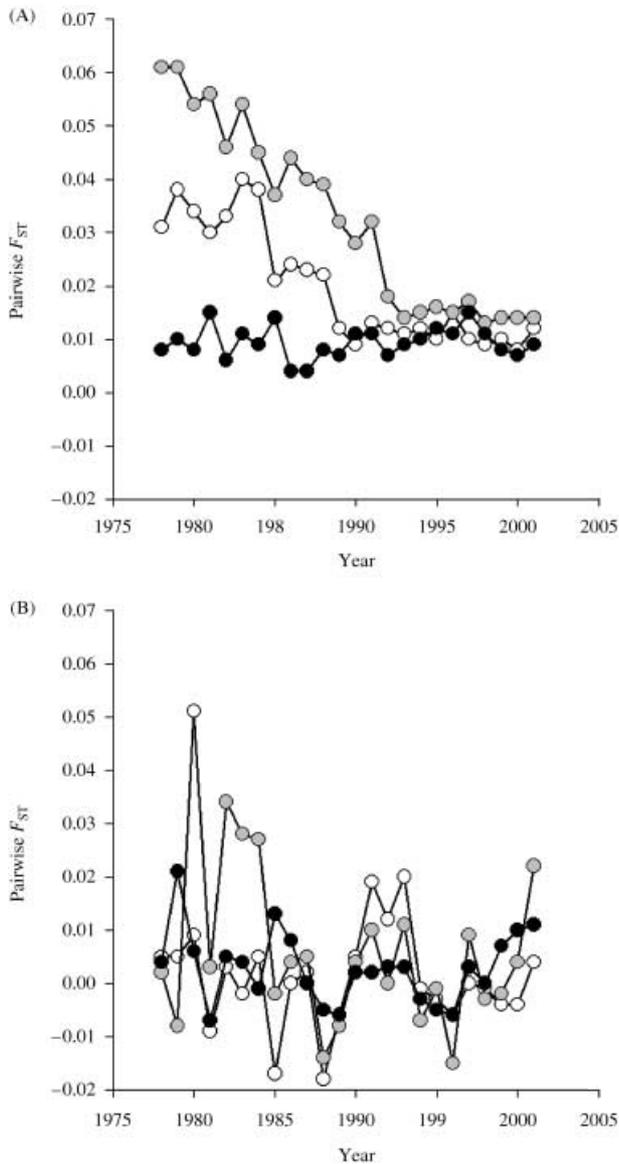


Fig. 5 Pairwise F_{ST} estimates comparing genetic differentiation between pairs of population subdivisions over time. (A) Females; the pairwise F_{ST} estimates between Shamhnan Insir (SI) and North Kilmory Glen (NKG) declines over time (white circles; $b = -0.0013 \pm 0.0002$ SE, $P < 0.001$), as do the SI-South Kilmory Glen (SKG) estimates (grey circles; $b = -0.0024 \pm 0.0002$ SE, $P < 0.001$). The NKG-SKG pairwise F_{ST} estimates remain constant and low across the study period (black circles; $b = 0.0000 \pm 0.0001$ SE, $P > 0.05$). (B) Males; no temporal trends apparent in either SI-NKG (white circles), SI-SKG (grey circles), or SKG-NKG (black circles) in pairwise F_{ST} estimates.

15.2, $P < 0.001$, Fig. 6A). The number of different males assigned paternities has also increased from around 20 in the late 1970s to between 30 and 40 in the last 5 years of the study ($F_{1,22} = 45.35$, $P < 0.001$, Fig. 6B).

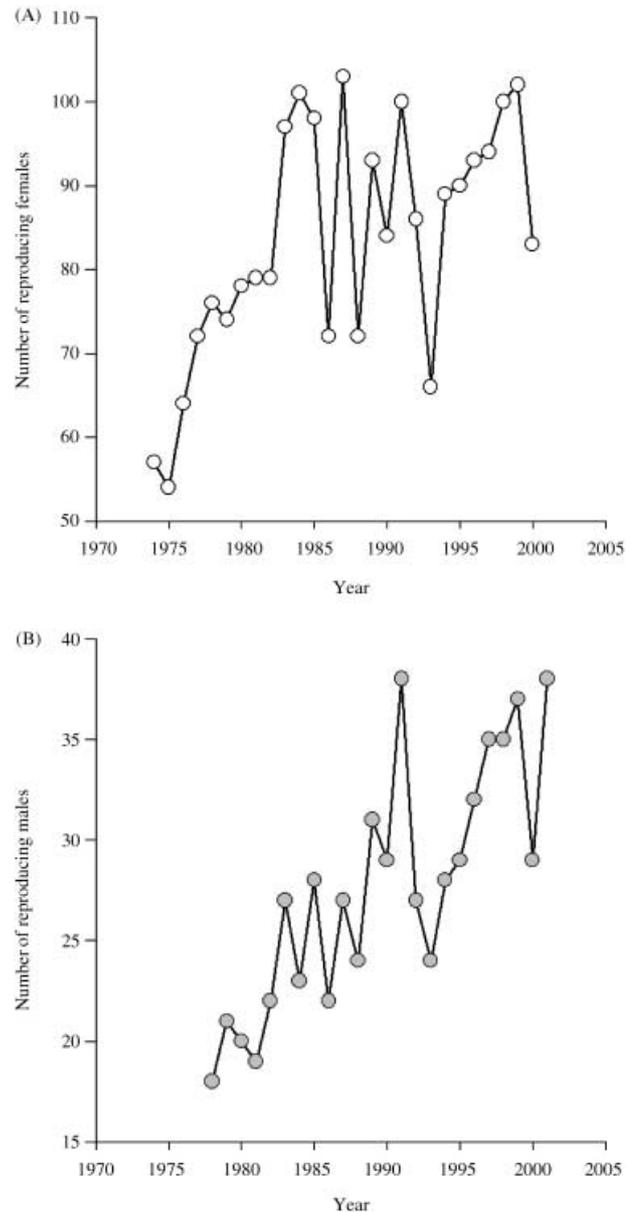


Fig. 6 (A) The number of females reproducing in each year has significantly increased since 1974 as overall female population density has increased in the population ($b = 1.10 \pm 0.28$ SE, $P < 0.001$). Note that this graph includes additional data for 1974–1977, as the main increase in female population size occurred immediately following the release from culling in 1973. (B) The number of different males assigned at least one paternity in a given year has increased across the study period ($b = 0.70 \pm 0.10$ SE, $P < 0.001$).

Dispersal. On average, only 11.7% of resident adult females were located outside their natal subdivision in a given year, compared to 30.0% for adult males. The numbers and direction of males and females dispersing from their natal subdivision are shown in Fig. 7. Movement of either sex

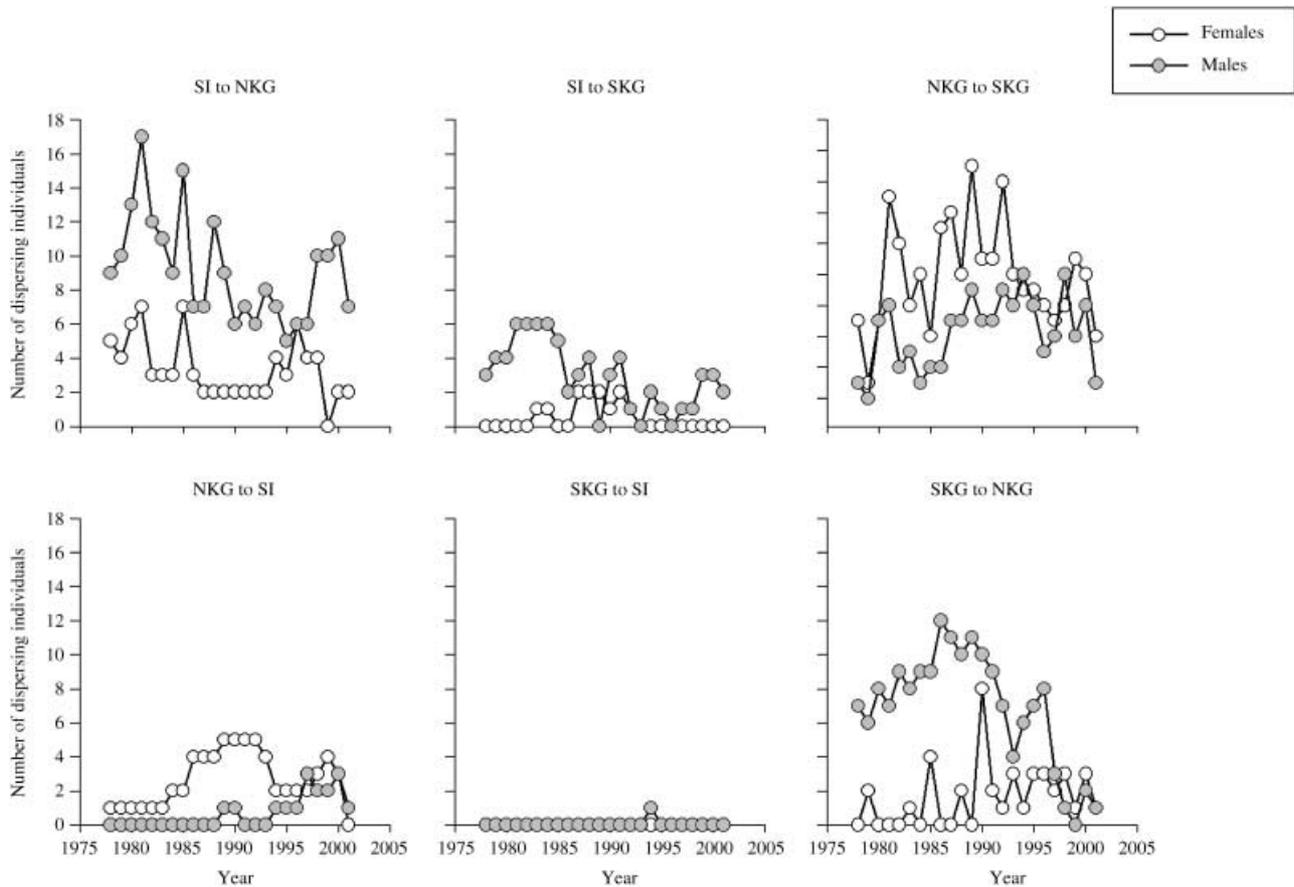


Fig. 7 Plot showing dispersal patterns in the North Block over time. Y-axes on each of the panels represent the number of adult deer found outside of their natal population subdivision for each of the six possible dispersal direction categories. Legends above each panel indicate dispersal direction, with natal subdivision followed by current subdivision. Numbers of dispersing females are indicated by white circles, numbers of males by grey circles. Subdivision abbreviations are as follows: SI, Shamhnan Insir; NKG, North Kilmory Glen; SKG, South Kilmory Glen.

between SI and SKG appears to be rare, as does movement from NKG to SI. Although higher levels of dispersal are observed between NKG and SKG and, for males at least, from SI to NKG, there is little indication of increases in dispersal capable of explaining the decline in female genetic structure. The only significant positive temporal trend in dispersal was for males dispersing from NKG to SI ($F_{1,22} = 28.87$, $P < 0.001$); however, no more than three males had dispersed in this direction in any year (Fig. 7). There were significant declines over time in male dispersal from SI to NKG ($F_{1,22} = 6.88$, $P < 0.05$) and SI to SKG ($F_{1,22} = 14.36$, $P < 0.01$), and in female dispersal from SI to NKG ($F_{1,22} = 5.31$, $P < 0.05$).

Polygyny. Variance in male ABS decreased over time ($F_{1,22} = 12.14$, $P < 0.01$, Fig. 8). This decline in the level of polygyny is most likely the result of the increase in the number of males gaining at least one paternity (Fig. 6B), rather than a change in the maximum ABS, which showed no relationship with year ($F_{1,22} = 0.59$, $P > 0.05$). The removal

of the four males with the largest lifetime breeding success from the data set resulted in a marginally nonsignificant decline in the variance in male ABS ($F_{1,22} = 3.14$, $P = 0.09$). The decline in polygyny was independent of the increase in the proportion of calves assigned paternities over time. In a multiple regression, the proportion of paternities assigned was not a significant predictor of the variance in male ABS ($F_{1,21} = 2.96$, $P = 0.10$), while year had a significant negative effect ($F_{1,21} = 11.33$, $P < 0.01$) on this measure of polygyny.

Discussion

Figure 3 clearly illustrates the presence of genetic structure at very fine spatial scales amongst female, but not male, red deer in the North Block study population. This was as predicted: a significant decline in genetic relatedness was observed over continuous space between pairs of the philopatric sex, and no spatial genetic structure was found between members of the dispersing sex. The presence of

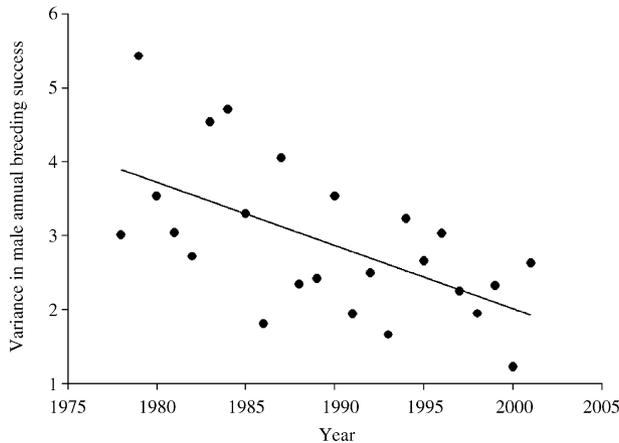


Fig. 8 Levels of polygyny have decreased over the study period. The plot shows the variance in male annual breeding success over time with a linear regression slope plotted ($b = -0.09 \pm 0.02$ SE, $P < 0.01$).

significantly positive F_{ST} and negative F_{IS} estimates across the study period imply population structure amongst females consistent with those in previous studies of mammalian population genetics (Storz 1999). In the only other study to examine genetic structure at such a fine scale in ungulates, Coltman *et al.* (2003) found similar differences between the sexes in Soay sheep on St Kilda, although the degree of spatial structure in females was lower in general and declined to zero at around 150 m. This difference between species could be explained by the fact that red deer possess a more obviously matrilineal social system (Clutton-Brock & Coulson 2002). However, it may also be the result of differences in feeding habitat and foraging behaviour: red deer on Rum have larger home ranges than Soay sheep on St Kilda.

We found significant partitioning of genetic variance between population subdivisions amongst females, but not males (Fig. 4). However, across our 24-year study period, we observed a decline in female genetic structure (Fig. 4A). Fixation indices may take many generations to reach mutation–drift equilibrium, and so it is possible that these temporal changes in genetic structure could be the product of events occurring before our study period began. F_{ST} estimates are influenced by factors such as dispersal, mating system, and effective population size. Previous work on the North Block red deer population suggests that these parameters have altered across our study period as a direct or indirect consequence of the cessation of culling (Clutton-Brock *et al.* 1982b, 1997; Albon *et al.* 1992). Increases in dispersal between population subdivision in either sex, increases in the breeding population size and decreasing polygyny levels would represent viable explanations for the observed decline in population genetic structure, although these would not represent mutually exclusive or exhaustive explanations for the observed trend.

Female population density in the North Block has increased threefold since the population's release from culling in the early 1970s. We have shown this to be concurrent with an increase in the number of females breeding in a given year (Fig. 6A). Although this increase took place mainly in the early part of our study period, the observed decline in F_{ST} and increase in F_{IS} values observed among females could be a direct result of these recent increases in effective female population size (Chesser 1991; Ballou 2004). Furthermore, as female numbers have risen, the population's female : male ratio has increased as the male bias in juvenile mortality and immigration have become more pronounced (Albon *et al.* 2000; Catchpole *et al.* 2004). As a consequence, competition for mates between males has decreased (Clutton-Brock *et al.* 1997). Our results showing a decrease in variance in male ABS, explained by an increase in the number of males obtaining at least one mating rather than an increase in maximal ABS, replicate the results for the period 1972–1990 of Clutton-Brock *et al.* (1997). The outcome of these changes has been a decline in polygyny (Fig. 8). Theoretical studies predict that reduced polygyny combined with increased numbers of reproducing females would substantially reduce co-ancestry within populations (Chesser 1991; Perrin & Mazalov 1999).

Increased dispersal of either sex from their natal population subdivision in response to rising resource competition would cause a decline in genetic structure (Slatkin 1987). While there is evidence of an overall density-driven increase in spacing between maternal relatives amongst females and in emigration amongst males in the population (Albon *et al.* 1992; Catchpole *et al.* 2004), our results do not support the hypothesis that an increase in dispersal between subdivisions is responsible for the observed breakdown in female genetic structure. Figure 7 shows little evidence of increases in dispersal in either male or female red deer within the North Block. Although dispersal patterns may not explain the decline in female global F_{ST} , the observation of relatively high levels of female NKG–SKG dispersal, compared to other possible directions, could explain the low and temporally stable pairwise F_{ST} estimates between NKG and SKG among females. This finding ties well with previous research suggesting a southward expansion of Kilmory Glen females as population density has increased to carrying capacity (Coulson *et al.* 2004). Such movement would make recent co-ancestry between females in the two subdivisions likely. Previous studies treating these two areas of the North Block as one subpopulation appear justified (Milner-Gulland *et al.* 2000).

Conclusions

Nonrandom spatial distribution of genotypes at small spatial scales can confound studies of allelic association and quantitative genetics, and may have important

evolutionary consequences such as the facilitation of kin selection and localized selection (Coltman *et al.* 2003). We found evidence of extremely fine-scale spatial structure amongst female red deer but not males, as would be expected for a typical mammalian system showing male-biased dispersal and female philopatry. Spatial structuring of genotypes amongst females declined over the course of our study period. This rapid decline in structure could be explained by both changes in female population density or levels of polygyny that are the result of the population's release from culling, but do not appear to be related to density-dependent changes in dispersal. Furthermore, we cannot be certain that the observed trends are not long-term consequences of events that took place prior to the start of our study. The analysis presented here is, to our knowledge, the first direct demonstration of a breakdown in the fine-scale genetic structure in a wild mammal population over time. The results represent an important step towards developing our understanding of the dynamic nature of population genetic structure and illustrate clearly that temporal stability in population genetic parameters cannot simply be assumed. Further research is now required to refine and expand our understanding of the interaction between the spatial distribution of genotypes, behaviour and the environment in free-living populations.

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