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Widespread gene flow and high genetic variability in populations of water voles *Arvicola terrestris* in patchy habitats

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Abstract

Theory predicts that the impact of gene flow on the genetic structure of populations in patchy habitats depends on its scale and the demographic attributes of demes (e.g. local colony sizes and timing of reproduction), but empirical evidence is scarce. We inferred the impact of gene flow on genetic structure among populations of water voles *Arvicola terrestris* that differed in average colony sizes, population turnover and degree of patchiness. Colonies typically consisted of few reproducing adults and several juveniles. Twelve polymorphic microsatellite DNA loci were examined. Levels of individual genetic variability in all areas were high (H_O = 0.69–0.78). Assignments of juveniles to parents revealed frequent dispersal over long distances. The populations showed negative F_{IS} values among juveniles, F_{IS} values around zero among adults, high F_{ST} values among colonies for juveniles, and moderate, often insignificant, F_{ST} values for parents. We inferred that excess heterozygosity within colonies reflected the few individuals dispersing from a large area to form discrete breeding colonies. Thus pre-breeding dispersal followed by rapid reproduction results in a seasonal increase in differentiation due to local family groups. Genetic variation was as high in low-density populations in patchy habitats as in populations in continuous habitats used for comparison. In contrast to most theoretical predictions, we found that populations living in patchy habitats can maintain high levels of genetic variability when only a few adults contribute to breeding in each colony, when the variance of reproductive success among colonies is likely to be low, and when dispersal between colonies exceeds nearest-neighbour distances.

Keywords: *Arvicola terrestris*, dispersal, microsatellite, patchy habitat, population dynamics, population genetic structure

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Introduction

The balance between habitat patchiness and dispersal ability of a species is considered to have important ecological and evolutionary consequences (Hanski & Gilpin 1997; Young & Clarke 2000). These processes define the degree of population genetic structure and the levels of local genetic diversity, which in turn influence how individuals might be affected by the negative effects of local inbreeding (Lande 1988; Nunney & Campbell 1993) and how populations and species can adapt to environmental change (Lacy 1997).

The relative effects of dispersal and population subdivision on the distribution of genetic diversity are likely to be complex. In classical population genetic models that ignore demography, a few migrants each generation will maintain levels of genetic variability (Wright 1943), and the level of genetic variation maintained in subdivided populations is higher than in a single, panmictic population of similar size (Li 1955; Nagylaki 1985). In contrast, models that incorporate a finite number of subpopulations (Takahata 1983), extinction-recolonization (Maruyama & Kimura 1980) or fluctuating subpopulation size (Vucetich & Waite 2000) predict a higher loss of genetic variability from

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subdivided populations. Even more sophisticated models that incorporate ecologically realistic modes of dispersal and population demography (e.g. allowing variation in fitness, migration, and turnover rates among demes and generations) suggest that population genetic structure will depend heavily on the degree to which dispersers share a common origin (Whitlock & McCauley 1990; Pannell & Charlesworth 1999) as well as on rates of extinction, recolonization and growth of subpopulations (Whitlock & Barton 1997). The effective population size will be heavily dependent on variance in reproductive success of individuals and subpopulations (Nunney 1999). The classic island model can be seen as an unrealistic case where the variance in reproductive success among demes is low because demes have exactly the same size. It therefore seems that in most cases, subdivision of natural populations is likely to induce some loss of genetic variability, and that the magnitude of the negative effect will be heavily dependent on how the subdivision impacts on local demography and thereby variance in reproductive success. However, Ray (2001) showed that if large population units are prone to extinction, even at low rates, then a structured population with many small colonies experiencing high local turnover rates may retain genetic variability at a higher rate than less subdivided populations. The predictions from such models are consistent with the similar genetic variability in populations of American pika in patchy habitat and continuous habitat (Peacock & Ray 2001). Moreover, the variance in effective population size around the expected outcome for a given degree of subdivision scenario is much larger than the difference in the average expectation from the different models. This highlights the importance of replication before conclusions about the effects of habitat fragmentation or natural patchiness on genetic variability can be drawn form empirical studies.

Although the predictions of models incorporating demography are becoming more specific, there is a lack of empirical testing with data from real patchy populations. The majority of studies examining the genetic structure of subdivided populations involve instances of recent, anthropogenic fragmentation (Hale *et al*. 2001; Keller & Largiadèr 2002). Empirical studies from ecologically well-characterized naturally patchy populations are therefore needed to derive general rules about the contribution of demography to the pattern of genetic variation in subdivided populations.

An ideal animal system in which to study the genetic structure of populations in natural patchy habitats is the water vole *Arvicola terrestris*. The water vole is a large (200–300 g), amphibious rodent that in mainland Britain exclusively occupies riparian habitat. Populations typically consist of small, discrete colonies comprising a few individuals and having a finite lifespan. Groups of colonies persist through dispersal and recolonization (Lawton & Woodroffe 1991; Aars *et al*. 2001; Telfer *et al*. 2001; Lambin *et al*. 2004) and therefore resemble a classic Levin's type metapopulation.

In the present study, we analyse the genetic structure of several water vole populations in patchy habitats that differ in the average number of breeders in each colony, the frequency of population turnover and the degree of separation between patches of suitable habitat. Genetic variability in populations in patchy habitats is compared to that of three populations in continuous habitats. We tested two contrasting hypotheses about the maintenance of genetic variability in naturally fragmented populations. According to the first hypothesis, patchy habitats reduce levels of genetic variability because dispersal is insufficient to counteract genetic drift caused by high local extinction rates and high variance in reproductive success. Conversely, the alternative second hypothesis purports that subdivision has no effect on the levels of genetic variability because dispersal is sufficient to counteract genetic drift and the variance in reproductive success among colonies is low in spite of the predicted impact of high local extinction rates. We examined genetic structure from both population-level parameters, such as classical *F*-statistics, and at an individual level, using parentage genetic assignment of individual juveniles to adults within populations to infer dispersal distances. As such, we can examine the extent to which increased patchiness of habitat and population subdivision are synonymous, and also gain insight into how mating systems relate to degrees of patchiness and may influence genetic patterns.

Materials and methods

Study areas and sampling

Populations of water voles in patchy habitats in two upland areas (Assynt, 58°8′N, 5°1′W and Grampian, 56°56′N, 3°27′W — low density) and one lowland area (Ythan, 57°23′N, 2°17′W — intermediate density) of northern Scotland were studied (see Fig. 1, Table 1). Data on population distribution and genetics are available for between 3 and 5 years depending on area (Table 1). In the Assynt and Grampians areas (hereafter referred to as upland when both areas are described, or as Assynt upland and Grampians upland when considered alone), water vole habitat consists of patches of grass or sedge species growing along slow-flowing stretches of waterways. Such patches are separated by unsuitable stretches of fast-flowing water and stony or heather-covered banks. Even in years when suitable patches were not occupied, the presence and size of these patches could be recognized not only by vegetation and topography, but also by the presence of old burrows that decay very slowly in the upland (Aars *et al*. 2001). Habitat patches were usually 30–400 m long and the

Fig. 1 Locations of the study populations in northern Scotland. All colonies were trapped within the squares marked on the left map, indicating different populations. Ythan corresponds to the intermediately fragmented lowland population, while the Grampian and Assynt populations correspond to the highly fragmented upland populations.

Table 1 Details of the study populations

Fragmentation	Area	*n*Years	*N*	*C*	n_A (SD)	A_R	H_O (SD)	Km²
Intermediate	Lowland	4	931	4–18	8.4 (2.9)	6.6	0.69 (0.07)	30
High	Grampian A	4	182	11–25	8.8 (2.2)	7.3	0.74 (0.07)	50
High	Grampian B	3	283	11–17	11.6 (4.9)	9.0	0.78 (0.06)	30
High	Assynt A, B, C	5	499	28–65	10.1 (3.3)	8.4	0.75 (0.06)	100
Continuous populations								
Riparian	England	1	45	1	6.0 (1.7)	5.6	0.74 (0.11)	1
Riparian	Alajoki, Finland	1	167	1	9.9 (4.7)	7.9	0.76 (0.07)	8
Fossorial	Alkkia, Finland	1	188	1	9.3 (4.2)	8.8	0.77 (0.12)	1

n Years, number of years (and samples); *N*, number of individuals; *C*, number of colonies; n_A, average number of alleles per locus; H_O, average observed heterozygosity per locus; km², area of populations trapped (in the case of Assynt, the area trapped is considerably smaller than the population range as the blocks are spread, see Fig. 1).

median number of adults was 1 ($n = 76$; range 1–5) (Lambin *et al*. 2004). The median nearest-neighbour distance between occupied patches varied between survey blocks and between years, ranging from 0.46 to 2.33 km (Lambin *et al*. 2004). Colony extinction rates were very high. Only 37% of habitat patches were occupied on average over survey years (219 out of 591), and 60% of the colonies went extinct from one year to the next. The extreme extinction rates were due to the very low colony sizes, and negative density dependence in colony growth rate preventing even the larger patches to host stable colonies over long periods (Poisson regression with colony size in year $t - 1$ as offset term, Log(colony size) – Log(last year colony size) = -0.0369 ± 0.2349SE $- 0.1129 \pm 0.0425$SE (last year colony size) ($\chi^2 = 7.0588$, d.f. = 1, $P = 0.0079$). In the lowland Ythan (hereafter referred to as lowland) area, water voles were found in narrow waterways with a bed substrate of silt and soft banks with a high total percentage cover of herbaceous vegetation, but no trees. There, occupied patches are separated by stretches of less-suitable but rarely wholly unsuitable habitat (Telfer *et al*. 2001). Habitat patches were usually 100–1000 m long and contained a median of four adults in the spring ($n = 26$; range 2–18) (Lambin *et al*. 2004). The median nearest-neighbour distance between colonies was much less variable in the lowlands, ranging from 0.62 to 0.70 km in the 4 years of survey. Colony extinction rates were much lower than in the two upland sites. Of the 22 habitat patches occupied by water voles at some point during the study, on average 77% were occupied each year, and only 17% of colonies went extinct annually. However, as in the upland, larger colonies in the lowland also suffered a larger per capita loss from a year to the next than smaller colonies (Poisson regression with colony size in year $t - 1$ as offset term, Log(colony size) – Log(last year colony size) = 0.1866 ± 0.1816SE

– 0.0297 ± 0.0139SE (last year colony size) ($\chi^2 = 4.590$, d.f. = 1, $P = 0.032$). However, the probability of a patch being occupied increased with the length of waterway occupied at that site in the year before, suggesting that larger populations were more likely to persist (Telfer *et al*. 2001).

Predation by American mink has a large influence on population persistence in the three Scottish areas, although to differing degrees. The Assynt upland populations lies to the north of the mink invasion front in Britain (Strachan *et al*. 2000) so its water vole populations are unaffected, while mink are controlled by gamekeepers in the Grampians upland area and water vole populations experience only occasional localized incursions by mink in the lower reaches of tributaries, leaving the headwaters unaffected (Aars *et al*. 2001). In the lowland area, mink are constantly present along the main river and some lower tributaries, leaving recently separated clusters of colonies in upper tributaries (Telfer *et al*. 2001).

Individuals were sampled by live trapping once between June and September (upland areas) or at monthly intervals between April and October (lowland area). Closed population models used to estimate population size provide estimates of capture rates and indicated that 73–92% of individuals within a local population were caught during a 4-day trapping session (S. Telfer, unpublished). Animals occupying the same habitat patch were categorized as members of the same colony. Animals born the previous year and animals born during the year of trapping and with visible signs of having bred were categorized as adults. Animals weighing less than 180 g and with no visible signs of reproductive maturity were categorized as juveniles. This weight criterion was chosen as animals born the consecutive year almost always were above this weight and reproducing, while animals of the year did not reach this body weight before, at earliest, late summer and only rarely reproduced before reaching this weight. A biopsy sample was taken from one ear of each animal and stored in 95% ethanol at ambient temperature. The trapping methods used and more detailed biological and demographic data on these populations are provided in Aars *et al*. (2001) for upland populations and Telfer *et al*. (2003a) for lowland populations. The difference in sample sizes between years in the lowland was mostly due to a difference in sampling effort. Sample sizes for the upland areas are more directly correlated to prevailing densities at the time of sampling. As most reproducing animals were born the year before and had high survival and high trappability (Aars *et al*. 2001; Telfer *et al*. 2003a), colony sizes based on number of adults are relatively comparable among areas.

We compared genetic structure between the fragmented upland and lowland populations in northern Scotland, with three continuous populations, one from southern England and two from western Finland (Table 1). The English population (river Itchen, Hampshire, 50°57′N, 1°20′W) occupies linear, riparian habitat and has high density and temporal stability (M. Jordan, personal communication, 1995). One Finnish population (Alajoki, South Ostrobotnia, 63°05′N, 22°55′E) occupies linear, riparian habitat (K. Norrdahl, personal communication, 1999) and the other (Alkkia, 62°11′N, 22°45′E) occupies two-dimensional, fossorial habitat (H. Henttonen, personal communication, 1999). Both Finnish populations show multi-annual fluctuations, and samples were taken during a peak phase.

Microsatellite genotyping

The genotypes of 12 microsatellite DNA loci (Stewart *et al*. 1998) were determined for all samples. For the nine loci whose alleles showed canonical differences of 4 bp (AV1, AV3, AV4, AV7, AV8, AV9, AV10, AV14 and AV15) typing was carried out as previously described (Stewart *et al*. 1999). Some alleles of the other three loci (AV11, AV12 and AV13) showed noncanonical differences of 1–3 bp. Genotyping of these loci was performed using long (40 cm) gels on an ABI automated DNA sequencer. The single peak morphology necessary for reliable scoring of 1 bp differences was ensured by PIG-tail modification (Brownstein *et al*. 1996) of the 5′ ends of the reverse primers (AV11R 5′-GTTT-CTTGAAGAGATGATGGATAGAAAGATGG-3′; AV12R 5′-GTTTCCAAGATGAGTTCCAAACAG-3′; AV13R 5′-GTTTCTTAACAATGAGAAGCCCAATGAC-3′). The 5′ ends of the forward primers for the latter three loci were labelled with fluorescent dyes (AV11 with HEX, AV12 with 6-FAM, AV13 with NED, PerkinElmer Biosystems). In one of the Finnish populations (Alkkia), AV11 showed a continuous distribution of one allele differences. We therefore chose to exclude AV11 from this population, and from all tests between populations involving Alkkia. Alleles of noncanonical differences, which in general were rare, were grouped together with the ones closest in length that matched a canonical distribution. This was carried out to reduce the risk of misinterpretations caused by, e.g. restricted gel resolution.

Statistical analyses

A two-level hierarchy of population units was defined. As most individuals stay in their natal colony (Telfer *et al*. 2003a), the lower unit was defined as the colony. The higher unit was defined as a population consisting of several colonies (Fig. 1). The whole lowland area consisting of a cluster of colonies was thus defined as one population. In the Grampians upland area, two subareas [Grampian A (50 km^2) and Grampian B (30 km^2)] were 30 km apart and separated by the recent extinction of colonies in the lower parts of the catchments, so these sections were defined as two different populations. In the upland Assynt area, we defined three populations. Assynt A encompassed a 50-km^2 area, although most of the colonies in the western part went extinct in 1999 or 2000, so the area occupied was

closer to 25–30 km² during later years. Assynt B (25 km²) and Assynt C (25 km²) were less than 10 km apart, and located 15–20 km south of Assynt A. No real barriers between these areas prevented gene flow (Fig. 1). Both upland areas, although geographically separated by up to 210 km, are ecologically similar. Where appropriate, both areas were thus pooled in comparison of upland and lowland systems. Samples from different years were analysed separately (referred to as 'annual groups' below) because water vole colonies typically undergo annual changes in genetic composition (Stewart *et al*. 1999) owing to annual bottlenecks in adult numbers (Lambin *et al*. 2004).

Levels of genetic variability were estimated as the average number of alleles, average observed heterozygosity per locus, expected heterozygosity, and allelic richness. *F*-statistics are according to Weir & Cockerham (1984). For these analyses, GDA 1.0 (Lewis & Zaykin 2000), GENEPOP (Raymond & Rousset 1995), and GENECLASS2 (Piry *et al*. 2004) were used. Confidence intervals of estimates were calculated in GDA by performing 1000 bootstraps over loci. For statistical comparisons of *F* values and diversity between samples we used FSTAT (Goudet 1995), which performs permutation tests with population (or colonies) as units. Hardy–Weinberg tests were performed in GENEPOP, and FSTAT was used to test for linkage between loci genotypes (with sequential Bonferroni correction).

Assignment of juveniles to parents was performed using CERVUS 2.0 (Marshall *et al*. 1998) for all genotyped individuals in the upland area. Young adults (less than 180 g, but with signs of having reproduced, and born in the study year) were also tested for assignment to older adults born the previous year. Similar analyses have been described previously for the lowland population (Telfer *et al*. 2003a). Due to the less frequent trapping in the uplands, we used more conservative assignment criteria than we had previously used for the lowland analyses. As there was an approximate 12-month delay between capture sessions within each population in the uplands, inferences about exact family relationships based on assignment between individuals caught in different years was difficult. Consequently, assignments were only conducted on individuals caught in the same year, with individuals classified as adults making up the candidate parent sets. In addition, we only assigned parentage if confidence in the assignment exceeded a threshold of 95% (as calculated by CERVUS) and allelic mismatches within parent–offspring dyads were not permitted. In cases where known parents and juveniles (unweaned juveniles trapped with mother) were compared, no mismatches were found, confirming minimal levels of mutation that could bias the strict approach we followed. To enable comparison of results between the lowland and upland systems, all the lowland results presented here conform to the same conservative criteria (assignment confidence levels 1 and 2 in Telfer *et al*. 2003b). From the assignment analyses we inferred dispersal distances by assuming that a parent (or both parents) stays and thus that the geographic distance between parents and offspring correspond to the distance the offspring have dispersed. This assumption holds well for lowland population as adults rarely move (Telfer *et al*. 2003a), but is slightly less robust for the upland populations as parents have been observed moving between patches (Lambin *et al*. 2004). When adults were observed moving by capture–recapture, or when one adult and one or more offspring stayed in one patch and the other adult was found in a different patch, the juvenile was assumed philopatric and the adult as a disperser.

Results from the parentage assignment were also used to assess individual reproductive success and mating patterns. In the lowlands, only individuals from populations trapped monthly were included (Telfer 2003a) in order to remove any variation due to differences in trapping effort. A litter was defined as a group of juveniles assigned to the same mother and with similar body masses indicating they were born on the same date. Typically the weight range within a litter was less than 15 g while the difference in average between two successive litters (20 days or more in age difference) was at least 30 g.

In addition to the *F*-statistics, genetic structure was studied by means of comparisons of geographic and genetic distance between pairs of individuals. This was carried out using Mantel correlograms in the program GENALEX (Peakall & Smouse 2001). We used the option allowing pairs to be compared within populations, but where the different relations from different populations and annual samples can be pooled into one correlogram. The approach assumes similar trends in the different populations. The shape of the correlogram should reflect distance and rate of dispersal. The correlogram should flatten out at the scale where dispersal is not connecting subpopulations by gene flow (isolation by distance), and steep negative slopes between distance classes would probably reflect common dispersal ranges out to these distances on a short timescale.

Results

Levels of genetic variability

All 12 microsatellites were highly polymorphic in the study populations. Levels of variability in the populations in northern Scotland were generally higher in the patchier upland habitat than in the less patchy lowland habitat (Table 1). Permutation tests (Goudet 1995) showed significant higher allelic richness ($P = 0.019$) and higher observed heterozygosity (H_O) ($P = 0.021$) in the upland populations than in the lowland population. Levels of allelic richness among the upland populations were comparable to levels in the continuous populations in southern England and Finland, with similar and overlapping values (permutation

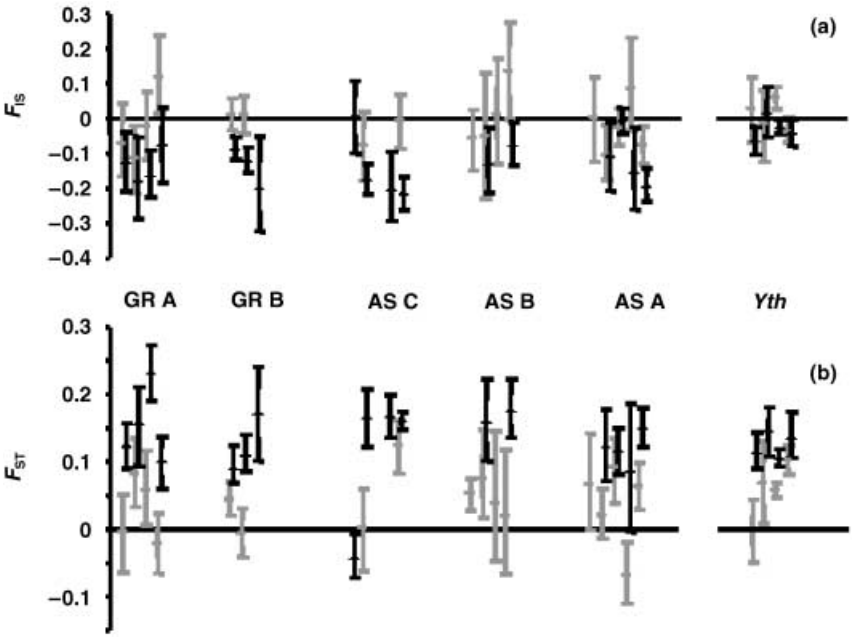


Fig. 2 *F*-statistics given as averages and 95% confidence intervals. The first five groups of estimates are for the upland populations: Grampian A 1999–2002, Grampian B 1998–2000, Assynt C 1998–2002, Assynt B 1998–2002, and Assynt A 1998–2002. The next four estimates are for the lowland (Ythan) 1995–1998. Values and bars in grey are for parents, and in black for juveniles. Within years and populations, the values overlap on the *x*-axis. In some cases, sample sizes were not sufficient for analyses of both adults and juveniles, in which case only one estimate is presented.

test, A_R = 7.4 for upland populations and 7.1 for continuous populations, P = 0.811). This result was also consistent with levels of observed heterozygosity (permutation test, H_O upland metapopulations = 0.749, continuous populations H_O = 0.762, P = 0.862). At the population level and within years, expected heterozygosity (H_E) values were considerably higher than H_O for the patchy lowland population (range H_E: 0.733–0.748, range H_O: 0.654–0.716, n = 4), but similar among 22 upland annual population samples (average H_O = 0.752, average H_E = 0.759, $F_{IT} > 0$ in 11 samples and < 0 in 11 samples). Compared to H_O (Table 1), levels of H_E among the continuous populations were higher for Alajoki (H_E = 0.788) and Alkkia (H_E = 0.796), but lower in the English population (H_E = 0.724). Hardy–Weinberg disequilibrium was found in all four lowland samples, in 15 out of the 22 upland samples, and in all the three continuous populations. Linkage disequilibrium was common over all types of populations. The number of comparisons between pairs of loci were 66, except for the Alkkia populations where it was 55 (11 loci only). The average numbers of loci pairs showing linkage disequilibrium (LD) were: for the lowland population 41 (range 11–65) and for the upland populations 7.9 (range 0–49). Numbers of LD pairs in continuous habitats were 1, 4, and 12 for England, Alajoki, and Alkkia, respectively. Further details on H_E, Hardy–Weinberg equilibrium, and linkage disequilibrium are provided in Table S1, Supplementary material.

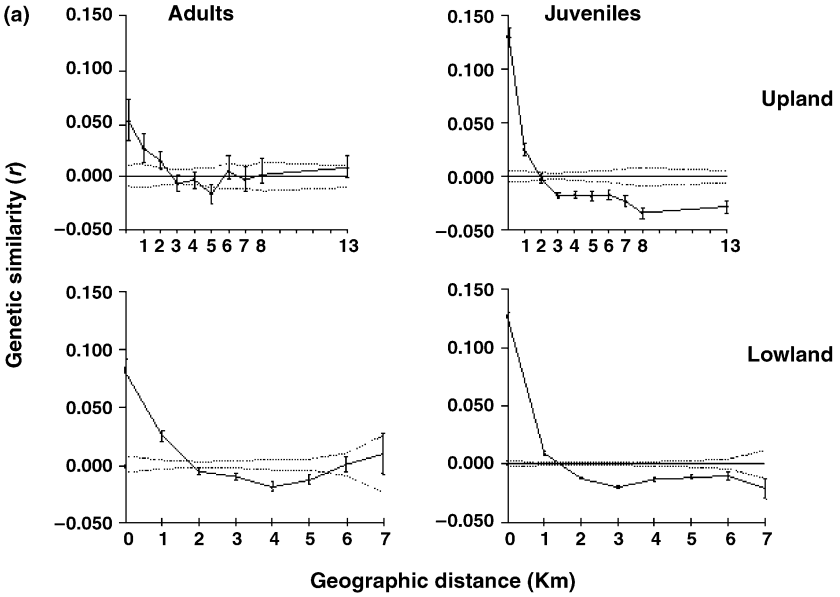
Population genetic structure

We characterized the genetic structure of the study populations using *F*-statistics calculated according to Weir & Cockerham (1984). As most dispersers are older juveniles (Telfer *et al*. 2003a), we analysed adults and juveniles separately. Mean F_{IS} values for juveniles were significantly negative in 14 out of 17 upland annual groups and in 3 out of the 4 lowland annual groups. For adults, mean values were almost invariably higher, and with no consistent trend (Fig. 2a). Over all colonies, the mean F_{IS} was –0.151 for the upland areas and –0.075 for the lowland area. In adults, the colony mean F_{IS} values were –0.027 for the upland and –0.003 for the lowland. We found a significant, positive relationship between the F_{IS} value of the juveniles, and the number of adults in a colony. The best linear model was F_{IS} = –0.1676 ± 0.0184 (SE) + 0.1176 ± 0.0419 (SE) * log(number of adults trapped), with a significant slope ($F_{1,158}$ = 7.87, P = 0.0057), but with considerable variation around the line (multiple R-square = 0.047). The logarithm of the number of adults gave a slightly better fit than the untransformed values. Addition of population type (upland or lowland), or population identity, did not improve the fit of the model.

Mean F_{ST} values for juveniles were uniformly higher than F_{ST} values for adults, in most cases with nonoverlapping confidence intervals (Fig. 2b). The F_{ST} values for adults were significantly higher than zero in only 9 annual groups out of 17 from the upland populations and in 3 out of the 4 annual lowland population groups. No significant differences were found between the different upland populations and the lowland annual groups ($P > 0.05$).

Genetic spatial autocorrelation of individuals

The Mantel autocorrelation diagrams (Fig. 3) show that within local areas, genetic similarities between individuals



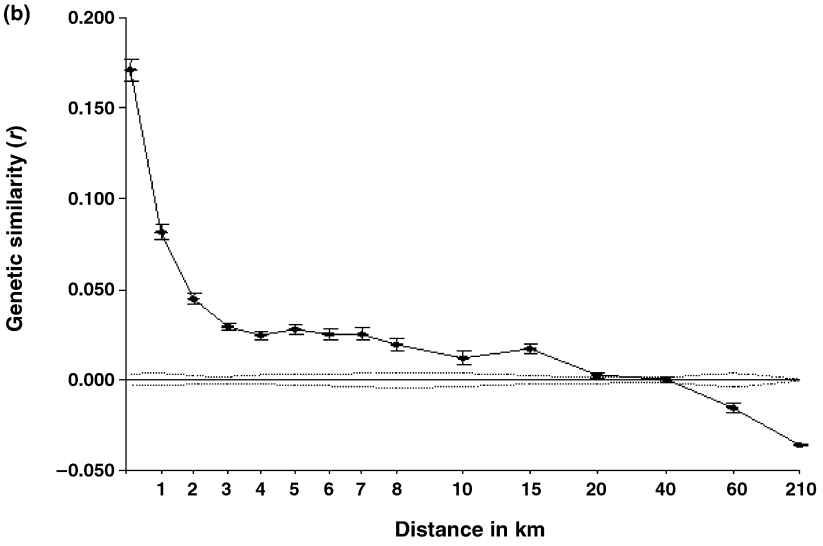


Fig. 3 (a) Mantel autocorrelation diagrams for juveniles and adults in the upland and lowland metapopulation. Data from all the areas and all the years are used, but the comparisons between individuals are from within populations and years. Zero km represents within-colony pairwise comparisons, and other estimates the comparisons between individuals in colonies separated by a distance from the previous up to the one given on the *x*-axis. Envelopes show the estimated 95% CI under the prediction of no structure. Error bars are 95% confidence limits around each estimate. (b) Correlogram for both the local scale within population, and on a large scale including comparison of individuals from different populations. Only the upland systems are included, and both juveniles and adults are included in the figure.

drop from within patches (zero km) and up to 3 km, and then flatten out. This pattern is consistent among lowland and upland fragmented populations. Juveniles show a similar pattern to adults, except for a higher similarity within patches and consequently a steeper drop in similarity out to 3 km (Fig. 3a). On a larger spatial scale among the upland systems (Fig. 3b), similarity dropped further on the scale of tens of kilometres. There is thus no isolation by distance at this scale.

Genetic drift of metapopulations

We calculated temporal F_{ST} values between samples from different years within the upland and lowland metapopulations. The F_{ST} values both for lowland and upland populations increased over time over the span of a few years (Fig. 4). The difference between lowland and upland populations was tested across a 3-year temporal span, as this was the maximum sampled for the lowland. After adjusting for the effect of timespan on F_{ST} ($F_{1,42} = 4.148$, $P = 0.048$), there was an additive effect of system, due to the higher F_{ST} values within upland metapopulations ($F_{1,42} = 4.490$, $P = 0.040$). There was no significant interaction between time span and system to indicate different slopes ($F_{1,41} = 0.207$, $P = 0.652$). The relations between time span in years and F_{ST} values were $F_{ST} = 0.004 \pm 0.005$ (SE) + 0.004 ± 0.003 (SE) ∗ time span for the lowland and $F_{ST} = 0.015 \pm$ 0.008 (SE) + 0.011 ± 0.004 (SE) ∗ time span for the upland (including all years). The three subareas in the Assynt region encompass an area small enough to expect transfer

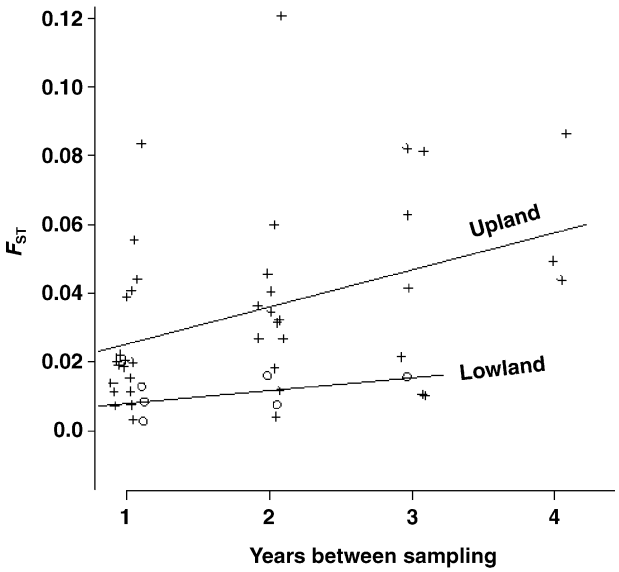


Fig. 4 Temporal F_{ST} values within metapopulations from the upland (crosses) and the lowland (open circles). The lines show the predicted slopes for the different systems predicted by the model.

of genes within this spatial scale over the 5 years of sampling, equivalent to a few generations. A separate test comparing spatial and temporal F_{ST} values within and between the subareas revealed that F_{ST} increased both with time ($F_{1,101} = 6.453$, $P = 0.013$) and geographic distance ($F_{1,101} = 69.773$, $P < 0.001$). We found no interaction between time and distance ($F_{1,101} = 0.869$, $P = 0.354$, illustration in Fig. S1, Supplementary material).

Assignment of individuals, and inferences of dispersal and reproduction

The rates of juveniles successfully assigned to at least one parent were high in upland populations (55%, $n = 629$) as well as in the lowlands (41%, $n = 675$). Among the juveniles successfully assigned, the proportions that had dispersed were: 22% of upland females ($n = 145$); 16% of upland males ($n = 192$); 11% of lowland females ($n = 123$); and 11% of lowland males ($n = 151$). Testing the differences in frequencies, dispersal rate was significantly higher in the upland than in the lowland for females ($\chi^2 = 4.62$, d.f. = 1, $P = 0.0316$), but not significant for males ($\chi^2 = 1.30$, d.f. = 1, $P = 0.2549$). As in the lowlands (Telfer *et al*. 2003a), there was a strong relationship between dispersal rates and size, a proxy for age, of the juveniles in the upland populations. Few juveniles less than 100 g had dispersed (females: 10%, $n = 84$ and males: 6%, $n = 113$). Among animals larger than 100 g, 44% of females ($n = 52$) and 33% of males ($n = 72$) had dispersed. Among the animals that had dispersed, the average distances of dispersal were: 2.18 ± 0.27 SE km for upland females; 1.65 ± 0.27 SE km for upland males; 1.04 ± 0.19 SE km for lowland females; and 1.50 ± 0.25 SE km for lowland males. These differences were significant between the upland and lowland systems for females ($F_{1,44} = 5.28$, $P = 0.0264$), and not for males ($F_{1,46} = 0.19$, $P = 0.6658$)

Among the adults that had juveniles assigned to them, males on average produced more offspring than females. The number of assigned juveniles per adult (hereafter termed RS) and the variance of these estimates were: upland females: 2.39 (var = 2.59, $n = 136$); upland males: 3.46 (var = 12.50, $n = 107$); lowland females: 2.45 (var = 4.83, $n = 73$); lowland males: 3.46 (var = 4.83, $n = 61$). The variance in RS was significantly higher for male adults compared to female adults in both upland populations ($F_{102,64} = 4.83$, $P << 0.0001$) and the lowland population ($F_{43,44} = 2.23$, $P = 0.0046$). Mating patterns tended to be more monogamous in the more fragmented upland populations compared to the moderately fragmented lowland population. Using only litters for which both parents were known, 13 out of 14 mothers with at least two successive litters had all juveniles sired by one father only in the upland. In contrast, 8 out of 9 mothers with two or more litters in the lowland had mated with two different fathers (test of difference in frequencies, $\chi^2 = 12.129$, d.f. = 1, $P = 0.0005$). Although the tendency was the same among male adults, it was less marked and nonsignificantly different between the systems, with 9 out of 15 males with more than one litter mating with only one female in the uplands, compared to 3 out of 9 in the lowlands ($\chi^2 = 0.711$, d.f. = 1, $P = 0.3991$). In no cases were multiple paternities observed within litters with more than one juvenile ($n = 24$ in the lowland and $n = 30$ in the upland).

Discussion

The primary goal of this study was to examine patterns of genetic diversity and structure across a group of water vole metapopulations that differed in their degree of habitat patchiness and turnover. In particular, we asked whether high habitat patchiness, low local densities, and high local rates of turnover would produce significant loss of population genetic variability.

Contrary to most theoretical predictions for subdivided populations, we found no support for the prediction of low levels of neutral genetic variability in extinction-prone populations inhabiting highly subdivided habitat. We found similar levels of genetic variability in the highly subdivided upland metapopulations as among continuous populations. There is no obvious explanation for lower allele richness and observed heterozygosity in the lowland population occupying moderately fragmented habitat than in the upland populations occupying highly dispersed and small habitat patches. This may reflect the impact of unknown historical events, or present local ecological conditions such as more restricted dispersal or

higher variance in female lifetime reproductive success in the lowland, in accordance with Ray (2001) (see below). However, it is difficult to generalize as we only have examined one population with this intermediate level of patchiness. The presence of American mink in the area and the associated loss of adjoining colonies over the last 10–20 years is another possible contributor, although it is unclear whether such a recent event could account for such a considerable loss of genetic diversity in a population of such size. In the annual population samples, H_E was consistently larger than H_O in the lowland, but not in the upland. Most populations were in Hardy–Weinberg disequilibrium, and typically also showed linkage disequilibrium. It is not surprising that these populations are not in Hardy–Weinberg equilibrium, as they consist of colonies with family groups as long as young juveniles are present. Linkage disequilibrium has earlier been shown to be common among water vole populations featured by local structure and strong genetic drift (Stewart *et al*. 1998).

Although the theoretical literature has dealt with the connection between population subdivision and effective population sizes for decades (e.g. Wang & Caballero 1999), empirical work to test the different predictions for animal populations has been rare. An exception is Peacock & Ray's study (2001) of American pika where fragmented and continuous populations had similar variability. Interestingly, the biology of pika populations in patchy habitat is similar to that of the water vole, with small colonies often built up around a pair of reproducing adults. Ray (2001) argues that low variance in reproductive success due to the small colonies is likely to have contributed to the high effective population size in the pika populations. Likewise, this could be the case for the water vole populations. Small and dispersed habitat patches make it hard for males to defend a territory with many females. Monogamy may thus become more common as the degree of fragmentation increases relative to a male home range size. Most patches are too small for successful mothers to help daughters to establish territories in the same area. Other studies of small rodents have indicated that mothers might increase the success of daughters that are allowed to stay (Lambin & Yoccoz 1998; Ims & Andreassen 1999), a strategy that will increase variance in female reproductive success. The larger colonies in the upland had almost the same extinction probability as the smaller ones from one year to the next due to the negative relation between colony size and colony growth (see Materials and methods). This could be due to either negative density-dependent survival, negative density-dependent immigration or both. Negative density-dependent immigration is a common trait observed in several mammalian species (Wolff 1997; Aars & Ims 2000; Ims & Andreassen 2000; Gundersen *et al*. 2001; Lambin *et al*. 2001), including the pikas in patchy habitat described above (Smith & Ivins 1984).

Metapopulations consisting of many very small colonies will experience high turnover rates owing to the impact of demographic stochasticity. Local extinction and colonization per se are expected to lower the effective population size (Hedrich & Gilpin 1997), primarily because they tend to increase the variance in reproductive success owing to more successful colonies exporting more colonists to empty patches than less successful ones. If, on the other hand, new colonies are made up of founders from many small colonies from a larger area rather than from a few larger colonies close by, as would be the case in a source-sink system, then the loss of variability expected could be low relative to that expected in a large continuous panmictic population of the same total size (Pannell & Charlesworth 1999). Such a process would be most effective when extinction is probable for colonies of all sizes, and thus might contribute to lower variance in reproductive success. Given the size of *Arvicola terrestris*, dispersal distances based on assignment data were long for both females and males with an average of about 2 km in the upland, despite no adjustment being carried out to correct for the fact that animals with the longest dispersal ranges had larger likelihood of being outside the study area, or to have dispersed into it from outside, and thus not being detected (see Koenig *et al*. 1996). Furthermore, spatial autocorrelation diagrams suggested widespread dispersal. The correlograms indicate frequent dispersal up to a few kilometres. Considering the lower estimated dispersal distances for females in lowlands (only 1 km) relative to the uplands (more than 2 km) and the similar dispersal distances for males, it is somewhat surprising that this difference was not reflected in the shape of the correlogram for population types. One should expect a drop in similarity out to a further distance in the upland based on the difference in dispersal ranges between the two systems indicated by individual assignment. The similarity highlights the fact that it is hard to translate spatial autocorrelation diagrams directly into dispersal patterns. Although dispersal necessarily influences the shape of the correlograms, we have not been able to find any reliable descriptions of how they can be directly translated into quantitative values of ranges and frequencies of dispersal.

Average distance between habitat patches is about 0.5 km in most upland areas (Aars *et al*. 2001). Thus animals frequently dispersed beyond the range of the closest neighbour patch. Low F_{ST} values among adults reflect a high rate and long range of pre-reproduction dispersal. Colony F_{IS} values are expected to be negative in small outbred colonies because of random differences in female and male adult allele frequencies (Rasmussen 1979; Pudovkin *et al*. 1996; Luikart & Cornuet 1999). Negative inbreeding coefficients have been reported on a small geographic scale within colonies or breeding groups of mammals in other studies (Selander 1970; Sugg *et al*. 1996; Dobson *et al*. 1997;

Goossens *et al*. 2001), but positive values or values close to zero are more common (Sugg *et al*. 1996). The values encountered here indicate that the dispersal mode in water voles in patchy habitats could be especially efficient at counteracting local inbreeding. If dispersal is highly sex biased, a further lowering of F_{IS} values is expected, as females and males from different areas tend to mate more often than when both sex disperse (Prout 1981). Dispersal in mammals including small rodents is commonly male biased, often strongly so (Greenwood 1980; Stenseth & Lidicker 1992). In several studies, sex-biased dispersal was proposed as the main reason for observed heterozygosity excess (Schwartz & Armitage 1980; Piertney *et al*. 1998; Aars & Ims 1999, 2000). Water vole dispersal in patchy habitat appears to show either no sex bias or only a slight male bias at moderate densities in the lowland areas (Telfer *et al*. 2003a), and even a slight female bias both in range and rate in the low-density upland metapopulations. Male bias in dispersal is thus unlikely to contribute to excess colony heterozygosity in water vole metapopulations. We do not have data confirming whether dispersal is male biased in more continuous populations, but it is probable that female dispersal is an adaptation to patchy habitat. Females are likely to improve their success by sampling the area for suitable habitat in a system where turnover rates in local patches are high. Indeed, the difference shown in this study between female dispersal rates in the moderately fragmented, low turnover lowlands and the highly fragmented, high turnover uplands supports this argument.

The ecological structure with dispersed small local colonies and large-scale movement suggest that water voles in areas of patchy habitat function more like larger mammals such as muskrats or beavers than like small rodents that tend to show small-scale philopatry. Here water voles thus show a difference to the pika populations described above. Pikas show a high degree of philopatry and dispersers tend to settle in patches close to where they were born (Smith & Ivins 1984). Whereas small rodents are typically present in hundreds or up to many thousands per km^2, water vole in the upland occur at densities usually less than five per km^2 (Aars *et al*. 2001). This sparseness contrasts with the very high densities fossorial water voles can reach (several hundred or thousand per km^2 in peak years) in the Alps (Saucy 1994), in Siberia (Evsikov *et al*. 1999) and on small British islands (Telfer *et al*. 2003b). Water voles thus show high plasticity to different habitat types and ecological conditions (Lambin *et al*. 2004).

Genetic drift is a powerful force that induces rapid loss of genetic variability in small populations. However, low density does not always imply small populations. In the upland of Scotland, most populations seem to be connected, as water voles are capable to disperse several kilometres between different waterways and even watersheds. The lack of a clear isolation-by-distance pattern in the large-scale spatial autocorrelation diagram suggests a large-scale network of connected areas. Although temporal F_{ST} values were considerable and increased over time within survey blocks, local drift on this scale apparently had not induced significant loss of variability. Interestingly, within the Assynt upland area, F_{ST} values within and between the three populations and five years sampled did not show any sign of temporal and spatial interaction. Had dispersal been restricted on this scale (up to 20 km) on this time frame (5 years), we should expect increased divergence due to independent drift. Migration thus seems to ensure efficient connection that should hinder long-term loss of variability due to inbreeding and drift, i.e. there should be larger and larger differences in F_{ST} between population pairs sampled with the same time difference (0, 1, 2, 3 or 4 years apart) as geographic distance increases. The absence of such statistical interaction thus imply that geographic areas at least as large as our sampling area should be the real genetic management units. It also suggests that metapopulation N_e may be large despite low densities, a conclusion also in accordance with the lack of any isolation by distance. Although studies of areas of smaller or similar size rarely indicated dispersal distances of similar scales to what we found here, there are exceptions (common shrew *Sorex araneus*: Wyttenbach *et al*. 1999; lemmings *Dicrostonyx groenlandicus*: Ehrich *et al*. 2001). Indeed, dispersal is likely to be strongly underestimated in many studies due to a limited spatial survey scale, especially where classical methods like capture–recapture are employed (Koenig *et al.* 1996). It is thus not unlikely that many species have the ability to counter the negative effects of patchiness in the habitat by a high and flexible dispersal ability.

In conclusion, this study suggests that populations in very patchy habitat can retain high levels of variability even compared to continuous populations of much higher densities. In the case of water voles, this is likely to be caused (i) by highly efficient frequent and long-distance dispersal over geographic ranges that ensure mixing of genes from larger areas and (ii) by low variance in reproductive success among females, due to small colonies with density dependent regulation, and maybe increasing tendencies for more monogamous mating systems, decreasing the variance of male reproductive success, as distances between occupied habitat patches increase. Organisms with similar ecological traits could therefore be expected to cope well in patchy habitats. A loss of genetic variability with increasing subdivision is still expected in species that have restricted dispersal ability relative to inter patch distances, or that exist in patches of highly variable size or quality, thus increasing variance in reproductive success. More studies on a range of species with different ecological traits are needed to test the general influence of subdivision on genetic variation. Species living in a range of habitat types, like the water vole and the pika, are the natural systems

to study, but comparisons between species living in habitat with different degrees of habitat patchiness could also contribute to test theoretical predictions on how subdivision may influence genetic variation and structure.

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Supplementary material

The supplementary material is available from
http://www.blackwellpublishing.com/products/journals/suppmat/MEC/MEC2889/MEC2889sm.htm

Table S1 Genetic diversity in 29 samples from nine water vole populations. Populations correspond to those with the same name in Aars *et al.*, Table 1. *N*, number of individuals successfully typed; H_E, expected heterozygosity; H_O, observed heterozygosity; F_{IT}, population inbreeding coefficient; HW, probability of Hardy–Weinberg equilibrium departure (NS = $P > 0.05$, *$0.05 > P > 0.01$, **$0.01 > P > 0.001$, ***$0.001 > P$); LD, the number of pairs of loci out of a total of 66 (55 for Alkkia) that departs from linkage disequilibrium (after sequential Bonferroni correction).

Fig. S1 The relationship between spatial and temporal F_{ST} values within and between the three populations (Assynt A, B, and C) in the Assynt upland area. Different lines show the average F_{ST} values for population comparisons sampled 0 to 4 years apart in time, and with up to 19 km interpopulation distance.

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