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ORIGINAL ARTICLE

Low genetic differentiation in a sedentary bird: house sparrow population genetics in a contiguous landscape

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The house sparrow *Passer domesticus* has been declining in abundance in many localities, including Finland. We studied the genetic diversity and differentiation of the house sparrow populations across Finland in the 1980s, at the onset of the species' decline in abundance. We genotyped 472 adult males (the less dispersive sex) from 13 locations in Finland (covering a range of 400 × 800 km) and one in Sweden (Stockholm) for 13 polymorphic microsatellite markers. Our analysis of Finnish ringing records showed that natal dispersal distances are limited (90% <16 km), which confirmed earlier finding from other countries. The Finnish populations were panmictic, and genetically very homogeneous and the limited dispersal was sufficiently large to maintain their connectivity. However, all Finnish populations differed significantly from the Stockholm population, even though direct geographical distance to it was often smaller than among Finnish populations. Hence, the open sea between Finland and Sweden appears to form a dispersal barrier for this species, whereas dispersal is much less constrained across the Finnish mainland (which lacks geographical barriers). Our findings provide a benchmark for conservation biologists and emphasize the influence of landscape structure on gene flow. *Heredity* (2011) **106,** 183–190; doi:10.1038/hdy.2010.32; published online 7 April 2010

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Introduction

To make long-term conservation decisions, we need information on population structure and connectivity (Moritz, 1994). Dispersal ability, geographic variation, level of genetic differentiation and adaptation to local conditions are key aspects of a species' ecology (Frankham *et al*., 2002; Hartl and Clark, 2007), but gathering information on these aspects through traditional methods is often laborious and costly, or simply infeasible (Lowe *et al*., 2004). In many organisms, individuals can be marked and followed to determine population structure and track the movement of individuals, but this method cannot be used for all species for practical reasons. For example, dispersal of birds can be studied by monitoring individuals marked by ringing (that is, attaching an individually numbered metal or plastic ring on the leg), but not all species are equally well represented in ringing records (Baillie, 1995). When information based on traditional ecological techniques is patchy, a genetic approach can complement the picture because the data required can be gained by sampling a small part of a population in a short time.

Due to their ability to fly, birds can move over large geographical scales and their populations are therefore often spatially more homogeneous than in some other taxonomic groups (Barrowclough, 1983; Evans, 1987; Ward *et al*., 1992). However, there are some striking exceptions from this general pattern. Senar *et al*. (2006) found two populations of the highly mobile citril finch *Serinus citrinella* to be significantly differentiated ($F_{ST} = 0.094$), even though their breeding areas were separated by only 5 km and the two populations mixed in a common overwintering area. Significant genetic differentiation ($F_{ST} = 0.043$) was found also among migratory Swainson's warbler populations *Limnothlypis swainsonii* (Winker *et al*., 2000).

The medium-sized passerine, house sparrow *Passer domesticus*, is one of the avian species most associated with humans, and familiar to many. It is a sexually dimorphic, social and very site-tenacious bird (Summers-Smith, 1988). Its natural range includes Europe, North Africa and parts of Asia such as Middle East, Indian subcontinent and a narrowing band from northern Asia toward the Pacific coast. From these areas its large-scale spread has been enabled by humans who have introduced it either intentionally or by accident to almost every corner of the world, including North and South America, South Africa, Australia and New Zealand (Summers-Smith 1963, 1988; Anderson, 2006). The house sparrow has been very abundant all over the world, but major declines in its abundance have been reported in large parts of Europe during the last few decades (Summers-Smith, 1999; Crick and Siriwardena, 2002; Hole *et al*., 2002; Anderson, 2006; de Laet and Summers-Smith, 2007). Also non-native populations have been reported to decline in, for example, North America

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(Peterjohn *et al*., 1994). Reasons for these declines are not fully understood.

Conservation efforts should take into account knowledge on genetic population structure and the amount of gene flow between them, and focus management on units that are significantly genetically differentiated (Moritz, 1994). Field observations in the United Kingdom and on island populations in northern Norway indicate that the house sparrow is a resident species with limited dispersal undertaken mainly by juveniles, and that females are also more likely to disperse from their native areas than males (Summers-Smith, 1988; Skjelseth *et al*., 2007). Using ringing recovery data in the United Kingdom, Paradis *et al*. (1998) found that a mean natal dispersal distance was less than 2 km. Furthermore, long-distance recoveries from Britain and Ireland showed that only 3% of dispersal events extend further than 20 km (Siriwardena *et al*., 2002). In Norway only 10% of female and 6% of male fledglings that were later recruited to the breeding population had left their native islands (Altwegg *et al*., 2000). Furthermore, Tufto *et al*. (2005) found that most house sparrows did not disperse from their natal farms, and of the ones that did, 90% dispersed less than 36 km. Low dispersal suggests that populations may also be spatially structured. Nevertheless, the number of migrants per generation needed to homogenize populations is relatively low (Franklin, 1980; Frankel and Soulé, 1981; Allendorf, 1983), and low dispersal indicated by the field data need not translate into genetic differentiation between populations. Significant genetic differentiation has been found in Norway on the scale of less than 100 km (F_{ST} among mainland populations 0.018, F_{ST} among island populations 0.025; Jensen *et al*., in preparation), but earlier allozyme studies have not found significant genetic differentiation (Fleischer, 1983; Parkin and Cole, 1984, 1985). Thus, it is currently not clear whether low observed dispersal in the field indeed implies that house sparrow populations are genetically differentiated on a modest spatial scale or whether high-resolution DNA microsatellite markers are better able to capture genetic differentiation across house sparrow populations than allozymes.

In this work, we carry out a DNA microsatellite analysis of the house sparrow from an extensive material covering the species' entire distribution in Finland. Our aim is to gain insight into the spatial structure and connectivity of the populations and the levels of genetic diversity within them. We used historical house sparrow material collected in the mid-1980s, when the species was highly abundant in Finland (estimated at 400 000 pairs; Väisänen *et al*., 1998) but starting to decline. We use national ringing records to show that estimated field-based dispersal is low, but our genetic data indicate that, in absence of geographical barriers, house sparrows are panmictic over several hundreds of kilometers. We discuss our findings in relation to previous studies and provide a conservation genetic outlook.

Materials and methods

Ringing records

Individually marking animals (for example, by ringing them) is a traditional ecological method for estimating dispersal rates and distances. In the house sparrows, most of the species' dispersal is conducted by juvenile birds. Ringing records from various localities have indicated that house sparrow natal dispersal is limited. We analyzed Finnish ringing records (obtained from the Ringing Bureau, Finnish Museum of Natural History, Helsinki) to summarize the available information on natal dispersal in Finnish house sparrows from 1930 to 2004. We considered data on individuals ringed as a nestling and either found dead or caught alive on or after 1 March in the year after hatching. Despite their high abundance, house sparrows are rarely ringed, probably because they nest at sites that are difficult to access and are sensitive to nest disturbance. Due to the paucity of ringing records of natal dispersal ($n = 87$), we simply pooled the entire data set and did not restrict analyses to any particular time period or sex.

In addition we looked at adult dispersal; that is, birds ringed as adults and caught the next calendar year or after that ($n = 1110$). Sex-specific dispersal was determined from individuals with known sex (males, $n = 543$; females, $n = 388$).

Sampling

Tissue samples used in this study were collected between 1983 and 1986 from 13 localities in Finland (Figure 1, Table 1). Sampled locations included both urban and rural sites. Birds were sampled with permission by catching with mist nets and killed with carbon dioxide. Skins were dried and bones were cleared from tissue and

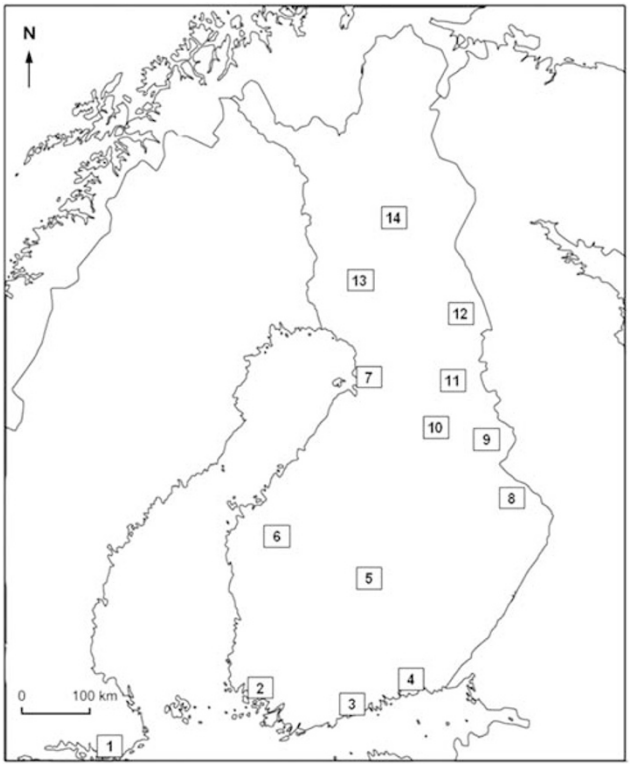

Figure 1 Map of Finland representing the sampling localities of house sparrows indicated by numbers from 1 to 14. Numbers refer to population names in Table 1. There are 13 sampling sites in Finland and 1 in Stockholm, Sweden. The edge of the map corresponds to north.

Table 1 Number of adult males sampled, by year, for the molecular analysis of this study

Population		*1983*	*1984*	*1985*	*1986*	*Total*
1	Stockholm				33	33
2	Turku	33	12			45
3	Helsinki	26	33			59
4	Myllykoski	7	22			29
5	Jyväskylä	23	12			35
6	Seinäjoki			30		30
7	Oulu			38		38
8	Lieksa		30			30
9	Kuhmo		36			36
10	Kajaani		25			25
11	Ämmänsaari		23			23
12	Kuusamo		14	7		21
13	Rovaniemi	29	19			48
14	Sodankylä			20		20

For these individuals, 11 or more loci were successfully genotyped.

preserved dry. Livers and kidneys were preserved at −18 °C. Samples were also collected in Stockholm (Sweden) for a comparison. For this study, we used only males, because these are supposedly the more sedentary sex (Summers-Smith 1988; Altwegg *et al*., 2000; Skjelseth *et al*., 2007). In addition, we selected only males that had survived their first winter (second calendar year or older, based on ossification of their skulls, Svensson, 1975) as they could be assumed to be resident individuals. Hence, the level of differentiation among the populations should be highest in this group.

Microsatellite genotyping

DNA was extracted from a small piece of liver tissue following the method described by Elphinstone *et al*. (2003), except that 70 μl of dH_2O was used to elute DNA in the last step.

The samples were amplified in PCR for 14 microsatellite loci in two parallel panels. Panel 1 included primers Pdoμ16, Pdoμ19, Pdoμ22, Pdoμ27, Pdoμ32, Pdoμ44 and Pdoμ47 (Dawson *et al*., in preparation) and panel 2 primers Ase18 (Richardson *et al*., 2000), Pdoμ1 and Pdoμ3 (Neumann and Wetton, 1996), Pdoμ10 (Griffith *et al*., 2007), Pdoμ33 and Pdoμ40 (Dawson *et al*., in preparation) and Pdoμ5 (Griffith *et al*., 1999). PCR was conducted with Multiplex PCR kit (Qiagen), where one PCR reaction contained 5 μl of Qiagen Master mix-solution (Qiagen, Hilden, Germany), 3 μl of extracted DNA and 2 μl of primer mix (containing 0.28–0.94 μM of each primer). PCRs for both panels were completed using the following touchdown protocol on a Satellite Thermal Cycler MBS 0.2G (Thermo Fisher Scientific, Waltham, MA, USA): one denaturing step of 15 min at 94 °C followed by 12 cycles of 30 s at 94 °C, 90 s initially at a temperature of 62 °C (then decreasing by 1° every cycle), and 60 s at 72 °C. This was followed by 20 cycles of 30 s at 94 °C, 90 s at 50 °C and 60 s at 72 °C. Finally there was an additional 5 min at 60 °C and an indefinite hold at 4 °C.

PCR products were separated and visualized with MegaBACE 1000 (Amersham Biosciences), and genotypes were scored using the software package Fragment Profiler 1.2 (Amersham Biosciences, Buckinghamshire, UK).

Statistical analysis

The 14 microsatellite loci were checked for Hardy–Weinberg equilibrium with the program Cervus 3.0 (Marshall *et al*., 1998; Kalinowski *et al*., 2007) where Bonferroni correction was used to evaluate the significance of any deviation from equilibrium. Linkage disequilibrium, that is, whether the loci are independent from each other in each population, was tested with statistical software Genepop 3.4 (Raymond and Rousset, 1995) using the default dememorization number (1000), 100 batches and 1000 iterations per batch.

Genetic diversity within the populations was described with three statistics: allelic richness (A_R), private allelic richness (A_{PR}) and expected heterozygosity according to Hardy–Weinberg equilibrium (H_E). Allelic richness and private allelic richness (A_R and A_{PR}) are genetic diversity measures that take into account uneven sample sizes by performing rarefaction, and calculate a statistic that is comparable across samples. These estimates were obtained using programs FSTAT 2.9.3 (Goudet, 2001) (for A_R) and HP-RARE (Kalinowski, 2005) (for A_{PR}). Expected heterozygosity, as well as the inbreeding coefficient (F_{IS}), was calculated for each population using FSTAT.

The level of genetic differentiation among the populations was assessed as F_{ST} (Wright, 1943) by using the θ estimator (Weir and Cockerham, 1984) as implemented in the software FSTAT 2.9.3 (Goudet, 2001). F_{ST} was estimated both globally and between all pairs of populations. To evaluate the significance of the pairwise tests, the program used randomizations (1820 times) for the genotypes. These *P*-values were then corrected with sequential Bonferroni correction that takes into account multiple tests instead of the standard Bonferroni correction that the program used. Mantel's test was used to test for isolation by distance; that is, correlation between the level of genetic differentiation and geographic distance. Only populations from Finland were used in this test.

The software Structure 2.2 (Pritchard *et al*., 2000; Falush *et al*., 2003a, 2007) was used to cluster populations into groups based on individual genetic data without any prior information on geographic sampling locality. Structure defines populations such that populations are more similar within the cluster than with populations in other clusters. Length of the burn-in period was set to 10 000 and the number of Markov chain Monte Carlo repetitions to 10 000. Simulation was ran 10 times for each values of *K*. Individuals were also assigned to populations using GeneClass 1.0.02 (Cornuet *et al*., 1999).

The program BOTTLENECK 1.2.02 (Cornuet and Luikart, 1996) was used to test whether study populations had gone through a decline in population size in recent history. In a bottlenecked population, allele numbers decline faster than heterozygosity, and the observed heterozygosity should be larger than the expected based on the allele count in the population. Here the expected heterozygosity was estimated by assuming the two-phase mutation model as recommended for microsatellite data. The variance of mutations was set to 30 and the proportion of mutations larger than one step to 30%. Significance of the mismatch between the observed and expected heterozygosities was tested by using the Wilcoxon test and the visual graphic test (Cornuet and Luikart, 1996).

Results

House sparrow dispersal in Finland based on ringing records

Median natal dispersal distance for house sparrows ($n = 87$) was 0 km, and only 10% of individuals dispersed further than 16 km (Figure 2). Hence, the available ringing records suggest that natal dispersal of Finnish house sparrows is highly limited. Furthermore, adult dispersal ($n = 1110$) was also expectedly low; that is, median was 0 km and only 10 % dispersed more than 3 km. When considering the sexes separately both had a median of 0 km, but from males 10% dispersed more than 2 km whereas from females 10% moved more than 5 km.

Samples

For testing the quality of the data (that is, linkage equilibrium, Hardy–Weinberg equilibrium and sufficiency of the loci), we used only individuals that were successfully genotyped for all 14 loci ($n = 391$). For all other analyses, we used individuals that had 11 or more loci successfully genotyped ($n = 472$). In this case for each population, 20–59 adult males were included adding up to a total of 439 individuals from Finland and 33 from Stockholm (Table 1). Some populations were sampled in two consecutive years (Table 1), but because there were no genetic differences between years (data not shown), all the analyses were carried out on the pooled data.

Testing loci

All loci were independent from each other when testing for linkage disequilibrium. All loci except Pdoμ32 were also in Hardy–Weinberg equilibrium (Table 2). There was a large and highly significant deficiency of heterozygotes in Pdoμ32 (Table 2). This may be due to null alleles decreasing the number of observed heterozygotes, and in this case the estimated frequency of null alleles was 0.17 (estimated following methods of Pemberton *et al*. (1995)). Consequently, Pdoμ32 was not included in the subsequent analyses.

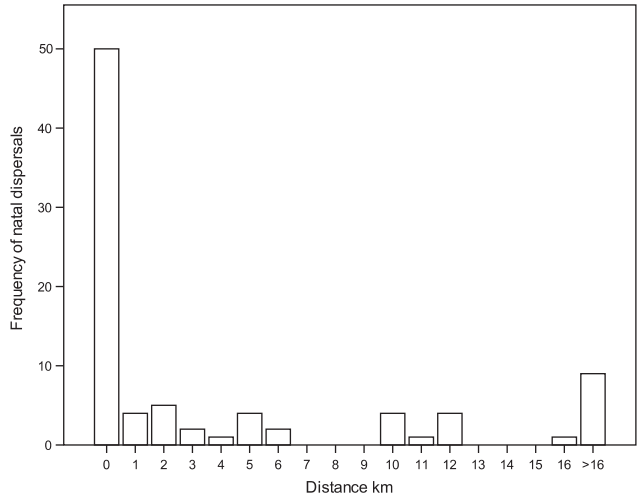

Figure 2 Distribution of natal dispersal distances of Finnish house sparrows based on ringing data from 1930 to 2004.

For testing the sufficiency of the number of loci used in this study, we calculated the change in F_{ST} and its standard error when loci were added one at a time (up to 13 loci). The standard error of F_{ST} was 0.008 with five loci and stabilized at 0.005 after the eighth locus was included. With 10 or more loci, the overall F_{ST} values did not change much. The quality and number of loci used were thus assumed to be sufficient for the analysis of genetic variability within and differentiation among the populations.

Genetic variability within populations

Basic population-level measures of genetic variability indicated that all populations were very similar with respect to intrapopulation levels of genetic variation (Table 3). Allelic richness ranged between 9.0 and 10.0 (on average 9.6) and private allelic richness between 0.02 and 0.29. Average expected heterozygosity, an unbiased estimate introduced by Nei (1987), was very similar in all populations (0.83–0.85). None of the inbreeding coefficients (F_{IS}) of the populations differed significantly from zero.

Table 2 Descriptive statistics of 14 microsatellite loci used

Locus	N_A	N	H_O	H_E	HW
Ase18	21	391	0.852	0.880	NS
Pdoμ1	20	391	0.854	0.869	NS
Pdoμ3	18	391	0.864	0.897	NS
Pdoμ5	19	390	0.854	0.874	NS
Pdoμ10	15	391	0.867	0.870	NS
Pdoμ16	14	391	0.877	0.889	NS
Pdoμ19	7	391	0.565	0.568	NS
Pdoμ22	16	391	0.655	0.733	NS
Pdoμ27	13	391	0.785	0.822	NS
Pdoμ32	18	391	0.575	0.814	***
Pdoμ33	23	391	0.928	0.915	NS
Pdoμ40	18	391	0.895	0.909	NS
Pdoμ44	18	391	0.905	0.888	NS
Pdoμ47	18	391	0.821	0.890	NS

Number of alleles per locus (N_A), number of individuals typed (N), observed and expected heterozygosities (H_O and H_E), deviance from Hardy–Weinberg equilibrium (HW significance indicated with stars, *** for $P < 0.001$).

Table 3 Basic population-level statistics of genetic variability

Population		N	A_R	A_P	A_{PR}	H_E	F_{IS}
1	Stockholm	33	9.59	3	0.208	0.849	0.013
2	Turku	45	9.76	1	0.088	0.844	0.025
3	Helsinki	59	9.58	3	0.161	0.842	0.000
4	Myllykoski	29	10.02	4	0.228	0.846	0.021
5	Jyväskylä	35	9.63	1	0.122	0.843	0.034
6	Seinäjoki	30	9.43	0	0.051	0.841	0.007
7	Oulu	38	9.47	2	0.096	0.834	0.062
8	Lieksa	30	9.57	0	0.023	0.845	0.011
9	Kuhmo	36	9.69	2	0.135	0.828	0.030
10	Kajaani	25	9.82	4	0.290	0.835	−0.013
11	Ämmänsaari	23	9.51	2	0.261	0.835	0.022
12	Kuusamo	21	9.82	0	0.088	0.832	0.019
13	Rovaniemi	48	9.98	2	0.100	0.851	0.018
14	Sodankylä	20	9.01	0	0.053	0.833	0.026

Number of individuals (N), allelic richness (A_R), number of private alleles (A_P), private allelic richness (A_{PR}), expected heterozygosity (H_E) and inbreeding coefficient (F_{IS}).

Table 4 Genetic differentiation (F_{ST} estimates) among population pairs below the diagonal

	Stockholm	*Turku*	*Helsinki*	*Myllykoski*	*Jyväskylä*	*Seinäjoki*	*Oulu*	*Lieksa*	*Kuhmo*	*Kajaani*	*Ämmänsaari*	*Kuusamo*	*Rovaniemi*	*Sodankylä*
Stockholm	—	0.0006	0.0006	0.0006	0.0006	0.0006	0.0006	0.0006	0.0006	0.0006	0.0006	0.0006	0.0006	0.0006
Turku	**0.025**	—	0.0055	0.1154	0.3198	0.3093	0.3121	0.0006	0.0022	0.0017	0.0011	0.0071	0.2539	0.0006
Helsinki	**0.027**	0.001	—	0.0039	0.0110	0.0006	0.0006	0.0006	0.0006	0.0082	0.0006	0.0006	0.0006	0.0006
Myllykoski	**0.027**	0.002	0.002	—	0.4670	0.0033	0.0140	0.1093	0.0824	0.0797	0.0039	0.1945	0.0747	0.0011
Jyväskylä	**0.023**	−0.001	0.001	−0.001	—	0.0121	0.0528	0.0791	0.0055	0.0137	0.0011	0.0082	0.0555	0.0022
Seinäjoki	**0.033**	−0.003	**0.002**	0.003	0.000	—	0.0368	0.0006	0.0006	0.0006	0.0006	0.0593	0.0055	0.0006
Oulu	**0.030**	0.000	**0.003**	0.005	0.000	0.002	—	0.0006	0.0165	0.0017	0.0033	0.0270	0.1478	0.0077
Lieksa	**0.024**	**0.003**	**0.007**	−0.001	−0.000	0.005	**0.005**	—	0.0077	0.0033	0.0006	0.0022	0.0011	0.0006
Kuhmo	**0.038**	0.007	**0.010**	0.003	0.006	**0.010**	0.007	0.005	—	0.0011	0.0011	0.0017	0.0022	0.0006
Kajaani	**0.031**	0.007	0.002	−0.000	0.002	**0.007**	0.006	0.005	**0.010**	—	0.0006	0.0187	0.0011	0.0006
Ämmänsaari	**0.034**	0.007	**0.007**	0.008	0.007	0.008	0.007	**0.012**	0.010	**0.012**	—	0.0061	0.0017	0.0011
Kuusamo	**0.032**	0.004	**0.005**	0.001	0.005	0.001	0.003	0.007	0.008	0.004	0.007	—	0.0022	0.0028
Rovaniemi	**0.031**	0.002	**0.004**	0.003	0.001	0.002	0.002	**0.007**	0.007	0.006	**0.008**	0.005	—	0.0028
Sodankylä	**0.032**	**0.008**	**0.007**	0.007	0.005	**0.013**	0.004	**0.011**	**0.014**	**0.013**	**0.007**	**0.008**	0.007	—

Uncorrected *P*-values (after 1820 randomizations) that program FSTAT provides given above the diagonal.
Significant F_{ST} values after sequential Bonferroni correction are in bold.

Genetic differentiation among populations

The levels of genetic differentiation (measured by F_{ST}) were very low both globally (F_{ST} among Finnish populations $= 0.004 \pm 0.001$ (s.e.)) and between all the population pairs (Table 4). Yet some of the pairwise F_{ST} estimates were significantly different from zero. Two rather centrally located populations, Myllykoski and Jyväskylä, did not differ from any other Finnish population, but the southern (Helsinki) and northernmost (Sodankylä) populations were significantly different from most other Finnish populations. The Stockholm population was significantly differentiated from all Finnish populations, with F_{ST} values ranging between 0.023 and 0.038.

The low level of genetic differentiation among populations within Finland was corroborated by a number of additional findings. First, there was no isolation by distance among the Finnish populations, as shown by zero correlation between genetic differentiation and geographic distance (Mantel $r = 0.0000$, $P = 0.941$). Second, all the Finnish sampling localities formed one cluster in the clustering analyses (posterior probability for $K = 1$ was Ln P(D) $= -26\,659.8$, which was better than for $K = 2$ for which Ln P(D) $= -26\,971.4$). Finally, the lack of differentiation was further shown by the assignment test where the assignment of individuals to their population of origin was only 24.7%.

Bottlenecks

Using the two-phase mutation model, we found none of the study population to have gone through a drastic decline in numbers in the past. The graphic test gave normal L-shaped distribution and the Wilcoxon test a probability of $P > 0.85$ for all populations.

Discussion

We studied the spatial structure of the house sparrow populations in Finland by using DNA microsatellite markers from the samples collected in mid-1980s, and found that populations were largely panmictic and homogenous over large areas at the time when the widespread decline in population sizes of this species had just started in Finland (Väisänen, 2003). We sampled and studied a large number of populations covering the whole country and a large number of individuals from each population. We focused on adult males, because they are the most sedentary sex and therefore the best indicator any differentiation. We also showed that the number of DNA microsatellite markers used was large enough to reach sufficient confidence for our genetic estimates.

Genetic diversity in the study populations

Genetic variability within house sparrow populations was very similar in all localities, including Stockholm. All measures of genetic diversity, allelic richness, number of private alleles and expected heterozygosity, were nearly equal (Table 3). None of the populations were inbred, which is not surprising given the large population sizes and strong gene flow between the populations (see below) indicated by this study. Also none of the populations had gone through a bottleneck in the recent past, which would have caused a reduction in genetic diversity. The measures of genetic diversity within house sparrow populations were in the same category as previously estimated for birds in general (Neff and Gross, 2001) as well for house sparrows (Neumann and Wetton, 1996; Griffith *et al*., 2007; Garnier *et al*., 2008). Because most populations were sampled only in 1 year, we could not estimate the effective population size formally from our data, but the equal genetic diversity across populations suggests that population sizes were of the same magnitude.

Spatial population structure

Despite the low dispersal indicated by the field data, the house sparrow populations showed hardly any spatial structuring across the Finnish range (about 400×800 km). We only found evidence of weak differentiation among some of the study populations, mainly concerning those at the southern (Helsinki) and northern (Sodankylä) edges of the region, but the global F_{ST} equaled zero showing no significant population structure overall (Table 4). Accordingly we could not differentiate any type of clusters of individuals within the data set by using the software Structure. Extensive homogeneity of populations was most likely due to populations being very large and possibly also better connected than field

data suggested. At the time of sampling, the house sparrow was highly abundant in Finland, the census population size of the whole country being in the order of 10^6 individuals and distribution covering most human-inhabited areas from small farms to cities (Väisänen *et al*., 1998). Genetic drift has a small effect in such populations, and they diverge only slowly in the neutral markers, such as DNA microsatellites. Dispersal of the house sparrows may also have been more frequent and may have covered larger distances than previous ringing records have suggested. Conversely, only a small number of migrants is enough to homogenize populations (Franklin, 1980; Frankel and Soulé, 1981; Allendorf, 1983) and only few dispersal events may maintain connectivity in an unobstructed landscape.

Thus, Finland could be considered as a rather contiguous landscape for the house sparrow in the 1980s, and our findings suggest that it formed a large and genetically homogenous population in most of its range. Accordingly, previous allozyme studies on the house sparrows have also shown only slight differentiation among populations in contiguous landscapes in the lowlands of eastern England ($F_{ST} = 0.014$) (Parkin and Cole, 1984), and among the introduced populations in New Zealand ($F_{ST} = 0.018$) and Australia ($F_{ST} = 0.024$) (Parkin and Cole, 1985). Also Fleischer (1983) found nonsignificant divergence ($F_{ST} = 0.076$) among five farm populations in Kansas in a microgeographic scale (12 km^2).

As adults rarely disperse, gene flow in the house sparrow is thought to be maintained by natal dispersal (Summers-Smith, 1988; Altwegg *et al*., 2000). Unfortunately, only few young birds are ringed in Finland and natal dispersal is poorly characterized. When looking at the limited data ($n = 87$), most of the house sparrows had not dispersed from their natal sites. This low natal dispersal is in good agreement with studies based on ringing data in other European countries (Paradis *et al*., 1998; Siriwardena *et al*., 2002; Tufto *et al*., 2005). Adult dispersal was also very low even though there were more ringing records ($n = 1110$). Nevertheless, dispersal distances based on recapture of marked individuals are underestimating connectivity (Koenig *et al*., 1996) and thus studies similar to this highlight the importance of genetic tools that can provide valuable information to be considered alongside with information gained by traditional ecological techniques. Finnish house sparrow may maintain gene flow over large geographical distances by a stepping-stone pattern of small migration distances in a fairly homogenously distributed population.

Another possible explanation for the low genetic differentiation between the house sparrow populations would be the colonization history of the house sparrow to Fennoscandia after the last ice age. Some species have shown less genetic variability as well as less genetic structuring in areas where they have expanded their ranges after the ice has retrieved (Hewitt, 2000). However, house sparrow populations in Norway have diverged from each other and because the ice seems to have retrieved approximately the same time from Norway and Finland (Kurtén, 1972; Koivisto, 2004), there should have been also time for the birds to colonize Finland and subsequently populations to diverge. We therefore believe that it is not so likely that a relatively recent postglacial recolonization explains the low genetic differentiation observed in Finland.

Despite the low differentiation on the scale of Finland (longest distance between sites 813 km), we also found that the distance of 250 km between Turku (Finland) and Stockholm (Sweden), including ca. 40 km of open sea, was sufficient to create significant genetic differentiation among the populations ($F_{ST} = 0.02$–0.04). This is in line with two studies made on house sparrow populations on the coast of Norway, where populations are separated by fjords and mountains. Bjordal *et al*. (1986) showed that populations separated by 10–200 km differed from each other based on genetic identity calculated from allozyme frequencies. Later, a microsatellite analysis found that island populations separated by less than 100 km were more differentiated from each other than mainland populations (mainland $F_{ST} = 0.018$, island $F_{ST} = 0.025$, Jensen *et al*., in preparation). These results underline the strong effect that landscape composition can have on dispersal: a species that in a contiguous landscapes forms a homogenous population on the scale of hundreds of kilometers can have rather strong spatial structuring on a much smaller scale when barriers (such as open sea) limit natal dispersal over intermediate distances. This also supports the idea that the house sparrow gene flow in the contiguous landscape occurs in a stepwise manner among nearby populations.

Relatively large populations and low levels of genetic differentiation are found to be common in many temperate zone passerines (Barrowclough, 1983). Merilä *et al*. (1996) found only weak genetic differentiation among greenfinch *Carduelis chloris* populations on the scale of Europe. No population structuring was detected in the great tit *Parus major* among populations as distant as Spain and Lapland (Kvist *et al*., 1999). Kvist *et al*. (1998) also studied Finnish and Swedish willow tit *Poecile montana* populations and found no genetic differentiation despite interpopulation distances of up to 1000 km. Furthermore, when studying willow tits more extensively in their Palaearctic distribution range, Kvist *et al*. (2001) found almost no differentiation between subspecies or geographical localities. This was considered to be due to high gene flow across relatively homogenous landscape lacking geographical barriers. This scenario applies probably to Finnish house sparrows and their environment as well.

Perspectives

The house sparrow is a highly successful avian species that has used much of the habitats humans have provided. However, the situation has recently changed, as the house sparrow populations have declined in many localities throughout Europe (BirdLife International, 2004). For example, between 1976 and 2002, the Finnish house sparrow populations had declined by 63% (Väisänen, 2003). The decline has been particularly pronounced in certain European cities (De Laet and Summers-Smith, 2007; Brichetti *et al*., 2008) and it has been suggested that different habitats (urban, suburban and rural) present different subpopulations in need of specific conservation actions (De Laet and Summers-Smith, 2007). Our findings imply that small-scale spatial distance associated with an urban to rural gradient are unlikely to be associated with significant genetic structuring in Finland. 'City sparrows' conceivably experience a different environment than their rural equivalents,

but they all seem to form one population because no difference was found between the urban and rural sites in Finland. However, Finland does not have any real metropolis unlike some other countries where these man-made habitats may have a role in genetic differentiation even between nearby populations.

In view of the species' decline, a comparison of the results on the onset of, its decline with contemporary data from the same localities in Finland will be interesting. Results obtained from this study form an important backdrop against which the population genetic consequences of the species' rapid decline in abundance can be evaluated (cf. Wandeler *et al*., 2007). A population decline may result in an increase in differentiation among populations (Bouzat *et al*., 1998; Muños-Fuentes *et al*., 2005; Martínez-Cruz *et al*., 2007). Knowledge of the population structure before a decline is essential, as sometimes the pattern of low genetic diversity can be present already in historical samples (Matocq and Villablanca, 2001). Whether decline-derived loss of genetic diversity is found, possible conservation actions need to be considered more population-wise; for example, is it better to manage diverged and unique populations or the larger and more connected ones. As the house sparrow is dramatically declining, the need for understanding key population biological processes, for example, through population genetic research, is increasing.

Conflict of interest

The authors declare no conflict of interest.

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