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Broad-scale latitudinal patterns of genetic diversity among native European and introduced house sparrow (*Passer domesticus*) populations

A. W. SCHREY,* M. GRISPO,* M. AWAD,* M. B. COOK,* E. D. McCOY,* H. R. MUSHINSKY,* T. ALBAYRAK,† S. BENSCH,‡ T. BURKE,§ L. K. BUTLER,¶[1] R. DOR,** H. B. FOKIDIS,†† H. JENSEN,‡‡ T. IMBOMA,§§ M. M. KESSLER-RIOS,¶¶ A. MARZAL,*** I. R. K. STEWART,††† H. WESTERDAHL,‡ D. F. WESTNEAT,††† P. ZEHTINDJIEV‡‡‡ and L. B. MARTIN*

**Department of Integrative Biology, University of South Florida, 4202 E Fowler Ave, Tampa Florida 33620, USA, †Department of Biology, University of Mehmet Akif Ersoy, Yeni Mah. İnönü Cad. No: 138 15030 Burdur, Turkey, ‡Department of Animal Ecology, Lund University, Zooekologiska avdelningen, Ekologihuset, Sölvegatan 37, 22362 Lund, Sweden, §Molecular Ecology Laboratory, The University of Sheffield, Western Bank, Sheffield S10 2TN, UK, ¶Department of Biology, Tufts University, 163 Packard Ave., Medford, Massachusetts 02155, USA, **Fuller Evolutionary Biology Program, Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14950, USA, ††School of Life Sciences, Arizona State University, PO Box 874601 Tempe, Arizona 85287, USA, ‡‡Department of Biology, Centre for Conservation Biology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway, §§National Museum of Kenya, P.O Box 40658 - 00100 Nairobi, Kenya, ¶¶Instituto de Ecologia, Universidad Nacional Autónoma de México, Apartado Postal 70-275, CP 04510, México DF, Mexico, ***Department of Zoology, Universidad de Extremadura, Avda. Elvas s/n, 06071 Badajoz, Spain, †††Department of Biology, University of Kentucky, 101 T.H. Morgan Building, 675 Rose St, Lexington, Kentucky 40506-0225, USA, ‡‡‡Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin Street, 1113 Sofia, Bulgaria*

Abstract

Introduced species offer unique opportunities to study evolution in new environments, and some provide opportunities for understanding the mechanisms underlying macro-ecological patterns. We sought to determine how introduction history impacted genetic diversity and differentiation of the house sparrow (*Passer domesticus*), one of the most broadly distributed bird species. We screened eight microsatellite loci in 316 individuals from 16 locations in the native and introduced ranges. Significant population structure occurred between native than introduced house sparrows. Introduced house sparrows were distinguished into one North American group and a highly differentiated Kenyan group. Genetic differentiation estimates identified a high magnitude of differentiation between Kenya and all other populations, but demonstrated that European and North American samples were differentiated too. Our results support previous claims that introduced North American populations likely had few source populations, and indicate house sparrows established populations after introduction. Genetic diversity also differed among native, introduced North American, and Kenyan populations with Kenyan birds being least diverse. In some cases, house sparrow populations appeared to maintain or recover genetic diversity relatively rapidly after range expansion (<50 years; Mexico and Panama), but in others (Kenya) the effect of introduction persisted over the same period. In both native and introduced populations, genetic diversity exhibited large-scale geographic patterns, increasing towards the equator. Such patterns of genetic diversity are concordant with two previously described models of genetic diversity, the latitudinal model and the species diversity model.

Correspondence: Aaron Schrey, Fax: (813) 974-3263;
E-mail: aschrey@cas.usf.edu; aaronschrey@hotmail.com
[1]Present address: Department of Biology, College of New Jersey, 2000 Pennington Road, Ewing, New Jersey 08628, USA

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Introduction

Introduced species offer unique opportunities to study evolution in new environments and particularly how genetic diversity changes with range expansion (Lee 2002; Cox 2004; Keller & Taylor 2008). In birds, introduced populations tend to have lower genetic diversity and greater differentiation in the introduced range than in native conspecifics; however, patterns of genetic differentiation are not consistent (Baker & Moeed 1987; Merilä *et al.* 1996; Cabe 1998; Hawley *et al.* 2006; Russello *et al.* 2008), as would be expected if a small number of individuals caused founder effects (Sirkkonaa 1983). For instance, if an introduced population was sufficiently large, multiple step-wise colonizations with associated founder events may be required to decrease genetic diversity and increase genetic differentiation (Clegg *et al.* 2002). On the other hand, if a few individuals were introduced, rare alleles would likely be lost, resulting in reduced heterozygosity (Sirkkonaa 1983). Also, if individuals were mixed during, or after, introduction, there could be less genetic differentiation in the introduced range (Peacock *et al.* 2009). In some cases, multiple introductions can increase genetic diversity by admixture (Kolbe *et al.* 2004, 2008), which could make some introduced populations better sources of subsequent colonizations (Kolbe *et al.* 2004). In some taxa, introductions have not been associated with a loss in broad-sense variation in quantitative traits (Dlugosch & Parker 2008). Reproductive characteristics, such as high fecundity, multiple-paternity, year-round breeding and/or sperm storage, can buffer losses of genetic diversity (Eales *et al.* 2008). Finally, a disposition towards high phenotypic plasticity might enable populations to persist in novel areas (Richards *et al.* 2006).

Wide-ranging introduced species also provide opportunities for understanding the mechanisms that generate or sustain macroecological patterns (Gaston 2009). For introduced species with broad distributions, native and introduced populations are likely to experience distinct selection pressures, which may generate unique patterns of genetic diversity. There are three commonly cited models regarding genetic diversity on such large scales. One, based on climate oscillations and species expansion pole-wards after glaciations, predicts a decrease in genetic diversity with increasing latitudes (hereafter referred to as the latitudinal model; Thingsgaard 2001; Martin & McKay 2004; Hughes and Hughes 2007; Miller *et al.* 2010; Saitoh *et al.* 2010). A second model predicts that the factors which contribute to species diversity may be correlated to genetic diversity (hereafter referred to as the species diversity model; Vellend 2003; Vellend & Geber 2005). This model is not mutually exclusive with the latitudinal model, and indicates that several factors could contribute to a latitudinal pattern in genetic diversity. The species diversity model indicates that ecological and demographic processes are important in determining genetic diversity. Thus, if these factors are correlated with latitude, one would expect correlations with genetic diversity. The third (hereafter referred to as the centre-marginal model) predicts that the centre of a species distribution will have the highest and the margins will have lowest genetic diversity (da Cunha *et al.* 1950; Brussard 1984; Eckert *et al.* 2008). The centre of the range is more likely to be in prime habitat and to experience gene flow, whereas range edges are more likely to be isolated, occur in patchy habitat, be more recently colonized and be less likely to receive immigrants. Indeed, Wisley *et al.* (2004) found that stepping-stone like range expansion generated a centre-marginal pattern in mammals. Recently, Miller *et al.* (2010) found the pattern of genetic diversity among tropical birds fit the centre-marginal model better than the latitudinal model.

In the present study, we sought to determine which model was more appropriate for the house sparrow (*Passer domesticus*), which should help reveal why this species has become one of the most broadly distributed birds. The native range of the house sparrow includes most of Europe and central Asia, and the introduced range now includes all continents but Antarctica. House sparrows were originally introduced into North America in the 1850's and multiple introductions, potentially from few source populations (Anderson 2006), occurred throughout the eastern United States between 1850 and 1870 (Robbins 1973). However, a good deal of uncertainty is associated with how many of the first introductions were successful and how many individuals were introduced (Moulton *et al.* 2010). Thus, it is possible that genetic diversity may have been increased due to admixture (Kolbe *et al.* 2004, 2008). By 1886 house sparrows were widely dispersed through the eastern United States, and by 1910 house sparrows were common in

most of the United States (Robbins 1973). It was not until about 1975 that birds became established in Costa Rica (Reynolds & Stiles 1982) and 1976 that the species was first recorded in Panama (Ridgely & Gwynne 1992). House sparrows are thought to have reached Mexico and Central America by natural range expansion rather than introductions.

In spite of their short history in most areas, house sparrows exhibit extensive phenotypic diversity across their range. Among both the native and introduced populations, house sparrows differ in body mass, sexual dimorphism, clutch size, metabolic rate, immune functions, stress hormone levels and other traits (Johnston & Selander 1964, 1973; Hamilton & Johnston 1978; Anderson 2006; Martin *et al.* 2004, 2005, 2006). Perhaps most intriguing is that many of these traits exhibit macroecological patterns, most notably varying as a function of latitude (Anderson 2006). Indeed in both Europe (native) and North America (introduced), house sparrow body mass, clutch size and immune function vary with distance from the equator, and in most cases, geographic patterns in house sparrows mirror trends observed in other (resident) songbirds. Although the factors driving observed patterns remain unreconciled, it is intriguing that such extensive phenotypic variation has arisen since the time of introductions (typically <150 years), suggesting that much of this phenotypic variation may be due to plasticity.

Given the introduction history of this species and its current distribution, we predicted that genetic diversity and degree of genetic differentiation would be reduced in the introduced compared to the native range. Also, we predicted that native populations would follow the latitudinal model whereas introduced populations would follow the centre-marginal model regarding genetic variation over continent-wide scales. To test these hypotheses, we compared microsatellite variation among native and introduced populations of house sparrow to determine: (i) the genetic structure of the introduced and native range, (ii) if genetic diversity changed after introduction, and (iii) if the changes were consistent over introduced populations. We then examined relationships between genetic diversity and latitude to determine: (i) if similar broad-scale patterns occurred between native and introduced populations, (ii) if patterns more closely resembled the latitudinal or centre-marginal model and (iii) if patterns of genetic diversity were concordant with known latitudinal clines in phenotypic variation.

Methods

Sample collection

We screened genetic variation in 316 adult individuals from 16 locations (Fig. 1; Table 1). Sample locations were classified as native (Norway, Sweden, Great Britain, Germany, Bulgaria, Italy, Spain, Turkey and Israel) or introduced (Massachusetts, Kentucky, Arizona and Florida in the USA, as well as Mexico, Panama and

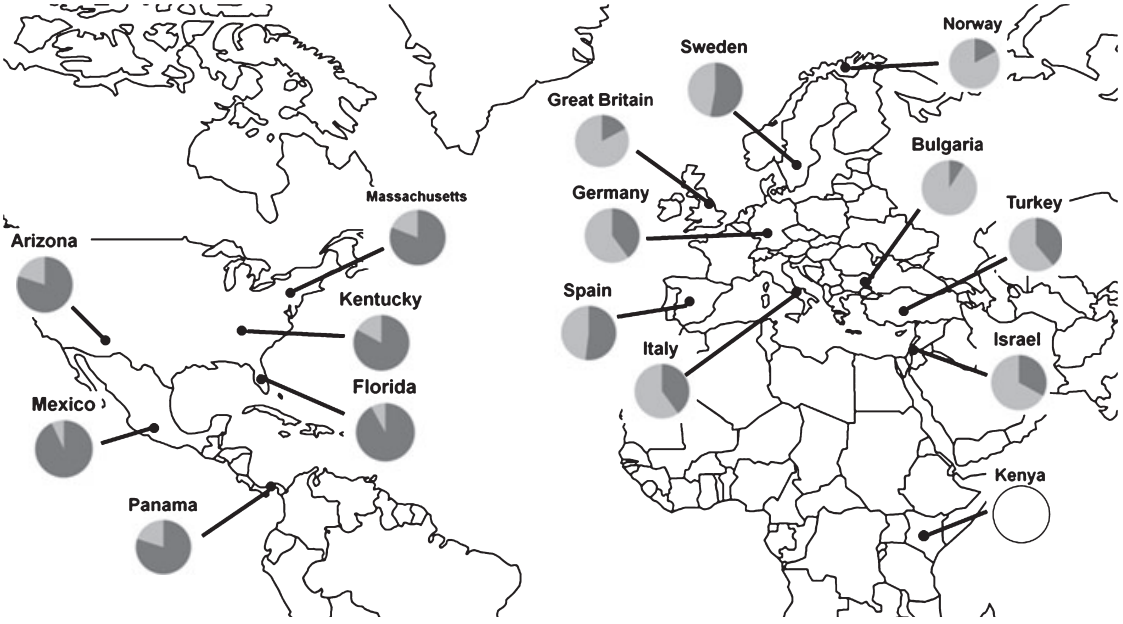

Fig. 1 Map indicating the 16 locations were house sparrows were collected, and the results of Bayesian clustering with the program Structure. Population assignment of individuals to three groups is represented by the shaded portion of the circle (native = light grey; North American = dark grey; Kenya = white).

Table 1 Locations sampled for house sparrow, with sample size (*N*), degrees latitude, degrees longitude and years since introduction (years introduced)

Sample	*N*	Latitude	Longitude	Years introduced	Na	Ar	pAr	H_e	H_o	F_{IS}
Native										
Norway	23	69N	29E	—	13.50	8.36	0.43	0.85	0.81	0.05
Sweden	15	55N	13E	—	11.38	8.68	0.46	0.85	0.77	0.09
G. Britain	30	53N	1W	—	14.38	8.13	0.50	0.86	0.85	0.01
Germany	16	48N	11E	—	13.13	8.66	0.61	0.81	0.82	−0.02
Bulgaria	11	44N	26E	—	9.26	8.06	0.31	0.82	0.84	−0.04
Italy	25	41N	14E	—	17.00	9.79	0.59	0.89	0.86	0.03
Spain	21	39N	6W	—	16.88	9.97	0.65	0.89	0.82	0.08
Turkey	23	37N	31E	—	16.88	10.06	0.41	0.90	0.86	0.04
Israel	9	31N	36E	—	9.88	9.29	0.93	0.86	0.89	−0.04
Mean					13.58	9.00	0.54	0.86	0.83*	0.02*
Introduced										
Mass.	16	42N	71W	150	12.50	8.46	0.37	0.81	0.78	0.04
Kentucky	24	38N	84W	150	14.00	8.15	0.48	0.82	0.74	0.11
Arizona	25	33N	111W	150	15.63	8.82	0.58	0.86	0.79	0.08
Florida	24	28N	82W	150	15.13	8.56	0.38	0.84	0.78	0.08
Mexico	15	19N	99W	90	12.88	9.08	0.53	0.85	0.81	0.06
Panama	20	9N	79W	50	15.50	9.40	0.76	0.87	0.78	0.10
Mean					14.27	8.75	0.52	0.84	0.78*	0.08*
Kenya	19	1S	37E	50	10.13	6.89	1.13	0.74	0.59	0.19

The range of observed number of alleles across loci (Na), and estimates of allelic richness (Ar), private allelic richness (pAr), expected heterozygosity (H_e), observed heterozygosity (H_o), and the inbreeding coefficient (F_{IS}) are provided for each sample (see text for definitions).

*Significant *t*-test between native and introduced samples.

Kenya). Of the locations sampled, house sparrows have most recently appeared in Panama and Kenya, both in the last ~50 years (Ridgely & Gwynne 1992; Anderson 2006). Based on Long (1991) and Summers-Smith (1988), we made conservative estimates on the date of introduction/colonization for all other non-native populations based on published sources (Summers-Smith 1988; Anderson 2006; Table 1). Individuals were bled at capture and collected blood was preserved in a saline solution (Fallon *et al.* 2003) and kept at room temperature until DNA extraction with a DNeasy kit (Qiagen, Valencia, CA, USA).

Data collection

Genetic variation was screened at eight microsatellite loci (Pdoμ1, Pdoμ3, Pdoμ4, Pdoμ5, Pdoμ6, Pdo8, Pdo9, Pdo10; Neumann & Wetton 1996; Griffith *et al.* 1999, 2007; Dawson *et al.* 2006). Griffith *et al.* (2007) found that Pdoμ6 and Pdo10 were located on the same chromosome. To determine if these loci were in linkage disequilibrium, we tested each pair of loci in each population for linkage equilibrium (LE) using FSTAT version 2.9.3 (Goudet 1995). We also tested each locus in each population for conformation to Hardy–Weinberg Equilibrium (HWE) with FSTAT. We observed no significant deviations from LE, nor did we observe linkage disequilibria between the loci Pdoμ6 and Pdo10. Further, no locus consistently deviated from HWE, and only two tests were statistically significant for heterozygote deficiency: Pdoμ4 in Kenya and Pdoμ6 in Spain. The significant tests suggest that small sampling error, or infrequent cases of allelic dropout may have occurred. Collectively though, data were not indicative of true deviation from HWE.

Microsatellite loci were amplified by multiplex polymerase chain reaction (PCR). PCR was conducted at a final volume of 10 μL, containing 1× PCR Buffer (50 mM KCl, 10 mM Tris HCl pH 9.0), 2 mM $MgCl_2$, 200 μM each dNTP, 0.1 unit Taq DNA polymerase, 0.9 μM of each PCR primer (forward primers labelled with 6-Fam, NED, or HEX) and 1–20 ng template DNA. Thermal cycles were 95 °C 2 min, then 95 °C 30 s, 50–56 °C 30 s, 72 °C 30 s, repeated 40 times and finally 70 °C 5 min. Reactions were diluted 1:1 with loading buffer (de-ionized formamide, blue dextran EDTA and MRK 500; The Gel Company, San Francisco, CA, USA), and electrophoresed on a ABI 377 (Applied Biosystems, Foster City, CA, USA) using 96-well upgrade, 36 cm well-to-read, 4.25% polyacrylamide gels. GENESCAN 3.2.1 and GENOTYPER v 2.5 (Applied Biosystems) were used to analyse gel images and define allele sizes. Resultant allele

size data were visualized on scatter plots and binned to specific allele categories.

Data analysis

Genetic diversity was compared among native and introduced populations. For each population, the number of alleles (Na), allelic richness (Ar) and private allelic richness (pAr) were calculated by HP-Rare (Kalinowski 2005b). Richness estimates were based on the smallest sample size of eight individuals (16 alleles) for each locus in each population. The *F*-statistic based system of mating inbreeding coefficient (F_{IS}), observed heterozygosity (H_o), and expected heterozygosity (H_e) were calculated for each population by GDA v 1.0 (Lewis & Zaykin 2001). A *t*-test was used to compare the mean of each genetic diversity estimate between native and introduced populations. Pearson correlation coefficients were calculated to compare genetic diversity estimates with time since invasion and degrees latitude.

Bayesian clustering was performed with Structure v 2.3 (Pritchard *et al.* 2000; Falush *et al.* 2003) to characterize population structure among individuals. Structure estimates the number of populations (k) present among individuals and identifies individual membership in each k using a model-based clustering approach. Structure was used to test for $k = 1–17$, with five independent runs at each k. The natural log probability of observing the data ln Pr($x|k$) method of Structure and the Delta k (Evanno *et al.* 2005) were used to determine the number of groups that best-fit the data. Clustering was performed with the admixture model, 30 000 burn-in steps, 1 000 000 post burn-in steps and allowed correlated allele frequencies. Individuals were assigned to groups using q-values. Individuals were assigned to the group with the highest q-value.

We calculated three estimators of genetic differentiation over samples for each locus. The *D* estimate (actual differentiation of Jost 2008) was calculated with SMOGD (Crawford 2010). We used 1000 bootstraps to estimate the 95% CI upper and lower bounds for each locus. We calculated an AMOVA with GENALEX-6 (Peakall & Smouse 2006) to compare Φ_{RT}, genetic differentiation among regions, defined as native and introduced North American populations (Kenya was excluded), to Φ_{PR}, genetic differentiation among populations within regions. We also calculated the θ_{ST} estimate (Weir & Cockerham 1984) with FSTAT. θ_{ST} was calculated pair-wise among all samples and the harmonic mean of D was calculated pair-wise among all samples. Statistical significance was estimated by permutation using the G-test as implemented in FSTAT. Sequential Bonferroni correction of $\alpha = 0.05$ was preformed for the multiple pair-wise tests (Rice 1989).

Results

Impact of introduction history on genetic diversity

House sparrow populations from the native European range, the introduced North American range, and one of the world's newest introductions (Kenya) had different levels of diversity (Table 1). Most notably, Kenya had the lowest allelic richness, highest private allelic richness, lowest expected heterozygosity, lowest observed heterozygosity and the highest inbreeding coefficient (Table 1). Native populations had significantly greater observed heterozygosity (*t*-test = 3.39, $P < 0.01$, d.f. = 13), significantly lower inbreeding coefficients (F_{IS}; *t*-test = 2.55, $P = 0.02$, d.f. = 13), yet native and introduced North American populations were similar at all other estimates of genetic diversity (Table 1). Thus, genetic diversity was similar among most populations with the exception of Kenya. Also, allelic richness ($r = -0.88$, $P = 0.01$, d.f. = 4) and private allelic richness ($r = -0.80$, $P = 0.03$, d.f. = 4) decreased with time since introduction among introduced North American populations, indicating that more recently introduced populations had more alleles and more private alleles.

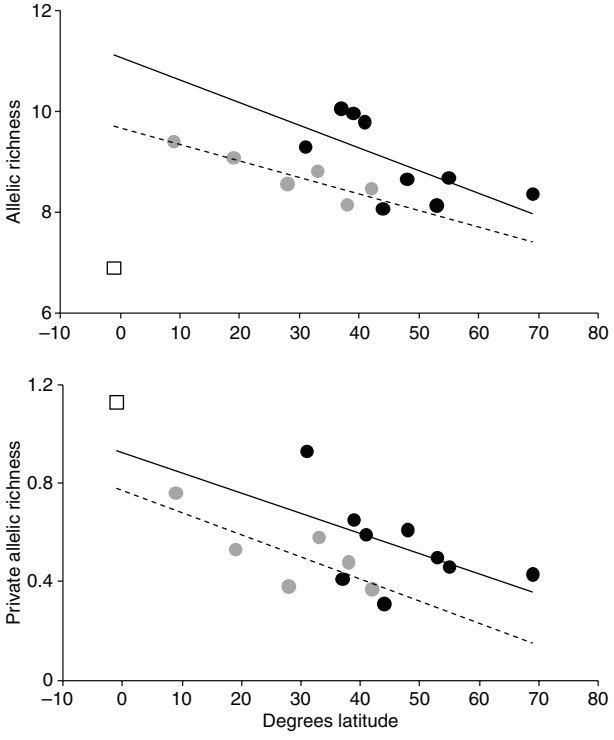

Fig. 2 Allelic richness and private allelic richness correlated with degrees latitude for native (black circles, solid line) and introduced North American (grey circles, dashed line). Kenya (open square) is plotted for reference.

Geographic patterns in genetic diversity

Among all locations, Kenya had the lowest genetic diversity and also was the lowest latitude population (Table 1; Fig. 2). When native and introduced North American populations were analysed together, but without Kenya, genetic diversity and private allelic richness was still the highest at low latitudes (Table 1; Fig. 2). Even when populations were split, latitudinal patterns persisted. In native populations, allelic richness ($r = -0.65$, $P = 0.03$, d.f. = 7), private allelic richness ($r = -0.52$, $P = 0.07$, d.f. = 7) and observed heterozygosity ($r = -0.68$, $P = 0.02$, d.f. = 7) decreased with increasing latitude. In introduced North American populations too, allelic richness ($r = -0.90$, $P = 0.01$, d.f. = 4), private allelic richness ($r = -0.77$, $P = 0.04$, d.f. = 4) and expected heterozygosity ($r = -0.84$, $P = 0.02$, d.f. = 4) decreased with increasing latitude.

Bayesian clustering

Bayesian clustering identified population structure between native and introduced house sparrows, and Kenyan house sparrows were highly differentiated from all other groups (Fig. 1). Structure identified three genetic groups with both the ln $Pr(X|K)$, mean K3 = −14156, and the Delta K, K3 = 193.15. The three groups consisted of one native group, one North American group and one Kenyan group (Fig. 1). All individuals from Kenya occupied a single, highly distinct group, yet 32% of native and 15% of North American individuals were assigned to the incorrect group (Fig. 1).

Table 2 Locus by locus estimates of D, with 95% confidence intervals, and θ_{ST}, with P-values for house sparrows from the native range and North America

Locus	D	95% CI	θ_{ST}	P
Native				
Pdoμ1	0.35	0.26–0.43	0.03	<0.0001
Pdoμ3	0.25	0.17–0.33	0.007	0.0500
Pdoμ4	0.84	0.79–0.88	0.02	<0.0001
Pdoμ5	0.36	0.27–0.44	0.03	<0.0001
Pdoμ6	0.68	0.61–0.75	0.02	<0.0001
Pdo8	0.58	0.51–0.65	0.08	<0.0001
Pdo9	0.26	0.16–0.37	0.02	<0.0001
Pdo10	0.35	0.28–0.44	0.04	<0.0001
North America				
Pdoμ1	0.41	0.26–0.54	0.05	<0.0060
Pdoμ3	0.28	0.18–0.38	0.02	<0.0060
Pdoμ4	0.74	0.65–0.82	0.004	<0.0060
Pdoμ5	0.23	0.14–0.35	0.03	<0.0060
Pdoμ6	0.51	0.41–0.62	0.006	<0.0060
Pdo8	0.21	0.12–0.33	0.03	<0.0060
Pdo9	0.24	0.14–0.35	0.02	<0.0060
Pdo10	0.17	0.09–0.37	0.01	<0.0060

Population differentiation

Estimators of genetic differentiation identified more population structure among native than North American populations, and Kenya was highly differentiated

Table 3 Pair-wise θ_{ST} estimates (below diagonal) and harmonic mean estimates of D (above diagonal) among house sparrow samples

	Norway	Sweden	G.B	Germany	Bulgaria	Italy	Spain	Turkey	Israel	Mass.	Kentucky	Arizona	Florida	Mexico	Panama	Kenya
Norway	—	0.23	0.20	0.33	0.27	0.11	0.12	0.16	0.22	0.20	0.24	0.23	0.19	0.19	0.24	0.65
Sweden	0.04*	—	0.14	0.11	0.15	0.20	0.09	0.13	0.18	0.21	0.18	0.10	0.23	0.26	0.30	0.55
G.B	0.04*	0.03*	—	0.22	0.28	0.15	0.09	0.15	0.04	0.09	0.15	0.16	0.19	0.16	0.18	0.66
Germany	0.06*	0.02	0.05*	—	0.19	0.16	0.15	0.18	0.26	0.16	0.24	0.19	0.20	0.32	0.32	0.46
Bulgaria	0.06*	0.02	0.05*	0.04*	—	0.27	0.21	0.12	0.28	0.36	0.22	0.23	0.39	0.32	0.41	0.46
Italy	0.03*	0.03*	0.03*	0.03*	0.04*	—	0.07	0.08	0.16	0.32	0.15	0.13	0.23	0.15	0.19	0.53
Spain	0.04*	0.02	0.02*	0.04*	0.03*	0.01	—	0.06	0.22	0.05	0.05	0.004	0.12	0.06	0.12	0.54
Turkey	0.04*	0.02*	0.03*	0.04*	0.03*	0.01	0.01	—	0.19	0.21	0.24	0.12	0.21	0.12	0.07	0.55
Israel	0.05*	0.03*	0.02*	0.05*	0.05*	0.02*	0.03*	0.03*	—	0.35	0.35	0.25	0.32	0.33	0.26	0.57
Mass.	0.05*	0.04*	0.03*	0.04*	0.07*	0.05*	0.04	0.04*	0.06*	—	0.10	0.06	0.06	0.04	0.12	0.66
Kentucky	0.04*	0.03*	0.03*	0.05*	0.06*	0.04*	0.02	0.04*	0.07*	0.03*	—	0.07	0.10	0.12	0.19	0.57
Arizona	0.04*	0.02*	0.03*	0.04*	0.05*	0.02*	0.02	0.02*	0.04*	0.03	0.02	—	0.08	0.09	0.11	0.36
Florida	0.04*	0.04*	0.04*	0.05*	0.06*	0.04*	0.03*	0.05*	0.05*	0.03	0.02	0.02	—	0.06	0.10	0.40
Mexico	0.04*	0.04*	0.03*	0.06*	0.05*	0.03*	0.02	0.04*	0.05*	0.03	0.03*	0.01	0.02*	—	0.07	0.60
Panama	0.04*	0.04*	0.03*	0.06*	0.06*	0.03*	0.02*	0.02*	0.05*	0.03	0.03*	0.01*	0.02*	0.02	—	0.45
Kenya	0.15*	0.12*	0.14*	0.12*	0.11*	0.11*	0.12*	0.12*	0.12*	0.16*	0.14*	0.10*	0.12*	0.13*	0.11*	—

G.B., Great Britain; Mass., Massachusetts.

*Statistical significance after Bonferroni correction of $\alpha = 0.05$.

from all other populations. Over loci, *D* ranged from 0.29 to 0.85 (no 95% CI included zero), and θ_{ST} ranged from 0.01 to 0.11 (all loci $P < 0.001$). Estimates were higher among native (*D* range 0.25–0.84; θ_{ST} range 0.007–0.08) than those in North America (*D* range 0.17–0.74; θ_{ST} range 0.004–0.05), however, confidence intervals of *D* overlapped for all but one locus (Table 2). AMOVA identified significant genetic differentiation among native and introduced North American regions ($\Phi_{RT} = 0.018$, $P = 0.001$), yet the genetic differentiation estimate was greater in the comparison done among populations within regions ($\Phi_{PR} = 0.048$, $P = 0.001$).

Pair-wise estimates of θ_{ST} identified significant differentiation among populations (Table 3); θ_{ST} ranged from 0.01 to 0.16 (101 of 120 comparisons significant) and the harmonic mean *D* ranged from 0.004 to 0.66. Again, Kenya was highly differentiated from all other locations (θ_{ST} range 0.10–0.16; all comparisons significant; *D* range 0.36–0.66). Pair-wise estimates also identified significant differentiation between native and introduced North American populations (Table 3). Pair-wise θ_{ST} ranged from 0.02 to 0.07 (50 of 54 comparisons significant) and the harmonic mean *D* ranged from 0.004 to 0.36. Pair-wise θ_{ST} tended to be greater in comparisons between native populations (range 0.01–0.06; 30 of 36 comparisons significant) than in comparisons between North American populations (range 0.01–0.03; six of 15 comparisons significant; Table 3). A similar pattern occurred for the harmonic mean *D* in comparisons between native (range 0.04–0.33) and between North American (range 0.06–0.19) populations (Table 3).

Discussion

Local patterns of genetic diversity

House sparrows exhibited the lowest genetic diversity in the Kenyan introduced population (Fig. 2, Table 1), a pattern consistent among several introduced bird species (Baker & Moeed 1987; Merilä *et al.* 1996; Cabe 1998; Hawley *et al.* 2006; Russello *et al.* 2008). North American introduced populations had similar genetic diversity to native populations. Only two estimates differed between native and introduced North American populations. Observed heterozygosity was higher in the native populations and the inbreeding coefficient showed the introduced North American populations' system of mating had more inbreeding (Table 1, Fig. 2). One intriguing observation for house sparrows though was that the most recent colonizations (Kenya, Mexico, and Panama) had different patterns of genetic diversity. House sparrow populations appeared to maintain or recover genetic diversity rapidly when they were from range expansions (Mexican and Panamanian populations likely stemming from US populations). In the Kenyan population, however, which likely originated from a single introduction to Mombasa in 1950 (Summers-Smith 1988), the signature of the introduction persisted. Kenya was genetically differentiated from all other locations, and it had the least observed genetic diversity. These characteristics are distinct from Mexico and Panama, which were not differentiated from, and had more similar genetic diversity to, other introduced North American populations. It is possible that the population introduced to Kenya was comparatively smaller, that no subsequent admixture has occurred (as no other introductions are known for that part of Kenya, and the closest other house sparrow populations occurs in Dar es Salaam, Tanzania; Summers-Smith, personal communication), or a combination of both factors. However, it is also possible that the immediate source population of Kenyan house sparrows was not sampled, making Kenya appear more differentiated from other locations. Presently, the former hypotheses are more plausible because most introductions came from Europe (i.e. Germany and England; Summers-Smith 1988). Nevertheless, as it is unclear from which areas Kenyan birds were introduced, ongoing analyses (e.g. sample collection from India and elsewhere in Africa and Europe) are underway to answer this question.

Macroecological patterns in genetic diversity

In native populations, genetic diversity followed the latitudinal model, with increased diversity at lower latitudes. Two factors likely contribute to this latitudinal gradient in the native range. First, house sparrow morphology, physiology, behaviour and life history characteristics change systematically with latitude in the native range (Johnston & Selander 1964, 1973; Hamilton & Johnston 1978; Anderson 2006). Second, house sparrows have declined throughout their native range in the past 20 years (Khera *et al.* 2010 and references therein), and the decline generally has been observed in more northern locations (i.e. a decline of almost 60% in Britain; Robinson *et al.* 2005). Thus, as predicted in the species diversity model, environmental and ecological differences may generate conditions favourable to increased genetic diversity at lower latitudes for the house sparrow, even though it is a close commensal of humans and thus expected to be shielded from some factors that would limit populations (e.g. food availability, climate factors). Interestingly though, introduced house sparrows also exhibited greater genetic diversity and more private alleles at lower latitudes. In North American populations, colonizations predominantly occurred north to south (Anderson 2006), so more

recent colonizations occurred towards the equator. Subsequently, the latitudinal pattern among introduced populations could be driven by multiple factors including latitude, favourable conditions for genetic diversity and admixture at the colonization front.

Unlike other latitudinal patterns in genetic diversity, the latitudinal patterns in house sparrows could not have been caused by post glacial expansion, because introductions occurred much more recently than glacial retreat and occurred in the opposite direction. Introduced populations also have latitudinal clines in morphology, physiology, behaviour and life history characteristics (Johnston & Selander 1964, 1973; Hamilton & Johnston 1978; Anderson 2006; Martin *et al.* 2004, 2005, 2006), so one plausible explanation of latitudinal trends in microsatellite variation may involve selection and adaptation. On the other hand, adaptation would have had to have happened rapidly as the first introductions happened just 150 years ago. Indeed, patterns of genetic diversity are concordant with, but unlikely causative of, observed phenotypic variation among populations. We note that the microsatellite markers screened in the present study may depict neutral variation. Thus, the markers may not display potential genetic variation underlying phenotypic variation in house sparrows, and plasticity may contribute to observed phenotypic variation. It is also possible that the rapid phenotypic variation could have been a result of selection on standing genetic variation, which has been demonstrated to generate parallel genetic evolution and potentially parallel phenotypic evolution in the threespine stickleback (Hohenlohe *et al.* 2010). We are currently investigating the potential role of epigenetic modification of gene expression as a driver of phenotypic variation in house sparrows (Bossdorf *et al.* 2008). However, we expect that a combination of more recent introductions at lower latitudes (Anderson 2006), which may have increased genetic diversity from admixture (Kolbe *et al.* 2008), plus phenotypic plasticity will explain many of the above trait clines.

Local patterns of population differentiation

House sparrows from the native European range were genetically differentiated from introduced populations, and native populations had higher estimates of genetic differentiation than the introduced North American range. However, the magnitude of genetic differentiation was similar among populations within the native European and introduced North American ranges. The notable exception was Kenya, which was highly differentiated from all other locations. Founder events likely occurred with introductions, generating some of the genetic differentiation between native and introduced populations. Yet in most cases the founder effects among introduced populations did not appear to have been severe enough to cause large magnitude genetic differentiation. Only in Kenya are genetic differentiation and diversity estimates indicative of a recent founder effect.

We note that, because of low sample sizes ($n < 20$) for some populations, some error likely occurred in our estimates of genetic differentiation. Increasing sample sizes has been shown to decrease the coefficient of variation of estimates of genetic differentiation for highly variable markers (Kalinowski 2005a). It is possible that our estimates underestimated, or overestimated, the actual amount of genetic differentiation among populations. However, multiple statistical approaches (Bayesian clustering, estimates of D, AMOVA, and pair-wise estimates of θ) support our findings that significant genetic differentiation occurs among native, introduced North American and Kenyan populations.

The high genetic differentiation in the native range supports the previous claims that house sparrow introductions to North America were likely derived from only a few source populations (Moulton *et al.* 2010; Anderson 2006). Bayesian clustering also indicated shared ancestry-history among introduced house sparrows in North America (Fig. 1), yet significant genetic differentiation was present among most locations. The estimates of genetic differentiation (Tables 2 and 3) indicate that populations have been established and are potentially in the process of differentiating. Thus, after introductions in the mid 1800's, house sparrows established populations and probably experienced low gene flow among populations. The development of multiple populations with low gene flow may promote or reinforce phenotypic diversification, as local adaptations that occur in newly colonized populations of relatively small size would not be diluted much by migration from nearby locations.

The magnitude and pattern of genetic differentiation observed also supports and extends previous genetic studies of this species. Allozyme variation indicated genetic structure in the native range (Johnston & Klitz 1977; Bjordal *et al.* 1986), but not among five samples over a very small area (12 km^2) in Kansas (Fleischer 1983). Allozyme loci also indicated similar allele frequencies among native (Germany and France) and introduced North American samples (Johnston & Klitz 1977). However, more alleles per locus were found in England and southwestern European populations compared with introduced populations from Australia and New Zealand (Parkin & Cole 1985). Heterozygosity was not different between native and either introduced population, yet New Zealand populations had less heterozygosity than the native England and introduced

Australian population. Also, significant genetic differentiation occurred among populations, with the New Zealand population being more strongly differentiated from English populations than Australian populations (Parkin & Cole 1985). Using four microsatellite loci, no differences were observed among house sparrow populations from Lundy, UK, Nottingham, UK and Kentucky, USA. (Griffith *et al.* 1999). Thirteen microsatellite loci identified very little genetic differentiation among house sparrows collected from 13 sites in Finland, yet the samples from Finland were differentiated from house sparrow from a single site in Sweden (Kekkonen *et al.* 2011). This study indicates that dispersal, while being low in magnitude, is sufficient to prevent genetic differentiation of house sparrows in Finland, while the open water separating Sweden and Finland may have served as a barrier to dispersal (Kekkonen *et al.* 2011).

Conclusions

Introduced house sparrows have differentiated genetically from native ones, especially in one of the world's most recent and likely isolated introductions: Kenya. Generally though, low levels of gene flow appear to be occurring among populations, native or introduced. At large spatial scales, genetic diversity decreased poleward, although the mechanisms producing such variation likely differed in the native and introduced range. Nevertheless, the presence of genetic differentiation among introduced populations presents an excellent opportunity to parse the genetic vs. epigenetic (plastic) basis of trait variation, especially as this species invades new areas and is exposed to new and different selective factors.

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The authors of this work are interested in studying various aspects of house sparrow biology. The work is a part of HOSPnet (house sparrow network), a global consortium of researchers interested in using one of the most broadly distributed avian species as a model to address large-scale ecological, behavioural and physiological questions.
