Contrasting levels of extra-pair paternity in mainland and island populations of the house sparrow (*Passer domesticus*): is there an ‘island effect’?

SIMON C. GRIFFITH*, IAN R. K. STEWART†, DEBORAH A. DAWSON†, IAN P. F. OWENS‡ AND TERRY BURKE‡

1Department of Biology, University of Leicester, Leicester LE1 7RH
2Department of Zoology, University of Queensland, St Lucia, Brisbane, QLD 4077, Australia

Despite the many studies that have investigated the genetic mating system of socially monogamous birds, very little is known about the underlying causes of extra-pair paternity and few studies have attempted to test those hypotheses which have been suggested. This study describes the analysis of the genetic mating system of two populations of the house sparrow (*Passer domesticus*), and uses the results from four other populations to test existing hypotheses using an intra-specific comparative approach. The parentage analysis was conducted using a combination of published and newly presented microsatellite loci isolated from the house sparrow. One population in Kentucky, U.S.A. was found to contain what may be considered to be a typical level of extra-pair paternity for this species (10.5%, 19/185 offspring). The second, a population on the island of Lundy, UK, exhibited a very low level (1.3%, 4/305 offspring), significantly lower than that in all the other populations studied so far. The finding of such diverse rates of extra-pair paternity, along with the existing estimates from other populations, has allowed us to test the effects of breeding density and genetic variation on the level of extra-pair paternity. We found no effect of either factor on the frequency of extra-pair paternity in the house sparrow, leaving the cause of this variation open to fresh ideas.

© 1999 The Linnean Society of London

ADDITIONAL KEY WORDS:—*Passer domesticus* — genetic variation — microsatellite loci — extra-pair paternity — island population.

CONTENTS

Introduction .................................. 304
Material and methods ......................... 305
The study populations ....................... 305
The Lundy population ....................... 306

* Corresponding author. Present address: Department of Evolutionary Biology, EBC, Uppsala University, S-752 36 Uppsala, Sweden, Email: simon.griffith@zoologi.uu.se
† Present address: Department of Animal and Plant Sciences, University of Sheffield, S10 2TN
INTRODUCTION

In passerine birds the advantages and restrictions of biparental care make alternative mating strategies one of the few ways in which males and females can augment their annual reproductive success (Gowaty, 1996). Males can significantly increase the total number of young fathered in a breeding season by indulging in extra-pair copulations (Trivers, 1972; Wetton et al., 1995). Females may benefit by improving the genetic quality or diversity of their offspring (Williams, 1966; Brown, 1997; Birkhead & Moller, 1992), assure fertility (Wetton & Parkin, 1991, cf. Lifjeld, 1994), or gain direct benefits in terms of access to resources (e.g. Gray, 1997).

Extra-pair paternity has been demonstrated to be a widespread alternative reproductive strategy common amongst birds. Owens & Hartley (1998) report that extra-pair fertilizations have been found in 69% of the 35 putatively monogamous passerine species in which molecular techniques have been used to determine paternity. Within the group of passerine species that has been studied, the high degree of variation in levels of extra-pair paternity (from zero to over 50%) has been attributed to several factors. Reviewed by Petrie & Kempenaers (1998), these include: differences in social mating systems, for example, monogamy, polygyny, and the more extreme polyandry and polygynandry; ecological differences between species (Birkhead & Moller, 1992); and the effects of breeding density and coloniality (Westneat & Sherman, 1997).

Additionally, Petrie & Lipsitch (1994) proposed that if females seek extra-pair paternity for good-genes reasons (Williams, 1966), then the costs and benefits of indulging in extra-pair paternity should vary in relation to the amount of genetic variation amongst the males in a population. This would result in an observable positive relationship between the amount of genetic variation in a population and the prevalence of extra-pair paternity. Like other theories, this is open to investigation through inter-specific comparative analysis (Petrie et al., 1998) and additionally through an intraspecific approach, comparing different populations of one species. This latter approach has rarely been used, primarily due to the lack of independent repeated measures within one species. Secondly, for those species in which multiple estimates of extra-pair paternity have been made, there is generally a strong correlation among the frequencies of extra-pair paternity observed in the different populations, such that the level of extra-pair paternity may be considered to be a species characteristic (Owens & Hartley, 1998).
Here we report the frequency of extra-pair paternity in two separate populations of the house sparrow, *Passer domesticus*. The addition of these two population estimates to those already in the literature allows a rare, intra-specific comparative analysis. The two populations presented here are a mainland population in Kentucky, U.S.A., and an ecologically-isolated population on Lundy, a small island in the U.K. While the frequency of extra-pair paternity found in the Kentucky population was consistent with that in other studies of the house sparrow, the level observed in the Lundy population is shown to be significantly lower than in any of the others. Assuming that the basic ecology of the house sparrow in each population is similar, the existing (non-mutually exclusive) hypotheses would predict that:

(a) The breeding density of house sparrows on Lundy was significantly lower than in the other populations (Westneat & Sherman, 1997).

(b) The genetic diversity was significantly lower within the Lundy population than within the other populations (Petrie & Lipsitch, 1994; Petrie et al., 1998).

To examine the effects of density a direct comparison of the reported breeding densities of the different populations was made. To examine its influence on extra-pair paternity, genetic variation was directly measured for the two study populations (Kentucky and Lundy). In addition, to increase the power of the analysis, the genetic variation of the Brackenhurst population near Nottingham, U.K., was assessed. This population should serve as a genetic benchmark for the Kentucky and Lundy populations as they were both founded historically by individuals from the British mainland population. The level of extra-pair paternity in this population was previously found to be 13% (Wetton & Parkin, 1991). Currently, all other factors invoked to explain variation in the level of extra-pair paternity rely on species-specific differences and will therefore not account for the variation between different populations of one species (see Petrie & Kempenaers, 1998).

**MATERIAL AND METHODS**

*The study populations*

The two study populations were on Lundy (an island, 51.11 N, 4.40 W), U.K., and in Kentucky (35.70 N, 83.20 W), U.S.A.

*The Lundy population*

The Lundy population, which has been studied by us since 1990, is on the island of Lundy, which is approximately 3 km² in area and is situated 20 km off the north coast of Devon, England. Although house sparrows have been present sporadically on the island for centuries, the current population became established following the breeding of an immigrant pair in 1972 and was subsequently supplemented by a low level of natural immigration (Lundy Field Society, unpublished). Reference to the records from the bird observatory between 1944 and 1978, a period during which there were initially no resident house sparrows, indicates that the natural rate of immigration to the island was estimated to average approximately three birds every 4 years (Lundy Field Society). Also, as house sparrow numbers on the mainland
have been declining since the 1960s (Gibbons et al., 1993), it is unlikely that this rate of immigration has increased. With such little movement in and out of the population, the Lundy house sparrows therefore constitute a behaviourally closed population, though not necessarily genetically closed.

During 1990–96 the size of the Lundy population remained stable at between 35 and 45 breeding pairs. Nestboxes were introduced in 1990 and by 1996 were used by all pairs. The population occupies an area of 1 km² centred on a village farm in the south-eastern corner of the island. The sparrows nested at relatively high density (40 pairs in 0.7 km²) in two main breeding areas: one around the farm buildings (45 boxes), the other in a neighbouring clump of trees (37 boxes). In any one year there were many unused nestboxes but their suitability for house sparrows was demonstrated by the observation that over the full period of study all were used for at least one breeding attempt (pers. obs.). Pair density ranged from ‘solitary’ pairs (nearest pair approximately 7 m) to ‘colonial’ pairs (nearest pair within 1 m). In both years, all females made at least one breeding attempt; however, there were approximately seven unpaired males (Griffith et al., 1999).

The Kentucky population

The Kentucky population was based around three storage barns at the University of Kentucky’s Agricultural Research Station on the outskirts of Lexington, Kentucky. Around 35 nestboxes had been in place since 1992, most of which were used in each successive season. The overall density of breeding pairs was approximately 30 pairs in 0.8 km². As on Lundy, the breeding density of individual pairs varied from ‘solitary’ pairs (nearest pair approximately five metres), to colonial pairs (nearest pair within one metre). The house sparrow was introduced into North America in 1852 (Long, 1981) and has since colonised most of the continent. In the area around the study site the house sparrow has a continuous range.

General field techniques

House sparrows do not hold territories, only defending the nest site, and the whole population will mix freely at communal feeding, bathing, and roost sites. Individuals in both populations were captured either prior to breeding or at the nest during chick-feeding and were uniquely colour-banded for individual recognition in the field. Additionally, they were ringed with a numbered metal ring (supplied by the British Trust for Ornithology or the United States Fish and Wildlife Service, as appropriate). Putative parentage was assigned by watching nests during chick-feeding. A minimum of two hours was spent recording at least ten visits to each brood by each parent. Only two adults were ever observed feeding each brood. The fieldwork reported in this paper was conducted contemporaneously between May and August in 1995 and 1996.

Molecular methods

A microsatellite-based genotyping system was employed to enable the assignment of paternity to chicks (Ellegren, 1992; Primmer et al., 1995). Approximately 30 μl of
blood was taken from the brachial vein of adult birds and 11-day-old chicks and stored in either 100% ethanol (Lundy) or 1 × TNE (50 mM Tris-HCl; 100 mM NaCl; 5 mM EDTA, pH 7.5) buffer (Kentucky). DNA was extracted from whole blood using a simple chelex resin-based extraction method, which makes small amounts of DNA available in solution (Walsh et al., 1991). In total, four highly polymorphic microsatellite loci were used: two previously published (Pdoμ3 and Pdoμ4; Neumann & Wetton, 1996), and two newly characterized loci (Pdoμ5 and Pdoμ6).

Microsatellite isolation and characterization

A ligation of pBluescript II plasmid to house sparrow DNA enriched for di- and tetranucleotide microsatellites was created using a method based on Armour et al. (1994) with the modification that the DNA fragments were not PCR-amplified before hybridization enrichment (as described in Gibbs et al., 1998). Briefly, MboI genomic DNA fragments (300–600 bp) were extracted from a pBluescript SK+ (Stratagene) library enriched for (CA)n and (TTTC)n sequences. Positive clones were sequenced using dye-deoxyte (Applied Biosystems) on an Applied Biosystems model 377 automated DNA sequencer. Primers were designed, using the PRIMER v0.5 software (Whitehead Institute for Biomedical Research), only for those sequences containing a pure microsatellite of at least 15 repeats for dinucleotides or 10 repeats for tetranucleotides. Each locus was then checked for observed heterozygosity and Mendelian inheritance using a panel of unrelated adults and three family groups, respectively.

Genotyping procedures

For each locus, the polymerase chain reaction (PCR) was carried out in a Perkin Elmer model 480 thermal cycler using the following PCR profile: an initial hot-start for 2 min at 94°C, followed by 35 cycles of 20 s at 94°C, 30 s at the annealing temp, and 60 s at 72°C. Annealing temperatures were 54°C for Pdoμ3 and Pdoμ4 and 59°C for Pdoμ5 and Pdoμ6. Each 15-μl mix included 0.1 unit of Taq polymerase (Applied Biotechnologies), 10 μl Jeffreys’ buffer (final concentration: 20 mM (NH₄)₂SO₄, 75 mM Tris-HCl pH 8.8, 0.15 mg/ml DNAse free BSA, 10 mM β-mercaptoethanol, 2.5 mM MgCl₂; Jeffreys et al., 1988), 0.8 μM of each primer and approximately 10 ng genomic DNA. Products were resolved on a 6% denaturing polyacrylamide gel alongside a 25-base-pair ladder (Gibco BRL) and visualized by silver staining (Bassam et al., 1991).

Alleles were categorized by comparison with the size marker (25-bp ladder). Although this did not allow for precise size determination, PCR products of similar size (± one base pair) could be identified. The accuracy of this approach was confirmed when individuals scored on different gels were consistently assigned the same genotype.

The probability of false paternal inclusion (P_{fa}) was calculated for each locus following Jamieson (1965).

The genetic variability in the three different house sparrow populations was compared using a random sample of 30 adults from each population. The 30 adults
TABLE 1. Characterization of four house sparrow microsatellite loci based on 48 adults from the Lundy population. $P_{pi}$ is the probability of false paternal inclusion, calculated from observed allele frequencies (see Jamieson, 1965). The size given is that of the original sequenced clone. *Characterization of Pdop5 is based on 26 adults from the Lundy population.

<table>
<thead>
<tr>
<th>Locus</th>
<th>Repeat motif</th>
<th>Primer sequences 5’–3’</th>
<th>Size (bases)</th>
<th>No. of alleles</th>
<th>Obs. het.</th>
<th>$P_{pi}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pdop3</td>
<td>(CCAT)</td>
<td>F: CTGTTCCATTAACGTACGGTG</td>
<td>140</td>
<td>10</td>
<td>0.78</td>
<td>0.283</td>
</tr>
<tr>
<td></td>
<td></td>
<td>R: AGTGGAAACTTTAATCCGTTG</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pdop4</td>
<td>(GAAAGAGA)</td>
<td>F: CGTATAGCCTGGATAGAGCTCCAC</td>
<td>375</td>
<td>16</td>
<td>0.90</td>
<td>0.159</td>
</tr>
<tr>
<td></td>
<td></td>
<td>R: CTTGGGAAGAGGATGACCTAGGA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pdop5*</td>
<td>(CA)</td>
<td>F: GATGTTGGCAGTCACGTCCCTTG</td>
<td>230</td>
<td>10</td>
<td>0.92</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>R: GCTGCTGTTAATGCTATGAAAATGG</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pdop6</td>
<td>(GAAA)</td>
<td>F: CAGATCGATGTAGGTGAAGCTGC</td>
<td>330</td>
<td>15</td>
<td>0.79</td>
<td>0.187</td>
</tr>
<tr>
<td></td>
<td></td>
<td>R: CAGATCCCTTAAGGCGAGTGG</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Previously published by Neumann et al. (1996); EMBL accession numbers X93505–X93506. Loci Pdop5 and Pdop6 were submitted to EMBL (accession numbers Y15125–Y15126).

from each population were genotyped together at each of the following loci: Pdop3, Pdop5 and Pdop6. All samples from a single population were run on a single gel for direct comparison of alleles. The total number of alleles and the level of heterozygosity were scored for each population. The samples were given new labels so that the individual conducting the genotyping did not know which population was being scored. The numbers of alleles and the heterozygosity in each population were used as measures of genetic diversity.

RESULTS

Microsatellite markers

In the analysis of the new microsatellite library, a total of 65 clones cross-hybridized to the dinucleotide and five to the tetranucleotide probes, of which 31 and five clones were sequenced, respectively. From these, eight primer sets were developed, of which only two gave clean, variable products and were characterized further in this study (Pdop5 and Pdop6; Table 1). A panel of 48 (26 in the case of Pdop5) unrelated adults was used to characterize each locus (Table 1). The cumulative probability of false paternal inclusion when using just three (Pdop3, Pdop4 and Pdop6) of the microsatellite loci in this population was found to be 0.0084, sufficient to score paternity. Therefore locus Pdop5 was only used to confirm the status of any suspect offspring (see below).

Extra-pair paternity in the Lundy population

In total, 112 broods were sampled from 71 different pairs. Thirteen of the 305 chicks mismatched with their putative parents at one or more loci. These 13 offspring and their parents were additionally genotyped at locus Pdop5 to determine the likely cause of the mismatches. Nine of these 13 mismatched at just one of the four loci,
Table 2. Frequency of extra-pair paternity in the Lundy and Kentucky populations. EPY is extra-pair young, EPP is extra-pair paternity.

<table>
<thead>
<tr>
<th></th>
<th>no. pairs</th>
<th>no. broods</th>
<th>total chicks</th>
<th>no. EPY</th>
<th>EPP% young</th>
<th>EPP% broods</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lundy</td>
<td>1995</td>
<td>30</td>
<td>107</td>
<td>2</td>
<td>1.9</td>
<td>5.3</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>41</td>
<td>198</td>
<td>2</td>
<td>1.0</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>total</td>
<td>71</td>
<td>305</td>
<td>4</td>
<td>1.3</td>
<td>3.6</td>
</tr>
<tr>
<td>Kentucky</td>
<td>1995</td>
<td>11</td>
<td>93</td>
<td>13</td>
<td>14.0</td>
<td>39.3</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>11</td>
<td>92</td>
<td>6</td>
<td>6.5</td>
<td>17.9</td>
</tr>
<tr>
<td></td>
<td>total</td>
<td>22</td>
<td>185</td>
<td>19</td>
<td>10.3</td>
<td>28.5</td>
</tr>
</tbody>
</table>

suggesting that the mismatches were caused by mutation. This idea was supported by the observation that in six of the nine cases the mismatched allele was one repeat unit different from one of the parental alleles, an observation in line with the expectations of the stepwise mutation model (Valdes et al., 1993). Additionally, five of the nine single-locus mismatches occurred at locus Pdop4, which is reported to have a high mutation rate (0.022, 95% c.i. 0.068–0.004; Neumann & Wetton, 1996) (the remainder mismatched at Pdop6). Just four individuals out of 305 mismatched with their putative parents at more than one locus: two of them mismatched at three of the four loci and the other two mismatched at all four loci. These four individuals all shared alleles in common with their putative mother at all loci, but not their putative father; they were therefore considered to be the products of extra-pair copulations as opposed to the result of intraspecific brood parasitism. Previous DNA fingerprinting analyses of parentage in house sparrows have likewise found no evidence for intraspecific brood parasitism (Wetton & Parkin, 1991; TB unpublished). With just four offspring out of 305 fathered outside the pair bond, the level of extra-pair offspring in the Lundy population was therefore 1.3%, with 3.6% (4/112) of broods being affected (Table 2).

Extra-pair paternity in the Kentucky population

In total, 56 broods were sampled from 21 different pairs. Twenty-one of the 185 nestlings mismatched with their father at one or more loci. Of the 21, one mismatched only at locus Pdop4 and one mismatched only at Pdop6 (consistent with mutation, see above). The remaining 19 mismatched at a minimum of two loci and were considered to be extra-pair offspring. The overall rate of extra-pair paternity was therefore 10.3% (19/185) offspring, occurring in 28.6% (16/56) of all broods (Table 2).

Comparison of extra-pair paternity in different populations

Including the two populations presented here, the frequency of extra-pair paternity as detected by DNA profiling methods has now been reported for six populations of house sparrows (Table 3). Overall, there was significant heterogeneity among the
The frequency of extra-pair paternity in six different populations of house sparrows including 95% confidence intervals calculated following Rohlf & Sokal (1969), assuming a normal distribution of extra-pair young within the sample. These confidence intervals allow a more objective comparison of the studies given the different sample sizes involved (see Fig. 1). Density is the approximate average nearest neighbour distance. This measure of breeding density will presumably represent the potential availability of extra-pair mating opportunities to females.

<table>
<thead>
<tr>
<th>Population</th>
<th>Sample size</th>
<th>Frequency of EPP (%)</th>
<th>95% c.i.</th>
<th>Nearest neighbour (m)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lundy, UK</td>
<td>305</td>
<td>4 (1.3)</td>
<td>0.2</td>
<td>4</td>
<td>this study</td>
</tr>
<tr>
<td>Kentucky, USA</td>
<td>183</td>
<td>19 (10.3)</td>
<td>6.8</td>
<td>5</td>
<td>this study</td>
</tr>
<tr>
<td>Villalba, Spain</td>
<td>171</td>
<td>12 (7.0)</td>
<td>3.7</td>
<td>&lt;5</td>
<td>J. Veiga &amp; L. Boto pers. comm.</td>
</tr>
<tr>
<td>Nottingham, UK</td>
<td>536</td>
<td>73 (13.6)</td>
<td>11.2</td>
<td>5</td>
<td>Wetton &amp; Parkin (1991)</td>
</tr>
<tr>
<td>Barcelona, Spain</td>
<td>109</td>
<td>25 (16.1)</td>
<td>5.0</td>
<td>17.3</td>
<td>Cordero et al. (1990)</td>
</tr>
<tr>
<td>New Mexico, UK</td>
<td>55</td>
<td>7 (12.7)</td>
<td>5.5</td>
<td>26.0</td>
<td>R. Kimball pers. comm.</td>
</tr>
</tbody>
</table>

Figure 1. The frequency of extra-pair paternity in six different populations of house sparrows (% of total offspring). Error bars represent the 95% confidence intervals around the estimates (see Table 3). The heterogeneity among the populations (due to the Lundy population) is highly significant ($\chi^2 = 37.2, P<0.0001$, d.f. = 5).

populations ($\chi^2 = 37.19, P<0.0001$; Table 3 and Figure 1). When the Lundy population was excluded, there was no significant difference among the other five populations ($\chi^2 = 6.28, P>0.15$), indicating that the rate of extra-pair paternity in the Lundy population was significantly lower than in all the others.

Comparison of genetic variation in three populations

There was no significant difference in heterozygosity at each of the three loci in the Lundy, Nottingham and Kentucky populations (combined $\chi^2 = 4.67, P>0.50$;
Table 4. Genetic variation in the Lundy, Nottingham and Kentucky populations of house sparrows measured by the level of heterozygosity and allelic diversity at three microsatellite loci. The observed heterozygosity ($H$) was calculated as the number of heterozygous individuals divided by the total number of individuals genotyped ($N$). Sample sizes varied slightly due to some PCR failure. It is assumed that the failure of PCR amplification for a sample will be random with respect to the alleles present and will therefore not bias the result. Allelic diversity ($a$) is used to allow a comparison of different sample sizes, being the number of alleles observed ($n_a$) divided by the total number possible ($2N$).

<table>
<thead>
<tr>
<th></th>
<th>Lundy</th>
<th>Nottingham</th>
<th>Kentucky</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P64a3$</td>
<td>$N$ 26</td>
<td>27</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>$H$ 0.923</td>
<td>0.920</td>
<td>0.958</td>
</tr>
<tr>
<td></td>
<td>$n_a$ 13</td>
<td>9</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>$a$ 0.250</td>
<td>0.200</td>
<td>0.167</td>
</tr>
<tr>
<td></td>
<td>$N$ 26</td>
<td>29</td>
<td>26</td>
</tr>
<tr>
<td>$P64a5$</td>
<td>$H$ 0.923</td>
<td>0.923</td>
<td>0.792</td>
</tr>
<tr>
<td></td>
<td>$n_a$ 9</td>
<td>11</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>$a$ 0.173</td>
<td>0.212</td>
<td>0.207</td>
</tr>
<tr>
<td></td>
<td>$N$ 25</td>
<td>30</td>
<td>25</td>
</tr>
<tr>
<td>$P64a6$</td>
<td>$H$ 0.864</td>
<td>0.810</td>
<td>0.966</td>
</tr>
<tr>
<td></td>
<td>$n_a$ 19</td>
<td>27</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>$a$ 0.380</td>
<td>0.500</td>
<td>0.540</td>
</tr>
</tbody>
</table>

Table 4). Additionally, there was no difference in allelic diversity among the three populations (combined $\chi^2 = 1.60$, $P>0.90$; Table 4).

DISCUSSION

The two populations studied here showed significantly different levels of extra-pair paternity. The frequency of extra-pair paternity in the Kentucky population was closely consistent with that in four other populations of house sparrows, supporting the assertion that in general extra-pair paternity is a species characteristic (Owens & Hartley, 1998). However, the Lundy population exhibited a significantly lower level than all the other house sparrow populations that have been studied to date. No difference was found in the level of genetic variation within the Lundy and Kentucky populations. In addition, there was no difference between these two and a third population (Nottingham), which we expect to be typical of the British mainland and therefore representative of the population from which each of the others were founded (see below). In a study of variability at allozyme loci, Parkin and Cole (1984) found rather little differentiation among British mainland populations.

The cause underlying the significantly lower level of extra-pair paternity of the Lundy population is not apparent. However, this study finds no support for the idea of density-dependence (see Westneat & Sherman, 1997). Pairs bred at high density in all of the populations. There were no detectable differences in the average breeding densities (Table 3), and the spatial distribution of nestboxes at the Lundy, Kentucky and Nottingham sites was highly comparable (TB & IRKS, pers. obs.). Unlike those passerines in which the effects of density on extra-pair paternity have been reported (Bjornstad & Lifjeld, 1997, and see Westneat & Sherman, 1997), male house sparrows do not establish breeding territories and there is a general mixing of all adults throughout the breeding season. Presumably this would provide
a female with ample opportunity to seek extra-pair matings. It may be expected therefore that in this species the density of nest sites will have little bearing on the level of extra-pair paternity.

There were no obvious fundamental differences in the basic ecology of the house sparrows in each of the six populations that might explain the difference in the level of extra-pair paternity. Although there will be slight differences, for example, in the food species exploited and species of predators present, it is difficult to see how such factors might account for a profound difference in the breeding biology. Additionally, the Nottingham and Lundy populations share essentially the same ecological environment.

Other factors have been proposed to explain why populations within a species may exhibit different levels of extra-pair paternity; for example, the degree of breeding synchrony within a population (Stutchbury & Morton, 1995), the levels of infertility (Wetton & Parkin, 1991), and the phenotypic variance of individuals within a population (Petrie & Lipsitch, 1994). There have been few unequivocal demonstrations supporting these ideas in any species and it is unlikely that the Lundy population would differ significantly, in the predicted direction, from the other populations with respect to any of these factors.

For example, if there had been a difference in the level of infertility between populations, Lundy might be expected to have had a higher incidence of infertility caused by occasional inbreeding or the accumulation of deleterious recessives. If it were to have an effect, this should have produced a higher level of extra-pair paternity on Lundy.

It is difficult to compare phenotypic data between the separate populations used in this study, due to different measurement techniques and samplers. However, we found no significant differences between the Lundy population of males and another mainland population living in Leicestershire (UK), with respect to the mean, and variance, of body mass, tarsus length and badge size (all individuals measured by SCG, unpublished data).

Asynchrony of breeding is unlikely to determine the level of extra-pair paternity in house sparrows for several reasons. They have an extended breeding season, with most pairs in each of the populations attempting at least three clutches. Even if all pairs start breeding synchronously, stochastic effects (failure of an attempt or the differing time it takes to rear small and large broods) lead to asynchrony. For this reason, and as whole breeding populations live as a freely mixing colony, there will always be some reproductively active males available for females seeking extra-pair copulations. Not surprisingly, we found no evidence for consistent differences in the degree of breeding synchrony between the two main study populations; furthermore, it is difficult to envisage what factor might have caused a consistent difference in breeding synchrony across both years and all clutches.

The single feature that clearly sets the Lundy population apart from the other five is its ecological isolation on an island. Due to a combination of founder effects, inbreeding, genetic drift, and low rates of dispersal, it is generally expected that island populations will have reduced genetic variability (Wright, 1931; Jaenike, 1973). Indeed, a recent comparative survey across many taxa reports this to be generally true for birds (Frankham, 1997). Therefore, superficially, the low level of extra-pair paternity on Lundy might appear to support the predicted relationship between extra-pair paternity and genetic diversity proposed by Petrie & Lipsitch (1994). However, our examination of the degree of genetic variation in Nottingham,
Kentucky and Lundy found no difference between the populations and therefore no relationship between extra-pair paternity and genetic variation.

The genetic homogeneity of the Nottingham, Lundy and Kentucky populations is interesting in itself given the history of the three populations. The individuals within the Nottingham population are part of the very large continuous British mainland breeding population estimated to be between 4 and 6 million pairs (Gibbons et al., 1993). It was from this population that individuals were taken for introduction onto the American continent (Long, 1981). Whether the current population of the US exhibits a comparable level of genetic variation to the parent population will depend on the numbers of individuals released and their subsequent survival, the origin of those individuals and the subsequent growth of the population. The large size of the initial introduced populations (totalling at least several hundred; Long, 1981) may have been sufficient to ensure that the majority of the variation in the parental population was transferred to North America.

Given that the Lundy population is ecologically isolated it is perhaps surprising that the level of genetic variation was found to be no different to that in the two mainland populations. There are perhaps several reasons for this finding. Firstly, although ecologically isolated (20 km from mainland), with a maximum of perhaps two immigrants annually, the population is probably not effectively genetically isolated. From Wright’s island model (Wright, 1931), we know that the difference in gene frequency between two populations will be reduced by the factor \((1-m)^2\), where \(m\) is the migration rate, in each generation. Consequently, a small rate of migration is sufficient to prevent genetic differentiation between two populations (see Hartl & Clark, 1989). As in other vertebrates, dispersal in house sparrows is predominantly in the first year of life (Summers-Smith, 1963). About two-thirds of fledglings that survive until the main period of dispersal in the autumn will survive to reproduce in the following spring, and as the annual adult survival rate is about 60%, the typical adult sparrow will reproduce for three seasons (Summers-Smith, 1963). The observed mean level of immigration (0.75 individuals every year), allowing for some mortality, will therefore equate to about 0.5 reproductive adults per year or about 1.5 immigrants per generation. This rate of migration should be sufficient to prevent significant divergence in allele frequencies occurring between the Lundy and mainland populations due to genetic drift (Allendorf, 1983).

Secondly, the microsatellite markers that were used to investigate the level of genetic variation are probably selectively neutral and are likely to have a higher mutation rate than other regions of the genome (Dallas, 1992). The combined effects of these characteristics will mean that following a genetic bottleneck there will be a faster recovery of variation at these regions of the genome than at those under selection. However, the speed at which genetic variation within a population will accumulate at microsatellite loci will of course depend on the mutation rate at each locus. From Wright (1931, 1969), the fixation index \(F = \frac{1}{4N(m+\mu)} + 1\) where \(N\) is the effective population size and \(\mu\) is the rate of reversible mutation. We have already argued that the number of immigrants per generation, \(Nm\), is approximately one. The effective population size will be less than the actual population size and is therefore unlikely to have exceeded about 80 (40 breeding pairs), giving an \(m\) of about 0.02. We know that one house sparrow microsatellite locus (Pdo4) has an exceptionally high mutation rate (0.022, 95% c.i. 0.068–0.004; Neumann & Wetton, 1996), comparable to the rate of migration. In the case of this locus, therefore, the high frequency of mutation alone might have prevented detectable differentiation.
between the Lundy and mainland populations; for this reason, we did not use locus Pldop4 in our analysis of genetic variation. Although very high relative to other locations in the genome, microsatellite mutation rates in general are of the order of $10^{-4}$-$10^{-3}$ (Dallas, 1992), several orders of magnitude smaller than our estimate of $m$. We therefore expect migration to be the factor that has had most influence on maintaining a high level of genetic variability on Lundy.

Although the analysis of genetic variation involved only three loci, the moderately large numbers of alleles at these loci potentially make them especially sensitive to any difference in genetic variability. There was no suggestion of a difference between Lundy and the other two populations. This indicates that overall genetic variability is not the underlying cause of the observed difference in the level of extra-pair paternity.

While a small rate of migration can prevent fixation due to drift at neutral loci, it might not be sufficient to prevent fixation at loci under selection. For the latter to occur, we would have to suppose that the selection acting on Lundy was either more consistent or stronger than that operating on the mainland. If this were the case, then it is quite conceivable that the selection at a single locus might outweigh the countervailing pressure due to an $m$ of 0.02. However, it seems probable that mate choice is mediated by a suite of morphological traits, and such traits are known to be influenced by a large number, perhaps many tens, of loci (Hartl & Clark, 1989), making homogenizing selection much less likely.

The failure of the current hypotheses to explain the variation observed in the level of extra-pair paternity in the Lundy population and other populations of house sparrows will we hope stimulate some fresh alternatives. A recent comparative analysis suggests that there is an ‘island effect’ on the level of extra-pair paternity (S. Griffith, personal obs.). One possibility is that the costs of indulging in extra-pair paternity are proportionately higher for island-dwelling females, perhaps because reproduction is more difficult and male help (which may be positively related to a male’s certainty of paternity; Dixon et al., 1994, Sheldon & Ellegren, 1998) is more crucial due to ecological constraints. We cannot exclude the possibility that genetic variation contributes to this phenomenon in some species (Petrie & Lipsitch, 1994), but our results in the house sparrow suggest that this is not necessarily the cause. Finally, if there is an effect of genetic variation on mate choice, then it seems unlikely to be determined by general genomic variation, but instead by variation at specific loci under selection. In a reasonably panmictic population, it is unlikely that such loci would be sufficiently tightly linked to marker loci for significant linkage disequilibria to occur. Investigation of a more precise hypothesis concerning the genetic variation at functional loci would require a knowledge of the many loci affecting the traits used in mate choice; this is well beyond our current understanding.

ACKNOWLEDGEMENTS

We thank the Landmark Trust, and Dave Westneat and the University of Kentucky for access to the Lundy and Kentucky field sites, respectively; Rebecca Kimball, David Parkin and José Veiga, for allowing us to consult unpublished data and manuscripts; Paula Smith for assistance in the lab; and Ben Sheldon for comments on the manuscript. This work was supported by NERC studentships (SCG and IRKS) and grants from the NERC and BBSRC.
REFERENCES


