

Genetic similarity, breeding distribution range and sexual selection

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Abstract

Large populations with extensive breeding distributions may sustain greater genetic variability, thus producing a positive relationship between genetic variation and population size. Levels of genetic variability may also be affected by sexual selection, which could either reduce levels because a small fraction of males contribute to the following generation, or augment them by generating genetic variability through elevated rates of mutations. We investigated to what extent genetic variability, as estimated from band sharing coefficients for minisatellite markers, could be predicted by breeding distribution range, population size and intensity of sexual selection (as reflected by degree of polygyny and extra-pair paternity). Across a sample of 62 species of birds in the Western Palearctic, we found extensive interspecific variation in band sharing coefficients. High band sharing coefficients (implying low local genetic variability among individuals) were associated with restricted breeding distributions, a conclusion confirmed by analysis of statistically independent linear contrasts. Independently, species with large population sizes had small band sharing coefficients. Furthermore, bird species with a high richness of subspecies for their breeding distribution range had higher band sharing coefficients. Finally, bird species with high levels of polygyny and extra-pair paternity had small band sharing coefficients. These results suggest that breeding distribution range, population size and intensity of sexual selection are important predictors of levels of genetic variability in extant populations.

Introduction

Species differ in the amount of genetic variability they harbour, and as genetic variability provides the raw material for evolutionary change, identifying the correlates of such differences is of interest both to evolutionary theory and to conservation. Some predictions of factors expected to affect genetic variability between species can be made. First, population size, as it reflects the number of individuals potentially making a genetic contribution to the subsequent generation. Second, extent of breeding distribution range, as it reflects the diversity of

environmental conditions experienced by a species. Third, sexual selection, as it might either erode genetic variability by reducing the variance in genetic contribution to the next generation (Roff, 1997), or increase it by causing elevated mutation rates (Møller & Cuervo, 2004; Petrie & Roberts, 2007). All these factors contributing to genetic variation are potentially confounded, and we treat each of these in the following paragraphs.

Breeding distribution range and population size are expected to affect the level of genetic variability for a number of reasons. First, widely distributed species with large populations will be more likely to experience environmental factors causing population subdivision and isolation, and hence divergence through drift. For example, more widely distributed species have a larger number of morphologically clearly identifiable subspecies than less widely distributed species, and such subdivision

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is also associated with reduced dispersal rate (Belliere *et al.*, 2002). Such subdivision of a global population creates many smaller subunits that each will be affected by increased levels of erosion of genetic variability due to each having a relatively small population size. Second, a large area of breeding distribution will generally provide more heterogeneity in selection pressures and hence greater differences in local adaptation. Such balancing selection can play an important role in maintaining genetic variation (Charlesworth & Hughes, 2000). For example, patterns of sexual selection in the barn swallow *Hirundo rustica* across the Western Palearctic are consistently directional by favouring long tails in males, although the intensity of selection shows a high degree of consistency in different sites (Møller *et al.*, 2006). Third, large populations may give rise to a larger number of heterozygous loci because the product of effective population size and mutation rate determines the level of standing genetic variation [which under certain assumptions can be approximated as $4N(e)\mu$, where $N(e)$ is the migration effective population size and μ designates the total mutation rate per gene; Nagylaki, 1998; Wakeley, 1998]. Because all populations are finite, genetic variability will be eroded with time through genetic drift, even in large populations. Therefore, the null expectation is that large populations will maintain greater levels of genetic variation than small populations. Thus, we can expect genetic variability to increase with breeding distribution area (because a larger breeding distribution due to smaller effects of drift in a large population will cause less erosion of genetic variation), heterogeneity in selection pressures across the breeding distribution range, and mutation rate. However, there are to the best of our knowledge no comparative studies of these predicted relationships.

Variance in mating success among males increases the intensity of sexual selection, reduces effective population size and reduces population levels of genetic variability due to fixation of alleles, as described by the so-called lek paradox (Borgia, 1979; Taylor & Williams, 1982). Extra-pair paternity (in contrast to genetic monogamy) increases the variance in reproductive success among males, predicting a reduction in genetic variation with higher levels of extra-pair paternity. Surprisingly, previous studies of extra-pair paternity and genetic variability in birds have shown that genetic variability in fact increases with the degree of extra-pair paternity across species (Petrie *et al.*, 1998). This poses the question of what mechanism is responsible for the generation of elevated genetic variability in species with the most intense sexual selection. Although mutation usually has slightly deleterious effects (review in Lynch *et al.*, 1999), mutation rates may evolve because the costs and benefits of mutations allow mutator alleles to accumulate (Taddei *et al.*, 1997). Mutation rates in sexually reproducing organisms are traditionally considered to be minimized because associations between mutability genes and

beneficial genetic variants tend to be broken up by recombination (Taddei *et al.*, 1997). However, the mutation rate is not necessarily at a minimum, because it may be greater in species with intense sexual selection. Intense sperm competition, an important component of sexual selection (review in Birkhead & Møller, 1998), may lead to an elevated male mutation rate (Møller & Cuervo, 2004; Petrie & Roberts, 2007). Increased sperm production is preceded by an increase in the number of mitotic germline cell divisions in the testes, probably resulting in a higher number of replication-dependent mutations per generation. The observed difference in mutation rate between the sexes (Miyata *et al.*, 1987; Ellegren & Fridolfsson, 1997; Bartosch-Härlid *et al.*, 2003) is likely to be due to similar differences in germline mitoses. Increased germline mitotic and meiotic rates may constrain the fidelity of replication, repair or recombination on a per division basis. Thus, mutational input for viability traits may increase as a direct consequence of intense sperm competition, and this may suffice to maintain genetic variability in fitness. Therefore, females may be able to continuously choose mates with high, genetically based viability if the mutational input increases with the intensity of sexual selection. Consistent with these arguments, Møller & Cuervo (2004) found that minisatellite mutation rates increased by a factor of five across rates of extra-pair paternity in birds. These theoretical and empirical arguments suggest that the amount of genetic variability increases with the degree of extra-pair paternity and polygyny.

The aims of this study were to investigate to what extent genetic variability among individuals in free-living breeding populations could be predicted by interspecific variation in population size, breeding distribution range and intensity of sexual selection. We used birds as a model system because standardized information is available on band sharing coefficients between unrelated adults in free-living populations for a large number of species. In addition, highly reliable information on breeding distribution range and population size is available for temperate zone birds. We statistically controlled for body mass as a confounding variable for breeding distribution range and population size (assuming that small species had larger breeding distribution ranges and population sizes than those of large species). In other words, inclusion of body mass as an additional variable tested whether relative breeding distribution range and population size contribute to explaining genetic variation. Furthermore, we controlled statistically for breeding distribution area, when analysing the effects of population size, given that a larger breeding distribution range should allow a larger population size to be maintained, and that population size controlled for breeding distribution range provides an estimate of local population density. In this context, it is important to note that Brown & Lomolino (1998) have shown that local and global population size is positively correlated across bird

species. We tested for the effects of sexual selection on genetic variation by using the frequency of polygyny and extra-pair paternity as estimates of the intensity of sexual selection (Andersson, 1994; Møller & Birkhead, 1998). The frequency of polygyny is an important measure of the intensity of sexual selection (Bateman, 1948; Payne, 1984). Likewise, studies of extra-pair paternity have shown that the variance in male reproductive success increases with the level of extra-pair paternity across species (Møller & Cuervo, 1998). Finally, we tested whether species with a high degree of morphological differentiation, as reflected by the number of subspecies, had a lower degree of genetic variability than species with little differentiation. We assumed that a high degree of differentiation would reflect a reduction in gene flow among populations since if that were not the case, morphological differentiation of subspecies would not be maintained. This assumption is supported by the observation that the number of subspecies per unit area is associated with a reduction in the extent of gene flow as reflected by geometric mean dispersal distance (Belliere *et al.*, 2000). A high degree of differentiation as reflected by subspecies richness would imply that local effective population size of a given species would be reduced compared to the situation when extensive dispersal allows genes to migrate freely within the entire range of a species.

We could not directly test whether band sharing coefficients were related to effective population sizes [population size corrected for unequal sex ratio, uneven family size, nonrandom mating, fluctuations in population size and many other factors (Roff, 1997)], because information on effective population size is only available for a handful of species. However, the magnitude of population fluctuations is an important factor reducing effective population size because it is the smallest size of a population that has a disproportionate effect on the genetic contribution to the next generation (Roff, 1997; Hartl & Jones, 2005). Such population fluctuations are determined by population growth rate and density dependence, and equal demographic and environmental stochasticity (Lande *et al.*, 2003). Recently, Sæther *et al.* (2005) showed across a sample of bird species that time to extinction was a decreasing function of clutch size through the effect of the latter (or the suite of life history traits with which it is correlated) on demographic stochasticity. We used this knowledge to make the prediction that if effective population size was an important determinant of band sharing in different species, then species with large clutch sizes should have greater fluctuations in observed population size and hence have smaller ratios of effective population sizes to observed population sizes than species with small clutch sizes. Thus, controlling the relationship between population size and band sharing for clutch size should remove the main effect of demographic stochasticity on genetic variability, and any remaining relationship between

band sharing and population size should be attributable to other factors such as reduced genetic variability due to genetic bottlenecks.

Materials and methods

Study species

We included all species with a breeding distribution within the Western Palearctic for which there was published information on band sharing coefficients. Although band sharing coefficients were available for many species from other geographical regions, these could not be included because we had no information on population size. Hagemeyer & Blair (1997) provided estimates of population sizes for all species in the Western Palearctic, all obtained in a consistent way, allowing for easy interspecific comparison. In addition, restricting the study to this region allowed us to extract information on breeding distribution area in a consistent manner, and to use information on phenotypic characteristics of species from a single source (Cramp & Perrins, 1977–1994). Again, this should make the comparative study homogeneous with respect to the sources of data. All species included had large, continental breeding distributions, removing any effects of island breeding distributions that are characterized by reductions in genetic variability in birds (Møller, 2001).

Estimating genetic variability

We did not have any direct estimates of local genetic variability, but instead used the inverse of genetic variability, genetic similarity among individuals, as a metric that would allow analysis of the predictions. We estimated genetic similarity for 62 species as the published band sharing coefficients between adults in a breeding population (usually dyads of pair members, but in cases where dyads of random adults in the population were also compared, results were very similar). Thus, band sharing coefficients and total number of bands were recorded from local populations that at most covered a few square kilometres, derived from an extensive survey of the literature using the Web of Science (2005) as a source, and all references are reported by Spottiswoode & Møller (2004) with the exception of those listed in the Appendix. Spottiswoode & Møller (2004) analysed hatching failure in relation to band sharing coefficients, taking care to match estimates of hatching success and band sharing coefficients from exactly the same study populations whenever possible. Here, we include all estimates of band sharing to ensure the most extensive coverage possible. However, we did not include estimates for populations that had recently gone through bottlenecks such as house sparrows *Passer domesticus* from North America or the great reed warbler *Acrocephalus arundinaceus* from Lake Kvismaren, Sweden.

The band sharing coefficient is an estimate of the number of shared minisatellite bands in relation to the total number of bands among adults, originally proposed by Wetton *et al.* (1987) as a measure of genetic similarity. A high band sharing coefficient implies that many bands are shared among individuals and hence that the genetic similarity in the population is relatively high. This estimate of band sharing has commonly been used as an index of genetic similarity among individuals within a species (Reeve *et al.*, 1990; Hoelzel, 1992; Blomqvist *et al.*, 2002). Here, we use species-specific mean band sharing values for comparative purposes. This approach is supported firstly by the highly significant repeatability (Becker, 1984) of band sharing coefficients among studies of the same species, based on 25 studies of nine species [$R = 0.55$ (SE = 0.20), $F_{8,16} = 3.90$, $P = 0.0099$; see also Møller (2001) and Spottiswoode & Møller (2004)]. This result demonstrates that band sharing estimates are consistent between populations of the same species when compared to variation between species. Secondly, Papangelou *et al.* (1998) have shown in a review of 129 published studies of 70 bird species that mean band sharing between dyads of unrelated individuals from populations or species defined as outbred on the basis of independent evidence was nearly 50% smaller than that for populations defined as small or inbred. In addition, mean band sharing between dyads of unrelated individuals in small or inbred populations was similar to that for dyads of first-order relatives in outbred populations (Papangelou *et al.*, 1998). This implies that mean band sharing coefficients of populations consistently reflect whether there is a high degree of genetic similarity within a species.

The number of fingerprinting probes ranged from one to three per study (mainly the minisatellite probes 33.15 and 33.36, but also *per*, M13 and others). This could potentially cause heterogeneity in estimates among analyses. Repeatability of band sharing coefficients among different probes used in the same study, based on 47 studies of 20 species, was highly significant [$R = 0.86$ (SE = 0.06), $F_{19,27} = 17.16$, $P < 0.0001$; see also Møller (2001) and Spottiswoode & Møller (2004)], suggesting that multiple probes should not cause any bias. Finally, band sharing coefficients were independent of the number of bands scored (Møller, 2001).

Estimating breeding distribution areas

We measured geographical range size in two ways that differed in degree of accuracy, and compared the resulting estimates. First, we estimated range size in the Western Palearctic alone by extracting files with breeding distributions of the species in the Western Palearctic from the electronic version of Cramp & Perrins (1977–1994). These are shown on the same standard map, making comparison of breeding distribution areas meaningful. We imported these maps into Adobe Photoshop, where

we saved them in exactly the same dimensions in separate files. We imported files containing single distribution patches in one colour into the program Image from NIH. In this program, we estimated the number of pixels occupied by the breeding distribution. Finally, we converted the number of pixels to square kilometre by estimating the area of five islands and peninsulas of known size: the British Isles, Iceland, Svalbard, Novaya Zemlya and the Iberian peninsula, using the same map as a reference.

Second, we estimated the total world geographical range of each species as the area of the shape bounded by the greatest span of latitude and longitude of each species' breeding range, as published in Cramp & Perrins (1977–1994). To take into account the curvature of the earth (which was assumed to be spherical), this area was estimated by the equation:

$$Area = R^2 \times (Longitude_1 - Longitude_2) \times [\sin(Latitude_1) - \sin(Latitude_2)],$$

where R is the radius of the earth (6366.2 km) and latitude and longitude are expressed in radians.

In widespread species Old and New World ranges were calculated separately and subsequently summed to exclude the area of the North Atlantic. The method proposed here over-estimates true geographical range due to inclusion of areas covered with water and due to the fact that breeding distribution borders are not straight lines, but the error should be random with respect to the variables under test. This estimate of total area was strongly positively correlated with geographical range size as calculated by counting one-degree grid cells overlain on published breeding distribution maps for a sample of 20 Palearctic and Nearctic bird species ($r = 0.871$, $P < 0.001$), and with range size as reported for a sample of 11 threatened species (Stattersfield & Capper, 2000) ($r = 0.976$, $P < 0.001$, based on log-transformed data).

Population size estimates

Population sizes were obtained from Hagemeyer & Blair (1997), who reported minimum, maximum and mean total number of breeding pairs in the Western Palearctic west of the Ural Mountains, obtained in a consistent way from national bird census programs in all countries. We used the mean of the minimum and maximum estimates in that source.

Sexual selection and life history

Data on extra-pair paternity reported as the proportion of offspring that were extra-pair offspring were obtained from Griffith *et al.* (2002) combined with more recently obtained information from the primary literature. If more than one estimate was available, we used the mean

weighted by sample size for the analyses, as data relying on larger sample sizes are more reliable than data from small samples.

The frequency of polygyny was estimated as the proportion of polygynous males in population studies, as reported by Cramp & Perrins (1977–1994). There was no significant relationship between polygyny and extra-pair paternity ($F_{1,58} = 0.11$, $P = 0.74$) indicating that the two estimates of sexual selection may reflect different phenomena. Extra-pair paternity may mirror the intensity of sperm competition, while polygyny involves factors that are shaped by sexual selection at the social level.

Data on mean clutch size were extracted from Cramp & Perrins (1977–1994), and if more than a single estimate was reported, we used the first mean estimate.

The number of subspecies was extracted from Cramp & Perrins (1977–1994). There are strong negative correlations between the relative number of subspecies and migratory habits and dispersal distance respectively (Belliere *et al.*, 2000). Hence, we did not include variables reflecting migratory habits and dispersal habits in the analyses.

Body mass was recorded as the mean mass of males and females from the breeding season, as reported by Cramp & Perrins (1977–1994). If more than a single estimate was reported, we used the mean values from the UK.

Comparative analyses

We \log_{10} -transformed breeding distribution area, population size, number of subspecies and clutch size, while the proportions polygyny, extra-pair paternity and band sharing were square-root arcsine-transformed before analyses.

We present analyses of band sharing coefficients predicted by breeding distribution area and population size separately and by both factors combined in a full model to provide readers with transparency concerning the effects of different variables. We only had information on population size from the Western Palearctic, whereas we had information on breeding distribution area from both the Western Palearctic and the total breeding distribution range. Hence, we were forced to analyse the independent effects of population size and breeding distribution area using data from the Western Palearctic, while we were able to analyse the effects of global breeding distribution area in a separate analysis.

Analyses of comparative data based on single species may provide misleading conclusions if sister taxa are more similar with respect to the variables under investigation than randomly chosen species. We used statistically independent standardized linear contrasts (Felsenstein, 1985), which controls for similarity among species due to common descent. The contrasts

were calculated using the software of Purvis & Rambaut (1995), implemented in the computer program *CAIC*. All regressions were forced through the origin (Garland *et al.*, 1992), as the dependent variable is not expected to have changed when the independent variable(s) has not changed (Felsenstein, 1985). Standardization of contrast values was checked by examination of absolute values of standardized contrasts vs. their standard deviations (Garland, 1992; Garland *et al.*, 1992). Plotting the resulting contrasts against the variances of the corresponding nodes revealed that these transformations made the variables suitable for regression analyses except band sharing. Alternative approaches, such as nonparametric statistics on the contrasts, and other phylogenetic methods gave very similar results.

Comparative analyses rely on a phylogenetic hypothesis. We used a composite phylogeny created by using information from Sibley & Ahlquist (1990). This phylogeny for higher taxa was supplemented with information from other sources to resolve relationships between species (Sheldon *et al.*, 1992; Seibold *et al.*, 1993; Leisler *et al.*, 1997; Cibois & Pasquet, 1999), which provided us with a tree containing dichotomous nodes only (Fig. 1). We applied branch lengths from the tapestry tree of Sibley & Ahlquist (1990) for higher taxonomic levels. Within families, the distance between different genera was set to 3.4 $\Delta T_{50}H$ units, and between species within genera to 1.1 $\Delta T_{50}H$ units (Sibley & Ahlquist, 1990; Bennett & Owens, 2002). We re-did the analyses using the taxonomy of Howard & Moore (1991), but that did not change the conclusions, suggesting that the findings were robust to changes in topology of the tree.

Statistical analyses of species-specific data and contrasts were based on Akaike's information criterion (AIC) as an estimate of the improvement in fit for addition of variables (Burnham & Anderson, 1998). In brief, we compared AIC for models with and without a specific variable. Delta AIC was defined as the change in AIC between the full model and the model excluding a given variable, and we adopted the criterion that a delta AIC >2.00 was indicative of an important effect of a variable on model fit (Burnham & Anderson, 1998).

Regression analyses require that models are not over-parameterized relative to the number of observations in the data set (Neter *et al.*, 1989; Sokal & Rohlf, 1995; Zar, 1996). Therefore, we attempted to reduce the number of variables as much as possible to strike a balance between having exhaustive models and models with a reasonable number of predictor variables. We made preliminary analyses of the number of minisatellite probes, the number of bands scored, and the number of individuals sampled, and none of these variables explained significant amounts of variance. Hence, we excluded these variables from all subsequent analyses. Likewise, we did

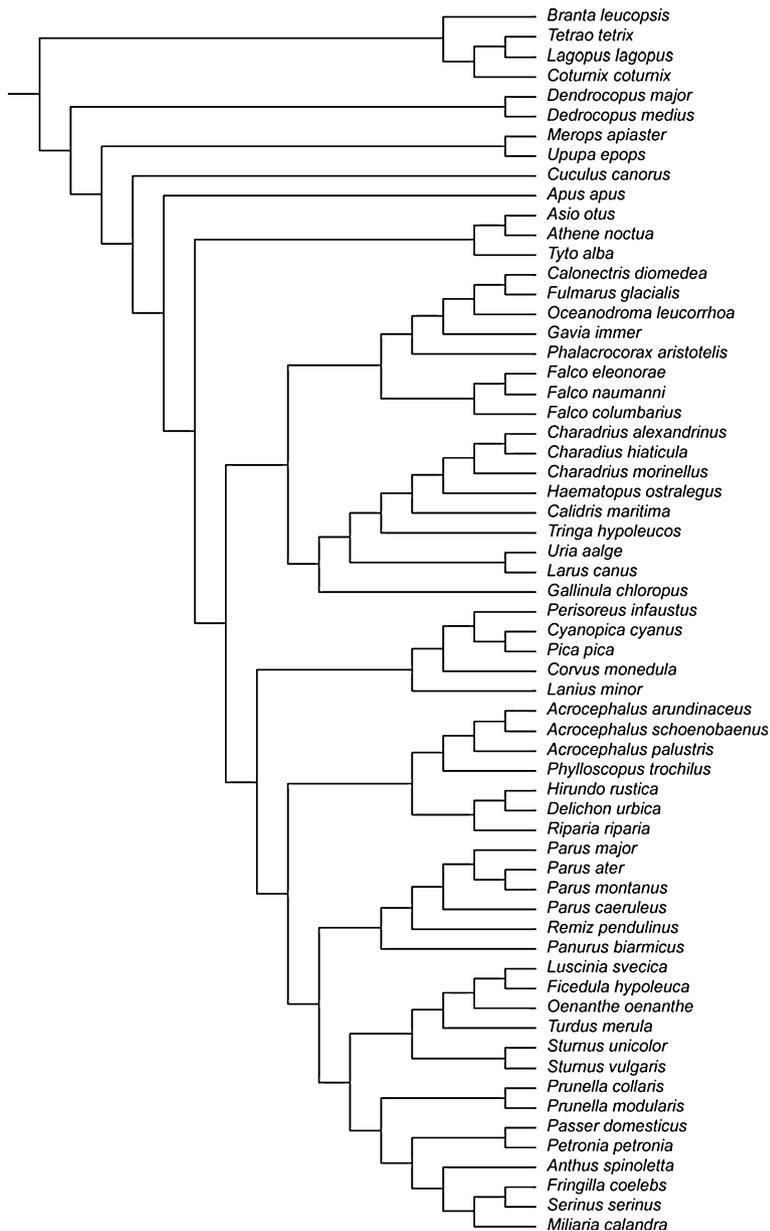


Fig. 1 Phylogeny of the species used in the analysis of population consequences of band sharing. The tree shows the topology obtained from a number of sources, as reported in Materials and methods.

not include information on migration distance and dispersal distance in the analyses, because the variable number of subspecies also included information on that aspect (see Belliure *et al.* (2000) for evidence), and it would have caused statistical problems due to multicollinearity.

In the analyses of population size, we controlled for breeding distribution area in the Western Palearctic by entering breeding distribution area as an additional predictor variable because population size estimates derived from that particular region, and because population size by necessity must be controlled statistically for differences in range size. Furthermore, population size

controlled for breeding distribution area provides an estimate of local population size.

Results

Band sharing and breeding distribution area

The total breeding distribution area of the 62 different species was on average 50.4×10^6 km² (SE = 4.6×10^6) with a range from 1.7×10^6 to 190.0×10^6 km². Breeding distribution area in the Western Palearctic varied from 1.19×10^6 to 82.85×10^6 km² [mean (SE) = 16.16×10^6 (1.27×10^6) km²] and was a strong predictor

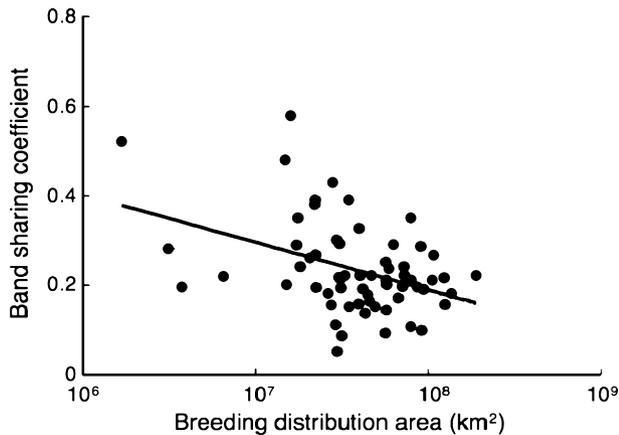


Fig. 2 Band sharing coefficients in relation to area of breeding distribution (km^2) in different species of birds. The line shows the logarithmic relationship.

of total breeding distribution area [$F_{1,60} = 110.12$, $r^2 = 0.64$, $P < 0.0001$, slope (SE) = 1.170 (0.112)]. Subsequently in this section, we present analyses that are based on total breeding distribution area. The band sharing coefficient was on average 0.234 (SE = 0.013), range 0.050–0.580.

Band sharing coefficients decreased with total breeding distribution area across species [Fig. 2; linear regression: $F_{1,60} = 10.15$, $r^2 = 0.14$, $P = 0.0023$, slope (SE) = -0.118 (0.037)]. This relationship remained significant when the effect of common ancestry was controlled statistically [linear regression forced through the origin and based on the phylogenetically independent contrasts: $F_{1,60} = 12.01$, $r^2 = 0.17$, $P = 0.0010$, slope (SE) = -0.122 (0.035)]. The predicted band sharing coefficient decreased from 0.37 to 0.16 across the range of recorded breeding distribution areas in this study.

Table 1 Multiple linear regressions between band sharing coefficient (dependent variable) and total breeding distribution area, body mass, polygyny and extra-pair paternity (independent variables).

Variable	Sum of squares	d.f.	F	P-value	Slope (SE)	Delta AIC
(A) Species						
Breeding distribution area	0.150	1	12.84	0.0007	-0.130 (0.036)	10.20
Polygyny	0.073	1	6.23	0.015	-0.136 (0.054)	5.80
Error	0.677	58				
(B) Contrasts						
Breeding distribution area	0.031	1	10.46	0.0021	-0.109 (0.034)	8.27
Body mass	0.014	1	4.82	0.032	-0.079 (0.036)	2.95
Polygyny	0.019	1	6.49	0.014	-0.163 (0.060)	4.58
Extra-pair paternity	0.014	1	4.71	0.034	-0.171 (0.079)	2.85
Error	0.161	55				

AIC, Akaike's information criterion.

The regression models had the statistics for (A) species $F = 8.53$, d.f. = 2,58, $r^2 = 0.13$, $P = 0.0006$, AIC = -268.54 and (B) contrasts $F = 7.34$, d.f. = 4,55, $r^2 = 0.12$, $P < 0.0001$, AIC = -340.50 .

Delta AIC is the change in AIC between the best-fit model and the model excluding a given variable.

In an analysis of the effects of extra-pair paternity and polygyny as predictors for species-specific data, only polygyny entered as a predictor according to the AIC criterion (Table 1A). The partial regression for total breeding distribution area explained most of the variation (Table 1A), with additional variance explained by polygyny (Table 1A). An analysis of independent contrasts produced a model that explained 12% of the variance (Table 1B). Total breeding distribution area was still the best predictor of the band sharing coefficient (Table 1B), with additional negative effects of body mass, polygyny and extra-pair paternity (Table 1B).

Band sharing and population size

Population size for the different species in the Western Palearctic was on average 11.9×10^6 pairs (SE = 3.2×10^6), range 3×10^2 – 120×10^6 . Population size increased with Western Palearctic breeding distribution area [linear regression based on log-transformed population size and breeding distribution area: $F_{1,56} = 9.55$, $r^2 = 0.15$, $P = 0.0031$, slope (SE) = 1.581 (0.511)], and a similar relationship was found after adjusting for log-transformed body mass [partial regression for breeding distribution area: $F = 6.54$, d.f. = 1,55, $r^2 = 0.11$, $P = 0.013$, slope (SE) = 1.164 (0.455)].

Band sharing coefficient decreased significantly with population size in the Western Palearctic adjusted for body mass [Fig. 3; partial regression: $F_{1,59} = 4.86$, $r^2 = 0.08$, $P = 0.031$, slope (SE) = -0.035 (0.016)]; analysis based on independent contrasts: $F_{1,59} = 11.99$, $r^2 = 0.17$, $P = 0.001$, slope (SE) = -0.059 (0.017)]. This relationship was robust to extreme data points as shown when the ranked values of contrasts of population size were used in the analyses [$F_{1,58} = 9.25$, $r^2 = 0.14$, $P = 0.0035$, slope (SE) = -0.0013 (0.00004)].

We made a full model with band sharing coefficient as the dependent variable and breeding distribution area in

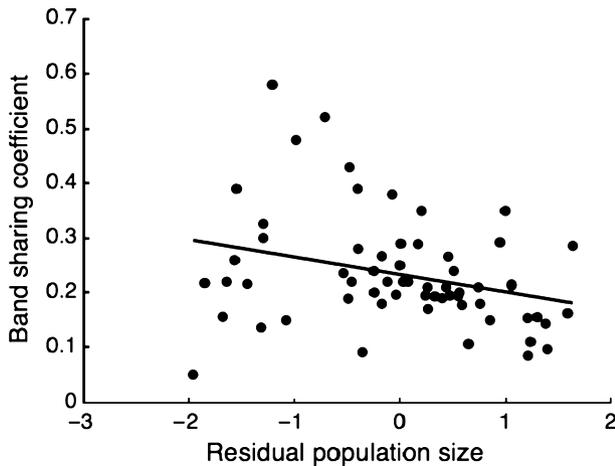


Fig. 3 Band sharing coefficients in relation to breeding population size in different species of birds, after adjusting for body mass. The line shows the linear relationship.

the Western Palearctic, population size in the Western Palearctic, body mass, extra-pair paternity, polygyny, clutch size and number of subspecies as additional predictor variables (Table 2A). Clutch size, extra-pair paternity, body mass and population size in Western Palearctic did not enter as predictors in the best-fit model based on species. The final model based on species-specific data explained 31% of the variance (Table 2A). Breeding distribution area in the Western Palearctic was larger in species with smaller band sharing coefficients (Table 2A). In addition, species with a large number of subspecies had larger band sharing coefficients (Table 2A). Finally, species with a high degree of polygyny had smaller band sharing coefficients (Table 2A).

An analysis of contrasts revealed a model that explained 14% of the variance in band sharing coefficients (Table 2B). Again, there were significant effects of breeding distribution area as expected, with species with larger breeding distributions having smaller band sharing coefficients (Table 2B). Independently, species with large population sizes for their breeding distribution range and body size had smaller band sharing coefficients (Table 2B). Furthermore, there were independent significant effects of degree of polygyny and extra-pair paternity, with species with more intense sexual selection having smaller band sharing coefficients (Table 2B). Finally, species with subdivided populations as reflected by relative subspecies richness for a given breeding distribution range had large band sharing coefficients (Table 2B). Bird species with large body mass had smaller band sharing coefficients than species with small body mass (Table 2B).

Discussion

The main results of this study were that a measure of local genetic similarity among adult breeders was negatively related to the breeding distribution range and population size of 62 species of common Western Palearctic birds, and that the intensity of sexual selection as reflected by degree of polygyny and extra-pair paternity was associated with further reductions in genetic similarity when controlling for similarity due to common descent. Furthermore, subdivision of populations as reflected by relative subspecies richness was associated with increased genetic similarity. These findings were robust to statistical control for covariation between traits, population fluctuations as reflected by clutch size and for similarity among taxa due to common descent. The null

Variable	Sum of squares	d.f.	F	P-value	Slope (SE)	Delta AIC
(A) Species						
Breeding distribution area	0.221	1	20.99	<0.0001	-0.178 (0.039)	17.13
No. subspecies	0.089	1	7.21	0.0094	0.089 (0.033)	5.27
Polygyny	0.098	1	9.28	0.0035	-0.160 (0.053)	7.20
Error	0.619	57				
(B) Contrasts						
Breeding distribution area	0.030	1	12.72	0.0008	-0.130 (0.036)	10.69
Population size	0.016	1	7.00	0.011	-0.043 (0.016)	5.32
No. subspecies	0.025	1	10.46	0.0021	0.110 (0.034)	8.63
Polygyny	0.018	1	7.55	0.0082	-0.149 (0.054)	5.86
Extra-pair paternity	0.019	1	8.16	0.0061	-0.207 (0.073)	6.45
Body mass	0.020	1	8.46	0.0053	-0.095 (0.033)	6.73
Error	0.124	57				

AIC, Akaike's information criterion.

The regression models had the statistics for (A) species $F = 8.70$, d.f. = 3,57, $r^2 = 0.31$, $P < 0.0001$, AIC = -277.81 and (B) contrasts $F = 8.66$, d.f. = 6,53, $r^2 = 0.14$, $P < 0.0001$, AIC = -351.57.

Delta AIC is the change in AIC between the best-fit model and the model excluding a given variable.

Table 2 Multiple linear regressions between band sharing coefficient (dependent variable) and world breeding distribution area, breeding population size in the Western Palearctic, body mass, polygyny, extra-pair paternity, clutch size and number of subspecies (independent variables).

expectation for these relationships were that larger local populations should be genetically more variable, assuming that large population size translates into large effective population size. Sexual selection should either cause a reduction in genetic variability because sexual selection increases the variance in mating success among males and hence effective population size. Alternatively, sexual selection may increase genetic variability if sexual selection causes an increase in mutation rate. In fact, we found an increase in genetic variation associated with sexual selection.

Nagylaki (1998) and Wakeley (1998) predicted that the number of heterozygous loci under certain assumptions is a function of effective population size [$N(e)$] and mutation rate (μ). Therefore, we will briefly discuss factors assumed to affect $N(e)$ and μ . Published estimates of effective population size only exist for a couple of the species included in our study. However, demographically stochastic variation in population size is strongly positively related to clutch size across bird species (Sæther *et al.*, 2005). Because large population fluctuations constitute an important factor reducing effective population size (Roff, 1997; Nagylaki, 1998), and because large reductions in population size are a cause of genetic bottlenecks, we assumed that variation in demographic stochasticity as reflected by clutch size would predict the level of genetic variability. However, population size was not significantly related to clutch size, providing no support for the prediction. We did find that large sized species had lower band sharing coefficients than smaller sized species. This result may appear to be counter-intuitive because large species generally have small population sizes (as we found in the present study). However, large body size is associated with high adult survival rate, long generation times and small clutch sizes, making such species less susceptible to the effects of demographic stochasticity, particularly because the annual probability of mating is much less important for demographic stochasticity as generation time increases (Legendre *et al.*, 1999).

The second component of the equation affecting the number of heterozygous loci is the mutation rate. Mutations are traditionally assumed to be rare and slightly deleterious (review in Lynch *et al.*, 1999). However, sperm competition may increase the mutation rate because elevated sperm production increases the number of germline cell divisions, causing mutation rates to be higher in males than in females (Miyata *et al.*, 1987), as also seen in birds (Ellegren & Fridolfsson, 1997; Bartosch-Härlid *et al.*, 2003). Furthermore, increased germline meiotic and mitotic mutation rates may constrain the fidelity of replication, DNA repair or recombination. Either way mutation rates are supposed to increase with the level of sperm competition. Consistent with this, Møller & Cuervo (2004) found that minisatellite mutation rates increased with increasing extra-pair paternity in birds. Here, we have found that both polygyny and

extra-pair paternity were associated with decreased band sharing coefficients for minisatellite markers across species of birds. The result for polygyny could potentially be reconciled with the theoretical background if the intensity of sperm competition was higher in socially polygynous than that in socially monogamous species, as has actually been reported (Hasselquist & Sherman, 2001).

Different species of birds have a highly variable number of subspecies, which indicates species differ greatly in the degree of intraspecific morphological differentiation they show. Given this and a previous finding that subspecies richness is associated with low dispersal rates (Belliere *et al.*, 2000), species with many subspecies can be expected to have experienced population subdivision and reduced rates of gene flow. As this should tend to erode genetic variability (because large panmictic populations are split into many smaller subpopulations), we predicted that high subspecies richness should be associated with low genetic variability within local populations. In accordance with this prediction, we found a significant positive relationship between relative subspecies richness of birds and band sharing coefficients, which accounted for 16% of the variance in the analysis of contrasts (Table 2B). Previous studies have also shown that higher subspecies richness in birds is associated with the evolution of more exaggerated secondary sexual characters (Møller & Cuervo, 1998), which suggests that sexual selection promotes morphological divergence while reducing genetic variability.

The present study relies on band sharing coefficients for minisatellites to provide a reasonable measure of genetic diversity among local breeding individuals. What is the evidence that this is so? We believe that our estimates of band sharing coefficients are reliable because they showed high repeatability among studies and among minisatellite probes, and because the degree of genetic similarity in populations of some species with high band sharing values can be considered to be high by any measure (Papangelou *et al.*, 1998). Moreover, previous comparative studies have found evidence consistent with the assumption that the band sharing coefficient provides an estimate of the degree of inbreeding (Møller, 2001; Spottiswoode & Møller, 2004), which would not be expected if it provided no biologically meaningful information about genetic similarity. Likewise, we can assume that the estimates of total population size of the different bird species are reliable given the extent of knowledge concerning breeding distribution and population density of the different species [see, e.g. Hagemeyer & Blair (1997) for an extensive discussion of these issues].

In conclusion, we have shown that the breeding distribution range and the population size of common and widespread bird species are correlated with a measure of genetic similarity in local populations, even when considering potentially confounding ecological variables. The intensity of sexual selection was an additional factor associated with a reduction in band sharing coefficients.

These findings have important ecological implications for studies of range size, as well as evolutionary implications for studies of comparative quantitative genetics.

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Appendix

Information on total breeding distribution area (km²), breeding distribution area in the Western Palearctic, mean population size, band sharing coefficient, mean clutch size, mean body mass, degree of polygyny, mean degree of extra-pair paternity and number of subspecies of European bird species. Population size is the mean value of the range. See Material and methods for sources. References for band sharing coefficients are reported by Spottiswoode & Møller (2001) or in the table for additional references.

Species	Total breeding distribution area (km ²)	Western Palearctic breeding distribution area (km ²)	Population size	Band sharing coefficient	Clutch size	Body mass (g)	Polygyny (%)	Extra-pair paternity (%)	No. subspecies	References
<i>Acrocephalus arundinaceus</i>	72532660	15323430	2200000	0.240	4.80	30.3	13.20	4.56	4	
<i>Acrocephalus palustris</i>	15087288	12986580	5000000	0.200	4.30	12.0	4.20	3.05	1	
<i>Acrocephalus schoenobaenus</i>	22251413	16946488	5900000	0.269	4.98	11.9	0.00	7.92	1	
<i>Actitis hypoleuca</i>	58944503	19601138	1520000	0.091	4.00	40.4	0.00	10.32	1	Blomqvist et al. (2002), Mee et al. (2004)
<i>Anthus spinoletta</i>	44557537	18290319	11950000	0.236	5.45	21.5	0.00	5.23	8	
<i>Apus apus</i>	57054530	20857812	595000	0.177	2.40	30.2	0.00	4.55	2	
<i>Asio otus</i>	73165616	14334508	930000	0.250	4.15	284.0	0.00	0.00	6	Marks et al. (1999)
<i>Athene noctua</i>	3110672	2917574	47500	0.220	3.60	219.0	0.00	0.00	12	
<i>Branta leucopsis</i>	20683254	8332116	51500	0.280	4.50	2120.0	0.00	0.00	1	
<i>Calidris maritima</i>	17232144	4029885	280000	0.260	3.91	97.3	0.00	1.22	1	
<i>Calonectris diomedea</i>	29702426	16378589	28500	0.289	1.00	535.0	0.00	0.00	3	
<i>Charadrius alexandrinus</i>	49403011	15177851	170000	0.050	3.00	47.7	0.00	0.59	6	
<i>Charadrius hiaticula</i>	39507955	13066263	26500	0.150	3.79	64.0	0.00	0.00	2	
<i>Charadrius morinellus</i>	31652899	17130066	10100000	0.156	2.92	113.0	0.00	4.55	1	Owens et al. (1995)
<i>Corvus monedula</i>	57146986	18225583	3750000	0.085	4.45	249.0	0.00	0.00	4	
<i>Coturnix coturnix</i>	79987916	18418485	6400000	0.210	10.20	121.0	-	-	5	Rodriguez-Teijeiro et al. (2003)
<i>Cuculus canorus</i>	1669659	1194274	360000	0.210	9.20	82.6	-	-	4	Gibbs et al. (2000)
<i>Cyanopica cyanus</i>	86520645	18408794	16950000	0.522	6.58	71.0	0.00	0.00	11	Gonzalez (1996)
<i>Delichon urbica</i>	79065128	19513932	15000000	0.195	4.10	19.5	0.00	16.85	5	
<i>Dendrocopos major</i>	14754777	11961770	225000	0.350	5.50	81.6	0.00	1.24	26	Michalak & Winkler (2001)
<i>Dendrocopos medius</i>	39702488	16526545	40000	0.480	5.64	59.0	0.00	0.00	4	Michalak & Winkler (2001)
<i>Falco columbarius</i>	6491767	3618799	6050	0.326	3.96	163.0	0.00	0.00	9	
<i>Falco eleonora</i>	30494411	13134238	33500	0.218	2.50	390.0	0.00	0.00	1	
<i>Falco naumanni</i>	31222685	17937280	16000000	0.216	3.83	152.0	0.00	3.44	1	
<i>Ficedula hypoleuca</i>	45934099	22446774	185000000	0.184	7.45	14.3	6.33	9.24	4	
<i>Fringilla coelebs</i>	27491825	14858207	3600000	0.162	4.30	24.2	0.00	17.00	17	
<i>Fulmarus glacialis</i>	107603464	82850373	1300000	0.154	1.00	750.0	0.00	0.00	2	
<i>Gallinula chloropus</i>	40351250	16122535	1500	0.266	6.58	246.0	0.00	0.00	12	
<i>Gavia immer</i>	46951330	20998321	375000	0.220	2.00	3150.0	0.00	0.00	1	Piper et al. (1997)
<i>Haematopus ostralegus</i>	79406476	18423470	26000000	0.220	2.78	531.0	0.00	1.54	3	
<i>Hirundo rustica</i>	30623543	10682560	2700000	0.106	4.40	19.1	0.00	24.88	6	
<i>Lagopus lagopus</i>	22100451	10527589	1060000	0.292	7.50	598.0	7.00	9.40	16	
<i>Lanius minor</i>	41869022	12299926	1045000	0.390	6.17	46.5	0.00	0.00	1	
<i>Larus canus</i>	63131559	17624545	6150000	0.190	3.00	336.0	0.00	3.64	4	
<i>Luscinia svecica</i>	94226129	13583929	740000	0.290	6.19	18.2	0.00	30.95	10	
<i>Merops apiaster</i>	26299101	15792159	14950000	0.189	6.00	55.1	0.00	0.70	1	Jones et al. (1991)
<i>Miliaria calandra</i>	15949651	7060654	170000	0.180	3.97	47.7	33.30	4.55	3	Hartley et al. (1993)
<i>Oceanodroma leucorhoa</i>	105524861	22419730	8800000	0.580	1.00	30.2	0.00	0.00	5	
<i>Oenanthe oenanthe</i>	29551674	13513024	360000	0.210	5.50	24.0	0.00	10.96	4	
<i>Panurus biarmicus</i>	67081983	17463049	20500000	0.300	5.86	15.3	0.00	14.40	2	
<i>Parus ater</i>	22374181	18836186	32000000	0.170	8.50	9.2	0.00	25.32	20	
<i>Parus caeruleus</i>	124262164	18706806	68500000	0.194	11.76	11.8	3.40	13.14	15	

Appendix (continued)

Species	Total breeding distribution area (km ²)	Western Palearctic breeding distribution area (km ²)	Population size	Band sharing coefficient	Clutch size	Body mass (g)	Polygyny (%)	Extra-pair paternity (%)	No. subspecies	References
<i>Parus major</i>	57808042	17013326	33000000	0.215	10.92	18.5	0.00	12.30	31	
<i>Parus montanus</i>	92054602	19222361	96500000	0.200	8.05	11.6	0.00	0.96	11	
<i>Passer domesticus</i>	27954938	9354488	5250000	0.097	4.00	30.4	5.00	8.78	12	
<i>Perisoreus infaustus</i>	32839062	12273404	2750000	0.430	3.70	84.7	0.00	0.00	16	
<i>Petronia petronia</i>	22003193	17091089	92000	0.220	5.70	32.9	12.00	32.04	7	Pilastro et al. (2002)
<i>Phalacrocorax aristotelis</i>	34702775	13133242	78000000	0.380	3.07	1790.0	0.00	9.30	3	
<i>Phylloscopus trochilus</i>	125873841	19417780	13250000	0.150	6.20	9.3	9.10	20.32	3	Bjørnstad & Lifjeld (1997)
<i>Pica pica</i>	43136324	12973326	140000	0.155	5.90	228.0	0.00	4.89	12	
<i>Prunella collaris</i>	18168515	17187814	19000000	0.136	3.50	42.3	15.00	0.00	11	
<i>Prunella modularis</i>	34607944	13988146	315000	0.240	5.10	19.0	15.00	0.80	7	
<i>Remiz pendulinus</i>	71056288	18437661	7450000	0.390	4.40	9.1	10.00	6.97	11	
<i>Riparia riparia</i>	17598255	12823702	14150000	0.196	4.78	13.1	0.00	14.37	4	
<i>Serinus serinus</i>	3716312	2134573	2600000	0.350	4.00	11.9	0.00	4.68	1	Hoi-Leitner et al. (1999)
<i>Sturnus unicolor</i>	57229673	21868439	39500000	0.195	4.10	90.6	36.36	15.90	1	Cordero et al. (2002)
<i>Sturnus vulgaris</i>	29140443	13396794	2850000	0.143	5.40	80.5	40.00	9.19	12	
<i>Tetrao tetrix</i>	56601323	18567443	1160000	0.110	7.91	1200.0	100.00	0.00	7	
<i>Turdus merula</i>	90485137	22419730	61000000	0.286	3.87	95.8	0.00	16.09	15	
<i>Tyto alba</i>	190152410	14949104	165000	0.220	5.70	308.0	0.00	0.47	34	Roulin et al. (2004)
<i>Upupa epops</i>	136372138	16140430	1295000	0.180	7.00	34.6	0.00	7.14	9	
<i>Uria aalge</i>	31020712	20786898	2350000	0.213	1.00	735.0	0.00	7.80	5	