MIGRATION DISTANCE IS POSITIVELY ASSOCIATED WITH SEX-LINKED GENETIC DIVERSITY IN PASSERINE BIRDS

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1. ABSTRACT

15

16   A recent comparative analysis of passerine birds found that the frequency of extra-pair

17   paternity was positively associated with neutral genetic diversity. It has been hypothesized

18   that migratory species have more extra-pair paternity than resident species, so we

19   reanalysed the same comparative data set to test whether migration distance could also

20   explain variation in genetic diversity. In this comparative analysis of 19 local populations

21   from 18 passerine species, spanning year-round residents to long-distant migrants, we found

22   that migration distance was positively correlated with sequence diversity at homologous

23   nuclear Z-linked (sex) introns, but not with autosomal intronic diversity. This pattern

24   contrasts with that of extra-pair paternity in the previous study where extra-pair paternity

25   was positively associated with autosomal diversity and not Z-linked diversity. We discuss

26   several possible explanations for the correlation between Z-linked diversity and migration

27   distance; effects that are specific to sex-linked genetic diversity may occur if migratory

28   behaviour infers different selective regimes in the sexes or affects population structuring.

29   These results suggest that significant amounts of genetic diversity at sex chromosomes and

30   autosomes are shaped by different processes, and should therefore be analysed and

31   interpreted independently in population genetics studies.

32   KEY WORDS: autosomes, female promiscuity, introns, seasonal migration, Z chromosome

2. INTRODUCTION

Genetic diversity is a prerequisite for evolutionary change and adaptations in populations (HUGHES et al., 2008; LEWONTIN, 1974). Understanding the various factors and processes that affect genetic diversity is therefore of fundamental importance in evolutionary biology. Genetic diversity is unevenly distributed across genomes (DAVIDSON et al., 2009), and the factors underlying loss and gain of genetic diversity may differ among loci (ELLEGREN, 2009), especially among chromosomes with different inheritance pattern (CORL AND ELLEGREN, 2012; ELLEGREN, 2009; ELLEGREN, 2009; KIRKPATRICK AND HALL, 2004; POOL AND NIELSEN, 2007; QVARNSTRÖM AND BAILEY, 2009; SÆTRE et al., 2003).

Current ecological hypotheses suggest that genetic diversity might be influenced by migratory behaviour in birds. Migratory species have greater breeding synchrony, which may facilitate extra-pair copulations (SPOTTISWOODE AND MØLLER, 2004), which in turn is expected to increase genetic diversity (GOHLI et al., 2013). Further, it has been proposed that genes controlling migratory behaviour undergo balancing selection in long-distance migrants, which would directly increase genetic diversity (FITZPATRICK, 1994). Additionally, migratory birds may be subjected to greater environmental heterogeneity and exposure to a more diverse parasite fauna than sedentary birds (JENKINS et al., 2012; MØLLER AND ERRITZØE, 1998; MØLLER et al., 2011), which would also select for increased genetic diversity (BERNATCHEZ AND LANDRY, 2003).

A recent comparative study on socially monogamous passerine birds documented a positive association between genetic diversity and female promiscuity for autosomal loci, but not for loci on the Z (sex) chromosome (GOHLI et al., 2013). Sex chromosomes differ from autosomes in both effective population (Ne; number of breeding individuals in an idealized population that exhibits the same amount of genetic drift or inbreeding as the actual population; ELLEGREN, 2009), the types of genes that map to them, mutation and recombination rates and their relative role in adaptive evolution (ELLEGREN, 2009; ELLEGREN, 2009; KIRKPATRICK AND HALL, 2004; QVARNSTRÖM AND BAILEY, 2009; SÆTRE et al., 2003). Differences in selective regimes in the sexes may cause discordant patterns of genetic diversity on sex-linked and autosomal loci. In the context of seasonal migration, such selection may be caused by differences in migratory strategies in the sexes, or sex specific selection inferred by parasites (DUNEAU et al., 2012) in long distance migrants (BERNATCHEZ AND LANDRY, 2003; GOHLI et al., 2013). Z-linked diversity may also be specifically affected if migratory behaviour affects effective population size (N_e ;number of breeding individuals in an idealized population that exhibits the same amount of genetic drift or inbreeding as the

67 actual population." (ELLEGREN, 2009)) since reductions in N_e is expected to reduce Z-linked

68 diversity more so than autosomal diversity (CORL AND ELLEGREN, 2012; ELLEGREN, 2009;

69 ELLEGREN, 2009; KIRKPATRICK AND HALL, 2004; POOL AND NIELSEN, 2007; QVARNSTRÖM

70 AND BAILEY, 2009; SÆTRE et al., 2003). Generally, in order to explain an effect of migration

71 distance on Z-linked genetic diversity, the driving factor must either infer sex-specific

72 selection or cause changes in effect population size, while also being affected by migratory

73 behaviour.

74   Here, we test for possible relationships between migration distance and genetic

75 diversity estimates from autosomal and Z-linked loci separately. There are many potential

76 covariates of both migration distance and genetic diversity. Female promiscuity in particular

77 is described as a covariate of both migration distance (SPOTTISWOODE AND MØLLER, 2004),

78 and genetic diversity (GOHLI et al., 2013; PETRIE et al., 1998). Further, the relationship

79 between migration distance and extra-pair paternity has been shown to differ between Eurasia

80 and America (STUTCHBURY et al., 2005), making continent of origin a potential confounding

81 variable in a study of migration distance and genetic diversity. Larger birds tend to migrate

82 further (NEWTON, 2007), making body mass a potential confounding variable in our study.

83 Protandry, i.e. the tendency of males to arrive prior to females at breeding grounds, may infer

84 selection at sex-linked genes and shape the associated genetic diversity. In this study we

85 control for all of the aforementioned factors when evaluating the relationship between

86 migration distance and genetic diversity.

87

88 ## 3. MATERIALS AND METHODS

89   Five Z-linked genes (ALDOB, BRM, CHDZ, PTCH, and VLDLR) and five autosomal

90 genes (CKB, GH1, LHCGR, RPL7A, and TM; BORGE et al., 2005) were sequenced in 18

91 passerine bird species (19 populations; Appendix 1; ≈4000 bp per species). The data set is the

92 same as used in a previous study (Gohli et al. 2013) in which species and populations were

93 selected on the availability of extra-pair paternity data (references can be found in Appendix

94 1) from the same study population. Intron sequences are available in GenBank (acc. no.

95 AJ890502-AJ890834 and JQ922568-JQ923421). Genetic diversity was estimated as

96 nucleotide diversity (π) from intronic single nucleotide polymorphisms (SNPs). These

97 estimates of genetic diversity were based on nine assumedly unrelated males from each study

98 population following Borge, et al. (2005; sampling localities are listed in Appendix 1).

99 Although larger sample sizes (>20) are optimal for accurately determining levels of genetic

diversity (PRUETT AND WINKER, 2008), uneven samples sizes are a far bigger problem (PETIT et al., 1998). In a study where genetic diversity was estimated using several different sample sizes, a sample size of 5 individuals performed poorly, while estimates from 10 individuals returned an interval which contained the correct value for genetic diversity (PRUETT AND WINKER, 2008). Thus, we deem nine males to be sufficient. Migration distance was measured as the distance from sampling location, to the midpoint of the wintering range. We evaluated distribution maps from several sources (CRAMP AND PERRINS, 1993; DEL HOYO et al., 2014; RIDGELY AND TUDOR, 2009) in order to determine the latitudinal and longitudinal restriction of wintering ranges. Mid-points were simply determined as equidistant from the southern and northern, and the western and eastern, boundary of the wintering ranges. When wintering and breeding ranges overlapped nearly perfectly, migration distance was set to zero. Although more extreme examples are indeed found among the passerines (CHERNETSOV, 2012), our focal species represent a wide range of migration distances (0-7800km). Data on body mass was also collected from literature (DUNNING, 2007; LYNX_EDICIONS, 2014), along with data on protandry (references in Appendix 1). Since protandry may vary in degree between populations of the same species, and since detailed data on protandry was not available for our specific sampling localities, we treated this variable as categorical. We were not able to locate data on protandry for *S. sialis*, only a reference stating that such data is lacking for this particular species. All analysed data are listed in Appendix 1. The phylogeny (Appendix 3) came from birdtree.org (JETZ et al., 2012). Birdtree.org did not have information on *Cyanistes teneriffae*, so it was coded as a closely related sister taxon to the two *C. caeruleus* populations. The two *C. caeruleus* populations were coded as sister taxa with miniscule branch lengths (0.1; total length of phylogeny is ≈66) separating them.

We performed phylogenetic generalized least squares (PGLS) tests (FRECKLETON et al., 2002; PAGEL, 1999) on the data set; autosomal and Z-linked genetic diversity estimates were separately regressed on migration distance, while controlling for the proportion of extra-pair young (EPY). In a test of migration distance against Z-linked diversity we also included two potential covariates of migration distance, namely body mass, and continent of origin, as fixed factors. Further, we included occurrence of protandry, which may be involved in selection, and hence genetic diversity, on sex-linked loci, in the model. In order to test whether Z-linked diversity was best explained by general genomic diversity, we also included autosomal diversity as a predictor of Z-linked diversity. We also tested for interaction effects between EPY and migration distance. Lambda (λ) was estimated as a measure of phylogenetic signal in our data. Figure 1 shows unadjusted (or raw) data together with the linear model,

which is adjusted for similarity in phenotype due to common phylogenetic descent. We checked that model assumptions were met by investigation of relevant model diagnostic plots (plots of residuals vs. fitted values). The analyses were done in R v. 2.15.3 (R DEVELOPMENT CORE TEAM, 2014).

4. RESULTS

Migration distance was significantly and positively correlated with Z-chromosome diversity but not with autosomal diversity (table 1a and 1b). In a regression model where we evaluated migration distance, EPY, body mass, continent and occurrence of protandry as predictors of Z-linked diversity, migration distance was the only significant factor (p=0.006; table 1a). Because this model included two categorical variables, we performed an ANOVA to obtain global p-values for all predictors, which revealed that migration distance was the only predictor explaining a significant amount of variance in Z-linked diversity ($F_{1,11}$=11.18, p-value=0.007; all other predictors had p-value>0.12). A simple model including only migration distance explained 41 % of the variance in Z-linked diversity (adj. R^2=0.41, p=0.002; figure 1). The same test with sedentary populations (migration distance=0) removed from the data was also significant (n=16, adj. R^2=0.42, p=0.004), yet when removing only the two species with the longest migration distances (*Hirundo rustica* and *Delichon urbicum*) from the dataset, the association between migration distance and Z-linked diversity was no longer significant (n=17, R^2=0.03, p=0.24). In a model where Z-linked diversity was regressed on migration distance and EPY, we found no evidence for a significant interaction effect between these predictors (p=0.21). Migration distance did not significantly explain any variance in autosomal diversity, (adj. R^2=0.01, p=0.28) regardless of whether EPY was included in the model (table 1c). The association between migration distance and EPY was statistically significant in our data set (p=0.040; table 1d). λ values were not significantly different from zero for all test, apart except for from the test which that included the many non-significant fixed factors (table 1a), which indicates that there is no significant phylogenetic dependency in the relationship between genetic diversity and the significant predictors. We performed all tests with an alternative proxy for sperm competition, the coefficient of between-male variation in sperm length (CV_{bm}) (LIFJELD et al., 2010), which produced similar test results (Appendix 2) as when using EPY. The previously documented correlation between female promiscuity (EPY) and autosomal diversity (GOHLI et al., 2013) retained statistical significance (p=0.045; table 1b) when migration distance was included in the model.

5. DISCUSSION

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170   Our analyses indicate that migration distance and female promiscuity are associated

171 with genetic diversity at different parts of the genome in a small sample of passerine birds.

172 Migration distance explained 41% of the variation in Z-linked diversity, but was ~~unrelated~~ not

173 significantly related to autosomal diversity. Female promiscuity, on the other hand, was

174 positively associated with autosomal genetic diversity, irrespective of the variation in

175 migration distance. Hence, we can conclude that, in our data set, migration distance is not a

176 confounding variable for the relationship between female promiscuity and autosomal diversity

177 reported in a previous study (GOHLI et al., 2013). Our results indicate that some variable,

178 which is associated with migration distance, affects Z-linked diversity specifically. These

179 results are based on a rather small dataset collected from the literature and should be viewed

180 as preliminary; we recommend further study to evaluate the reliability of the correlation

181 between migration distance and genetic diversity.

182   A number of researchers have proposed hypotheses that link genetic diversity and

183 migration. Fitzpatrick (1994) introduced the hypothesis that genes coding for migratory

184 behaviour are under fluctuating directional selection given the fluctuating suitability of

185 different overwintering habitats, resulting in more genetic diversity in migrants. Migratory

186 birds may also encounter greater environmental heterogeneity and a more diverse parasite

187 fauna (JENKINS et al., 2012; MØLLER AND ERRITZØE, 1998; MØLLER et al., 2011), which

188 would select for increased genetic diversity (BERNATCHEZ AND LANDRY, 2003; GOHLI et al.,

189 2013). However, unless genes linked to migration, defence against parasites, or tolerating

190 heterogeneous environments map to the Z- chromosome, none of these hypotheses explain

191 why migration distance correlates with Z-linked, but not autosomal diversity. That such genes

192 are Z-linked seems unlikely, since Z-linked genes typically are involved in sex-related

193 functional traits like sexual dimorphism, reproductive compatibility, secondary sexual traits,

194 and mate choice (KIRKPATRICK AND HALL, 2004; QVARNSTRÖM AND BAILEY, 2009; SÆTRE et

195 al., 2003). It is also important to note that sex-biased gene expression is widespread across the

196 genome, and is not restricted to the sex chromosomes (ELLEGREN AND PARSCH, 2007).

197   Spottiswoode and Møller (2004) proposed that migratory species have higher

198 breeding synchrony, which allows females to assess more potential partners, and hence obtain

199 more extra-pair paternity, which is associated with genetic diversity (GOHLI et al., 2013;

200 PETRIE et al., 1998). We found that migration distance is significantly and positively

associated with female promiscuity (EPY) in our dataset, but female promiscuity is

specifically correlated with autosomal genetic diversity and not to Z-linked diversity (GOHLI

et al., 2013), so the aforementioned causal pathway cannot explain the observed correlation

between migration distance and Z-linked diversity. However, increased breeding synchrony

may increase the level of male-male sexual competition (likely unrelated to extra-pair

paternity given our results). ~~This will infer sexual selection~~, which will lead to increased

variation among males (PETRIE AND ROBERTS, 2006). If the loci targeted by this sexual

selection maps to the Z-chromosomes, one would expect an increase in genetic diversity

specifically at Z-linked loci.

There are some sex-difference in migratory behaviour, such as ~~of~~ protandry (sex-

differences in arrival time at breeding ground) (MØLLER et al., 2009) and differential

migration (one class of individuals, e.g. females, is more prone to migrate) (ALERSTAM AND

HEDENSTRÖM, 1998). If genes coding for protandry are situated on the Z chromosome and

undergo balancing selection or divergent selection in the two sexes, Z-linked genetic diversity

would increase in migratory species, however, we used a crude categorical classification of

protandry~~have~~ in order to controll~~ed~~ for the occurrence of protandry in this study and found it

to be unimportant in the association between migration distance and Z-linked diversity (table

1a). Similarly, when females are more prone to migrate than males, such as in dark-eyed

junco (*Junco hyemalis*; HOLBERTON AND ABLE, 2000) or chaffinch (*Fringilla coelebs*;

LINNAEUS, 1758), divergent selection in the sexes on migratory genes may generate genetic

diversity. However, this type of differential migration is not seen in long-distance migrants,

who are obligatory migratory. Thus, the divergent selection, and corresponding greater

genetic diversity, should be observed in birds with intermediate migration distances, which is

inconsistent with our results (figure 1).

Genetic diversity may be influenced by other factors, such as population bottlenecks

(POOL AND NIELSEN, 2007), and mating system (BAZIN et al., 2006). Because Z-linked loci

are more sensitive to decreasing population sizes than autosomal loci (CORL AND ELLEGREN,

2012; ELLEGREN, 2009; ELLEGREN, 2009; KIRKPATRICK AND HALL, 2004; POOL AND

NIELSEN, 2007; QVARNSTRÖM AND BAILEY, 2009; SÆTRE et al., 2003), differences in the

occurrence of bottlenecks between migratory classes could explain the differences in genetic

diversity at Z-linked loci. However, we found that the relationship between migration distance

and Z-linked diversity was dependent on the two species with the longest migration distances,

and the removal of the sedentary species did not significantly change the results. Hence, if

bottlenecks are to explain the association between migration distance and Z-linked diversity

235   the occurrence of bottlenecks must be small for long distance migrants and substantial for

236   both sedentary species and intermediate-distance migrants. Mating system may affect Z-

237   linked and autosomal loci differently through a sex-specific reduction in number of

238   reproducing individuals (CHARLESWORTH, 2001). However, all species analysed in this study

239   are socially monogamous, and there is no significant association between EPY and Z-linked

240   diversity (GOHLI et al., 2013).

241   The correlation between migration distance and Z-linked diversity may also be

242   explained by differences in population structuring. Populations of sedentary birds may

243   constitute metapopulations of many allopatric or parapatric subpopulations with reduced gene

244   flow, whereas populations of migratory birds should have more gene flow and thus less

245   population structuring (ARGUEDAS AND PARKER, 2000; ROCKWELL AND BARROWCLOUGH,

246   1987). Smaller populations are expected to have less genetic diversity (AMOS AND

247   BALMFORD, 2001; BAZIN et al., 2006; SPIELMAN et al., 2004), which is also true for

248   subpopulations of structured populations because there is greater probability of mating within

249   subpopulations than between subpopulations (WANG AND CABALLERO, 1999). The idea that

250   migration distance can be associated with population structure, which in turn can affect

251   genetic diversity, is supported by the observation that dispersal ability is negatively correlated

252   with higher subspecies diversity (BELLIURE et al., 2000). The negative effect of smaller

253   population size on genetic diversity will be stronger at Z-linked loci than at autosomal loci,

254   due to the lower effective population size (N_e) of Z-linked loci compared to autosomal loci

255   (CORL AND ELLEGREN, 2012; ELLEGREN, 2009; ELLEGREN, 2009; KIRKPATRICK AND HALL,

256   2004; POOL AND NIELSEN, 2007; QVARNSTRÖM AND BAILEY, 2009; SÆTRE et al., 2003). N_e

257   has several definitions (CHERRY AND WAKELEY, 2003); here N_e is defined as a theoretical

258   quantity: "Number of breeding individuals in an idealized population that exhibits the same

259   amount of genetic drift or inbreeding as the actual population." (ELLEGREN, 2009). Lower N_e

260   will result in more alleles being lost due to drift, and since the N_e of Z-linked loci are already

261   low, the Z-specific reduction in genetic diversity will be larger (POOL AND NIELSEN, 2007).

262   Such relative changes in autosomal and Z-linked genetic diversity resulting from changes in

263   population size are expected to be rapid and substantial (POOL AND NIELSEN, 2007). One

264   should note that population structuring is expected to increase overall diversity (for the entire

265   metapopulation) through isolation among subpopulations. However, because our sampling

266   was done on a restricted local scale, such an effect will not be present in our dataset.

267   Population structuring may not only reduce genetic diversity in sedentary species at a local

268   scale, but can perhaps also increase genetic diversity in migrator species at the same scale. If

269 suitable breeding habitat in northern temperate regions is fragmented during glaciations,
270 isolation may result in fixation of different alleles in different localities. Given good dispersal
271 ability, as in seasonal migrants, these alleles may spread in the entire metapopulation during
272 periods with no glaciation. The pattern would be observable only on Z-linked loci due to the
273 effects of smaller effective population size (increased fixation of alleles through drift).

274 We have found that migration distance is strongly associated with Z-linked genetic
275 diversity, but that the relationship is driven mainly by the two species with the longest
276 migration distances. These two species (*Hirundo rustica* and *Delichon urbicum*) are quite
277 closely related (Appendix 3), but as we control for phylogeny in all statistical tests, this
278 should not have affected our results. The association between migration distance and Z-linked
279 diversity may be explained by differences in the occurrence of bottlenecks, breeding
280 synchrony or population structuring. The notion that differences in population structure could
281 be responsible for the differences in Z-linked diversity between long- and short-distance
282 migratory species could be tested more explicitly by comparing F_{ST} values estimated from
283 population pairs, with the prediction that short distance migrants will have higher F_{ST} values.
284 Our estimates for genetic diversity are based on only five Z-linked introns; follow-up studies
285 could implement next-generation sequencing data to get better estimates of genetic diversity
286 for the entire Z chromosome. Regardless of the causal factors involved, our findings indicate
287 that sex chromosomes and autosomes are affected by different processes. Therefore, one
288 should take care to treat these genomic regions as separate entities in population genetics
289 studies.

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7. LITERATURE

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409

8. TABLES

Table 1

	response variable	predictor variables	estimate	SE	t-value	p-value	R^2 (adj.)	df	λ
a)		migration distance	7.68E-07	2.24E-07	3.43	**0.006**			
		EPY	-1.80E-03	3.86E-03	0.47	0.649			
	Z-linked diversity	autosomal diversity	-2.42E-02	1.66E-01	0.15	0.887	0.38	11	~0.85[0.6,0.01]
		protandry*	1.77E-04	8.68E-04	0.20	0.842			
		body mass	5.40E-05	3.39E-05	1.59	0.140			
		continent**	-1.11E-03	8.44E-04	1.32	0.214			
b)	Z-linked diversity	migration distance	4.98E-07	1.36E-07	3.66	**0.002**	0.41	17	~0[1, 0.01]
c)	autosomal diversity	migration	2.93E-08	2.89E-07	0.10	0.920	0.20	16	~0[1, 0.01]
		EPY	1.11E-02	5.10E-03	2.18	**0.045**			
d)	EPY	migration	2.69E-05	1.21E-05	2.22	**0.040**	0.18	17	~0[1, 0.01]

Table 1: Phylogenetic generalized least square tests where (a) Z-linked diversity was regressed on migration distance, EPY, autosomal diversity, occurrence of protandry, body mass, and continent on which the species were sampled, (b) Z-linked diversity was regressed only on migration distance, (c) autosomal diversity was regressed on migration distance and EPY, and (d) EPY was regressed on migration distance. R^2 is the amount of variance explained by the model. Lambda (λ) indicates the level of phylogenetic dependency in the data, with superscripts giving p-values from likelihood ratio tests of λ=0 and λ=1 respectively. *Reference: No protandry, **Reference: America.

9. Figure legends

Figure 1

Migration distance plotted against Z-linked genetic diversity. The plotted data points are not controlled for phylogeny. The predicted line shows the generalized least square model where migration distance was the only predictor (table 1b), which is controlled for phylogeny.

14