

Why is there a tropical–temperate disparity in the genetic diversity and taxonomy of species?

Andrew A. Chek,¹ James D. Austin² and Stephen C. Loughheed^{2*}

¹*Organization for Tropical Studies, Duke University, Box 90630, Durham, NC 27708-0630, USA and*

²*Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada*

ABSTRACT

Studies over the last few decades have suggested that neotropical vertebrate taxa may have greater genetic disparity than their nearctic counterparts. Here, a robust test of this suggestion using bootstrap resampling of allozyme data for 53 passerine (16 nearctic and 37 neotropical) species confirms the pattern. This disparity could be due to taxonomic artifacts or to differences in the rate or history of genetic processes between regions. In contrast, a selection-based explanation emphasizes negative feedback of species richness on rates of phenotypic, but not molecular, evolution in neotropical species.

Keywords: allozymes, biodiversity, bootstrap, genetic disparity, latitudinal gradient, Nearctic, Neotropics, phenotype, species richness, taxonomy.

INTRODUCTION

Recent work on some neotropical vertebrate species has shown surprising genetic variability at assayed neutral loci, variability that is typically much more pronounced than in nearctic vertebrates of the same taxonomic rank and class (e.g. birds: Gerwin and Zink, 1989; Escalante-Pliego, 1990; Seutin *et al.*, 1993; frogs: Heyer and Maxson, 1982; Hass *et al.*, 1995; Mulcahy and Mendelson, 2000; rodents: da Silva and Patton, 1993). The most extensive discussion of this apparent geographic discrepancy was provided by Hackett and Rosenberg (1990), who observed that ‘species of neotropical birds are [genetically] structured differently from those of temperate birds’ (p. 482); they attributed this pattern to the putatively greater age of neotropical species. Such claims of genetic disparity between realms have been made without any formal statistical test. Moreover, explanations for the disparity have generally considered only a few possibilities, with the relative age of neotropical taxa suggested to be the primary candidate (Hackett and Rosenberg, 1990; Klicka and Zink, 1997).

Here we present a comprehensive statistical test of the suggested difference in genetic disparity between neotropical and nearctic species using allozyme data from passerine birds, arguably the world’s best-known animal group. Our aims were to determine if there

* Author to whom all correspondence should be addressed. e-mail: loughheed@biology.queensu.ca
Consult the copyright statement on the inside front cover for non-commercial copying policies.

is a genetic disparity between nearctic and neotropical passerine birds and, if there is, to explore the mechanisms responsible for the disparity between the two realms. Emphasis to date has focused on historical mechanisms as the primary cause of the discrepancy in genetic disparity. However, differences in taxonomic practice or ecological context may also contribute to the generation of the discrepancy between the two realms (see Discussion).

METHODS AND RESULTS

Within-species allozyme-based studies were compiled from the literature (16 species in 12 nearctic genera representing five families; 37 species in 31 neotropical genera representing 14 families) (see Appendix). Although the number of methods for surveying neutral genetic variation has increased, the largest cohesive and comparative passerine genetic data set is still from allozyme studies (Butlin and Tregenza, 1998). Furthermore, for a statistically robust estimate of genetic divergence, it is important to survey many independent loci. While the data from DNA-based markers (e.g. sequence, microsatellites) are rapidly expanding, there is still nothing comparable to allozymes in numbers of loci and taxa.

We limited our study to intraspecific comparisons principally to reduce the probability of polyphyly and confounds that could result in erroneously high genetic distances. Studies were included only if they used Nei's (1978) corrected genetic distance and more than 20 putative loci. Thus, we used a reduced sample size for our test in favour of better estimates of genome-wide variation. For each selected study and species, the mean Nei's genetic distance across populations was used as a measure of intraspecific genetic divergence.

We took two approaches to test for the potential disparity in genetic divergence between biogeographic realms. First, we compared mean Nei's D within species for all data using a Mann-Whitney U -test. Second, we reduced potential outlier and phylogenetic bias (Harvey and Pagel, 1991) by bootstrapping the data. In each of 1000 pseudoreplicates, eight species were chosen from each of the neotropical and nearctic samples subject to the constraint that a genus could only be represented once per sample. Several other factors could confound our analyses. We have addressed these as follows: First, islands often represent extremes in genetic and phenotypic evolution (e.g. Wagner and Funk, 1995). Thus, we excluded studies exclusively employing island populations and, for studies containing both island and continental populations, we re-calculated distance statistics using only mainland populations. Second, the average geographic scale of studies (i.e. the distance among populations sampled within a study), if different between realms, could produce spurious results because distance alone may correlate with genetic differentiation (isolation by distance; Wright, 1931). Third, a difference in the number of subspecies included in samples from the two realms could confound the pattern. This is because subspecies designation implies phenotypic distinction and possibly elevated genetic distance, assuming a positive correlation between phenotype and neutral genetic diversity (Soulé and Yang, 1973; Barrowclough, 1980; Thorpe, 1983; Soulé and Zegers, 1996; Butlin and Tregenza, 1998; Johns and Avise, 1998; Waldman and Andersson, 1998; but see Reed and Frankham, 2001). Bootstrap analyses were used to determine whether either geographic distance among sampled populations or number of subspecies could have biased our results.

Our analyses indicate that neotropical populations within surveyed species are more

genetically disparate than their nearctic counterparts (total data set comparison: Mann-Whitney $Z_{\text{approx}} = -3.52$, $N_1 = 16$, $N_2 = 37$, $P = 0.0004$; Fig. 1a). This pattern is supported by bootstrap analysis. The mean intraspecific genetic distance for neotropical species exceeded that of nearctic species in 999 of 1000 replicates (neotropical minus nearctic: median = 0.035; range 0.0892 to -0.0028 ; Fig. 1b).

Several potential confounds did not account for the greater average genetic differentiation within neotropical species. Geographic distance among sampled populations tended to be greater in the Nearctic (median difference across replicates for geographic distance = -926 km), a conclusion supported by bootstrap analysis (Fig. 2a). Greater geographic separation among nearctic populations should, if anything, increase genetic distance among them and so reduce any difference between neotropical and nearctic species. We also examined *a posteriori* the relationship of species range size (log-transformed) and Nei's D to determine whether, at comparable range sizes, neotropical species were more genetically disparate than their nearctic counterparts. Although the relationship between species range and Nei's D did not differ significantly between realms and the slope was not significantly different from zero, this analysis did show that, for any given range size, genetic disparity was higher for neotropical species (results of analysis of covariance not shown).

Genetic disparity between the two realms could be related to the average number of subspecies. The median difference (nearctic – neotropical) across replicates for subspecies was -0.25 , suggesting slightly more subspecies were included in nearctic surveys (Fig. 2b). In so far as character differences used to delimit subspecies may correlate with differentiation in genetic markers, the slightly larger number of subspecies in nearctic samples

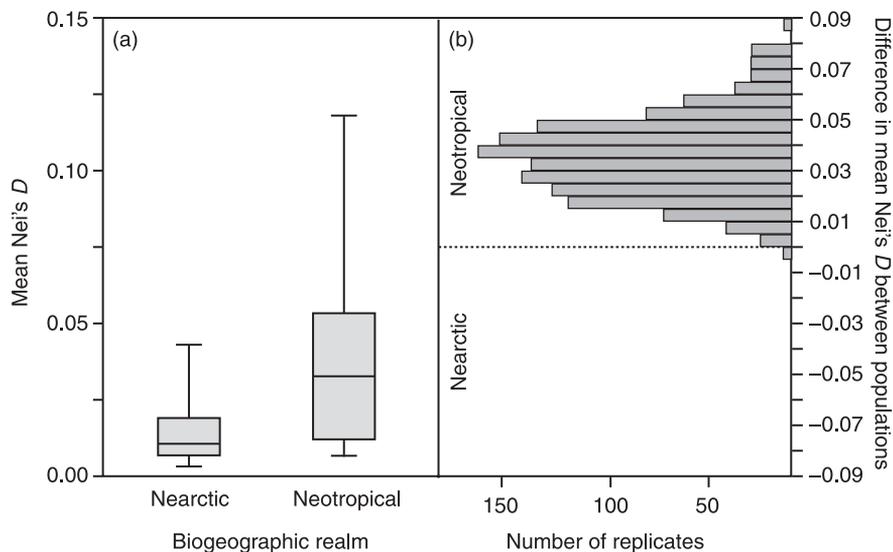


Fig. 1. (a) Boxplots of average Nei's genetic distance among populations within species (nearctic, $n = 16$; neotropical, $n = 37$). (b) Distribution of mean difference (neotropical – nearctic) in average Nei's genetic distance across 1000 re-sampling replicates. All but one replicate showed a higher average Nei's D among neotropical populations.

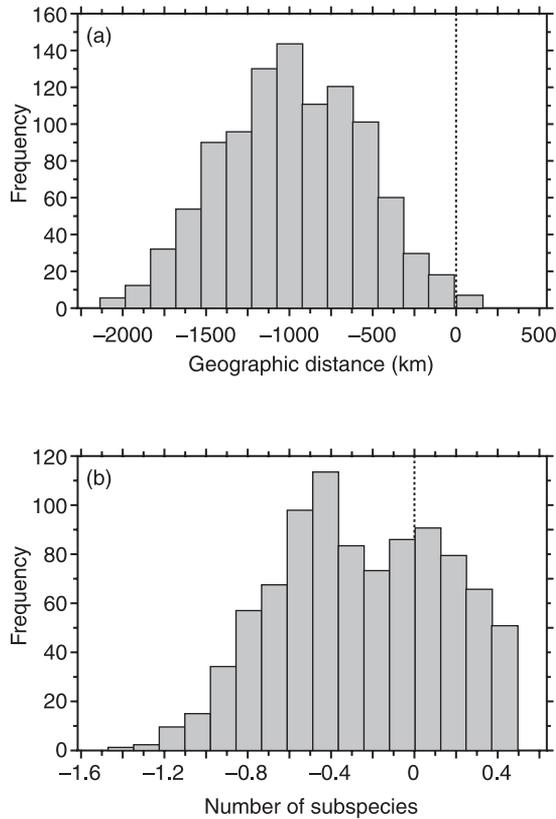


Fig. 2. Distribution of (a) interpopulation geographic distance and (b) number of subspecies across 1000 re-sampling replicates. All but six replicates showed greater interpopulation distances among nearctic populations, while differences in numbers of subspecies was similar across nearctic and neotropical species, with 634 replicates having a greater number of subspecies within nearctic samples. These results suggest that neither interpopulation distance nor the number of recognized subspecies should account for the greater average genetic divergence within neotropical species (see text).

should again reduce the difference in genetic disparity between the two realms. Note that insufficient intensity of sampling precludes analysis of potential differences in within-subspecies variation. Ultimately, the greater geographic separation among nearctic populations, and the inclusion of greater numbers of subspecies in the nearctic data, make our tests more conservative. Four genera in the nearctic sample contained long-distance migrants that winter in the Neotropics (*Empidonax*, *Vireo*, *Dendroica*, *Geothlypis*). Re-analysis after removal of these species did not change our results. The ecological type of birds sampled (generalist *vs* specialist) was not obviously different between the neotropical and nearctic studies surveyed. Finally, the number of loci was slightly greater in nearctic studies (median difference across replicates = -2.6 loci), but is unlikely to be the cause of the difference in average genetic differentiation because the mean number of loci in both samples exceeded 30.

DISCUSSION

Our analyses suggest that current taxonomy (i.e. described species) does not equivalently summarize genetic variation in passerine species of the Neotropics and Nearctic. There are, then, two classes of explanation for this phenomenon. First, taxonomic practice has not been applied equally in the two realms (e.g. undersplit tropical species). Second, the relationship between taxonomy, the phenotypic characters (e.g. morphology, calls) upon which it has overwhelmingly been based (Templeton, 1994; Butlin and Tregenza, 1998; Johns and Avise, 1998), and neutral genetic markers differs between the two realms.

We see three main possibilities, which are not mutually exclusive but are presented separately for clarity:

1. Taxonomic practice has not consistently partitioned phenotypic differentiation in the two realms and any apparent difference in genetic disparity is an artifact of this inconsistency.
2. Taxonomic practice has consistently partitioned phenotypic variation but the rate of neutral genetic divergence is different in the two realms
3. Taxonomic practice has consistently partitioned phenotypic variation; however, the correlation between phenotypic evolution and neutral genetic marker differentiation differs between the two realms

Effects of taxonomic practice

Significant ‘intraspecific’ phenotypic disjunctions in the Neotropics may have been overlooked. One could argue that populations in our sample might have been recognized as separate species if they occurred in the Nearctic or they had been studied with the same intensity as those in the Nearctic. If true, we are comparing populations at different taxonomic levels (e.g. species *vs* genera). However, most neotropical taxa were originally described by scientists also working with nearctic fauna. Moreover, many taxonomists now have extensive field and museum-based familiarity with both temperate and tropical biotas. This argues against the systematic under-splitting of the neotropical fauna as an explanation for the pattern found here. Certainly, where taxonomy (using either genetic or phenotypic data) has been reinterpreted using new species concepts (i.e. evolutionary or phylogenetic species), there is a trend for an increase in the number of species (e.g. ‘American Ornithologists’ Union, 1997; Hanken, 1999; Peterson and Navarro-Sigüenza, 1999). Yet, this has been the case for both temperate and tropical taxa, and it is unclear whether re-defining species will have a disproportionate effect in tropical and temperate biotas, either erasing the genetic disparity revealed here or magnifying it. Regardless, if the greater genetic divergence in the Neotropics is due to taxonomic under-splitting, then for a well-known group of neotropical organisms (passerine birds), the number of species has been greatly underestimated. If neotropical taxa are under-split, then the consequences include a steeper slope to the latitudinal gradient in species richness and a decrease in the average range of neotropical species. Practically, this would complicate neotropical conservation efforts because the absolute number of taxa to be conserved would increase, while the redundancy (shared species) between areas would decrease. The converse explanation is possible: nearctic passerine species may be over-split. The latitudinal gradient in species richness would still change but the considerations for conservation would be markedly different. Such complications would be magnified if a bias in taxonomic practice extended to other

vertebrate groups for which latitudinal richness gradients are reported (reviewed in Rosenzweig, 1995).

Effects of demography and history

Neotropical species could have smaller effective population sizes, be less vagile than their nearctic counterparts (Hackett and Rosenberg, 1990), or their evolution could be dominated by founder-type events. If any of these is true, then the rate of fixation of alleles in a population and the rate of genetic divergence among populations should be faster (Mindell and Thacker, 1996). Neotropical populations may also be more genetically differentiated if they simply have longer independent histories than nearctic populations. This is the most common explanation for differences in genetic disparity between realms (e.g. Hackett and Rosenberg, 1990; Klicka and Zink, 1997). Although comparative data are sparse, data accumulated thus far do suggest that some neotropical avian taxa are older than their nearctic counterparts (Gaston and Blackburn, 1996; Klicka and Zink, 1997).

The pattern of genetic variation is often used to infer both the demography and history of a species. Independent data are lacking that would allow us to examine the relative importance of the above factors (e.g. population size, age). Nevertheless, all these explanations suggest that neotropical populations are essentially older or genetically accelerated versions of the nearctic populations. If so, then nearctic populations, undisturbed for long enough, should achieve similar levels of genetic differentiation as neotropical populations, but without enough correlated phenotypic evolution to require designation as separate species. At present, there are insufficient data to test this prediction. However, the average Nei's D reported among nearctic congeneric species ($D = 0.044$; Barrowclough, 1980) is only marginally greater than the average for neotropical populations in our sample ($D = 0.041$; Fig. 1a). This does not support the idea that nearctic and neotropical populations are simply at different stages in the same evolutionary trajectory.

Effects of species richness

Previous explanations have concentrated on factors that might affect the rate of genetic evolution and so explain the disparity between the Neotropics and the Nearctic. None have considered an explanation based on a difference in the rate of phenotypic evolution. However, this seems the logical alternative because the claim of a genetic disparity assumes that equivalent taxonomic entities (species) are being compared. As we have noted, taxonomy has been dominated by the description of phenotypic differences.

Why should the phenotype of neotropical species evolve on average more slowly than that of their nearctic counterparts? An intriguing possibility is that higher species richness typical of many neotropical environments might retard phenotypic evolution (i.e. a species-richness hypothesis). Connell (1980) argued that co-evolution between competitors was less likely in tropical regions because the frequency and duration of particular species-pair interactions (selection pressures) are not as predictable as in regions with lower diversity. There are simply more combinations of species that can occur at a particular time and place within an area having a richer species pool. In so far as phenotypic evolution is shaped by interactions of a population with other species, a slowing of phenotypic but not neutral molecular evolution among populations of many neo-

tropical species should then occur. Hence, deep genetic divisions could develop among neotropical populations with a slower appearance of the morphological differences that would otherwise see divergent populations elevated to species status. This implies that speciation (i.e. phenotypically diagnosed species) may slow as greater numbers of *morpho*-species accumulate. Thus, the tropics may indeed act as a 'museum' of species diversity (Gaston and Blackburn, 1996); the tempo of speciation (as reflected by phenotypic distinction) is slowed independent of neutral genetic diversity, concomitant with reduced population extinction rates.

The species-richness hypothesis emphasizes selection on the phenotype through inter-specific interactions. Socially selected characters (e.g. those used in mate attraction) may be relatively more impacted by *intraspecific* dynamics (West-Eberhard, 1983). Therefore, such characters may be less affected by variation in species richness and continue to diverge. Accordingly, a greater proportion of species designations in the Neotropics may have relied more on characters that are the targets of social selection than has been the case in the Nearctic. Unfortunately, the role of sexual selection in speciation in the tropics has not yet been thoroughly explored (Price, 1998; Moritz *et al.*, 2000), although a comparison of the extent to which secondary sexual characteristics figure in taxonomic descriptions should be possible.

CONCLUSION

We have presented a robust test of the assumption that neotropical species show greater genetic disparity than their nearctic counterparts. These results may reflect a difference between the Neotropics and Nearctic in the delimitation of species and this may be an indication of how relatively understudied the Neotropics are, with primarily quantitative implications for conservation. Alternatively, a qualitative difference results from a geographically based disparity in evolutionary process or even in what 'molecules versus morphology' actually reveals about organisms. Such a disparity in processes would further complicate discussions of species definition and increase the difficulty comparing and conserving species.

ACKNOWLEDGEMENTS

Thanks to A. Baker, P. Boag, J. Bogart, C. Eckert, P. Handford, E. Lougheed, B. Lyon, R. Montgomerie, T. Nudds, K. Omland, H. Proctor and R. Rapasky for careful review and useful discussions. D. Kosciński and L. Neidrauer helped with library work. Thanks especially to Stuart Pimm, who provided encouragement during the early stage of this work's evolution and who helped improve this paper. Our effusive thanks to Lisa Manne for providing us with the range size data. The authors also thank the Queen's Grad Club for its unique contribution. This work was undertaken while the authors were supported, in part, by NSERC (Canada) grants to J.P. Bogart, P.T. Boag and S.C. Lougheed.

REFERENCES

- American Ornithologists' Union. 1997. Forty-first supplement to the checklist of North American birds. *Auk*, **114**: 542–552.
- Barrowclough, G.F. 1980. Genetic and phenotypic differentiation in a wood warbler (genus *Dendroica*) hybrid zone. *Auk*, **95**: 655–691.

- Butlin, R.K. and Tregenza, T. 1998. Levels of genetic polymorphism: marker loci versus quantitative traits. *Phil. Trans. R. Soc. Lond. B*, **353**: 187–198.
- Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, **35**: 131–138.
- da Silva, M.N. and Patton, J.L. 1993. Amazon phylogeography: mtDNA sequence variation in arboreal Echimyid rodents (Caviomorpha). *Mol. Phylogenet. Evol.*, **2**: 243–255.
- Escalante-Pliego, B.P. 1990. Genetic differentiation in yellowthroats (Parulinae: *Geothlypis*). In *Acta XX Congressus Internationalis Ornithologici* (B.D. Bell, R.O. Cossee, J.E.C. Flux, B.D. Heather, R.A. Hitchmough, C.J.R. Robertson and M.J. Williams, eds), pp. 333–341. Wellington: New Zealand Ornithological Trust Board.
- Gaston, K.J. and Blackburn, T.M. 1996. The tropics as a museum of biological diversity: an analysis of the New World avifauna. *Proc. R. Soc. Lond. B.*, **363**: 63–68.
- Gerwin, J.A. and Zink, R.M. 1989. Phylogenetic patterns in the genus *Heliodoxa* (Aves: Trochilidae): an allozyme perspective. *Wilson Bull.*, **101**: 525–544.
- Hackett, S.J. and Rosenberg, K.V. 1990. Comparison of phenotypic and genetic differentiation in South American antwrens (Formicariidae). *Auk*, **107**: 473–489.
- Hanken, J. 1999. Why are there so many new amphibian species when amphibians are declining? *Trends Ecol. Evol.*, **14**: 7.
- Harvey, P.H. and Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.
- Hass, C.A., Dunski, J.F., Maxson, L.R. and Hoogmoed, M.S. 1995. Divergent lineages within the *Bufo margaritifera* complex (Amphibia: Anura; Bufonidae) revealed by albumin immunology. *Biotropica*, **27**: 238–249.
- Heyer, W.R. and Maxson, L.R. 1982. Neotropical frog biogeography: paradigms and problems. *Am. Zool.*, **22**: 397–410.
- Johns, G.C. and Avise, J.C. 1998. A comparative summary of genetic distances in the vertebrates from the mitochondrial cytochrome b gene. *Mol. Biol. Evol.*, **15**: 1481–1490.
- Klicka, J. and Zink, R.M. 1997. The importance of recent Ice Ages in speciation: a failed paradigm. *Science*, **277**: 1666–1669.
- Mindell, D.P. and Thacker, C.E. 1996. Rates of molecular evolution: phylogenetic issues and applications. *Annu. Rev. Ecol. Syst.*, **27**: 279–303.
- Moritz, C., Patton, J.L., Schneider, C.J. and Smith, T.B. 2000. Diversification of rainforest faunas: an integrated molecular approach. *Annu. Rev. Ecol. Syst.*, **31**: 533–563.
- Mulcahy, D.G. and Mendelson, III, J.R. 2000. Phylogeography and speciation of the morphologically variable, widespread species *Bufo valliceps*, based on molecular evidence from mtDNA. *Mol. Phylogenet. Evol.*, **17**: 173–189.
- Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics*, **89**: 583–590.
- Peterson, A.T. and Navarro-Sigüenza, A. 1999. Alternate species concepts as bases for determining priority conservation areas. *Conserv. Biol.*, **13**: 427–431.
- Price, T. 1998. Sexual selection and natural selection in bird species. *Phil. Trans. R. Soc. Lond. B*, **353**: 1–12.
- Reed, D.H. and Frankham, R. 2001. How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. *Evolution*, **55**: 1095–1103.
- Rosenzweig, M.L. 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.
- Seutin, G., Brawn, J., Ricklefs, R.E. and Bermingham, E. 1993. Genetic divergence among populations of a tropical passerine, the Streaked Saltator (*Saltator albicollis*). *Auk*, **110**: 117–126.
- Soulé, M.E. and Yang, S.Y. 1973. Genetic variation in the side-blotched lizards on islands in the Gulf of California. *Evolution*, **27**: 593–600.

- Soulé, M.E. and Zegers, G.P. 1996. Phenetics of natural populations. V. Genetic correlates of phenotypic variation in the pocket gopher (*Thomomys bottae*) in California. *J. Hered.*, **87**: 341–350.
- Templeton, A.R. 1994. The role of molecular genetics in speciation studies. In *Molecular Ecology and Evolution: Approaches and Applications* (B. Schierwater, B. Streit, G.P. Wagner and R. DeSalle, eds), pp. 455–477. Basel: Birkhäuser Verlag.
- Thorpe, J.P. 1983. Enzyme variation, genetic distance and evolutionary divergence in relation to levels of taxonomic separation. In *Protein Polymorphism: Adaptive and Taxonomic Significance* (G.S. Oxford and D. Rollinson, eds), pp. 131–152. Systematic Association No. 24. New York: Academic Press.
- Wagner, W.L. and Funk, V.A. 1995. *Hawaiian Biogeography. Evolution on a Hotspot Archipelago*. Washington, DC: Smithsonian Institution Press.
- Waldmann, P. and Andersson, S. 1998. Comparison of quantitative genetic variation and allozyme diversity within and between populations of *Scabiosa canescens* and *S. columbaria*. *Heredity*, **81**: 79–86.
- West-Eberhard, M.J. 1983. Sexual selection, social competition, and speciation. *Quart. Rev. Biol.*, **58**: 155–183.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics*, **16**: 97–159.

