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GENETIC AND MORPHOMETRIC DIFFERENTIATION IN INTRODUCED POPULATIONS OF COMMON CHAFFINCHES (*FRINGILLA COELEBS*) IN NEW ZEALAND[1]

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Abstract. Approximately 400 Common Chaffinches (*Fringilla coelebs*) were introduced last century into New Zealand from England. These founders and their descendents have been such successful colonizers that they are now among the most abundant and widespread passerine species in the region. To assess the amount of differentiation that has developed in the period of about 90–120 years, we sampled populations in the North and South islands of New Zealand, and a population isolated on Chatham Island 800 km to the east. Chaffinches have differentiated very little genetically and morphometrically, in sharp contrast to colonizing species such as House Sparrows (*Passer domesticus*), Common Mynas (*Acridotheres tristis*), and European Starlings (*Sturnus vulgaris*) introduced contemporaneously. Population differentiation does not fit geographically ordered patterns such as clines or isolation-by-distance, and there is no convincing evidence of selection for climatic adaptation or non-selective environmental induction. Random drift is implicated as the primary causal agent for the haphazard pattern of geographic variation, which implies that genetic and morphometric characters are now effectively neutral with respect to selection. Comparison with populations in Europe, North Africa, and the Atlantic islands suggests that microevolutionary processes of population divergence in New Zealand can be extrapolated through time to explain intraspecific and interspecific diversity in chaffinches.

Key words: Common Chaffinch; electrophoresis; genetic differentiation; morphometrics; colonizing species; microevolution.

INTRODUCTION

Populations of animals and plants introduced by humans to regions of the world remote from their natural ranges provide evolutionists with unparalleled opportunities to study processes of microevolutionary change over known time frames. The theoretical significance of such studies derives from the contention that gradual adaptive divergence among populations can be extrapolated to account for speciation and macroevolutionary phenomena, a basic premise of the neo-Darwinian synthesis. This view has been challenged as an exclusive mode of evolution by proponents of rapid founder-induced change (Mayr 1954, Carson and Templeton 1984) and punctuated equilibrium (Eldredge and Gould 1972, Gould 1982). It seems possible that these divergent viewpoints can be reconciled simply as different perspectives through time on cumulative microevolutionary changes, coupled with differential rates of extinction in different clades (Turner 1988). The development of population differentiation in colonizing species can thus provide an extremely valuable assessment of the magnitude of microevolutionary change, and give insights into its macroevolutionary potentiality (Baker and Moeed 1979, Baker 1980).

New Zealand populations of the Common Chaffinch (*Fringilla coelebs*) are ideal subjects for investigating processes of microevolution because the populations were introduced from England late last century. About 400 birds were liberated between 1862 and 1877 (Thomson 1922). Primary introductions were made at Auckland and Wellington in the North Island, and at Nelson, Christchurch, and Dunedin in the South Island. Approximately 100 chaffinches each were released at Auckland, Wellington, and Dunedin, 23 at Nelson, and the rest at Christchurch. Private individuals and bird dealers then secondarily introduced this expanding stock to other centers. They have been such successful colonizers that they are now among the most abundant passerine birds there (Jenkins and Baker 1984), and are the only introduced passerine species that has successfully penetrated native forests. Chaffinches have now colonized many offshore islands in the region of New Zealand,

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TABLE 1. Samples of Common Chaffinches used in this study.

Locality	Abbreviation	Collection date	Sample size
North Island			
Woodhill	WOOD	February 1984, November 1985	36
Taupo	TAUP	December 1985	25
Wellington	WELL	November 1985, January 1986	20
South Island			
Nelson	NELS	November 1985, January 1986	26
Eyrewell	EYRE	November 1985	36
Herbert	HERB	November 1985	31
Longwood	LONG	November 1985	30
Chatham Island			
Tuku	TUKU	November 1985	23
		Total	227

reaching as far east as the Chatham Islands (800 km). The apparently natural colonization of the Chathams occurred around 1900 (Williams 1953), but there are no records of the numbers of founders involved. An earlier study based on learned song suggested that the Chathams were colonized by a small number of founders because extant populations have a depauperate pool of syllables relative to their New Zealand conspecifics (Baker and Jenkins 1987).

In this paper we report on the amount of genetic differentiation that has developed in chaffinch populations in the North and South islands of New Zealand, and compare them with a population isolated in the Chatham Islands. We assess the roles of gene flow, selection, and random genetic drift in promoting this level of differentiation in the period of approximately 90–120 years. We then compare these short-term microevolutionary changes to longer-term changes observed in populations isolated in the Atlantic islands (Azores, Madeira, and Canaries) for about a million years (Baker et al. 1989). Finally, we argue that processes of genetic differentiation in small to moderate-sized populations extrapolated through time are sufficient to account for the evolution of intraspecific and interspecific diversity in chaffinches.

MATERIALS AND METHODS

SAMPLES OBTAINED

Samples of adult chaffinches were collected from eight different populations covering nearly all the range of the species in the New Zealand region. Three populations were sampled in the North Island, four in the South Island, and one on Chatham Island. Details of the samples obtained for genetic and morphometric analysis are provided in Table 1, and their geographic locations are shown in Figure 1.

ELECTROPHORETIC METHODS

Samples of liver, heart, and pectoral muscle were removed from each specimen immediately after death and stored in cryogenic tubes in liquid nitrogen until they were transported back to the Laboratory of Analytical Systematics in the Royal Ontario Museum. The samples were then stored at −70°C until they were electrophoresed. Tissue samples from all 227 birds were surveyed for genetic variation at 44 presumptive loci using running buffers optimized for chaffinches (details of running conditions can be obtained from the first author). Gels were run overnight for 16 hr at 4°C, and were then stained using the methods detailed in Harris and Hopkinson (1976), Barrowclough and Corbin (1978), and Cole and Parkin (1980). Electromorphs were assumed to be products of different alleles. Alleles from each population were calibrated by running them side-by-side on the same gel. Loci were numbered sequentially with integers beginning with 1 for the most anodal form, and alleles were designated alphabetically (with A for the most common one).

ANALYSIS OF GENETIC DATA

Genotypes scored for all populations were analyzed with the computer package BIOSYS-1 (Swofford and Selander 1981). All the loci screened in this study were autosomal except cytoplasmic aconitase (Aco-1). In chaffinches this

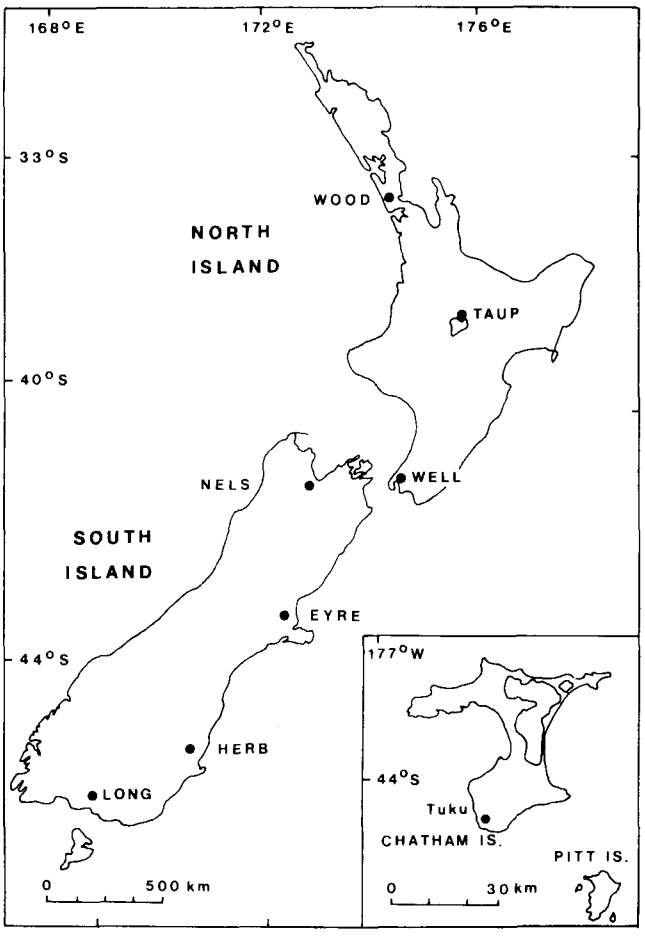

FIGURE 1. The location of sites where samples of Common Chaffinches were collected for this study. The Chatham Island sample at Tuku is shown in the inset.

locus is Z-linked (Baker et al. 1989), so we therefore deleted genotypes for the heterogametic sex (females) from the data set for this locus in all analyses. For each population, observed (direct count) and expected (based on Hardy-Weinberg equilibrium) heterozygosities were calculated and averaged across all loci. Because there were no significant differences between average observed and expected heterozygosities (Kruskal-Wallis test, $P > 0.05$) in any of the populations, we have only reported the theoretically preferable latter estimate beyond. To test for departures from expected Hardy-Weinberg proportions of genotypes within samples, we employed chi-square tests with pooling of all uncommon alleles to guard against inflation of the chi-square values when cells had expected frequencies of less than one (Swofford and Selander 1981). Exact probabilities for small samples were used in evaluating the chi-square statistics (Vithayasai 1973).

Geographic heterogeneity in allele frequencies among all populations was tested at each locus with contingency chi-square analysis, using the method of Workman and Niswander (1970). The extent of population structuring and genetic differentiation was investigated with F-statistics (Wright 1965, 1978). Differentiation in different regions was assessed by averaging F-statistics over all polymorphic loci for (1) the North Island, (2) the South Island, and (3) all New Zealand populations and Chatham Island.

Multilocus genetic comparisons were made among populations by computing Rogers' (1972) genetic distances and clustering them with UPGMA cluster analysis (Sneath and Sokal 1973). Cluster analysis of our data set resulted

in some distortion of the original distance matrix (matrix correlation $r_{dd*} = 0.766$) in the 2-D phenogram, so we also ordinated the samples in 3-D space with nonmetric multidimensional scaling (Kruskal 1964). To guard against the scaling solution becoming trapped in local optima, we used a principal coordinates ordination (Gower 1966) as an initial configuration. A minimum spanning tree based on the full dimensional genetic distance matrix was then superimposed between the sample projections to indicate relationships and to reveal any distortions in the reduced 3-D space. Genetic distances were also calculated using the formula given by Nei (1978) for comparison with published values in other studies of birds.

ANALYSIS OF MORPHOMETRIC VARIATION

Morphometric variation in the eight New Zealand populations of chaffinches was restricted to the 180 specimens of males because females were too few in number for adequate statistical treatment. Twelve measurements were made on each specimen as follows: (1) premaxilla width (PREW), transversely across the premaxilla where the jugals meet the lateral wings of the premaxilla; (2) cranium depth (CRAD), medially as the minimum vertical distance between the basisphenoid and the top of the cranium; (3) cranium length (CRAL), laterally from the posterior tip of the supraoccipital ridge to the posterior border of the orbit; (4) mandible length (MAND), from the articular fossa to the anterior tip of the mandible; (5) humerus length (HUML), the minimum distance between the the tip of the head and the entepicondylar fossa; (6) ulna length (ULNA), from the olecranon to the distal intercondylar fossa; (7) sternum length (STER), medially from the manubrium to the caudal edge of the sternum; (8) coracoid length (CORA), the minimum distance from the head to the sternal facet; (9) femur length (FEML), the minimum distance between the neck and the intercondylar fossa; (10) tarsometatarsus length (TARS), from the trochlea for digit II to the proximal tip of the hypotarsus; (11) synsacrum length (SACL), lateromedially between the anterior and posterior tips of the ilium; (12) synsacrum width (SACW), the minimum dorsal distance between the acetabula. All measurements were made with dial calipers to the nearest 0.05 mm.

Geographic variation was assessed univariately among populations using single classification analysis of variance. Nonsignificant subsets of population means were delimited with Duncan's multiple range test to quantify the extent and pattern of geographic variation in individual characters. Multivariate analogs of these tests were also conducted to elucidate geographic patterns of character variation and covariation. We used multivariate analysis of variance (MANOVA) to determine whether population centroids differed significantly in location, and then defined maximally connected subsets of centroids with MANOVA-STP (Gabriel 1968). To facilitate comparison with the genetic data, we also ordinated the morphometric data with nonmetric multidimensional scaling, based on an initial configuration obtained from a principal coordinates analysis of a matrix of average taxonomic distances (Sneath and Sokal 1973).

ENVIRONMENTAL VARIATION

The association between environmental variation and population differentiation was investigated using separate linear regressions of morphometric variables and allele frequencies on 12 environmental variables, as follows: (1) mean annual rainfall, (2) mean January (summer temperature), (3) mean July (winter) temperature, (4) mean maximum January temperature, (5) mean maximum July temperature, (6) mean minimum January temperature, (7) mean minimum July temperature, (8) mean annual temperature range, (9) latitude, (10) longitude, (11) isophane, and (12) relative humidity at 09:00. Weather data were taken from New Zealand Meteorological Service reports based mostly on 25- to 30-year summaries to 1970. Weather stations were located in the forests in which we collected, or were nearby (usually within 5 km).

RESULTS

GENETIC VARIABILITY

Twenty-seven of the 44 loci surveyed in this study were monomorphic and fixed for the same allele in all populations: Aco-2, Acp-2, Acp-3, Ak-1, Ak-2, Ak-3, Ck-1, Es-4, Es-5, Got-1, Got-2, Gpd-2, Gpi, G6pd, Icd-2, Ldh-1, Ldh-2, Mdh-1, Mdh-2, Pgm-1, Pt-1, Pt-2, Pt-3, Sdh, Sod-1, Sod-2, and Sod-3. Allele frequencies for the remaining 17 polymorphic loci are shown in Table 2. The same common allele occurs in all populations except for the Aco-1 locus, where some South Island samples (Nelson, Eyrewell, and Longwood) have a clear preponderance of the alternative allele (B). The Woodhill sample alone has

TABLE 2. Allele frequencies for 17 polymorphic loci in eight New Zealand populations of Common Chaffinches.

Locus (EC number)	ALLELE	Population WOOD	TAUP	WELL	NELS	EYRE	HERB	LONG	TUKU
Aco-1	A	0.46	0.66	0.50	0.23	0.29	0.46	0.22	0.50
(4.2.1.3)	B	0.50	0.34	0.50	0.77	0.71	0.54	0.78	0.50
	C	0.04							
Acp-1	A	0.95	1.00	1.00	0.92	1.00	1.00	0.97	0.98
(3.1.3.2)	B	0.01			0.08			0.03	0.02
	C	0.04							
Ada	A	0.87	0.90	0.94	0.66	0.90	0.81	0.85	0.87
(3.5.4.4)	B	0.01							
	C	0.09	0.08	0.03	0.20	0.04	0.05	0.08	0.04
	D	0.03	0.02	0.03	0.14	0.06	0.14	0.07	0.09
Ck-2	A	1.00	1.00	1.00	0.98	0.92	0.94	0.90	0.83
(2.7.3.2)	B				0.02	0.08	0.06	0.10	0.17
Es-1	A	0.92	0.98	0.98	0.94	0.96	1.00	0.95	1.00
(3.1.1.1)	B	0.08	0.02	0.02	0.06	0.04		0.05	
Es-2	A	0.56	0.80	0.58	0.58	0.65	0.57	0.60	0.70
(3.1.1.1)	B	0.32	0.12	0.25	0.34	0.32	0.43	0.33	0.16
	C	0.12	0.08	0.17	0.08	0.03		0.07	0.14
Es-3	A	1.00	0.92	0.88	1.00	0.90	0.95	0.98	0.96
(3.1.1.1)	B		0.08	0.12		0.08	0.05	0.12	0.02
	C					0.01			0.02
Gda	A	0.95	0.94	1.00	0.98	0.99	0.95	1.00	0.83
(3.5.4.3)	B	0.05	0.06		0.02	0.01	0.05		0.17
Glud	A	1.00	1.00	1.00	1.00	1.00	0.97	1.00	1.00
(1.4.1.3)	B						0.03		
Gpd-1	A	0.99	0.94	1.00	1.00	1.00	1.00	1.00	1.00
(1.1.1.8)	B	0.01	0.06						
Icd-1	A	0.96	0.96	0.98	0.90	0.85	0.89	0.93	0.89
(1.1.1.42)	B	0.04	0.04	0.02	0.08	0.07	0.06	0.05	0.11
	C				0.02	0.08	0.05	0.02	
Mpi	A	0.66	0.77	0.82	0.73	0.60	0.61	0.58	0.65
(5.3.1.8)	B	0.34	0.23	0.18	0.27	0.40	0.39	0.41	0.35
Np	A	0.99	1.00	0.90	0.90	0.93	0.87	0.77	0.96
(2.4.2.1)	B	0.01		0.10	0.10	0.07	0.13	0.23	0.04
Pep-A	A	1.00	0.98	0.98	1.00	1.00	1.00	0.95	1.00
(3.4.11)	B		0.02	0.02					
	C							0.05	
Pep-B	A	0.63	0.60	0.70	0.56	0.69	0.68	0.60	0.64
(3.4.11)	B	0.04		0.02	0.04	0.07	0.10	0.05	
	C	0.33	0.40	0.28	0.40	0.24	0.23	0.35	0.36
Pgd	A	0.81	0.76	0.82	0.94	0.79	0.78	0.75	0.84
(1.1.1.44)	B	0.18	0.20	0.18	0.06	0.17	0.19	0.25	0.09
	C	0.01	0.04			0.04	0.03		0.07
Pgm-2	A	1.00	1.00	1.00	0.96	0.97	0.98	0.98	1.00
(2.7.5.1)	B							0.02	
	C				0.04	0.03	0.02		

rare alleles at three loci (Aco-1, Acp-1, and Ada). Another feature of the allele frequency data in Table 2 is that the Tuku sample from the peripherally located Chatham Islands is extremely similar to the mainland New Zealand populations in its allelic profiles at each locus.

Chi-square analysis revealed statistically significant departures from Hardy-Weinberg proportions at six loci (Acp-1, Es-1, Es-3, Gda, Icd-1, and Pgm-2). Sampling error is implicated as the cause for these deviations because they all emanate from small deficiencies of heterozygotes involving rare or uncommon alleles. Levels of genetic variability within populations are sum-

TABLE 3. Genetic variability at 44 loci in eight New Zealand populations of Common Chaffinches.

Locality	Mean sample size per locus	Mean number of alleles per locus	Percentage of loci polymorphic 0.95	Percentage of loci polymorphic 0.99	Average heterozygosity ± SE
North Island					
Woodhill	38.5	1.4	20.5	27.3	0.071 ± 0.024
Taupo	24.8	1.3	20.5	27.3	0.061 ± 0.019
Wellington	19.8	1.3	18.2	25.0	0.061 ± 0.021
South Island					
Nelson	25.8	1.4	22.7	29.5	0.077 ± 0.024
Eyrewell	35.7	1.5	22.7	29.5	0.077 ± 0.023
Herbert	30.9	1.4	20.5	29.5	0.079 ± 0.023
Longwood	29.8	1.4	25.0	31.8	0.084 ± 0.025
Chatham Island					
Tuku	22.8	1.4	20.5	29.5	0.077 ± 0.022

marized in Table 3. There are no significant differences among the populations in the mean number of alleles/locus, percentage of polymorphic loci (0.95 or 0.99 criteria), and average heterozygosity (t-tests, $P > 0.05$). The Chatham Island population sampled at Tuku has similar levels of genetic variability as obtain in mainland New Zealand populations.

GENETIC DIFFERENTIATION

Based on a conservative probability level of 0.01, contingency chi-square analysis detected significant heterogeneity in allele frequencies among all eight populations. Significant geographic variation in allele frequencies occurs at six loci (Aco-1, Ck-2, Es-2, Gda, Gpd-1, and Np). The geographic structuring of populations is primarily due to genetic differentiation between populations in the North and South islands of New Zealand; within each of these islands the populations are not significantly heterogeneous in their allele frequencies, the mean F_{st} values over all loci are about half that for all New Zealand localities, and the mean genetic distances among populations are lower (Table 4). The small scale of the among-population component of genetic variance in the New Zealand region is reflected in the mean F_{st} value of 0.040. It is noteworthy that the inclusion of the Chatham Island sample adds little to the various measures of genetic differentiation, indicating that this population has not diverged from its mainland counterparts to any significant degree.

Genetic distances among all populations are shown in Table 5. UPGMA cluster analysis of Rogers' (1972) genetic distances illustrates the limited differentiation of populations in the North and South islands, although the northernmost North Island sample at Woodhill is clustered with South Island samples (Fig. 2). The 3-D multidimensional scaling ordination shows clearly, however, that the Woodhill sample is actually genetically intermediate between North and South island samples (Fig. 3). Both the ordination and the cluster analysis group the Chatham Island sample (Tuku) with the North Island populations.

MORPHOMETRIC VARIATION

Means and standard errors of the 12 skeletal characters for the eight New Zealand populations of chaffinches are listed in Table 6. Analysis of variance detected statistically significant geographic variation in only two of the morpho-

TABLE 4. Summary of genetic differentation in eight New Zealand populations of Common Chaffinches.

Measure	North Island ($n = 3$)	South Island ($n = 4$)	Mainland New Zealand ($n = 7$)	All populations ($n = 8$)
F_{st}	0.027	0.021	0.040	0.040
D_R	0.021	0.022	0.025	0.026
No. loci geographically	0[a]	0[b]	4	6

[a] Two loci, Es-3 and Np approach significance ($0.01 < P < 0.05$).
[b] Two loci, Glud and Ada, approach significance ($0.01 < P < 0.05$).

TABLE 5. Genetic distances among eight New Zealand populations of Common Chaffinches. Above the diagonal are Nei's (1978) unbiased genetic distances, and below the diagonal are Rogers' (1972) genetic distances.

Population	WOOD 1	TAUP 2	WELL 3	NELS 4	EYRE 5	HERB 6	LONG 7	TUKU 8
1 WOOD	—	0.002	0.002	0.001	0.000	0.001	0.001	0.001
2 TAUP	0.022	—	0.000	0.004	0.003	0.007	0.004	0.001
3 WELL	0.023	0.017	—	0.004	0.002	0.006	0.003	0.002
4 NELS	0.019	0.033	0.031	—	0.002	0.002	0.001	0.003
5 EYRE	0.019	0.029	0.024	0.025	—	0.000	0.000	0.001
6 HERB	0.025	0.037	0.033	0.027	0.016	—	0.000	0.005
7 LONG	0.019	0.034	0.031	0.023	0.018	0.021	—	0.003
8 TUKU	0.023	0.023	0.028	0.031	0.024	0.031	0.029	—

metric characters, cranium depth (CRAD) and synsacrum width (SACW). The magnitude of this differentiation can be judged from the individual variance components; for CRAD 13.3% of the character variation is distributed among populations, and the corresponding value for SACW is 5.2%. The variance components for the remaining characters are all small or zero, attesting to the very limited scale of morphometric differentiation among populations.

Duncan's multiple range test revealed that only the populations from Woodhill (with the largest mean) and Herbert (with the smallest mean) differ significantly for CRAD. Additionally, the Woodhill, Eyrewell, and Herbert population means for SACW are significantly larger than the corresponding Wellington mean. MANOVA confirmed that there are significant differences in the location of the population centroids in multivariate space (F-transformation of Wilks' lambda = 1.643, df = 84 and 780, $P < 0.001$). In parallel with the univariate tests, MANOVA-STP identified only two maximally connected subsets of centroids, confirming multivariately the small degree of geographic variation in morphometrics. One subset contained all population centroids except Woodhill, and the other contained Woodhill, Eyrewell, and Tuku. Since the latter subset contains centroids from the three different islands, it is apparent that among-population variation is not based on geographic contiguity of populations.

Average taxonomic distances among populations are shown in Table 7. A principal coordinates analysis produced a good data-analytic reduction of the full-dimensional morphometric distance matrix to three dimensions, with the first three eigenvalues cumulatively explaining 87.2% of the total variation in the matrix. Nonmetric multidimensional scaling of this 3-D model produced the optimized ordination in Fig-

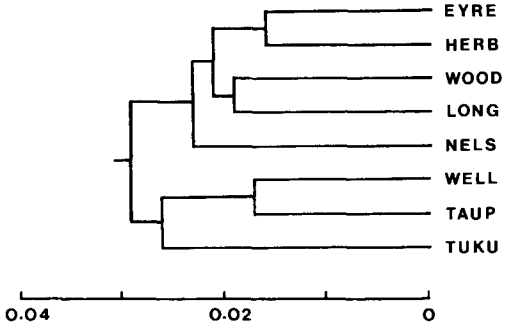

FIGURE 2. UPGMA cluster analysis of Rogers' (1972) genetic distances among eight New Zealand populations of Common Chaffinches. See Table 1 for key to abbreviations.

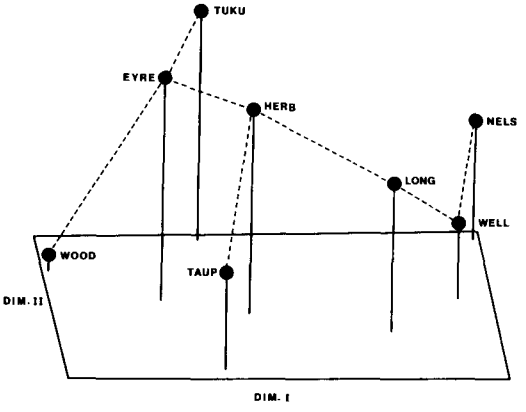

FIGURE 3. Three-dimensional ordination with nonmetric multidimensional scaling of Rogers' (1972) genetic distances among eight New Zealand populations of Common Chaffinches. Dimension III is represented by the height of the population projections. See Table 1 for key to abbreviations.

ure 4. Populations from the North and South islands do not group separately in different regions of morphometric space, and the Chatham Island sample (TUKU) is not well differentiated from its mainland New Zealand counterparts.

POPULATION DIFFERENTIATION AND ENVIRONMENTAL VARIATION

Environmental variables successfully predict the pattern of geographic variation in only one morphometric variable, cranium depth (CRAD). Mean January, mean minimum January, and mean minimum July temperatures, and the correlated variables of mean annual temperature range and isophane, all have significant linear regressions ($P < 0.05$) on cranium depth. These regressions 'explain' up to 55% of the among-population variation in CRAD. Principal component I based on the population means for the 12 morphometric variables is a rough index of geographic variation in body size, although bootstrapping revealed that cranium depth and mandible length do not load significantly on this axis. No significant regressions were found between environmental variables and PC I of the morphometric variables.

Allele frequencies at geographically variable loci are also poorly aligned with environmental gradients. Only three of 78 regressions were significant ($P < 0.05$), a result expected by chance alone. Geographic variation in the common allele at Aco-1 was predicted by longitude ($r^2 = 0.55$), and at Np by latitude ($r^2 = 0.61$) and longitude ($r^2 = 0.81$).

ASSOCIATION OF GENETIC AND MORPHOMETRIC DIVERGENCE

To investigate whether genetic and morphometric variation among populations were associated, we conducted Mantel's tests using Rogers' genetic distances and average taxonomic distances. As an approximate test of an isolation-by-distance model, we also carried out Mantel's test with the above matrices and a geographic distance matrix computed from a Gabriel connected graph among populations (available on request from the senior author). Based on the normalization procedure outlined in Smouse et al. (1986), genetic and morphometric distances among populations are not significantly correlated ($Z = -0.206$, $P = 0.315$). Neither genetic distances ($Z = 0.248$, $P = 0.287$) nor morphometric distances ($Z = -0.023$, $P = 0.910$) are

TABLE 6. Percent variance components, means, and standard errors of 12 skeletal measurements from eight New Zealand populations of male Common Chaffinches.

Measurement	% variance component	Population							
		WOOD ($n = 18$)	TAUP ($n = 23$)	WELL ($n = 15$)	NELS ($n = 23$)	EYRE ($n = 30$)	HERB ($n = 29$)	LONG ($n = 23$)	TUKU ($n = 19$)
PREW	0.0	6.58 ± 0.04	6.56 ± 0.04	6.51 ± 0.05	6.53 ± 0.05	6.60 ± 0.05	6.54 ± 0.04	6.57 ± 0.07	6.58 ± 0.03
CRAD	13.2	11.94 ± 0.06	11.64 ± 0.06	11.80 ± 0.06	11.80 ± 0.05	11.67 ± 0.05	11.58 ± 0.06	11.66 ± 0.06	11.79 ± 0.06
CRAL	4.0	20.20 ± 0.09	20.03 ± 0.10	19.85 ± 0.08	19.85 ± 0.10	19.98 ± 0.07	20.06 ± 0.08	19.90 ± 0.09	20.14 ± 0.10
MAND	2.9	21.01 ± 0.12	21.40 ± 0.13	21.21 ± 0.12	20.88 ± 0.13	21.12 ± 0.10	21.19 ± 0.14	21.22 ± 0.16	21.02 ± 0.10
HUML	3.0	18.69 ± 0.08	18.60 ± 0.08	18.32 ± 0.14	18.36 ± 0.08	18.53 ± 0.08	18.51 ± 0.08	18.55 ± 0.07	18.46 ± 0.11
ULNA	2.4	23.43 ± 0.10	23.37 ± 0.08	23.15 ± 0.16	23.02 ± 0.12	23.28 ± 0.11	23.15 ± 0.10	23.24 ± 0.11	23.19 ± 0.12
STER	0.8	21.62 ± 0.14	21.31 ± 0.19	21.19 ± 0.16	21.14 ± 0.19	21.42 ± 0.13	21.39 ± 0.16	21.11 ± 0.13	21.45 ± 0.13
CORA	0.0	16.74 ± 0.09	16.72 ± 0.08	16.60 ± 0.13	16.58 ± 0.10	16.76 ± 0.09	16.71 ± 0.07	16.54 ± 0.09	16.76 ± 0.14
FEML	0.0	15.33 ± 0.08	15.36 ± 0.06	15.22 ± 0.12	15.22 ± 0.10	15.42 ± 0.10	15.37 ± 0.08	15.28 ± 0.08	15.24 ± 0.11
TARS	0.0	18.32 ± 0.12	18.29 ± 0.15	18.02 ± 0.12	18.01 ± 0.16	18.28 ± 0.13	18.12 ± 0.11	18.00 ± 0.14	18.06 ± 0.16
SACL	2.1	16.47 ± 0.10	16.51 ± 0.07	16.38 ± 0.11	16.41 ± 0.12	16.71 ± 0.11	16.48 ± 0.09	16.48 ± 0.12	16.76 ± 0.13
SACW	5.2	10.48 ± 0.10	10.32 ± 0.08	10.20 ± 0.11	10.26 ± 0.09	10.52 ± 0.08	10.51 ± 0.07	10.40 ± 0.06	10.44 ± 0.06

TABLE 7. Average taxonomic distances among eight New Zealand populations of Common Chaffinches based on 12 skeletal measurements.

Population	1	2	3	4	5	6	7	8
1 WOOD	—							
2 TAUP	0.182	—						
3 WELL	0.258	0.179	—					
4 NELSON	0.266	0.236	0.105	—				
5 EYRE	0.154	0.126	0.207	0.219	—			
6 HERB	0.180	0.121	0.165	0.185	0.103	—		
7 LONG	0.237	0.140	0.111	0.144	0.165	0.124	—	
8 TUKU	0.166	0.181	0.193	0.188	0.114	0.129	0.177	—

significantly correlated with geographic distances among populations.

DISCUSSION

EXTENT OF POPULATION DIFFERENTIATION IN NEW ZEALAND

The major finding in this study is the very limited amount of genetic and morphometric differentiation that has developed in chaffinch populations that have colonized New Zealand in the last 90–120 years. Only six allozyme loci and two morphometric characters display significant geographic variation. The small scale of population structuring that has developed derives from differences among populations in the North vs. the South islands in New Zealand, whereas the peripherally isolated population on Chatham Island has not diverged noticeably from its mainland ancestral counterparts. This result is surprising because an earlier study of cultural evolution in songs of New Zealand and Chatham Island chaffinch populations had reported that the latter had a depauperate syllable pool, consistent with a small innoculum of founders possessing only a subset of the syllables found in a typical New Zealand population (Baker and Jenkins 1987). Thus we might have anticipated reduced levels of genetic variation on Chatham Island, but this is clearly not the case in the extant population. Part of the explanation resides in the smaller effective population size for songs (and thus syllables) than for genes because only males sing and transmit syllables to males in subsequent generations. Consequently, cultural transmission of songs is analogous to a haploid genetic system like mitochondrial DNA, which has only one-fourth the effective population size of diploid nuclear gene systems (Birky et al. 1981). It is also possible that many founders were females or young males who had not learned their songs before they emigrated to Chatham Island.

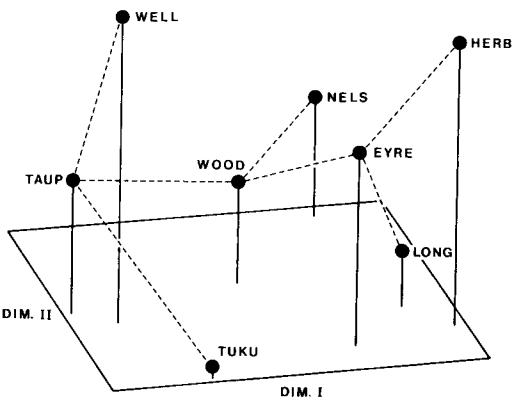

FIGURE 4. Three-dimensional ordination with nonmetric multidimensional scaling of average taxonomic distances among eight New Zealand populations of Common Chaffinches. Dimension III is represented by the height of the population projections. See Table 1 for key to abbreviations.

The scale of genetic and morphometric differentiation among populations of chaffinches can be gauged by comparison with populations of other introduced passerines that have been studied in New Zealand. Contemporaneous populations of House Sparrows (*Passer domesticus*) and European Starlings (*Sturnus vulgaris*), sampled over the same geographic range as chaffinches, have clearly differentiated morphometrically much more than the latter (Baker 1980, Ross and Baker 1982). For example, House Sparrows and European Starlings have developed significant geographic variation in 13 of 16 and eight of 14 skeletal characters, respectively. The corresponding average added variance component for these skeletal suites is 5.32% and 5.96%. In marked contrast, chaffinches have differentiated in only two of 12 skeletal characters, and the

average added variance component is about half (2.80%) that in the other species. Populations of Common Mynas (*Acridotheres tristis*), although restricted to the northern two-thirds of the North Island, have also differentiated much more than have chaffinches over the whole of New Zealand (Baker and Moeed 1979). In Common Mynas, 17 of 28 skeletal characters have developed significant geographic variation, and the average added variance component is 5.29%.

Comparable genetic data are available only for starlings (Ross 1983); six loci show significant geographic variation in New Zealand and the mean F_{st} is 0.032. Similar values pertain to chaffinches, with four loci showing significant heterogeneity in mainland New Zealand (six loci if Chatham Island is included), and the mean F_{st} is 0.040. The mean value of Nei's (1978) unbiased genetic distance of 0.0022, although small, is nevertheless equivalent to that among much older continental populations of birds (see Barrowclough 1980). Similarly, the mean F_{st} of 0.040 in New Zealand chaffinch populations is typical of most continuously distributed bird populations (Barrowclough 1983). Thus we can conclude that the introduced populations of chaffinches have developed levels of genetic structuring typical of continental demes of birds, and furthermore, this weak structuring has occurred in the short period of about 100 years.

INFERENCE OF PROCESSES OF POPULATION DIFFERENTIATION

Both genetic and morphometric variation among New Zealand populations of chaffinches do not fit geographically ordered patterns such as clines or isolation-by-distance, because neither correlates with geographic distances among sample sites. Not only is the pattern of geographic variation haphazard for both genetics and morphometrics, but they are also independent of one another. With the exception of cranium depth, which increases in warmer northern localities, morphometric variation does not align with environmental variation, the latter being essentially a north-south temperature gradient. Similarly, allele frequencies are not convincingly associated with environmental variation, although the limited genetic differentiation that has evolved is attributable to differences between populations in the North and South islands. As noted by Schnell and Selander (1981) and Zink (1986), it would be surprising if one could not find some environmental variable(s) that covaried significantly with allele frequencies at polymorphic loci, as we found between latitude and the common alleles at Aco-1 and Np. This covariation is very likely spurious because such a result is expected by chance under our multiple comparisons design.

Thus the geographic variation patterns exhibited in extant populations do not accord with selection for climatic adaptation (as deduced for House Sparrows and Common Mynas from morphometric data alone—see Baker [1980] and Baker and Moeed [1979] for rationale), or for nonselective environmental induction (Gould and Johnston 1972). All of the specimens used in this study were collected in exotic forests of predominantly *Pinus radiata* planted by the New Zealand Forestry Service in the last 40 years or so, and it is therefore very unlikely that the seed-eating chaffinches are responding morphometrically to geographically random patterns of seed size in different forests.

The haphazard pattern of genetic differentiation implicates random genetic drift as the principal causal agent for geographic variation at the molecular level, as has been invoked previously for Common Mynas and European Starlings (Baker and Moeed 1987, Ross 1983). The incipient North Island/South Island differentiation, however, is probably attributable to restricted gene flow across the Cook Strait water barrier between the two islands. Unfortunately, the time frame since the introduction of chaffinches into New Zealand is too short to allow the establishment of equilibrium between gene flow (or migration) among populations and mutational input within populations, and thus we cannot use indirect methods (Slatkin 1985, 1987) to calculate levels of gene flow between populations in the North and South islands. However, the syllable pools of the North and South island populations are very different, reinforcing the contention that the interisland water barrier is limiting dispersal (Baker and Jenkins 1987, unpubl. data).

The very small scale and haphazard pattern of geographic variation in morphometric characters is consistent with presently neutral evolution of these characters (see Lande 1985, Lynch and Hill 1986, Lynch 1988). At the morphometric level, cranium depth alone is aligned with environmental temperature gradients. It is extremely unlikely that directional selection for cli-

matic adaptation would operate only on cranium depth and leave other characters unaffected (given genetic covariances among characters), especially since the tendency for increased average cranium depth in warmer northern locales is the opposite to that predicted by Bergmann's rule and has no obvious functional explication. We therefore favor the view that this single character association with among-locality temperature gradients is fortuitous, and is consistent overall with random drift of effectively neutral morphometric characters. This does not mean, however, that phenotypic evolution in New Zealand chaffinch populations will not eventually be ordered by natural selection, especially if they switch to markedly different habitats or if they encounter environmental perturbations in the future.

The near geographic uniformity in morphometrics of chaffinches contrasts sharply with the more pronounced geographic variation exhibited in many characters by House Sparrows, European Starlings, and Common Mynas that have also been introduced into New Zealand in the last 100 years or so. The species name *coelebs* (or bachelor male) refers to the relative sedentariness of male chaffinches (in Europe in winter), whereas females disperse more widely (Bannerman 1953). If the New Zealand populations have retained female-biased dispersal within the two major islands, then this might partly account for the limited differentiation in chaffinches relative to more sedentary species. This parallels the striking contrast between the geographically structured Fox Sparrow (*Passerella iliaca*) and the geographically uniform Green-tailed Towhee (*Pipilo chlorurus*), which are syntopic in many parts of the western United States. The latter is much more continuously distributed, however, implying that the smoothing effect of gene flow is much more important in this species than in the more subdivided Fox Sparrow. Additionally, as pointed out by Zink (1986), these species may also differ in their degree of geographic variation because of intrinsic differences in phenotypic canalization, or species-specific differences in phenotypic plasticity (Via and Lande 1986), and the same line of reasoning can be applied to the colonizing species of passerines in New Zealand. Although the innovative studies conducted by James (1983) have revealed an unexpectedly large nongenetic component to geographic variation in the Red-winged Blackbird (*Agelaius phoeniceus*), we clearly need more investigations of the developmental constraints on geographic variation in a broad range of species with different population structures (see Smith et al. 1985).

INTRASPECIFIC AND INTERSPECIFIC DIVERGENCE

The evolutionary potential of population divergence in New Zealand chaffinches is difficult to assess, especially given the short time frame for the development of genetic and morphometric differentiation. This study, however, was designed as part of a more comprehensive research program to investigate whether cumulative microevolutionary changes could be extrapolated to explain intraspecific and interspecific divergence in *Fringilla* populations with different colonization histories. Specifically, the objective was to compare short-term changes in New Zealand populations with longer-term changes in continental populations in Europe and North Africa, and their derivatives in the Atlantic islands. The latter are particularly relevant here because chaffinches from the continents colonized the Azores, Madeira, and the Canaries in about the last million years (Grant 1979, 1980).

Genetic and morphometric studies (Baker et al., in press) revealed that continental populations in Iberia and Morocco, representing subspecies that are phenotypically very distinctive, are only weakly structured genetically (F_{st} = 0.092). The limited genetic differentiation of these subspecies suggests that they may have diverged in about the last 100,000 years following their isolation on either side of the Mediterranean Basin by Pleistocene climatic events. A high level of homogenizing gene flow between these populations is an unlikely explanation for this restricted allozyme divergence because it would have counteracted the substantial morphological divergence unless strong selective forces acted on phenotypes (which seems implausible for plumage characters, for example).

The peripherally isolated Atlantic island populations have diverged further (F_{st} = 0.321) than continental ones, consistent with their long period of isolation. Much of this subdivision is owing to the marked divergence of the Canaries subspecies, and this in turn likely emanates from much lower long-term effective population sizes in this archipelago. Finally, differences among subspecies grade into interspecific differences between *F. coelebs* and the Blue Chaffinch (*F. teydea*), but speciation has apparently not involved

bottlenecks (Baker et al., in press). Viewed from this perspective, the small-scale differentiation in New Zealand appears to be an early phase of a gradual process of divergence in populations of moderate size. We conclude that although bottlenecks can accelerate divergence (see Baker and Moeed 1987), the critical factor in the evolution of intraspecific and interspecific divergence in chaffinches has been the restriction or cessation of homogenizing gene flow among populations.

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