

A genetic assessment of the human-facilitated colonization history of black swans in Australia and New Zealand

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Abstract

Movement of species beyond their indigenous distribution can fundamentally alter the conservation status of the populations involved. If introductions are human-facilitated, introduced species could be considered pests. Characterizing the colonization history of introduced species can therefore be critical to formulating the objectives and nature of wildlife management strategies. The black swan (*Cygnus atratus*) is native to Australia but is considered a reintroduced species in New Zealand, where the endemic population was reported extinct during the 19th century. After the reintroduction of a small number of individuals from Australia, the New Zealand population expanded unexpectedly rapidly, which was attributed to simultaneous waves of migration from Australia. An alternative, but hitherto unformalized, hypothesis is that local extant populations remained and admixed with introduced individuals. To contribute to our understanding of the reintroduction history of the species, we investigated dispersal patterns and demographic histories of seven populations from Australia and New Zealand, using population genetic inferences from a microsatellite dataset. Our results on genetic structure, dispersal rates, and demographic histories provide mixed evidence on the origin of New Zealand black swans. The hypothesis that reintroduced individuals mixed with remaining local individuals and that the subsequent dramatic population expansion may have been due to genetic rescue of the inbred indigenous population cannot be discarded and needs further investigation.

KEYWORDS

conservation, *Cygnus atratus*, kakianau, pest species, phylopatry

1 | INTRODUCTION

The introduction of a species to a new environment can result in a complex series of ecological consequences. Non-native species can outcompete or prey upon indigenous species, alter ecological processes, and ultimately lead to species extinctions (Lowry et al., 2013;

Sakai et al., 2001). In contrast, humans can benefit immensely from the exploitation of introduced species (e.g., crops; Sax et al., 2007), while introduced species in the wild may benefit native species by, for example, controlling other pests (e.g., Glen & Dickman, 2005; Kerr, 2012) or providing critical habitat or food resources (e.g., van Dongen et al., 2012; Toone & Hanscom, 2003). Where species introductions

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are carefully monitored, they can provide important insights into evolutionary and ecological processes in real time (Sax et al., 2007). Documenting the introduction history of species beyond their traditional distribution is critical to understanding their ecological impacts on novel environments, helps predict problematic introductions, and potentially guides proposals to translocate species in the face of climate change. Uncertainty regarding provenance may even lead to controversies about whether a species is native or introduced, a designation that radically alters the management goals (e.g., extermination versus conservation) and attention afforded to species (Grosser et al., 2016).

While archeological evidence or historical records provide important insights into the introduction history of non-native species (Middleton, 2012), genetic studies allow direct hypothesis testing of various evolutionary scenarios (Pool et al., 2010) based, for example, on historical accounts of a species' introduction into a new environment. These scenarios can then be tested via analyses of extant genetic variation to reveal insights uncovered by nongenetic research techniques.

Black swans (*Cygnus atratus*), a common wetland species throughout much of Australia and New Zealand, represents a challenging case study for molecular and introduced species ecology, with direct consequences for wildlife management. The population status of the species as native in Australia is uncontroversial, although reports from the 17th century suggest that the species was rare in Western Australia, subsequently increasing in abundance after introductions during the 19th century from eastern Australia (Marchant & Higgins, 1990). Contrarily, no consensus exists on the origins of the current New Zealand population. Fossil records from the early to late Holocene indicate that the species historically occurred in New Zealand, but it was believed extinct by the 19th century (Thomson, 1922; Worthy, 1998, 2004). Several attempts of reintroduction from Australia took place 1864–1870, to control aquatic weeds in rivers, and for ornamental and hunting purposes (Thomson, 1922; Williams, 1964). Birds were released always in small groups of 1–8 units, with one big release of 42 individuals in 1867, with a total of 86 individuals reportedly released (Thomson, 1922). After reintroduction, the population grew unexpectedly rapidly, dispersed hundreds of kilometers from liberation sites (Miers & Williams, 1969), and was already common throughout the entirety of New Zealand in the first decades of the 20th century (Thomson, 1922).

Propagule pressure (i.e., the number of individuals introduced or the number of introductions) stemming from a few introduced individuals of a species with a relatively low reproductive output, such as the black swan (Braithwaite, 1981), may not have been sufficient to establish a viable population (von Holle & Simberloff, 2005; Colautti, Grigorovich, & MacIsaac, 2006). It was therefore hypothesized that the quick proliferation of the black swan in New Zealand was due to spontaneous migration from Australia during the same period as the human-driven reintroductions (Kirk, 1895). However, while individuals may move hundreds of kilometers, most remain near their natal site, and adults are highly site faithful (van Dongen et al., 2015; Payne et al., 2012; Williams, 1977). Another possibility is that New Zealand

black swans were mistakenly declared extinct and that a native population was still extant at the time of the reintroduction. This population may have then subsequently admixed with the newly arrived individuals leading to the dramatic increase in population growth through genetic rescue of the inbred indigenous population (Tallmon, Luikart, & Waples, 2004). Relevant information on the origin of current New Zealand black swans most likely resides in genetic data and might have important implications for species management. Black swans are protected from widespread hunting in Australia under state legislation (e.g., the New South Wales National Parks and Wildlife Act 1974; Victorian Flora and Fauna Guarantee Act, 1988), although occasional regulated culls occur under a strict licensing system (Donavon, 2008). In contrast, the species, being considered a pest in New Zealand, as it does in some parts of Australia, causes considerable agricultural damage to crops (in NZ since the early twentieth century; Lever, 2005). It is also declared as game under the New Zealand Wildlife Act (1953) and is commonly hunted (Nugent, 1992). The only exception is for the species on the Chatham Islands (NZ) despite reports that the population there is also nonindigenous, having arrived some time before 1922 (Thomson, 1922). Competing hypotheses, that is, whether the populations are introduced (the prevailing assumption) or whether they may at least in part be indigenous (an untested proposition), regarding the origin of current New Zealand populations have not yet been tested using genetic data.

Here, we conducted genetic typing of 12 short tandem repeat (STR) loci in samples collected from seven different geographic locations, spanning Australia and New Zealand. Using these data, we performed a variety of population genetic inferences to explore whether a recent reintroduction of black swans in New Zealand (i.e., a founder effect followed by a rapid population expansion) is unambiguously the most likely scenario. We show that alternative hypotheses could also explain the observed genetic patterns, thus questioning the current notion of New Zealand black swans being an introduced species. This study is the first large-scale contribution to the understanding of the evolutionary and reintroduction history of the iconic black swan across Australia and New Zealand using genetic data.

2 | MATERIALS AND METHODS

Black swans are currently distributed throughout New Zealand, and through all of Australia except northern Cape York Peninsula, with an apparently range gap in the central and western deserts (Marchant & Higgins, 1990). It inhabits fresh and low-energy marine wetlands, where it breeds with partial seasonality, mostly in pairs, with a modal clutch size of 5 – 6 eggs; longevity, fidelity to partner and site, and capacity to multiclutch are poorly documented (Marchant & Higgins, 1990).

2.1 | Sample collection

Individual black swans ($N = 189$; 105 males and 84 females) were sampled between 2000 and 2008, at seven localities across their

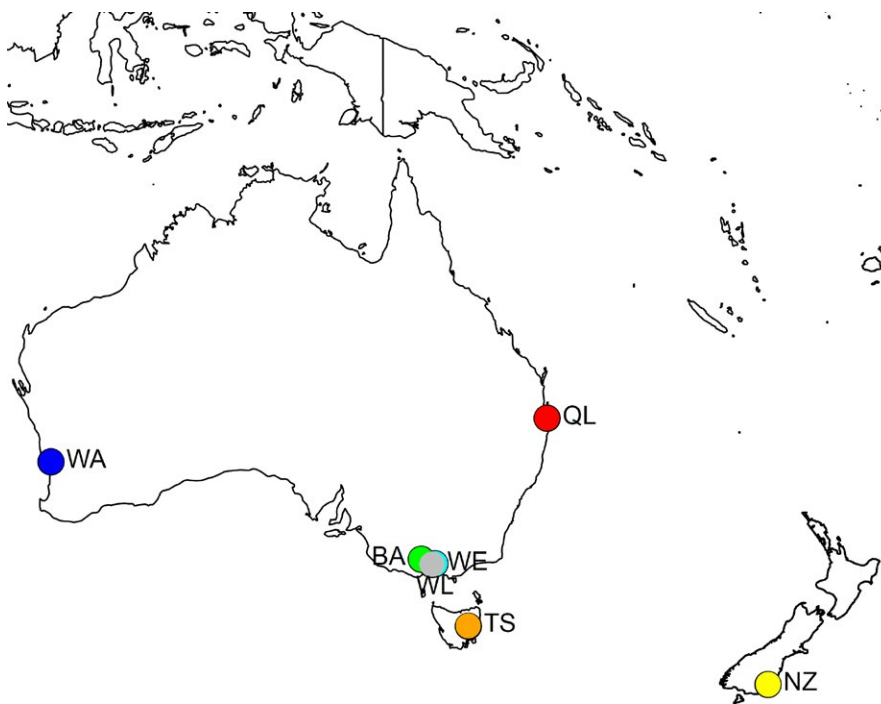


FIGURE 1 Georeferenced map of the seven sampled locations from Australia and New Zealand. Name abbreviations of localities are as in Table 1

TABLE 1 Migration rates among localities estimated with BIMr. Recipient populations are in columns, and immigrating populations are in rows. Standard deviations are reported in parentheses

Emigration/Immigration rates								
Pop	Into	BA	NZ	QL	TS	WA	WE	WL
From								
BA		1($\pm 4e-6$)	6e-11($\pm 3e-10$)	6e-11($\pm 3e-10$)	6e-11($\pm 3e-10$)	6e-11($\pm 3e-10$)	6e-11($\pm 3e-10$)	6e-11($\pm 3e-10$)
NZ		7e-4($\pm 3e-3$)	0.99($\pm 7e-2$)	5e-4($\pm 7e-2$)	2e-3($\pm 1e-2$)	6e-4($\pm 3e-3$)	2e-3($\pm 1e-2$)	6e-4($\pm 3e-3$)
QL		6e-11($\pm 2e-10$)	6e-11($\pm 2e-10$)	1(NAN)	6e-11($\pm 2e-10$)	6e-11($\pm 2e-10$)	6e-11($\pm 2e-10$)	6e-11($\pm 2e-10$)
TS		4e-11($\pm 2e-10$)	4e-11($\pm 2e-10$)	4e-11($\pm 2e-10$)	1($\pm 2e-10$)	4e-11($\pm 2e-10$)	4e-11($\pm 2e-10$)	4e-11($\pm 2e-10$)
WA		3e-11($\pm 4e-9$)	4e-11($\pm 8e-9$)	4e-11($\pm 8e-9$)	3e-11($\pm 2e-9$)	1($\pm 1e-6$)	4e-11($\pm 4e-9$)	4e-11($\pm 6e-9$)
WE		7e-11($\pm 2e-10$)	7e-11($\pm 2e-10$)	7e-11($\pm 2e-10$)	7e-11($\pm 2e-10$)	7e-11($\pm 2e-10$)	1($\pm 6e-6$)	7e-11($\pm 2e-10$)
WL		6e-11($\pm 2e-10$)	6e-11($\pm 2e-10$)	6e-11($\pm 2e-10$)	6e-11($\pm 2e-10$)	6e-11($\pm 2e-10$)	6e-11($\pm 2e-10$)	1($\pm 4e-9$)

geographic distribution, six within Australia and one within New Zealand (Figure 1). Sampled populations included one population near the western limit of the species' distribution (Western Australia [WA], 43 samples), three populations from southeastern mainland Australia (Ballarat [BA], Werribee [WE], and Williamstown [WL]: 50, 21, 8 samples, respectively), one population from Tasmania (TS; 10 samples), another from the northeast of mainland Australia (Queensland [QL]; 20 samples), and one from the southern island of New Zealand (NZ, 37 samples; Figure 1; Table S1). Samples collected from multiple localities within close proximity to each other (i.e., within 20 km) were pooled to increase sample size. Tissue samples from Tasmania were collected from individuals shot as part of crop protection culls, while tissue samples from New Zealand were provided by hunters who legally shot the birds. All other birds were captured by hand and fitted with a metal band displaying a unique identification code supplied by the Australian Bird and Bat Banding Scheme. A blood sample was

taken from these hand-captured birds via the tarsal vein. University of Melbourne ethics application numbers concerned to our sampling are as follows: UoM 06,186, UoM 97,146, UoM 0,705,887, and UoM 05,122.

2.2 | Molecular analysis

DNA was extracted from blood and tissue samples using the salting-out procedure (Bruford et al., 1992). We genotyped swans at 12 microsatellite loci consisting of Cam2, Cam3, Cam4L, Cam5, Cam9, Cam10L (Carew, Adcock, & Mulder, 2003), TTUCG5 (Cathey, DeWoody, & Smith, 1998), TSP.1.20.9, TS.1.29.32 (St John et al., 2006) and TS.1.29.57, Caudo24 (Huang et al., 2005), and Bcau11 (Buchholz et al., 1998), following the protocols that are well established for this species (van Dongen et al., 2015; Kraaijeveld et al., 2004). Loci were amplified using fluorescently labeled primers using

the protocols in the references outlined above, with subsequent fragment analysis on a Beckman Coulter 8000XL automated sequencer. Fragment sizes were scored using an automated binning system in the Beckman Coulter 8000XL fragment analysis software, which were also confirmed visually. This binning system is well established for these loci and has previously been used elsewhere for this species (van Dongen et al., 2015; Kraaijeveld et al., 2004).

2.3 | Summary statistics

Genetic summary statistics for samples and loci were calculated with R package *adegenet* (Jombart, 2008) and R package *hierfstat* (Goudet, 2005). Observed heterozygosity was tested from departure from expected heterozygosity using a two-sided Student's *t* test. Pairwise F_{ST} between populations were estimated with *adegenet*, while pairwise G_{ST} (Hedrick, 2005) and pairwise Jost's D (Jost, 2008) were estimated using R package *mmod* (Winter, 2012). Concordance and correlation among distance matrices (F_{ST} , G_{ST} , and D) was tested using the CAMD (Legendre & Lapointe, 2004) function of *ape* R package (Paradis, Claude, & Strimmer, 2004) with 10 k permutations. A bootstrap analysis with 10 k permutations was performed to obtain *p-values* for the pairwise genetic distances using a customized R script. A principal component analysis was produced with R package *ade4* (Dray & Dufour, 2007), using allele frequencies calculated per population.

To test the correlation between individual genotypes and geography, a redundancy analysis was run in the R package *vegan* (Oksanen et al., 2015) and R package *fossil* (Vavrek, 2011), where genotypes are the dependent observations and geography is used as the independent explanatory variable. Latitude and longitude were tested together and separately, for the latter case using matrices of linear distances calculated as the pairwise difference of each coordinate. An ANOVA test was run with 10 k permutations to evaluate statistical significance of the fraction of explained variance (Legendre, Oksanen, & ter Braak, 2011). A Mantel test, implemented in R package *ape* (Paradis et al., 2004), was added to quantify the proportion of genetic distance that may depend on physical distances.

2.4 | Population structure

We used STRUCTURE 2.3.3 (Pritchard, Stephens, & Donnelly, 2000) to estimate the number of genetic clusters (K) in our dataset. STRUCTURE assigns each individual to a cluster with probability q . Ten independent analyses were performed for $1 \leq K \leq 10$ using a Markov chain of 600 k iterations, discarding the first 100 k as burn-in. To avoid potential biases, we assumed the admixture model without including prior knowledge of the origin of samples. Correlated allele frequencies were also assumed.

2.5 | Spatial analysis

A spatial analysis was carried out using the R package *SpaceMix* (Bradburd, Ralph, & Coop, 2016), which estimates admixture due

to long-distance movement versus common shared ancestry. The method assumes that covariance among populations should be lower with increasing geographic distance. Higher covariance than expected on the long distance is interpreted as the result of gene flow, and lower genetic covariance than expected at short distances is interpreted as isolation. The *SpaceMix* algorithm provides information on how gene flow among observed genetic units (in this case our geographic localities) compares to actual geographic distances and gives an estimate of the genetic admixture among populations. The results are visualized with a "geogenetic" map of "perceived" genetic distances based on the estimated gene flow among populations superimposed on actual geographic distances. Default setting values were used. Total run length was set to $10e7$. Five parallel runs gave convergent results.

2.6 | Testing geographically driven dispersal

Bayesian estimates of migration rates among localities were obtained using BIMr (Faubet & Gaggiotti, 2008). The software calculates recent gene flow from the gametic disequilibrium that usually derives from immigrant alleles (Faubet & Gaggiotti, 2008), while linkage equilibrium is considered a lack of recent migration. To set initial search parameters for the Bayesian analysis with BIMr, twenty pilot runs of 50 k iterations are performed, starting from the default parameter set (Faubet & Gaggiotti, 2008). Thus, a burn-in of 100 k was performed and the final parameter search was conducted for 5 million iterations. Ten parallel replicates were performed and output files were analyzed with Tracer_v1.6 (Rambaut & Drummond, 2007) to evaluate the posteriors. Internal convergence of single runs and convergence of parallel runs were tested with R package *coda* (Plummer et al., 2006). After conversion checking, five convergent runs estimated the best posterior parameters and quantiles for migration rates and inbreeding coefficients.

2.7 | Effective population size and time to the most recent common ancestor

We used a coalescent-based estimator of population size changes over generational time (*MsVar*; Beaumont, 1999). We used version 1.3, which directly estimates mutation rate (μ), population effective sizes (current and ancestral, or N_0 and N_1 , respectively), the time since the population started growing or declining (τ_a), and the time of the most recent common ancestor (TMRCA), relying on user-defined prior distributions. Prior for mutation rate was based on general values for microsatellites (10^{-2} - 10^{-6} ; Anmarkrud, Kleven, Bachmann, & Lifjeld, 2008). *MsVar* 1.3 provides absolute number of individuals and number of years since the change in population size commenced. The coalescent model is written for microsatellites loci and implements a single stepwise mutational model. Two different size change models are considered: a gradual linear change (model 0) and an exponential change (model 1) with only one population demographic event allowed. The parameters (θ_0 and θ_1) and the TMRCA are assumed to vary among loci. The TMRCA is expressed in coalescent units, so that

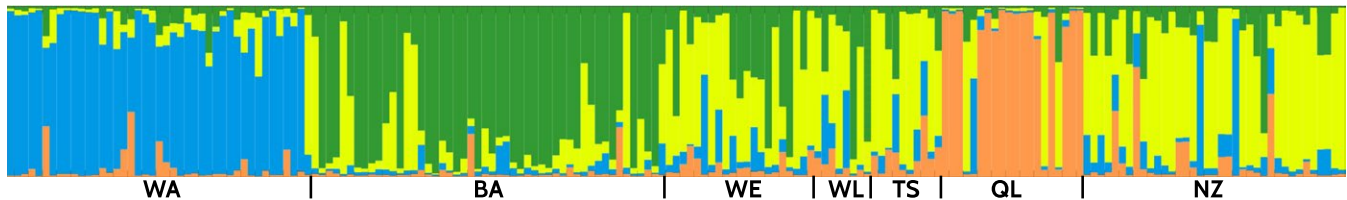


FIGURE 2 Distruct plot of STRUCTURE posterior cluster assignment probabilities among black swans. Each vertical line represents one individual, and color indicates probability of belonging to each of the four genetic clusters

the value of current population size needs to be used to convert the units in number of generations.

Pilot runs for model 0 and model 1 showed likelihood values $10e2$ times lower than for model 0; thus, we based our results on model 1. Prior parameters and run length are reported in an example input file (SFile 1). Four parallel runs per population (28 independent runs) were checked with *coda R* package to assure internal chain convergence (Geweke diagnostic) and parallel chain convergence of independent runs (Gelman diagnostic; Plummer et al., 2006). Independent runs are obtained by shuffling the random file number and changing some of the starting values in the input file. Convergence was reached for all independent runs using a running time of $12e10$ iterations (SFile 1). Following Beaumont (1999), Bayes factor was used to evaluate the probability of declining versus expanding population size changes. Modes and confidence intervals of posterior parameters were estimated with R package *modest* (Poncet, 2012).

2.8 | Bootstrap analysis of the dataset

We selected a subset of 70 random samples from our genotypes to be analyzed with *MsVar*, using the same prior parameters and running time as in our populations. The number of samples per subdataset was the same as in observed populations (Table S1), with each sample repeated 10 times. This analysis allowed us to build general distributions of posterior population parameters for the whole meta-population of black swans and to use them to test the likelihood of demographic parameters for our populations. We also tested the effect of number of samples on the estimates.

The logical flow behind our statistical approach has been summarized in a paragraph provided in Supplementary Material. The main R scripts used in this study are provided in Dryad repository.

3 | RESULTS

3.1 | Genetic variation and population differentiation

A similar level of internal heterozygosity occurred across populations and loci (Tables S2 and S3). No substructure was observed for pooled locations (see Materials and Methods and Table S1) using the *find.cluster* function in R package *adegenet* (Jombart, 2008). Both observed and expected heterozygosities per population range between ~ 0.6 – 0.7 and are nonsignificantly different (all p -values $\gg .05$).

Hardy–Weinberg equilibrium locus-by-locus per population is reported in Table S4. Private alleles are detected for Tasmania (3 of 79, $\sim 3.7\%$), Western Australia (2 of 81, $\sim 2.5\%$), Werribee (2 of 89, $\sim 2\%$), and New Zealand (1 of 94, $\sim 1\%$).

A bootstrap analysis of pairwise genetic distances indicated that samples from different locations were statistically significantly differentiated except for WE, which was undifferentiated from BA, WL, NZ, and TS, although values of genetic distances for this population are not much lower than for WL or TS (see F_{ST} , Table S5). Based on the PCA plot (Fig. S2C), WA, QL, BA, and NZ are the most separated from the other localities, while QL, TS, WL, and WE are more closely grouped together on the PCA plot. The first and second components explain 74.0% and 15.2% of the variance, respectively, and are differentiated by several loci (Fig. S3). There are three alleles that most weight on PC1 (locus TS1 allele length 191, locus Bcau 11 allele 166, and Cam10 allele length 350; Fig. S3).

Redundancy analyses of genotypes versus geographic coordinates revealed that geography explains a small but significant fraction of genetic distances (proportion of inertia explained with geography = 0.043, $e \ll 0.001$). When geography is summarized into a single factor (i.e., sampling locality), 9% of the variance in the distribution of allele frequencies is explained ($p < .001$). A Mantel test indicated a lack of correlation between the matrix of geographic distances and the genetic distances ($p > .12$). However, latitude taken alone seems to explain genetic distances ($p < .00$), while longitude is nonsignificantly correlated with genetic ($p > .189$), as shown in plots of genetic distances against physical distances, using distances in kilometers for the two-coordinate system and absolute distance in degrees for latitude and longitude separately (Fig. S2D–F).

3.2 | Genetic structure

Genetic clustering analysis with STRUCTURE detected four genetic clusters among the samples (Fig. S1). Location differentiation detected with F_{ST} (>0.01) is sufficient to obtain a reliable estimate of the genetic structure (Coleman, 2014). The most likely number of clusters in the dataset was estimated by calculating ΔK following the procedures of Evanno, Regnaut, and Goudet (2005), which estimates the most likely number of clusters based on the rate of change in log-likelihood probabilities for each K . ΔK was greatest for four clusters, although ΔK for two clusters was also relatively high (Fig. S1). Following Pritchard et al. (2000), we assumed four clusters as this created a more biologically likely clustering than when two clusters were assumed. In the latter

case, samples from WA and QL would be clustered together, which is geographically and ecologically very unlikely. Individuals generally displayed admixed origins; however, QL, WA, and BA appear to be the most internally homogenous and thus displayed greater differentiation compared with other localities (Figure 2). The remaining four localities show similar within-group composition, although WE and WL are more admixed than the two island localities (TS and NZ) where most individuals belong to one cluster (Figure 2). This common ancestry could be a wide southeast component, with exception to be made for Ballarat (see discussion below in this regard). The STRUCTURE analysis is therefore in good agreement with both the F_{ST} and PCA results, which show less differentiation for southeastern Australian samples.

3.3 | Admixture and spatial origin of the populations

SpaceMix estimated a very weak degree of genetic admixture among populations (see “geogenetic” map in Figure 3). The map showed that the spatial origin of distant samples (NZ, QL, WA, WE, and WL) is a good approximation of genetic covariance, indicating that greater physical distances and genetic distance can be explained by genetic ancestry. On the other hand, two of the closest localities (BA and TS) are more scattered on the genetic than on the geographic map. This pattern indicates that BA is more differentiated than would be expected under a simple isolation-by-distance model, while TS seems to be more closely related to mainland samples than expected given the physical distances. Therefore, SpaceMix analysis complements the results obtained with our previous analyses, and clarifies why the Mantel test failed to detect a linear correlation between geographic distance and genetic distance matrices.

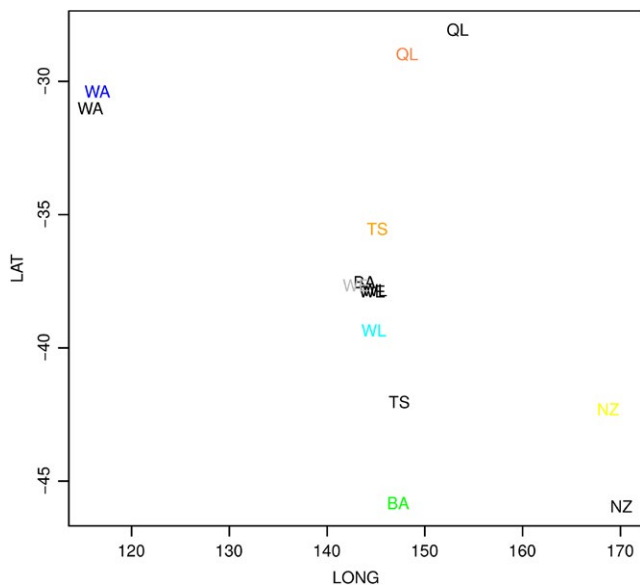


FIGURE 3 SpaceMix analysis plot. Population names are abbreviated as in Table 1. The black names represent the geographic location based on coordinates, while color-coded names represent the “geogenetic” distances (i.e., the distances perceived by the populations depending on their genetic covariances)

3.4 | Estimates of recent asymmetric migration rate

Bayesian estimates of multilocus migration rates confirmed a lack of recent ongoing gene flow among black swans. As for the STRUCTURE analysis, the F_{ST} values observed among the seven populations fall between 0.01 and 0.05 (Table S5), a range for which the estimator gives acceptable results, although posterior estimates improve with increasing genetic differentiation (Faubet & Gaggiotti, 2008). Five of ten parallel runs were convergent. The results indicate migration from one locality to another to be < 1% (Table 1). These estimates give a quantitative perspective on the degree of current isolation among our samples. Closer localities appeared to be as isolated as more distant ones, which further supports the outcome of the SpaceMix analysis. Interestingly, the remaining five nonconvergent runs differed from those that converged only for the NZ results. Each of these runs indicated some degree of gene flow into NZ from all other locations, although the total amount of gene flow substantially changed from one run to the other.

3.5 | Population size changes over time

Coalescent inferences of population size changes over time indicated that all populations underwent a decline during a relatively recent time. While prior distributions are equal for both current and ancestral effective population size to give an equal probability of both population decline and growth, posterior distributions of current population sizes are systematically lower than posteriors for ancestral population sizes, with no overlap (Fig. S4). Given this, a model of population growth has virtually zero likelihood compared to a model of population decline (Beaumont, 1999). As a substructure in the sample may produce a false signal of population decline, Chikhi et al. (2010) proposed that random subsamples of the metapopulation can be analyzed to verify whether the signature is also detected at the metapopulation level to confirm decline in subpopulations. Thus, a bootstrap test was run on 70 sub-datasets, which showed that the signature of strong decline is also detected in the metapopulation (black diamonds in Fig. S4).

The absolute values of current effective population sizes range from ~50 to ~150 individuals (Table 2). The ratio between current and ancestral effective population sizes (r ; Table 3) shows a very strong decline for all populations, with ancestral populations on the order of 10^4 times larger than current ones (~290 k to ~430 k individuals; Table 2). Both current and ancestral population effective sizes of the simulated sub-dataset show that modal values for the observed populations fall in the range of estimates from the metapopulation (Table 2). No statistically significant difference was detected for the modal values obtained from different sample sizes. MsVar 1.3 also provided a posterior estimate of an average mutation rate across loci, which was very similar for all populations. The mean mutation rate of modal values for the 70 sub-datasets is 2.21×10^{-4} , a rate that falls into the expected range of values for microsatellite loci (Thuillet et al., 2002).

TABLE 2 Modal and quantile values (0.05q and 0.95q) of population demographic parameters obtained with MsVar 1.3

POP	BA	NZ	QL	TS	WA	WE	WL	SIM
μ								
Mode	2.10e-4	2.14e-4	2.16e-4	2.18e-4	2.13e-4	2.12e-4	2.16e-4	2.19e-4
0.05q	4.56e-5	5.71e-5	4.91e-5	5.82e-5	4.69e-5	5.62e-5	5.72e-5	8.71e-5
0.95q	6.14e-4	6.47e-4	6.08e-4	6.71e-4	6.69e-4	6.87e-4	6.95e-4	5.59e-4
N_0								
Mode	59	104	56	156	76	96	101	115
0.05q	7	16	9	22	12	13	16	19
0.95q	1,137	943	896	1,657	675	768	890	1,067
N_1								
Mode	374,515	406,408	425,553	430,121	300,566	340,729	328,885	399,334
0.05q	98,515	91,921	118,644	115,007	57,847	60,574	55,600	104,097
0.95q	1,401,102	1,331,849	1,713,129	1,612,378	1,170,865	1,199,667	1,152,973	1,280,827
τa								
Mode	1,113	1,298	1,056	1,498	1,151	1,195	1,271	1,436
0.05q	129	244	236	307	218	210	221	421
0.95q	16,929	10,565	17,512	15,752	9,431	8,840	9,967	6,922

μ , mutation rate averaged across loci; N_0 , current effective population size; N_1 , ancestral effective population size; τa , time since the population is growing/declining in coalescent units.

Quantile values are obtained for all convergent runs across all loci. The posterior distribution for all loci of all convergent runs is unimodal.

Output results are on a log scale and are here reported as absolute numbers.

TABLE 3 Converted modal and quantile values of TMRCA (T) and rate of population decline (r) since time τa

POP	BA	NZ	QL	TS	WA	WE	WL	SIM
T								
Mode	498,799	657,086	463,484	663,040	526,152	441,539	387,202	579,390
0.05q	5,667	14,620	74	12,754	17,385	3,420	2,758	14,651
0.95q	219,371,978	89,615,526	120,254,365	98,035,298	72,376,234	64,095,780	72,766,120	72,058,378
r								
Mode	1.71e-4	2.55e-4	1.32e-4	3.60e-4	2.55e-4	2.82e-4	3.06e-4	2.96e-4
0.05q	7.05e-5	1.73e-4	7.95e-5	1.90e-4	2.11e-4	2.22e-4	2.79e-4	1.81e-4
0.95q	8.11e-4	7.08e-4	5.23e-4	1.02e-3	5.77e-4	6.20e-4	7.72e-4	8.33e-4

T is expressed here in number of years, equal to the number of coalescent units outputted by MsVar multiplied by the effective current population size and generational time (Table 3), while r is modal and quantile values of the distribution of the ratio N_0 to N_1 .

3.6 | Time to population decline and time of the most recent common ancestor

In MsVar 1.3, the generation time is specified in the input file and the posterior estimates of time since population size change are converted into number of years. Black swans can reproduce twice per year once sexual maturity is reached (18–36 months); their age of first successful reproduction can vary between 2 and 5 years (Coleman, 2014). Following a simple ecological definition of generational time as the time passing between two of the same stages of the life cycle (Bienvenu & Legendre, 2015; Fu, 2001), we can consider observed time to first successful reproduction as an estimate of generational time. Using this

estimate, our results indicate that all populations started declining ~1–2 kya (Table 2).

Coalescent inferences also allowed us to estimate time to the most recent common ancestor per population. Posterior estimates across loci give the number of coalescent units since the local population may have originated for each sampling site. The oldest coalescent time is detected for Tasmania and New Zealand samples (Table 3). Confidence intervals are high for all populations. Samples from Ballarat and Queensland show the most uncertain estimates, while confidence intervals for other localities are close to those estimated for the 70 randomly sampled datasets (Table 3).

4 | DISCUSSION

While the ecology and population biology of black swans have enjoyed substantial research effort, little is known regarding the species' molecular ecology and genetics (see van Dongen et al., 2015; Kraaijeveld et al., 2004). We used a combination of inferential evolutionary tools to document patterns of ongoing gene flow among populations across Australia and New Zealand and examine the long-term population demography of the species. Our results highlight three important findings: (i) a lack of substantial dispersal between populations, (ii) a strong demographic decline across all populations, approximately 1–2 kya, and (iii) a more ancient origin of New Zealand and Tasmania samples compared to samples from most Australian localities. Our results may question the prevailing notion that the black swan is a highly mobile species that originated in Australia, which owes its high current abundance in New Zealand to a coincidence of human-driven releases and spontaneous, novel, and substantial immigration from Australia.

Our multivariate analyses, coupled with multilocus inference of recent migration rates and a landscape analysis of covariation between genetic ancestry and geographic distances, indicate that dispersal rates of this species are low, despite the capacity of the species to fly long distances (Williams, 1977). In support of this, van Dongen et al. (2015) report significant genetic differentiation between two swan populations separated by only 30 km (see also Oyler-McCance, Ransler, Berkman, & Quinn, 2007). Linkage disequilibrium (LD) was not tested on our microsatellite dataset as it is driven by many factors (e.g., population structure, population decline, and inbreeding), that are unrelated to physical linkages among loci. So, testing a priori for LD may be highly misleading unless a physical map of loci into the genome is available.

Within local population units (i.e., sampling areas), migration rates were very low, which indicates that allele frequencies are not altered by incoming migrating genotypes. These patterns may relate to the fact that several of the populations sampled (Ballarat, Western Australia, and Queensland) were from generally permanent waterbodies with largely resident populations. These swans were captured by hand, which may favor the sampling of habituated resident birds that readily approach humans. However, this was not the case for many of the other populations. For example, New Zealand and Tasmanian samples were collected from shot individuals, which are unlikely to be biased toward habituated, resident birds, while birds from Werribee were captured at their nests. As expected given the pervasive homoplasy that can occur in microsatellite markers (Balloux et al. 2000), absolute values of genetic distances detected here are not strikingly high, but the bootstrap test based on observed genetic profiles does support significant population differentiation. Even being low, but still present despite homoplasy, some private alleles in Tasmania, Western Australia, Werribee, and New Zealand support isolation occurring among the populations analyzed here. Werribee and Ballarat appear to be the least and most isolated populations, respectively. While Werribee could act as a sink locality for black swans, such scenario is not mirrored in our estimates of migration rates. On the other hand,

Ballarat is characterized for being the highest location of our sampling and in general one of the highest cities in Australia. This may suggest a role of altitude in shaping black swans' genetic diversity, a topic that would deserve further investigation.

Overall, the results suggest that this species does not disperse long distances when local environmental conditions are satisfactory, although long-distance dispersal may be more likely when local conditions deteriorate or are less stable (Williams, 1977). The fact that latitude seems to be more correlated with genetics than longitude was expected from previous studies on bird dispersal, as latitude is more correlated with environmental factors, that is, temperatures and precipitations, than longitude (Masello et al., 2015). Such a strategy is typical of many Australian birds which rely on waterbodies, and is also observed in environments where rainfall can be temporally and spatially unpredictable (e.g., Roshier, Asmus, & Klaassen, 2008; Roshier, Robertson, & Kingsford, 2002). Although we could not formally test an hypothesis relating climatic variables to genetic differentiation in black swans, our results points to an indirect correlation of genetic differentiation with physical distances. Indeed, even if the longitudinal dispersal (1139–3334) of our population is much higher than the latitudinal range (501–1009), latitude turns out to be a better predictor than longitude for genetic differentiation. Thus, climatic differentiation along a south to north gradient could influence genetic differentiation more than physical distances. We thus suggest that this hypothesis could be tested also in other Australian aquatic birds in relation to dispersal and genetic differentiation. Other swan species also tend to remain at the same site year round and not disperse from breeding sites between breeding events (e.g., Włodarczyk et al., 2013). We found pronounced differentiation between Western Australian swans and the other populations despite reports that the population may have at least partly arisen from introductions from eastern states (Marchant & Higgins, 1990).

Our results also indicate that all populations examined have declined over the last 1–2 kya. We found no signature of an increase in population size in New Zealand or Western Australia that would be expected from the reported population increases. This may be due to a lack of statistical power in our analyses to detect such a recent changes in population size. It is also to note that the expansion has occurred over few generations. Alternatively, the decrease in population size over the last 2,000 years may have overwhelmed the signature of the more modest contemporary increase. In the absence of experimental studies, drivers of population change are correlative and speculative, but we propose climate changes and hunting pressure as a possible explanation of detected population decline. Studies on the paleoclimatic changes in Australia during the Holocene (Neolithic) indicate a period of peak moisture 5–8 kya during which wetland water levels were higher than present (Quigley et al., 2010). Aridification commenced approximately 5 kya, where levels of salt lakes in mainland Australia fluctuated between moderate to low and then dropped drastically over the last 1 ky (Bowler, 1981; Quigley et al., 2010). This presumably resulted in severe fragmentation of swan habitat, followed by isolation of habitats and local populations. Indeed, the incomplete population structure and the lack of recent gene flow we report

indicate that the current populations might have resulted from recent geographic isolation followed by population divergence. The effects of habitat change on population structure may be continuing in the present day, with widespread wetland loss or conversion (Anonymous, 1988; Goodrick, 1970).

In addition to the onset of aridification in Australia, the last 5 kya in Australia has also been characterized by a rapid acceleration in human population growth (Johnson & Brook, 2011). Indigenous Australians hunted black swans for food (e.g., Clarke, 2003), and the rapid expansion of the European population may have accelerated the species' population decline via increased hunting pressure. The apparent coincidence of these two processes, coupled with our coalescent inferences of population decline in black swans, would suggest a reasonable ecological explanation for the decline of swans. Similarly, the decline in black swans in New Zealand may be at least partially attributed to the arrival of human populations approximately 800 years ago (Wilmshurst, Anderson, Higham, & Worthy, 2008). The arrival of the Maori leads to rapid landscape transformations (McWethy et al., 2010) and was coupled with a high extinction rate of indigenous avifauna due to hunting pressure (Duncan & Blackburn, 2004), including the hunting of black swans (Horn, 1983).

From a population genetics perspective, estimates of population size changes over time may often be biased by the confounding effect of population structure (Chikhi et al., 2010; Mazet et al., 2016), as most methods designed to estimate this parameter, including *MsVar* (Beaumont, 1999), assume panmictic populations. However, no population substructure could be detected among our population units. In addition, a bias toward detecting population bottlenecks with *MsVar* has been reported by Chikhi et al. (2010), but a simulation study by Girod et al. (2011) showed that the method can reliably detect reductions in population sizes when the bottleneck was strong, meaning that the population size reduced by a factor of at least $10e3$, which seems to be the present case. Excess immigration into the population could also misleadingly lead to a signal of recent bottleneck (Excoffier & Heckel, 2006). However, all our analyses indicate little to no gene flow among populations and the population reduction detected did not begin recently, as supported by simulation studies ($\log \tau a < 1$; Girod et al., 2011). This is further corroborated by our simulation approach based on 70 random datasets, following Chikhi et al. (2010), rendering our inferences of meta-population decline highly reliable.

Finally, our results indicate that the current black swan population in New Zealand originated approximately 660 kya and, along with Tasmania, was the most ancient population sampled. The absolute values of coalescent times appear very old, a known characteristic of *MsVar* estimates when populations under decline are detected (Girod et al., 2011). However, the same bias is expected to affect all analyzed samples, which makes the relative comparison of TMRCA reliable between samples. The use of fossil records to calibrate the mutation rates of the black swan STRs for the coalescent simulations would refine our population age estimates. Moreover, the bootstrap datasets that we analyzed suggest that the coalescing times of the two island populations are on average higher than random subsets of the

populations. Indeed, while all other localities appear less ancient than the average of the random subsets, coalescing times of New Zealand and Tasmania samples fall in the upper quantile of the modal distribution of population age of our bootstrapped datasets.

Although the exact origin of the species remains unclear, our results may challenge the prevailing view that the New Zealand population consists solely of newly introduced individuals. We acknowledge that confidence intervals for TMRCA are very high, which does not exclude the possibility that population ancestry is less old for island compared with continental populations. Moreover, we could not estimate population divergence. Our results may be compatible with the hypothesis that the current NZ population originated from an admixture from individuals introduced from Australia during the 1860s and extant populations in New Zealand that were otherwise assumed extinct. Indeed, old TMRCA times could be interpreted such that parental populations of the current NZ population were derived from distantly isolated Australian units, but the old TMRCA time could also reflect a native NZ parental population, as the modal TMRCA value is still older than what obtained on average for the random datasets that we drew from all populations. In addition, our structure analysis highlights genetic similarity between NZ samples and the samples from WE, WL, TS, which all seem to share common ancestry. A parental native population coming from this area of Australia (WE, WL) and admixed with introduced individuals may also explain the reported rapid increase in abundance of the species after the introductions in both New Zealand and Western Australia. In fact, genetic rescue, whereby unrelated individuals are introduced into an inbred population, can lead to dramatic increases in the population's fitness, including individual survival, reproductive output, and ultimately population size (e.g., Bouzat et al., 2009; Hogg, Forbes, Steele, & Luikart, 2006; Madsen, Shine, Olsson, & Wittzell, 1999; Tallmon et al., 2004). The population's sudden increase may also have been related to other factors such as the simultaneous, substantial, and novel immigration of swans from Australia (Kirk, 1895) or changes in ecological conditions (e.g., changes in land use) that encouraged population growth (Crookes & Soulé, 2001). However, our results do not support a scenario of spontaneous migration from Australia to New Zealand.

Some of our samples are representative of extended geographic areas, such as Queensland, Western Australia, Tasmania, and indeed New Zealand. These distant populations are appropriate to study long-range dispersal and infer local population demographic history. In particular, assuming that black swans were recently reintroduced in New Zealand and thus expanded rapidly across the country, each locality should potentially have been populated starting from the same recent ancestral population, making a random sample suitable for population genetic investigation. However, our results highlight the need for a more extended analysis of genetic diversity of current black swan populations across New Zealand, which might indeed derive from a more complex demographic history than previously thought and thus be characterized by unexpected genetic variation.

Overall, the results presented here may contradict the general consensus that the New Zealand black swan is an introduced (pest and game species) from Australia. Instead, the New Zealand population

appears to be at least partly derived from a natural, and not a feral, population; thus, it may constitute an evolutionary significant unit (ESU; Moritz, 1994). A test of mtDNA reciprocal monophyly of NZ, TS, WE, and WL samples could provide more insightful evidence on the definition of ESU (Moritz, 1994). The designation of species as invasive and non-native is complex and the nuances of population histories need to be considered (Crees & Turvey 2015). In particular, approaches to actively managing “native” invaders require addressing social and political considerations (Carey, Sanderson, Barnas, & Olden, 2012). Our results suggest that, in the nuanced framework of Crees and Turvey (2015), the black swan in New Zealand is “xenonative” (rather than “returned” or “restored” native), that is, native but restocked from external populations. The management strategies and legislation regarding the conservation and hunting status of the swan in New Zealand may accordingly need to be reviewed. While swans are currently numerous in New Zealand, extirpation would lead to the loss of genetic variation attributable to more ancient endemic swans, and as such should perhaps be avoided, or at least a more nuanced decision made regarding desirable outcomes for the species’ population.

5 | FUTURE DIRECTIONS

Our study is the first in-depth assessment of the population demographic history of the black swan and provides the first convincing evidence that the current black swan population in New Zealand may be partly derived from indigenous populations. However, the complex evolutionary scenarios that we propose in the present work will require additional analyses to provide further clarification. The availability of a precise historical record on the reintroduction of black swans in New Zealand allows the collection of samples from exact localities where the individuals were captured (Australia) and released (New Zealand). Such a sample could then be typed for higher-resolution genomic loci than microsatellites, such as radSeq data, or the whole mitochondrial genome, which was published in 2010 for *C. atratus* (Jiang et al., 2010) and might reveal unambiguous phylogeography of Australian and New Zealand lineages. Such dataset will likely have enough power to run in-depth hypothesis tests to verify our indications of a New Zealand or Tasmanian origin of *C. atratus*, including the possibility to detect past sporadic migratory event between Australia, New Zealand, and Tasmania and their intensity.

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AUTHOR CONTRIBUTIONS

P-JG, RAM, RWR, and MAW conceptualized the project and study design. P-JG, RAM, and WFDvD conducted field work. P-JG conducted the laboratory work. VM, WFDvD, and MC analyzed the data. P-JG, RAM, RWR, MAW, VM, and WFDvD interpreted the findings, WFDvD, VM, and MAW wrote the manuscript. All authors read and contributed to the manuscript.

DATA ACCESSIBILITY

The microsatellite data used for this study and an R script for the data analysis are available from Dryad Digital Repository: <https://doi.org/10.5061/dryad.ct8j4>. Any specific question about data analysis will be answered upon request to the corresponding author.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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