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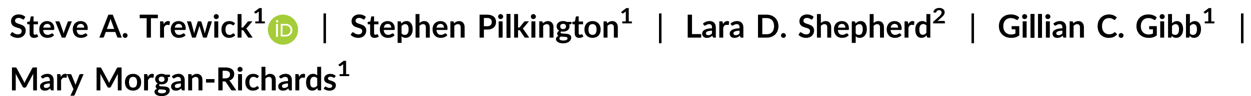
Closing the gap: Avian lineage splits at a young, narrow seaway imply a protracted history of mixed population response



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Abstract

The evolutionary significance of spatial habitat gaps has been well recognized since Alfred Russel Wallace compared the faunas of Bali and Lombok. Gaps between islands influence population structuring of some species, and flightless birds are expected to show strong partitioning even where habitat gaps are narrow. We examined the population structure of the most numerous living flightless land bird in New Zealand, Weka (*Gallirallus australis*). We surveyed Weka and their feather lice in native and introduced populations using genetic data gathered from DNA sequences of mitochondrial genes and nuclear β-fibrinogen and five microsatellite loci. We found low genetic diversity among extant Weka population samples. Two genetic clusters were evident in the mtDNA from Weka and their lice, but partitioning at nuclear loci was less abrupt. Many formerly recognized subspecies/species were not supported; instead, we infer one subspecies for each of the two main New Zealand islands. Although currently range restricted, North Island Weka have higher mtDNA diversity than the more wide-ranging southern Weka. Mismatch and neutrality statistics indicate North Island Weka experienced rapid and recent population reduction, while South Island Weka display the signature of recent expansion. Similar haplotype data from a widespread flying relative of Weka and other New Zealand birds revealed instances of North Island—South Island partitioning associated with a narrow habitat gap (Cook Strait). However, contrasting patterns indicate priority effects and other ecological factors have a strong influence on spatial exchange at this scale.

KEYWORDS

biogeography, cospeciation, feather lice, fibrinogen, flightless, microsatellite, New Zealand, phylogeography

1 | INTRODUCTION

Habitat gaps exert their influence on biotic composition through the interaction of their longevity and spatial scale with biological attributes of potential inhabitants (e.g., Bacon et al., 2013; Gillespie & Roderick, 2002; Jønsson, Lessard, & Ricklefs, 2015). At all spatial scales, regional biotas evolve through three processes summarized as colonization, speciation and extinction. Their relative contributions depend on physical (e.g., habitat patchiness) and biological (e.g., competition) factors that result in a continuum of outcomes with respect to diversity and distinctiveness. Global (e.g., Dowle, Morgan-Richards, & Trewick, 2013), continental (e.g., Jønsson et al., 2015),

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insular (e.g., Lamichhaney et al., 2015) and landscape (e.g., Prugh, Hodges, Sinclair, & Brasharesa, 2008) systems present assemblages with many and varied characteristics that challenge unifying explanation. However, the dual treatment of islands as habitat patches subject to a colonization lottery, and as evolutionary laboratories reflects the importance of gene flow in all situations. Here we examine the correlation between population genetic structure of a flightless bird and other endemic avifauna, and a narrow seaway that divides continental islands (Cowie & Holland, 2006). Does this geologically young feature indicate a significant barrier to gene flow allowing the accumulation of neutral genetic differences or does it represent a recent and ephemeral separation of populations?

Dispersal of individuals and establishment of populations allows species' ranges to change and extend across habitat gaps, and can result in distinct lineages (taxa) occupying different places or regions (Trewick, 2011). Disjunct distributions can also arise when populations are divided by environmental change that alters gene flow, such as rising sea level creating islands from formerly continuous habitat (e.g., Jones & Jordan, 2015; Runemark, Hey, Hansson, & Svensson, 2012). The persistence and divergence of separate populations depend on rates of gene flow, which in turn depend on ecological attributes (prior occupancy, competition, resource diversity, dispersal ability: Lenormand, 2002; Edelaar & Bolnick 2012; Richardson, Brady, Wang, & Spear, 2016). Gaps are conceptually linked with biogeographic boundaries or barriers where they are associated with biotic compositional differences, but may be coincidental not causal (Edwards, Crisp, Cook, & Cook, 2017). For example, phenotypic evidence for adaptive ecological partitioning across a seaway without correlated neutral genetic signal suggests the habitat gap acts as a region of low density, into which the frequency cline of ecological traits under selection has rapidly moved (Trewick & Olley, 2016). And, despite the absence of habitat gaps or species dispersal limitation, strong spatial genetic structure suggests animal behaviour can be influential in controlling gene flow (Morinha et al., 2017).

Well-documented cases such as the abrupt difference in avifauna of adjacent islands (Bali and Lombok) that are just 35 km apart indicate that even narrow habitat gaps are profound and persistent biogeographic barriers (Sclater, 1858; Wallace, 1859, 1860). This implies restricted biological exchange that is apparently inconsistent with the idea that close-proximity and high mobility favour exchange and thus similarity of assemblages (Carlquist, 1974; MacArthur & Wilson, 1967). In fact, a gap itself may not prevent exchange, whereas ecological interaction (e.g., prior occupancy) is likely to limit successful establishment. Indeed, only about 30% of bird, reptile, amphibian, butterfly and snail species are distinct to one side or another of Lombok Strait (Mayr, 1944). The majority of taxa are shared by Lombok and Bali, and phylogeographic data demonstrate some plants and animals have experienced numerous exchanges of individuals across Lombok Strait (e.g., Tänzler, Toussaint, Suhardjono, Balke, & Riedel, 2014; Thomas et al., 2012). Even well-recognized features such as Wallace's line involve a mixture of ecological and evolutionary processes in their maintenance (e.g., Condamine et al., 2015).

The New Zealand archipelago attracts biogeographers because of the seemingly paradoxical continental geology of the islands (Trewick, Paterson, & Campbell, 2007), and a biota with mixed patterns of spatial structure, depth, endemicity and relatedness outside New Zealand (Goldberg, Trewick, & Paterson, 2008; Wallis & Trewick, 2009). Among birds, the eclectic fauna includes several phylogenetically and ecologically distinctive taxa, but also many naturally widespread species that show the capacity of land birds to disperse and colonize over 1500 km of ocean (Trewick, 2011; Trewick & Gibb, 2010; Trewick & Morgan-Richards, 2016). Even during recorded history since European settlement (~200 years) several bird species have self-colonized New Zealand from Australia (Trewick, 2011) and extended their ranges through the main islands (e.g., *Zosterops*—Clegg et al., 2002). Also, European bird species brought to mainland New Zealand by settlers have reached offshore islands in the region (>800 km away) by their own efforts (Heather & Robertson, 1996). Contrary to this evidence of numerous colonization and establishment, there are numerous endemic bird species and some have distinct races on different islands in the New Zealand region, including the two main islands separated by a sea strait (Buller, 1868; Trewick & Olley, 2016).

Within the New Zealand archipelago, the Cook Strait seaway between North Island and South Island is as narrow as 22 km (Lewis, Carter, & Davey, 1994). To the west, the depth is about 100 m, but plunges eastwards to 3,000 m in the Hikurangi Trough. Tectonic activity associated with the Australian-Pacific continental plate boundary caused rapid uplift of mountain ranges in the area during the last 1 million years (Lewis et al., 1994; Trewick & Bland, 2012). Uplift in what is now southern North Island gradually closed older seaways further north, and in effect drove subsidence southward. By late Pleistocene interglacial periods, the landscape was configured much as it is today, but during the last glacial maximum global sea level was sufficiently low to allow land connection of North and South islands (Lewis et al., 1994; Trewick & Bland, 2012). Although geologically young, the Cook Strait gap might be a biogeographic boundary if it reflects older north/south division of New Zealand geography (Trewick & Bland, 2012). Geologically recent temporary closure of Cook Strait could have enabled terrestrial animals to bridge the gap, but this would not necessarily have obscured phylogeographic signal from older north/south division. Variation in ecological competition and genetic compatibility would influence the extent of introgression.

We considered the relevance of a young but ecologically significant landscape feature to insular evolution. Is recent restriction of gene flow the primary driver of current population structure or merely coincident with an older landscape feature that shaped the distribution of diversity? To do this, we assessed population genetic variation in the Weka (*Gallirallus australis* Sparrman, 1786), one of the few flightless New Zealand birds surviving today (Worthy & Holdaway, 2002) and the most abundant. The occurrence of Weka on both main islands of New Zealand could indicate recent colonization of one main island from the other (crossing the gap), or mixing of two or more distinct and deeply diverged lineages. Concordance

of independent neutral markers (e.g., Lefebvre et al., 2016; Zamudio, Bell, & Masona, 2016) provides the best evidence that physical features of the landscape have shaped the distribution of genetic diversity by preventing gene flow. We used traditional mtDNA haplotype markers, developed novel microsatellite loci and targeted the single copy, autosomal gene β-fibrinogen that has been informative in other bird species (e.g., Gonçalves, Rodrigues, Ferrari, Silva, & Schneider, 2007; Weston & Robertson, 2015). We further increased our sample of independent loci by examining mitochondrial variation of two ectoparasites of Weka. Although exclusion of paternal mtDNA during fertilization reduces diversity passed from one generation to the next in both birds and lice, in birds with biparental care lice are transmitted from both parents to their offspring (e.g., Lee & Clayton, 1995; Brooke 2010). Weka chicks produced by parents of mixed ancestry will receive only the avian mtDNA of their mother's lineage, but they could receive lice from either or both parents. Transmission requires physical contact of birds, and therefore, landscape barriers to the host will separate parasites too. Lice therefore add capacity to test for concordant patterns of divergence and reveal host admixture (Koop, DeMatteo, Parker, & Whiteman, 2014). We compare our findings from weka and their parasites with data representing a flying near relative of Weka in the western Pacific and codistributed birds across the Cook Strait gap in New Zealand. We assess evidence that gene flow facilitated by dispersal ability results in genetically homogenous populations on either side of the Cook Strait. Recent isolation of north and south populations might be concordant with older divisions and predict the flightless lineage and its associated ectoparasites will be more sensitive to spatial partitioning than its flying relatives.

2 | METHODS

2.1 | Phylogenetic and taxonomic background

Phylogenetic analysis of mitochondrial and nuclear DNA sequence data from rails (Aves: Rallidae) highlights that *Gallirallus* is especially rich in flightless and often recently extinct species (Garcia-R, Gibb, & Trewick, 2014a; Trewick, 1997a,b). The flightless members of this clade live(d) on islands in the western Pacific, and the New Zealand region is notable for the former existence of morphologically diverse species (Ripley, 1977) (Figure 1). The only surviving flightless *Gallirallus* in the New Zealand archipelago, and one of the few survivors in the entire clade, is the Weka (*Gallirallus australis*). It is phylogenetic distinct, and it is not sister to other New Zealand species (Garcia-R, Gibb, & Trewick, 2014b; Garcia-R, Joseph, Adcock, Reid, & Trewick, 2017; Garcia-R et al., 2014a) (Figure 1). Fossils of Weka are missing from Miocene New Zealand deposits that contain evidence of a taxon similar to the extant, volant Pacific species *Gallirallus philippensis* (Worthy, Tennyson, Jones, McNamara, & Douglas, 2007). Much younger Holocene fossils show that just before human colonization (~800 years ago), Weka (*G. australis*) were widespread in New Zealand (Holdaway, Worthy, & Tennyson, 2001) although the ranges of the subspecies are not known with precision (Figure 1). The current range is much reduced (Figure 1), but historical records show that Weka lived in habitats from coastal beaches to upland forest and open country, throughout the main islands of New Zealand (Oliver, 1930). Decline has been substantial since human colonization as a result of habitat modification and introduction of mammalian predators (Beauchamp, Butler, & King, 1999).

Four subspecies of Weka (*Gallirallus australis* (Sparrman, 1786)) are currently recognized on the basis of plumage variation associated with distinct geographic distributions (Figure 1): North Island Weka *Gallirallus australis greyi*; Western Weka *G. a. australis*; Buff Weka *G. a. hectori*; and Stewart Island Weka *G. a. scotti* (Beauchamp et al., 1999; Kinsky, 1970; Turbott, 1990). Previously, six species (in *Ocydromus*) were recognized by Hutton (1873) and five by Buller (1888). Only one taxon (*Ocydromus greyi* Buller, 1888 = *G. a. greyi*) has been considered to exist in North Island (Buller, 1888). Modern conservation management has also recognized distinct populations within *G. a. australis* including Weka with particularly dark plumage from the Fiordland area (southwest South Island), but there is speculation about the basis of plumage variation (e.g., Beauchamp et al., 1999; Henderson & Goodman, 2007; Oliver, 1955). For example, it has been suggested that the pale "isabella brown" (Hutton, 1873) of *G. a. hectori* was "merely" a colour variant of *G. a. australis* (Scarlett, 1970), suggesting that plumage differences might be environmentally induced phenotypes, or population polymorphism.

Today, Weka are more abundant and widespread in South Island than North Island and have at various times been introduced to small islands near the mainland coast, but in most cases, the origin of these populations is not known. For example, twelve Weka (*G. a. hectori*) are recorded as being introduced to Chatham Island in 1905 (Lindsay, Phillips, & Watters, 1959), giving rise to a large modern population. Weka on many small islands near Stewart Island are thought to have been introduced by whalers and sealers for food during the 1800s, and it is presumed that these birds came from Stewart Island before their extirpation in the 1990s (Brothers & Skira, 1984; Miskelly & Powlesland, 2013). We group together Weka samples from these islands that are the nesting places of Tītī or *Puffinus* shearwaters, which are traditionally harvested as chicks. North Island *G. a. greyi* are recorded as being introduced to Mokoia Island in Lake Rotorua from near Gisborne during the 1950s (Axbey, 1994; Owen, 1997), but despite being the most translocated species in New Zealand, few have been successful (Miskelly & Powlesland, 2013). Although IUCN Red-listed as vulnerable, many populations have subsequently been removed from offshore islands so these mammal-free habitats can be used for conservation management of other native species.

Weka subspecies are therefore included in our analyses on the basis that they were collected from native (distribution resulting from natural process) mainland populations, with the exception of *G. a. hectori* that putatively exists only as the Chatham Island population derived from translocated birds. Other translocated populations of uncertain origin are treated separately, and we also consider in our analysis regional groupings of native *G. a. australis* in South Island.

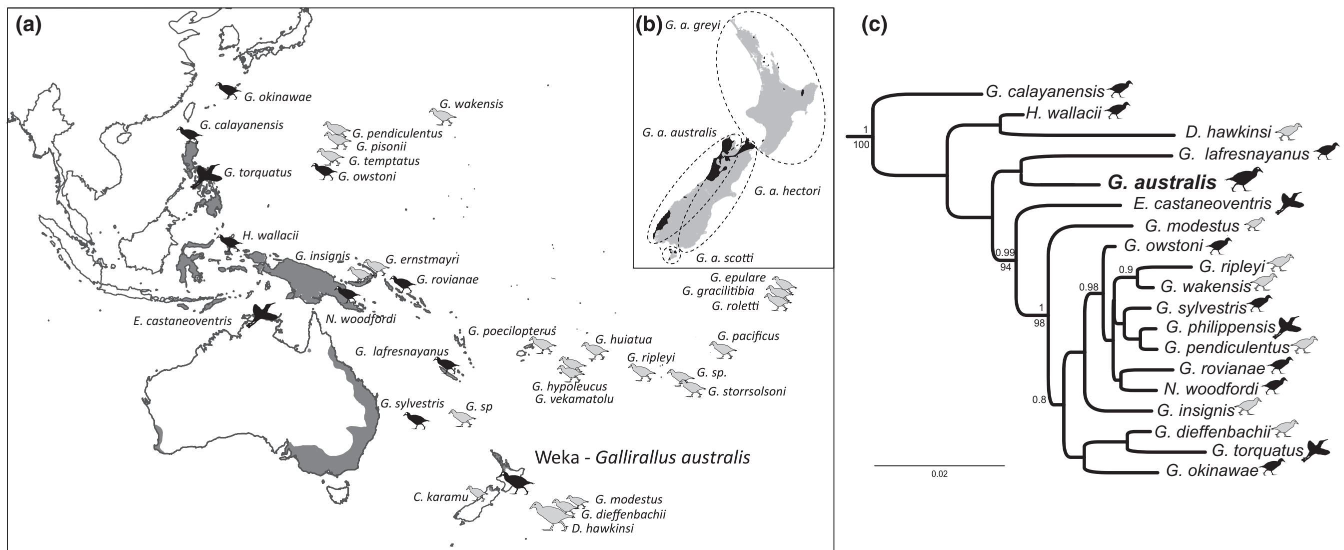


FIGURE 1 (a) The approximate distribution of flightless (walking bird icon) and flying (flying bird icon) *Gallirallus* species in the southwest Pacific region. Grey icons indicate recently extinct species, and dark grey fill the approximate range of the widespread buff-banded rail (G. *philippensis*). (b) Approximate former distribution of the four subspecies of Weka (*G. australis*) currently recognized indicated with dotted lines. Black areas indicate approximate current ranges of Weka based on observations in the period 1999–2004 (Robertson, Hyvönen, Fraser, & Pickard, 2007 Webatlas via nzbirdsonline.org.nz). (c) Multigene phylogeny of living (black icons) and extinct (grey icons) flightless and flying *Gallirallus* in the southwest Pacific showing the placement of the Weka lineage (Garcia-R, Elliott, Walker, Castro, & Trewick, 2016). Note that *Habroptila wallacii*, *Eulabeornis castaneoventris*, *Diaphorapteryx hawkinsi* and *Nesoclopeus woodfordi* are nested within *Gallirallus*

2.2 | Sampling Weka

Because Weka are threatened, sampling was necessarily restricted. We obtained material from the full geographic range of the species to examine the relative biogeographic significance of Cook Strait. Blood samples were collected by Department of Conservation (DoC) staff from Weka at 15 sites around New Zealand and stored at −80°C. In addition, we obtained liver or muscle tissue from Weka that were accidentally killed in traps for feral predators on conservation land (including Chatham Island) or struck by cars on public roads (Freeman, 2010). Chest feathers were collected from live Weka on eight offshore islands in the vicinity of Stewart Island (Tītī islands) by DoC staff. Toe pad tissue was obtained from Weka skins preserved in the collection of the Museum of New Zealand Te Papa Tongarewa representing locations where the species is extinct or rare today (Table S1). A Holocene fossil bone held in the Waitomo Caves Discovery Centre collection was also sampled. The toe bone used (one of nine) came from a set of material collected together in a limestone cave at Matira, Waikato (Accession # 17876k).

2.3 | DNA extraction

Genomic DNA was extracted from Weka blood and liver tissue using the High Pure™ PCR Template Preparation Kit (Roche Applied Science, Manheim, Germany) according to the manufacturer's instructions. Alternatively, DNA was obtained from approximately 25 mg of macerated liver tissue or approximately 5 μl of whole blood incubated at 55°C with CTAB extraction buffer (2% Hexadecyl Trimethyl Ammonium Bromide, 100 mM Tris-HCl, pH 8.0, 1.4 M NaCl, 20 mM EDTA) and Proteinase K. Purification used an equal volume of Tris-equilibrated Phenol and then Phenol-Chloroform-Isoamyl alcohol (25:24:1). Cut feather tips were incubated overnight at 55°C with 200 μl SET buffer (100 mM NaCl, 1 mM EDTA, 100 mM Tris), 10 μl Proteinase K (20 mg/ml), 5 μl 1 M Dithioreitol (DTT) and 10 μl 20% (w/v) Sodium Dodecyl Sulphate (SDS), and purified with Phenol-Chloroform-Isoamyl alcohol (25:24:1). DNA was precipitated from the resulting aqueous solution with 3 M NaOAc (pH 5.2) and cold absolute Ethanol.

Toe pad samples from museum skins were treated as ancient DNA sources and were handled in a dedicated and physically separate aDNA laboratory. These samples were incubated at 55°C overnight in 2.5 ml extraction buffer (10 mM Tris-HCl pH 8.0 and 1 mM NaCl), 250 μl of 10% SDS, 15 μl of 200 mg/ml DDT and 25 μl of 50 mg/ml Proteinase K. DNA extractions were purified with Tris-saturated Phenol followed by Chloroform-Isoamyl alcohol (24:1) and then concentrated to 100 μl on a Vivaspin-30 membrane (Viva Science, UK). An additional clean-up step using the Qiagen DNA mini kit was performed as per manufacturer's instructions to remove copurifying PCR inhibitors from samples that did not initially amplify. Blank DNA extractions and PCRs were routinely screened for contamination. Genomic data were obtained from a bone (Waitomo Caves Discovery Centre collection #17876k) preserved in Holocene sediments in a cave at Matira using specialist methods (Delsuc et al., 2016), followed by high-throughput Illumina sequencing and assembly to reference data (details to be reported elsewhere).

2.4 | Weka sequence markers

Preliminary data were generated for partial sequences of mtDNA Cytochrome b (Cytb) to determine the level of sequence variation within Weka, and for phylogenetic inference. Partial sequences of Cytb were amplified from a subset of Weka (Table S1) using primers AV15017F (5′ CAT CCG TTG CCC ACA CAT GYC G 3′) and Av16065R (5′ GYG RTC TTC YGT CTT TGG TTT ACA AGA C 3′).

To examine population genetic structure, we looked for concordance in mitochondrial and nuclear markers. For mtDNA haplotype analysis, we targeted the most variable part of the mitochondrial Control Region (CR) (Garcia-R et al., 2014b) with primers K1 (5′ AAT CAC CGC GGC ATG TAA TC 3′- Kirchman, 2009) and Av522DloopR (5′ CTG GTT CCT AAG TCA GGG CCA 3′- Slack, Janke, Penny, & Arnason, 2003). We chose a variable nuclear locus β-fibrinogen intron 7 (FGB-7- Morgan-Richards et al., 2008), amplified from a subset of Weka using primers Fib-BI7U (5′ GGA GAA AAC ACA ATG ACA ATT CAC 3′) and Fib-BI7L (5′ TCC CCA GTA GTA TCT GCC ATT AGG GTT T 3′) (Prychitko & Moore, 1997), to genotype representative population samples. Polymerase chain reactions were in 10 μl volumes containing 1 μl 10× DreamTaq™ buffer, 1 μl 10 μM dNTP mix, 0.5 μl each 10 μM primer, 0.15 μl DreamTaq™ DNA Polymerase and 1 μl template DNA, with 35 cycles of 94°C for 20 s, annealing at 51 [–54]°C for 30 s, 72°C for 45 s and a final extension step of 72°C for 10 min.

Sequencing was performed using BIGDYE version 3.1 chemistry (Applied Biosystems, Foster City, CA, USA), with products purified using CleanSeq® magnetic beads (Agencourt Bioscience) and analysis on an ABI 3730 automated capillary sequencer. Sequence data were edited in SEQUENCHER version 4.9 (GeneCodes Corporation, Ann Arbor MI) with alignment in GENEIOUS version 9.1 (Kearse et al., 2012). Phylogenetic analysis of Cytb included appropriate outgroup sequences from GenBank (Garcia-R et al., 2014a) using GENEIOUS version 9.1 to implement maximum-likelihood analyses in PHYML and MRBAYES. PHYML used a general time reversible model of DNA evolution estimating a proportion of invariant sites, four rate categories model and bootstrapping with a random seed and 100 repetitions searching for the best tree. MRBAYES used a standard DNA 4 × 4 nucleotide model, Nst of 6 with a Dirichlet prior and an invariable gamma (default settings). Markov Chain Monte Carlo (MCMC) started from a random seed and run for 5 million generations, sampling every 2,000 generations. Minimum-spanning and median-joining networks (Bandelt, Forster, & Röhl, 1999) were inferred for Weka haplotypes in PopArt (Leigh & Bryant, 2015) and colour-edited in Adobe Illustrator. We downloaded published mtDNA Control Region sequence for seven other New Zealand bird taxa that span the Cook Strait (Dussex, Sainsbury, Moorhouse, Jamieson, & Robertson, 2015; Goldberg, Trewick, & Powlesland, 2011; Miller & Lambert, 2006; Robertson, Steeves, et al., 2007; Shepherd et al., 2012; Trewick & Olley, 2016) and inferred haplotype networks for each using minimum-spanning and median-joining networks.

Summary statistics were obtained for the Weka CR data using ARLEQUIN version 3.5 (Excoffier & Lischer, 2010) after grouping samples in three different ways: (i) regional population samples, (ii) haplotype data grouped by current classification of four Weka subspecies, (iii) the pattern of spatial clustering indicated by phylogenetic analysis of mtDNA Cytb sequence data (north/south). Fu's *Fs* (Fu, 1997) and Tajima's D statistics (Tajima, 1989) were used to assess the consistency of observed genetic variation with a neutral model of evolution in each sample site and over all sample sites combined for each subspecies with 1,000 permutations, using ARLEQUIN version 3.5. Fu's *Fs* statistic is sensitive to population demographic expansion, which generally leads to large negative Fs values, and significant *D* values may be due to population expansion and bottlenecks. Genetic population structuring among sample populations was examined using the comparison of Φ_{ST} (Excoffier, Smouse, & Quattro, 1992), and tested to see whether estimates were significantly >0 using 1,000 permutations.

Demographic history of Weka was investigated by examining the shape of frequency distributions of pairwise genetic distances using Weka CR sequences (Rogers & Harpending, 1992) using DNASP version 5.0 (Librado & Rozas, 2009; Rozas, Sánchez-DelBarrio, Messequer, & Rozas, 2003). Harpending's raggedness index (Harpending, 1994; Harpending, Sherry, Rogers, & Stoneking, 1993) and the sum of squared deviations (SSD—Schneider & Excoffier, 1999) between the observed and expected mismatch were calculated using ARLEQUIN version 3.5 (Excoffier & Lischer, 2010) with 1,000 bootstrap resamples. Populations in demographic equilibrium are expected to show a unimodal distribution, so a nonsignificant result indicates deviation from this null due to recent population expansion (Slatkin & Hudson, 1991).

Within the alignment of FGB-7 sequences, we identified sites of ambiguity that could be reliably diagnosed as representing alleles by comparison of homozygotes and heterozygotes. We scored the frequency of alleles in population samples.

2.5 | Weka microsatellites

A modified enriched microsatellite library protocol was used to develop nuclear markers for population genetic analysis. Whole genomic DNA from Weka blood obtained from Nukuwaiata Island (one of the Chetwode group in the Marlborough Sounds) was digested with the endonuclease BfuC1 and fragments ligated to linker sequences using T4 ligase. PCR enhanced copy number of the ligated fragments prior to their hybridization to biotin-labelled dinucleotide (CA_{36} and GA_{36}) probes, which enriched the retained DNA with the aid of Streptavidin Magnesphere paramagnetic beads (Promega) and washes of increasing stringency. PCR generated the second strand and the enriched library was transformed into competent *E. coli* cells via the TOPO TA cloning kit (Invitrogen). Standard culture techniques and PCR with M13 primers were used to identify potential microsatellite loci based on product size and sequencing. Locus-specific PCR primers were initially developed for 22 CA repeat loci and 16 GA repeat loci and tested on DNA from 8 Weka. Eight reliable loci were identified and screened across 90 Weka individuals (Table S1).

Microsatellite PCRs for selected loci were multiplexed for genotyping according to size and fluorescent label (6-FAM or HEX), with allele sizes determined using an ABI3730 automated sequencer with an internal LIZ size standard (Applied Biosystems). Results were scored using GENEMAPPER® version 4.7 (Applied Biosystems), and data from each population were tested for amplification errors due to null alleles, large allele dropout and stuttering using 10,000 randomizations in MICROCHECKER version 2.2.3 (van Oosterhout, Hutchinson, Wills, & Shipley, 2004). Tests for departures from Hardy–Weinberg proportions within loci and linkage disequilibrium between loci in each population were conducted on the largest population sample ($n = 11$) of Western Weka (*G. a. australis*) using a Markov chain method implemented in GENEPOP version 4.2 online software (Raymond & Rousset, 1995; Rousset, 2008). All pairs of loci were tested, with 10,000 dememorizations and iterations and 1,000 batches used. A sequential Bonferroni correction (Rice, 1989) was implemented to reduce the chance of type 1 errors.

Diversity measures (number of alleles, observed and expected heterozygosity) were calculated using ARLEQUIN version 3.5 (Excoffier & Lischer, 2010). Population pairwise F_{ST} values were calculated (Weir & Cockerham, 1984) and used to test for significant departure from zero in ARLEQUIN version 3.5, using 1,000 permutations and adjusted significance level due to multiple pairwise tests. If taxonomically meaningful, we expected different Weka population samples grouped by putative subspecies to have pairwise F_{ST} estimates >0. AMOVA was implemented in GENODIVE version 2b27 (Meirmans & van Tienderen, 2004).

We tested the contrasting hypothesis that Weka population structure reflected only spatial proximity using a Mantel test of the correlation of pairwise geographic distances and pairwise genetic differentiation with the five loci combined. Such a scenario is plausible for native Weka populations because the sea strait between North Island and South Island was closed in the late Pleistocene. Associations between $F_{ST}/(1\text{-}F_{ST})$ (Rousset, 1997) and log transformed geographical distance were assessed with Mantel tests implemented in IBDWS version 3.16 (Jensen, Bohonak, & Kelley, 2005) with 10,000 randomizations of the data. Geographic distance was taken as the linear metric between the centres of each sample area.

A Bayesian assignment approach was used to assess population structure based on clustering of individual microsatellite genotypes with a method that determines the posterior probability of the data for a given number of genetic groups (STRUCTURE version 2.3.4 - Pritchard, Stephens, & Donnelly, 2000). The optimal number of populations (*K*) was estimated in STRUCTURE by performing ten independent runs for each hypothetical *K* between 1 and 8, with a burn-in of 100,000 steps to ensure likelihood convergence, and 3,000,000 MCMC repetitions. No prior population information was used, and allelic admixture was assumed. Allele frequencies among clusters were assumed to be independent to prevent overestimation of the number of clusters (Falush, Stephens, & Pritchard, 2007). Replicate iterations for each K value were formatted and optimal K selected (Evanno, Regnaut, & Goudet, 2005) using Structure Harvester (STRUCTURE HARVESTER WEB version 0.6.92) (Earl & Von Holdt, 2012), and averaged using CLUMPP version 1.1.2 (Jakobsson & Rosenberg, 2007). The "Greedy" Search Method was used with random input orders and 100,000 repeats. The output files from CLUMPP were processed with DISTRUCT version 1.1 (Rosenberg, 2004) to generate graphical summaries of assignment probabilities at each K. We also used GENODIVE version 2b27 (Meirmans & van Tienderen, 2004) to implement K-Means clustering.

2.6 | Sampling ectoparasites

To further examine the influence of the Cook Strait gap as a biogeographic barrier, we included two independent ectoparasite lineages from Weka. Weka chicks are populated by feather lice from their parents and so concordance between host and parasites genetic structure is expected (Clayton, Bush, & Johnson, 2016). Shorter generation times in ectoparasites compared to their hosts (e.g., Hafner et al., 1994; Johnson et al., 2014) mean that even the constrained mitochondrial COI gene has potential to inform population genetic history. Frozen road-kill Weka carcasses collected by DoC staff were searched for feather lice (Phthiraptera) by hand or by vigorous washing individually in ample water with detergent as a wetting agent. A series of laboratory sieves (8 mm to 212 microns) were used to separate feather barbules and other matter from ectoparasites. Additional specimens of lice were obtained opportunistically by DoC staff handling live weka. The resulting samples were preserved in 95% ethanol, identified and counted under a dissecting microscope. Lice belonging to two genera in separate suborders (Ischnocera: *Rallicola harrisoni* and Amblycera: *Pseudomenopon pilgrimi*) have previously been recorded on Weka (Price, Hellenthal, Palma, Johnson, & Clayton, 2003), although the southern-most population of Weka (*Gallirallus australis scotti*) lacks records of *Pseudomenopon* (Paterson, Palma, & Gray, 1999).

2.7 | Feather louse mtDNA

Representative feather lice were subjected to DNA extraction using the Qiagen DNeasy Blood and Tissue Kit (Clayton & Johnson, 2003; Toon & Hughes, 2008). Each louse was carefully bisected between the third pair of legs and the abdomen using a sterile scalpel. Both parts were placed in a 2.5-ml microfuge tube with 180 μl of buffer ATL and 20 μl of 10 mg/ml Proteinase K to be incubated at 56°C for 48–72 hr. The standard protocol was followed but DNA was eluted in two stages using a total of 50 μl of AE buffer. Remaining cuticles were ideal for morphological examination. A ~380-bp fragment of louse mitochondrial COI was amplified by PCR using primers L6625 (5′ CTT YGR TTY TTY GGN CAY CC 3′) and H7005 (5′ CCG GAT CCA CAN CRT ART ANG TRT CRT G 3′) (Hafner et al., 1994). Reactions in 20 μl volumes (11.5 μl sterile Milli-Q H_2O, 2 μl 10× McLAB Taq buffer, 2 μl 10 μM dNTPs, 1 μl each 10 μM primer, 0.2 μl 25 mM MgCl, 0.3 μl McLAB Taq DNA Polymerase and 2 μl template DNA) were treated to 40 cycles of 94°C 20 s, 45°C 20 s, 72°C 45 s, with a final extension step of 72°C for 10 min. DNA sequencing was as described above.

To provide outgroup data for preliminary phylogenetic analysis of the two louse lineages, we also collected congeneric lice *Rallicola ortygometrae* and *Pseudomenopon scopulacome* from buff-banded rails (*Gallirallus philippensis*) sampled on Great Barrier Island with the assistance of DoC, and *R. lugens* and *P. concretum* from swamphens (*Porphyrio porphyrio*) sampled from Palmerston North road kills (Garcia-R & Trewick, 2015). These were subjected to the same type of DNA extraction and PCR as Weka lice and resulting sequences were aligned with Weka louse data. Phylogenetic trees were obtained for each taxon using ML analysis via the PHYML algorithm implemented in GENEIOUS version 9.1 using a GTR+I+G model.

3 | RESULTS

Maximum-likelihood phylogenetic analyses (PHYML and MRBAYES) of an alignment of Weka sequences with an outgroup comprising published MtDNA Cytb sequences (GenBank: *Eulabeornis castaneoventris* KF644583, *G. philippensis* KF7014058, and *G. okinawae* AP010821) confirmed monophyly of Weka (Figure 2). Cytb sequences (841 bp) from twelve representative Weka from the widest geographical range (Table S1) revealed five haplotypes with a maximum GTR+I+G distance of 0.0148 (GenBank MF539888–MF539891). Two clusters of Weka Cytb sequences were revealed, comprising northern (Kapiti Island, Opotiki and Gisborne) and southern samples (West Coast South Island, Chetwode Islands, Stewart Island, Chatham Island) (Table S1).

3.1 | Control region haplotypes

Given the low genetic divergence detected at Cytb, we sequenced the less conserved Control Region for all Weka samples (Figure 2). A mtDNA Control Region (CR) alignment (343 bp) was obtained from 223 Weka, revealing 20 different haplotypes (A–T, Table S1, Table 1) comprising 23 parsimony informative sites (GenBank MF539892–MF539811). Genetic distance (Jukes-Cantor) among haplotypes reached 5.8% (Table S2). As indicated by analysis of Cytb sequences, two main clusters of CR variation were apparent with no sharing of haplotypes between the North and South Island samples. The sample of North Island Weka (*G. a. greyi*) from native sites in Gisborne, Matawai and Opotiki ($n = 11$) contained five haplotypes (B, C, D, F, G). Unique haplotypes were found in populations derived from translocated North Island Weka on Mokoia Island (E) and Kapiti

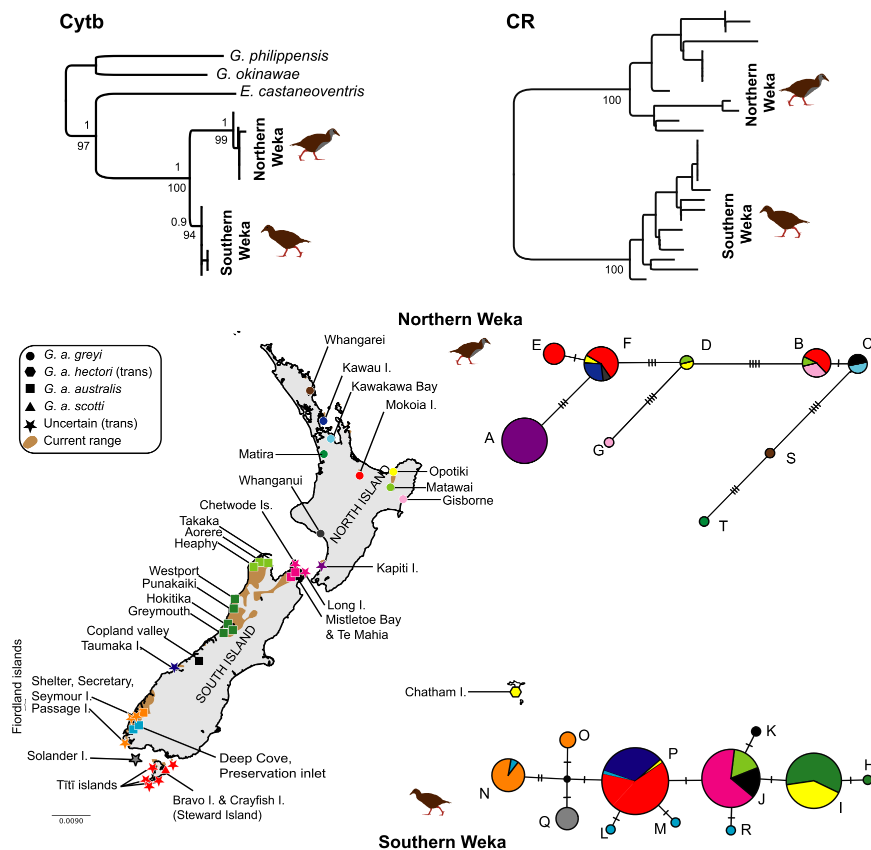


FIGURE 2 Mitochondrial diversity of New Zealand Weka (*Gallirallus australis*). Phylogenetic analysis of Cytb and CR sequences from Weka indicating two lineages. Sampling of Weka with networks of the two clusters of mtDNA CR haplotypes associated with the North Island and the South Island. Colours on the map correspond to haplotypes for each network, with symbol shapes indicating putative taxa for native and translocated (trans) populations. The approximate current ranges of Weka are based on observations made in the period 1999–2004 (Robertson, Hyvönen, et al., 2007 Webatlas via nzbirdsonline.org.nz)

TABLE 1 Mitochondrial Control Region haplotype diversity among population samples of the New Zealand Weka (*Gallirallus australis*), indicating sample size (*N*), nucleotide site diversity (π), haplotype diversity (Hd) and number of polymorphic sites (S)

						Haplotype																			
Location		*N*	π	Hd	S	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
North Island	Gisborne	8	0.00916	0.75	9		4	2	1			1													
	Opotiki	5	0.0035	0.4	3				4		1														
	Mokoia I.	18	0.0099	0.686	8		5			5	8														
	Kawau I.	4	0	0	0						4														
	Kawakawa Bay	2	0	0	0			2																	
	Kapiti I.	23	0	0	0	23																			
South Island	Punakaiki	2	0.0029	1	1								1	1											
	Hokitika	6	0	0	0									6											
	Westport	12	0	0	0									12											
	Greymouth (Ahaura)	3	0	0	0									3											
	Mistletoe Bay (Marlborough Sounds)	4	0	0	0										4										
	Long Island (Marlborough Sounds)	5	0	0	0										5										
	Te Mahia (Marlborough Sounds)	3	0	0	0										3										
	Titirangi (Marlborough Sounds)	1													1										
	Chetwode Islands	14	0	0	0										14										
	Tasman	7	0	0	0										7										
	Copland Valley	8	0.00073	0.25	1										7	1									
	Deep Cove (Doubtful Sound)	2	0.0058	1	2												1	1							
	Passage I. (Chalky Inlet)	4	0	0	0														4						
	Shelter Islands (Doubtful Sound)	8	0	0	0														8						
	Secretary I. (Doubtful Sound)	1																		1					
	Seymour I. (Doubtful Sound)	2	0	0	0															2					
	Taumaka (Open Bay Islands)	18	0	0	0																18				
Stewart Island/s	Bravo Islets	10	0	0	0																10				
	Tītī islands	23	0	0	0																23				
	Codfish Is	1																			1				
	Solander Island	6	0	0	0																	6			
Chatham Island	Chatham Island	15	0	0	0									15											
aDNA	Fiordland	1																					1		
	Takahe Valley	1																			1				
	Preservation Inlet	1																						1	
	Whangarei	1									1														
	Whanganui	1																							
	Waitomo	1																							1
	Oenga (Chatham)	1																			1				
∑		222				23	9	4	5	5	14	1	1	37	41	1	1	1	13	3	54	6	1	1	1

Island (A). Mokoia Weka (n = 18) were polymorphic, but all those sampled from Kapiti (n = 23) carried just haplotype A. Haplotype F also occurred in the one sample from the extinct Whanganui population putatively collected in 1964. Unique CR haplotypes were obtained from a museum skin from Whangarei (S) and a bone from a prehuman deposit at Matira (T), again, part of the northern cluster (Figure 2).

The southern cluster included haplotypes found in Weka assigned by their location to the three other Weka subspecies; *G. a. australis*, *G. a. scotti* and *G. a. hectori*. Haplotype I occurred in 22 putative *G. a. australis* (West Coast South Island) and all 15 putative *G. a. hectori* samples (from Chatham Island). Putative *G. a. scotti* from the Bravo islets (n = 10) close to Stewart Island and the nearby Tītī islands (n = 23) all had haplotype P. Haplotype P was the only one found in 18 Weka from the introduced Taumaka Island population near west coast South Island. Solander Island Weka (n = 6) had a unique haplotype (Q). Unique, but closely related, haplotypes (K, L, M, N, O) were found in Weka from Copland valley and the Fiordland sounds in southwest South Island. However, the Copland sample (n = 7) included Weka with a haplotype (J) that was otherwise found in birds from the north end of South Island in Marlborough (n = 13), the Chetwode islands (n = 14) and Tasman (n = 7). A unique haplotype (R) was found in a museum skin putatively from Fiordland (Figure 2).

Haplotype diversity (Hd) and nucleotide diversity (π) were highest in population samples from northeast North Island where native populations of Weka remain and, excluding very small population samples ($n < 3$), Copland valley had the highest diversity in South Island (Table 1). Offshore island populations had minimal diversity, usually comprising a single haplotype even when sample sizes were relatively large such as Kapiti (n = 23), Taumaka (n = 18), the Chetwodes (n = 14) and the Tītī islands (n = 23). In contrast, the inland island Mokoia in Lake Rotorua in North Island had among the highest diversity recorded (Hd = 0.686, π = 0.0099). Comparison of genetic composition of populations revealed significant departure of Φ_{ST} from zero. When data were grouped to represent the four putative subspecies, the lowest pairwise Φ_{ST} was between South Island (*G. a. australis*) and the translocated population on Chatham Island (putative *G. a. hectori*) (Table 2). No two southern haplotypes were separated by more than six steps, whereas up to 18 steps differentiated northern clade haplotypes.

We examined the contrasting patterns of mtDNA diversity seen in North Island and South Island Weka using neutrality and mismatch statistics. Population samples were grouped for each mainland island with offshore populations excluded (Table 3). Despite similar sample sizes for North Island (n = 60) and South Island (n = 67), diversity indices for the North were higher. As a result neutrality statistics for the two islands were very different with North Island population samples having positive values (Tajima's D = 0.932 and Fu's Fs = 3.262) compared to negative values for South Island Weka (Tajima's D = −1.189 and Fu's Fs = −2.147). Although not statistically significant at the $p < .05$ level, negative values are consistent with population expansion following a bottleneck, whereas relatively large positive values are indicative of rapid population contraction. Mismatch statistics show a similar contrast with a higher demographic expansion factor (τ) for North Island than South Island, but the estimated number of migrants (M) being larger for South Island (Table 3). The mismatch distribution of haplotypes from North Island was multimodal, consistent with demographic equilibrium, in contrast to the unimodal distribution for South Island Weka showing a close fit to the expectation for an expanding population (Figure 3).

TABLE 2 Pairwise Φ_{ST} for mtDNA Control Region variation among Weka (*Gallirallus australis*) representing four putative subspecies from different regions of New Zealand

		North I.	South I.	Stewart I.
North Island	*G. a. greyi*			
South Island	*G. a. australis*	0.822		
Stewart Island	*G. a. scotti*	0.812	0.386	
Chatham Island	*G. a. hectori*	0.823	0.153	1.000

3.2 | β-fibrinogen intron 7

The 972-bp alignment of 59 homologous FBG-7 sequences contained variation at just three nucleotide positions consistent with

TABLE 3 Patterns of mtDNA Control Region variation and demographic modelling among northern and southern New Zealand Weka (*Gallirallus australis*)

		North	South
Polymorphic sites		13	6
Gene diversity		0.7780	0.5246
		±0.034	±0.044
Nucleotide diversity		0.0107	0.0019
		±0.0061	±0.00163
Mismatch statistics		Group 1	Group 2
Spatial expansion model	Tau	4.4	0.5
	Theta	0.389	0.231
	M	3.297	11493.0
	SSD	0.031	0.013
	SSD P	0.490	0.070
	Raggedness	0.116	0.141
	Raggedness P	0.540	0.450
Neutrality statistics			
Tajima's D	*N* individuals	60	67
	S	13	6
	Pi	3.681	0.636
	Tajima's D	0.932	−1.189
	Tajima's D p	0.852	0.099
Fu's FS test	*N* alleles	7	6
	Theta_pi	3.681	0.636
	Exp. no. alleles	10.987	3.576
	FS	3.262	−2.147
	FS p	0.891	0.089

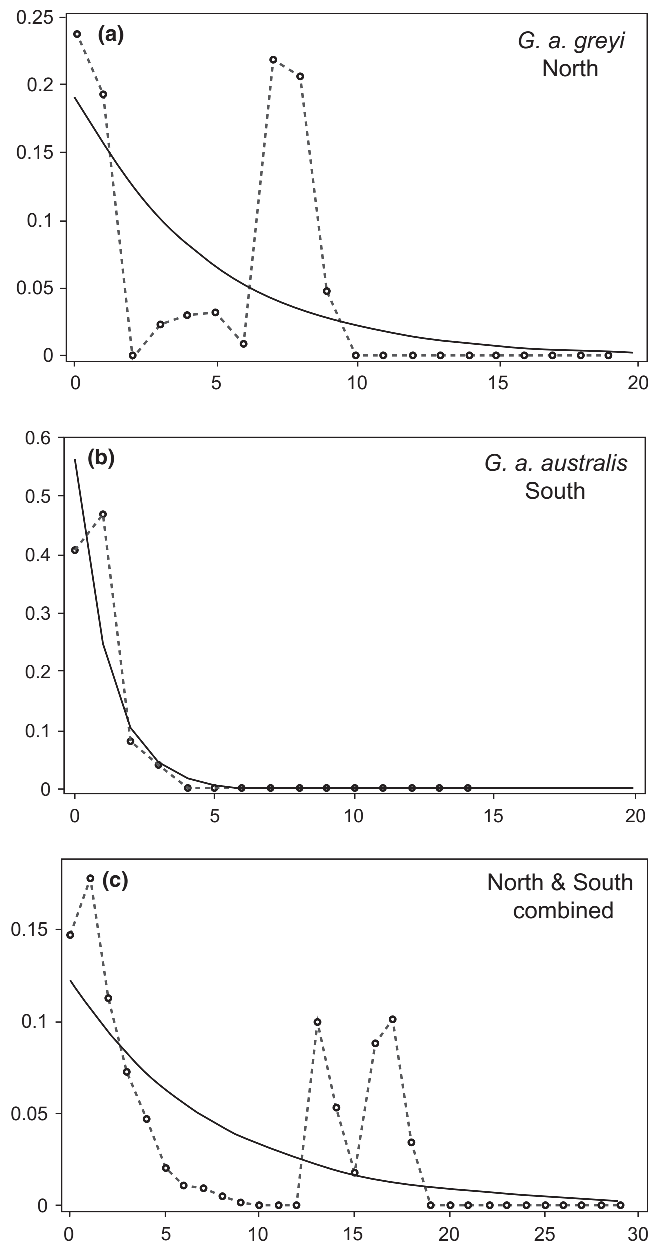


FIGURE 3 Mismatch distributions of mtDNA Control Region haplotypes from Weka (*Gallirallus australis*) in (a) the North Island (*G. a. greyi*), (b) South Island (*G. a. australis*) and (c) data combined

three alleles (A–C) (GenBank MF539912–MF539914). The frequency of alleles and genotypes was scored for each population sample examined (Table 4). All North Island (*G. a. greyi*) Weka were homozygous for one allele (B), while Weka from populations south of Cook Strait were more varied and mostly lacked this allele (Figure 4). Heterozygosity was therefore higher in the south, with two and sometimes three alleles present in a population sample. To test the null hypothesis of a single population of Weka, we assessed allele frequencies for Hardy–Weinberg equilibrium, which was rejected (χ^2 = 24.9162, *p* = .000145). However, the same analysis applied to the data from just the southern Weka could not reject the null suggesting that southern Weka belonged in the recent past to a single panmictic population (χ^2 = 5.6297, *p* = .34004).

3.3 | Microsatellites

After initial screening, five microsatellite loci were selected that showed no evidence of large allele dropout, abnormal frequency of null alleles or significant linkage disequilibrium (Table S3). These five nuclear loci were used to genotype 85 Weka including representatives of the four recognized subspecies (Table S1; DRYAD https://doi.org/10.5061/dryad.r1b48). The highest levels of heterozygosity were in the small Copland Valley sample (*n* = 4), but the highest number of alleles was in the sample from the native North Island populations (*n* = 6) (Table 5).

Overall F_{ST} (0.243) differed significantly from zero ($p < .001$), and pairwise F_{ST} among population samples included many that were significantly >0 ($p < .05$) (Table 5). Treated independently no population sample was significantly differentiated from all other populations according to the pairwise F_{ST} values, but offshore island populations tended to be well differentiated. Notably, comparisons of North Island and southern populations did not all show significant departures from $F_{ST} = 0$ (Table 5). It was expected that Weka population genetic structure would be consistent with subspecies taxonomy, but AMOVA applied to data for individuals assigned to one of four subspecies (*n* = 56) revealed that only a small part of variation (15%, *p* = .001) was partitioned among the four subspecies.

Bayesian assignment of 85 Weka genotypes scored for five microsatellite loci indicated that five clusters (*K* = 5) fitted the data best (Figure 5). These clusters did not correspond precisely with spatial distribution or current taxonomy. North Island and South Island samples did for the most part belong to different clusters (the exceptions being at the boundary between North and South), but South Island Weka populations showed a high degree of admixture. In contrast, low variation on Taumaka Island and the Tītī islands suggested recent genetic bottlenecking. To examine this further, we cropped the data set to include various permutations of location samples (not shown) and repeated analyses. We excluded genotypes of Weka population samples of the most-questionable origin and retained putatively native *G. a. greyi* from North Island, *G. a. australis* from South Island and the Chetwode islands, putative *G. a. scotti* from the Bravo islets and *G. a. hectori* from Chatham Island (no native populations of the latter remain). For these data, Bayesian assignment resulted in the selection of a model with two clusters (*K* = 2). *K*-Means clustering (Meirmans, 2012) also favoured two genotype clusters (pseudo-F statistic; Caliński & Harabasz, 1974) over larger values of *K*. Strikingly, the two clusters did not correspond to the north/south partition indicated by mtDNA CR haplotype analysis (Figure 5). Instead, the sample of putative *G. a. hectori* Weka from Chatham Island showed more similarity to northern *G. a. greyi* than South Island Weka. Nevertheless, there were significant departures of F_{ST} from zero when Chatham Island and Chetwode island population samples were each compared to North Island population samples (Table 5).

We tested the null hypothesis that all mainland Weka were part of a panmictic population subject only to isolation by distance. A Mantel test of genetic and geographic distances showed no compelling correlation (R^2 = 0.22, *p* = .1437), which is consistent with the result from Bayesian assignment of genotypes (i.e., $K > 1$).

TABLE 4 Frequency of nuclear β-fibrinogen intron 7 (FGB-7) genotypes and alleles in regional samples of Weka (*Gallirallus australis*). Na = number of different alleles, H = observed heterozygocity

		Genotype frequency							Allele frequency				
	N	AA	BB	CC	AB	AC	BC		A	B	C	H	Na
Gisborne	3		3					6	0	1	0	0	1
Opotiki	3		3					6	0	1	0	0	1
Mokoia !.	8		8					16	0	1	0	0	1
Kapiti I.	4		4					8	0	1	0	0	1
Wesport	6	2			1	2	1	12	0.58	0.17	0.25	0.67	3
Copland V.	4	1			1		2	8	0.38	0.38	0.25	0.75	3
Fiordland	4	3					1	8	0.75	0.13	0.13	1	2
Stewart I.	5	2	1					10	0.6	0.4	0	0.33	2
Chatham I	12			5	2	5		24	0.29	0.08	0.63	0.58	3
Taumaka	7	5			2	2		14	0.83	0	0.17	0.5	2
Long I.	1	1						2	1	0	0	0	1
Solander I	2	1			1			4	0.75	0.25	0	1	2

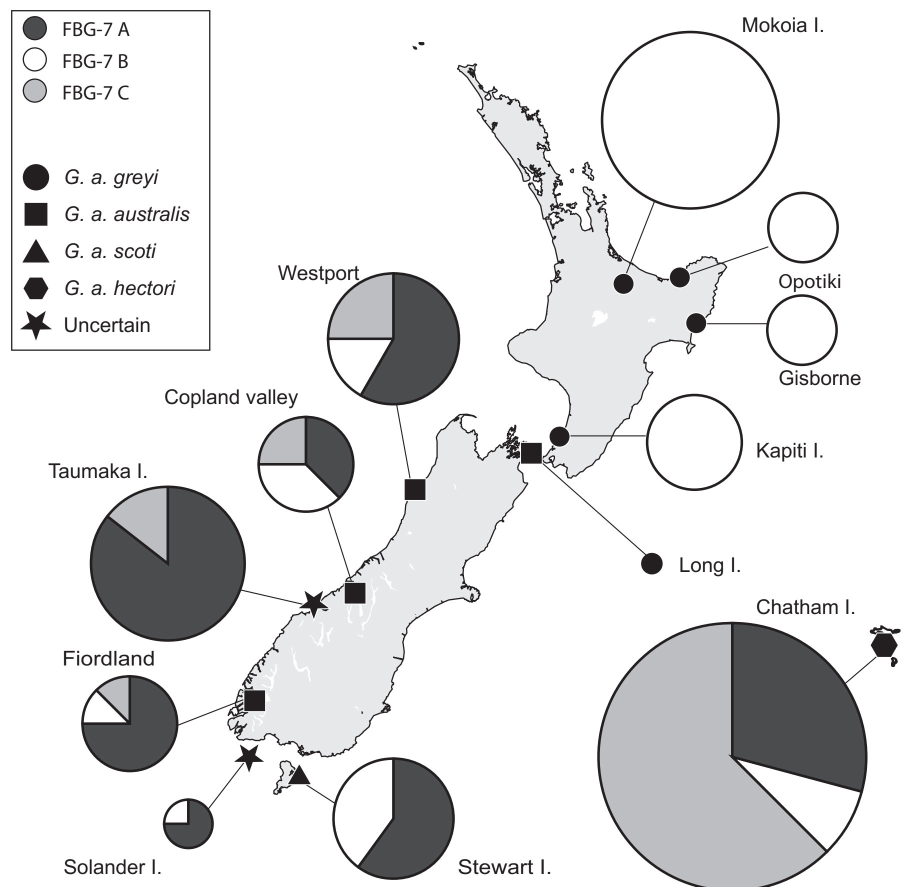


FIGURE 4 Distribution of three β-fibrinogen intron 7 (FBG-7) alleles identified in DNA sequences from Weka (*Gallirallus australis*) at locations in the North and South islands of New Zealand. Pie sizes are proportional to relative allele frequency, and symbol shape indicates putative taxon (see Table 4)

3.4 | Feather louse mtDNA

Using a combination of hand searching live or dead birds and washing dead birds, we gathered Phthiraptera feather lice from 22 individual Weka (Table S4). Microscopic examination revealed that our sample of >1,200 adult lice included representatives of two genera in different suborders; *Pseudomenopon* (Amblycera) and *Rallicola* (Ischnocera). The abundance of lice on each host varied considerably, and of those Weka washed and searched exhaustively, the number of lice ranged from 13 to 522 per host. *Rallicola harrisoni* (93%) were more abundant than *Pseudomenopon pilgrimi* (7%), but frequencies varied among individual hosts, with five Weka from the

TABLE 5 Diversity and pairwise F_{ST} among microsatellite genotypes from regional samples of Weka (*Gallirallus australis*). Number of individuals sampled (N), total number of alleles detected (N_A), Average number of alleles detected (AvN_A), observed heterozygosity (H_O) and expected heterozygosity (H_E). Estimates of pairwise F_{ST} that are significantly >0 are in bold

Population	N	NA	HO	HE	AvN_A	Stewart I.	Tītī is.	Chatham I.	Gisborne	Mokoia I.	Kapiti I.	NW South I.	Marlborough	Chetwode is.	Taumaka I.	Fiordland is.
Stewart I.	10	12	0.620	0.442	2.4											
Tītī is.	12	11	0.810	0.610	2.4	**0.955**										
Chatham I.	4	9	0.750	0.700	2.2	**0.928**	0.000									
Gisborne	6	23	0.767	0.758	4.6	**0.248**	**0.700**	**0.538**								
Mokoia I.	5	12	0.870	0.714	3.2	**0.452**	**0.590**	**0.391**	0.016							
Kapiti I.	2	12	0.900	0.700	2.4	0.531	0.756	0.515	−0.004	−0.061						
NW South I.	10	15	0.492	0.506	3	0.152	**0.710**	**0.592**	0.034	0.135	−0.046					
Marlborough	10	17	0.409	0.483	3.4	**0.277**	**0.632**	**0.501**	0.004	0.020	−0.098	−0.004				
Chetwode is.	7	15	0.771	0.588	3	**0.731**	**0.819**	**0.710**	**0.325**	0.195	0.469	**0.525**	**0.429**			
Taumaka I.	13	12	0.794	0.547	2.4	**0.670**	**0.469**	0.348	**0.297**	0.200	0.244	**0.433**	**0.335**	**0.481**		
Fiordland is.	3	13	0.667	0.600	2.6	0.388	**0.726**	0.509	−0.063	−0.048	−0.204	−0.036	−0.081	**0.422**	0.198	
Copland V.	4	16	0.938	0.741	3.2	−0.056	**1.000**	**1.000**	0.199	0.391	0.515	0.122	0.251	**0.710**	**0.638**	0.329

Tītī islands near Stewart Island hosting only *R. harrisoni*. Both species of louse were found on a sample of 12 Weka from west coast South Island (near Hokitika and Westport) with the most similar numbers on a single Weka being 125 *R. harrisoni* and 31 *P. pilgrimi*. (4 : 1) A Weka from Chatham Island had 125 *R. harrisoni* and five *P. pilgrimi*, (25 : 1) and the lousiest host was among three Weka from near Opotiki (North Island), which carried 488 *R. harrisoni* and 34 *P. pilgrim* (14 : 1) (Table S4).

MtDNA COI sequences were obtained from 33 lice (25 *Rallicola harrisoni* and eight *Pseudomenopon pilgrimi*) including representatives of both genera from the same Weka individuals (GenBank MF539919–MF539926 and MF539915–MF539918 respectively). Alignments of 330 bp (*Rallicola*) and 337 bp (*Pseudomenopon*) had 59 and 31 parsimony informative sites, respectively. Maximum genetic distances (Juke Cantor) among haplotypes were substantially higher in the sample of *R. harrisoni* (0.2) than the *P. pilgrimi* (0.098). Nevertheless, minimum-spanning networks revealed two clusters of variation in *R. harrisoni* and *P. pilgrimi*, each associated with sampling from North Island and South Island Weka hosts (Figure 6a). We also obtained homologous mtDNA COI sequences from specimens of the same louse genera living on congeneric rails in New Zealand. The Weka louse clades were confirmed as sister groups within both genera (Figure 6b).

4 | DISCUSSION

4.1 | Concordance of genetic markers and Cook Strait

We found an overall signal in the genetic data from Weka for just two primary lineages among the extant populations (Figure 2), suggesting an accumulation of genetic differences during prolonged separation. These lineages are partitioned by the most prominent, and yet geologically young, geophysical feature in the New Zealand landscape; the Cook Strait seaway. MtDNA genetic diversity was lower among southern Weka, comprising three putative subspecies, than northern Weka (Table 1 and 2, Table S2). Associated with this were different inferences of demographic history. North Island Weka that have today the more restricted range gave a signal of recent population reduction, and novel haplotypes in extinct populations show diversity as well as range has been lost recently. In contrast, southern Weka appear to have experienced recent population expansion (Figure 3).

Corresponding north and south lineages were evident in the mtDNA variation of two independent Weka ectoparasites. Although feather lice are not attached permanently to their hosts or carried within their cells, the close association means that lice share many evolutionary features with host mitochondria. Multiple lice individuals live on each host and are transmitted primarily from parents to offspring (vertically). Rarer opportunity and priority effects limit horizontal transfer although this also requires close physical proximity and would therefore also retain a signal of host spatial distribution (Clayton et al., 2016). Feather louse lineages therefore represent

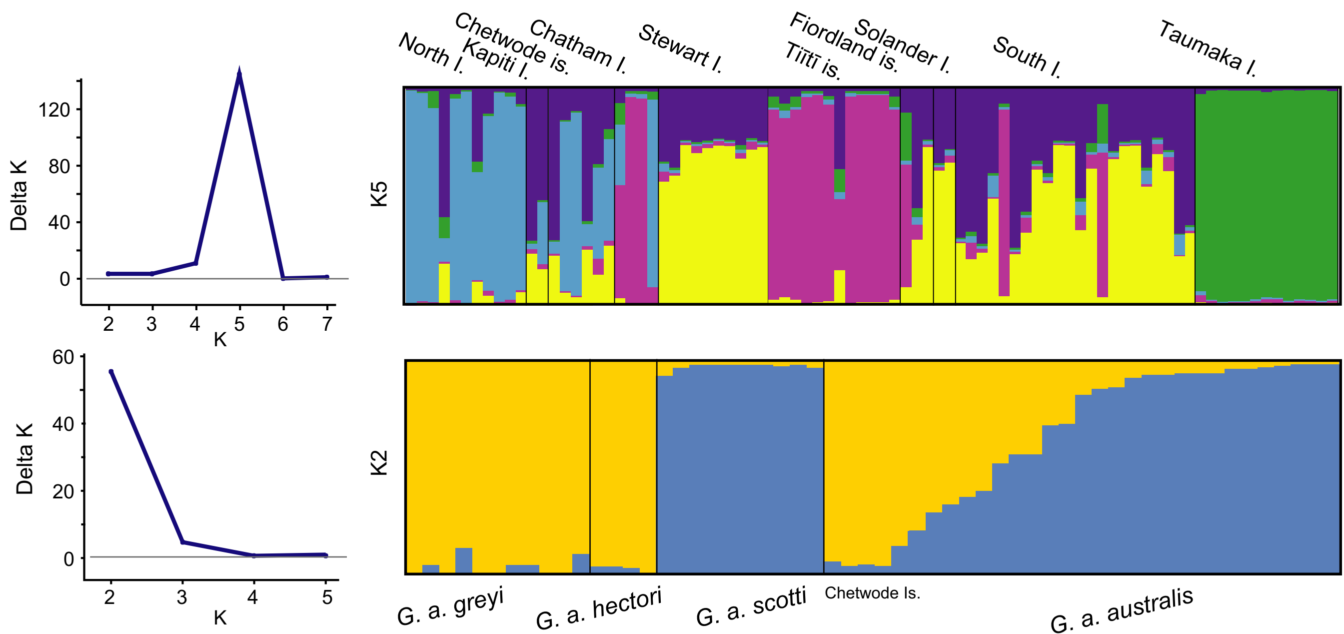


FIGURE 5 Bayesian clustering of genotypes from five microsatellite loci for all Weka (*Gallirallus australis*) surveyed (upper) and those Weka representative of four recognized subspecies (lower). Evanno DeltaK plots are shown on the left indicating strongest support for $K = 5$ and $K = 2$, respectively

independent evolutionary histories that coincide through shared host ancestry (Clayton et al., 2016; Toon & Hughes, 2008). The two distantly related host-specific louse taxa that we surveyed from Weka (*Rallicola harrisoni*, *Pseudomenopon pilgrimi*) each had sister lineages associated with North Island and South Island (Figure 6). We noted the correspondence between relative census abundance of the two louse lineages and the number of haplotypes detected in each (although sample sizes were small—Table S4), consistent with coalescent expectations (Charlesworth, 2009). Higher genetic distances between north and south louse mtDNA sequences than between north and south hosts likely reflects life history differences such as the shorter generation time of lice compared to their Weka hosts (e.g., Hafner et al., 1994; Whiteman, Kimball, & Parker, 2007; Whiteman et al., 2009).

Weka and Weka louse mtDNA implicate the North/South division of New Zealand that existed before and during the Pliocene (and into the early Pleistocene), prior to opening of the current narrow Cook Strait. Recent land connections during the last glacial maximum of the Pleistocene allowed contact between north and south populations, but apparently did not result in sufficient mixing to obscure this pattern. However, although nuclear markers indicated a similar degree of clustering among mainland Weka as their mitochondrial variation, the distribution of diversity was more complex. Bayesian assignment of microsatellite genotypes indicated that native populations of Weka comprised just two clusters partitioned approximately north and south. The northern group included Weka from North Island and a few west coast South Island individuals, as expected if recent land connections facilitated some gene flow between north and south populations. When included in the analysis some of the translocated Chatham Island and Marlborough Sounds island Weka genotypes were assigned to the northern group (Figure 5). The southern cluster comprised Stewart Island birds and most Weka from the South Island. Analyses including genotypes from translocated Weka populations (whose ancestry is not known) resulted in support for more genotypic clusters (Figure 5). There were distinct clusters for Weka from Taumaka Island and the Tītī islands that are likely to have been subject to genetic bottlenecking during population establishment, resulting in fewer alleles occurring in unique permutations. Similar distinct small-island genotypes have been observed in flying New Zealand bird species including Kokako (*Anthornis melanura* - Baillie, Ritchie, & Brunton, 2014), Tieke (*Philesturnus carunculatus* - Taylor, Jamieson, & Wallis, 2007) and Kaka (*Nestor meridionalis* - Dussex et al., 2015). Island populations had mtDNA haplotypes consistent with their location, being the same or most similar to Weka haplotypes in the nearby mainland region.

4.2 | Conservation of genetic diversity and human assisted gene flow

> *"...they are so very tame or foolish, as to stand and stare at us till we knocked them down with a stick..... and eat very well in a pye or fricassée." Cptn. James Cook* (Maver, 1813)

The genetic data do not support putative *G. a. hectori* as representing a distinct lineage or subspecies, corroborating previous interpretation of plumage variation (Scarlett, 1970). Indeed, consistent signal differentiating the three southern subspecies from one

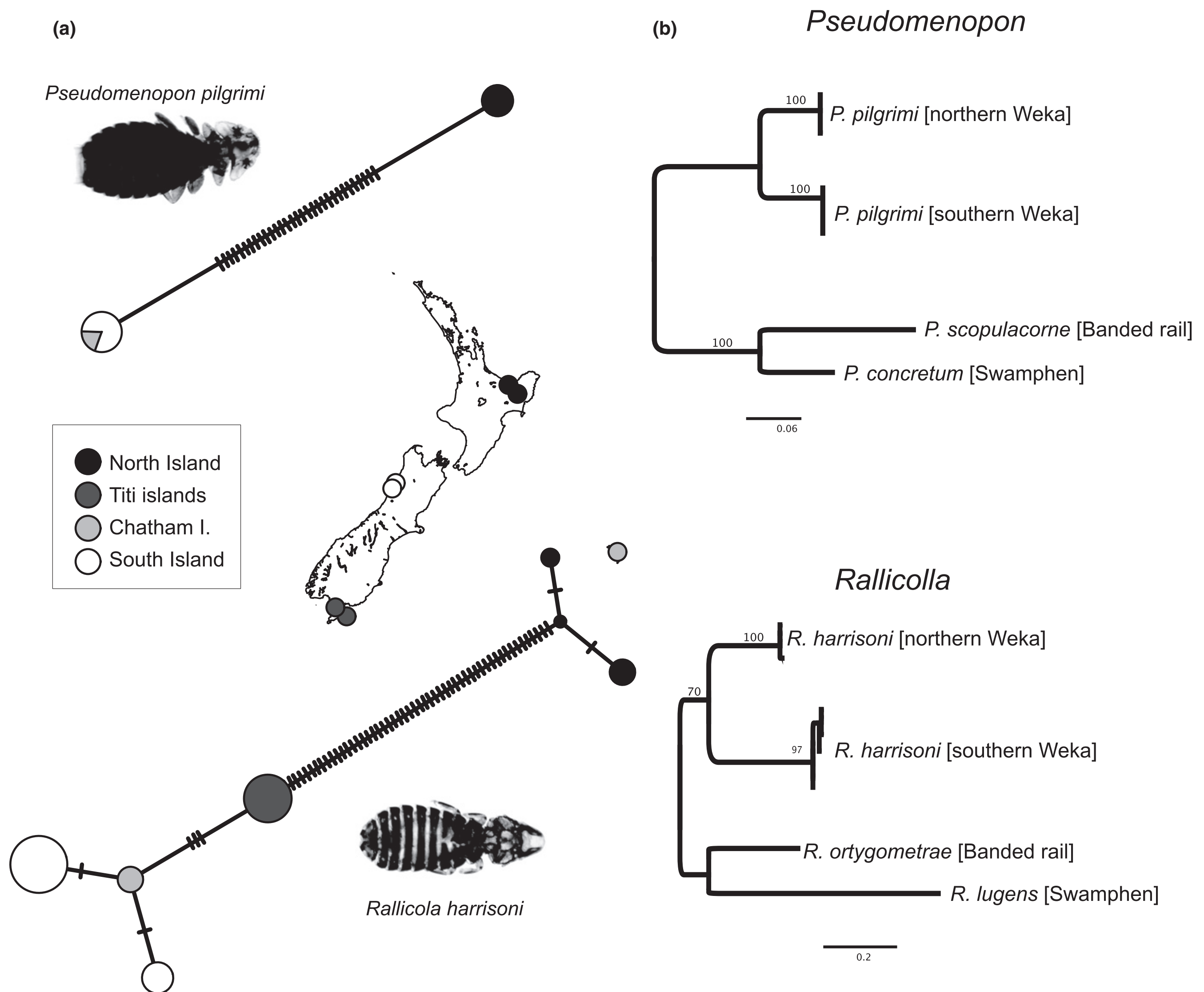


FIGURE 6 Haplotypic variation at the mtDNA COI locus in two genera of feather lice (Phthiraptera) from Weka (*Gallirallus australis*) hosts in New Zealand. (a) Networks showing the extent of sequence difference between lice from North Island and southern Weka. (b) Maximum-likelihood analysis (GTR+I+G) of mtDNA COI sequences with outgroup data from *Rallicola* (left) and *Pseudomenopon* (right) lice on buff-banded rail (*Gallirallus philippensis*) and swamphen (*Porphyrio porphyrio*). Host names in [square brackets]. Numbers at nodes are bootstrap support from 100 replicates

another is absent. The Weka species (= *Rallus australis*) was first described by Sparrman (1786) as inhabiting southern New Zealand. As such the name *Gallirallus australis* (Sparrman, 1786) applies to Weka generally and as the nominate species the southern subspecies would remain *G. a. australis*. Just a single North Island taxon has long been recognized (*G. a. greyi* (Buller, 1888)). We do not at this stage consider the north and south Weka lineages as distinct genotypic clusters (species - Mallet, 1995) because nuclear loci are equivocal about the history of admixture (c.f. Tavares, de Kroon, & Baker, 2010), and consistent discriminating phenotypic traits have not been confirmed. Additional morphological or nuclear genetic markers are required to determine whether the north and south louse lineages should be recognized as separate species, but their level of mtDNA sequence divergence is consistent with them being given taxonomic distinction (Johnson, Reed, Hammond Parker, Kim, & Clayton, 2007).

Although there are perceived conservation conflicts associated with the presence of omnivorous Weka on islands that could provide “predator-free” habitat for other endangered species (Miskelly & Beauchamp, 2004), these island populations of Weka contribute important genetic diversity to this declining species. For example, Mokoia in Lake Rotorua supports a population of about 100 Weka, derived from birds translocated in the 1950s from Gisborne (Axbey, 1994; Owen, 1997). The unique haplotype there has likely been fixed stochastically and may formerly have existed in the Gisborne area. Alternatively, it is possible that the haplotype reached the island from a closer but now extirpated population by swimming Weka (Riddell & Riddell, 2012). Similarly, the Kapiti Island Weka haplotype belongs to the North Island lineage (Figure 2), but was not encountered in any other population. This suggests that at least some of the females on Kapiti came from a North Island population

that is now extinct, but persisted in southern North Island near Kapiti into the European era (1920s - Beauchamp et al., 1999).

Like Kapiti, Solander Island off southwest South Island has Weka with a haplotype not recorded on the mainland, but related to haplotypes on nearby islands in Fiordland (Figure 2). In contrast, west coast Taumaka Island has a haplotype that is otherwise most abundant among Weka originating from Stewart Island (putatively *G. a. scotti*). This could imply translocation of Weka from Stewart Island to Taumaka, but museum specimens from Fiordland show the haplotype here, formerly existed on the mainland in this region (Figure 2). The Chatham Island population has the common South Island west coast haplotype and southern ectoparasite lineages, but mixed microsatellite genotypes and high FBG-7 diversity. Given its supposed origin from 12 *G. a. hectori* trapped at a single locality in eastern South Island, the modern population has unexpectedly high genetic diversity. This could reflect former South Island genetic diversity, and/or subsequent undocumented introductions from several sources including North Island. The small founding population could conceivably have retained high genetic diversity if it was initially diverse and population size increased rapidly without selection (e.g., Zenger, Richardson, & Vachot-Griffin, 2003).

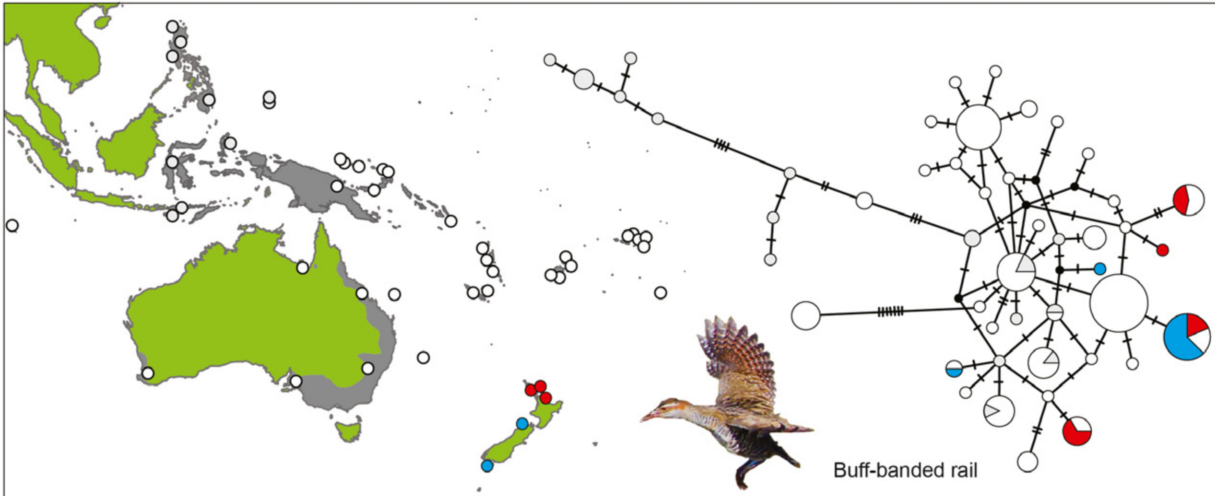
Mixed signal from mtDNA and nuclear markers is consistent with the different effective population sizes of the genomes tending to result in more rapid coalescence of mtDNA (Palumbi, Cipriano, & Hare, 2001). It might also indicate sex-biased dispersal (Dobson, 2013) and different dispersal behaviour of male and female Weka could be associated with observed uneven effective sex ratio (Freeman, 2010). We noted that despite having southern mtDNA haplotypes, Weka on the Chetwode, Chatham and Tītī islands appear to have genotypes indicating admixture with northern Weka (K = 2), or clustering of Chatham Island and Tītī island Weka (K = 5) (Figure 5). Similarly, Kapiti island Weka had a northern mtDNA haplotype, but nuclear genotypes more like southern Weka suggesting natural admixture during the last glacial maximum when the two main New Zealand islands were connected (Figure 7). However, as Kapiti and Chetwode Weka populations are presumed to have been derived from translocation, mixing might also have resulted from both indigenous practice (Miskelly, 1987) and more recent translocation for conservation.

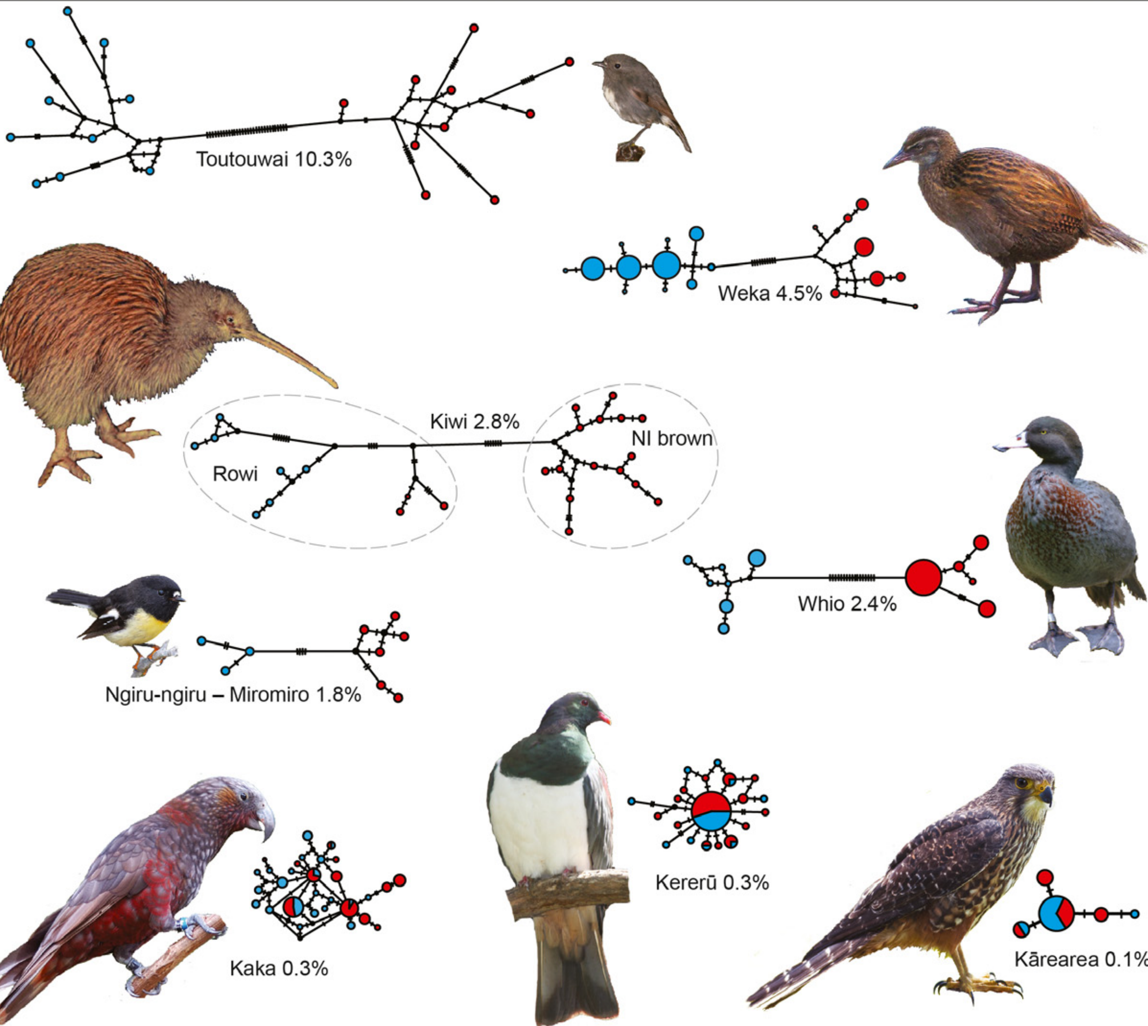
4.3 | Congruent lineage splits in other birds

The most abundant flying relative of Weka, the buff-banded rail (*Gallirallus philippensis*), comprises many races distributed among islands in Oceania (Garcia-R et al., 2017). Sharing of mtDNA Control Region sequences among populations on widely spaced Pacific islands including New Zealand, shows rampant, recent and potentially ongoing dispersal of this species (Figure 7). Large oceanic gaps between islands do not prevent this (Garcia-R et al., 2017) or other (Trewick & Gibb, 2010) species in the region reaching and colonizing suitable habitat.

Available genetic data for New Zealand endemic birds show north-south haplotype structure in species with diverse ecology including Whio the river duck, Toutouwai the forest robin and the flightless Weka (Figure 7). In many cases, the north-south split corresponds with the limits of the two main islands and recognized taxa, but in the brown Kiwi complex, one taxon spans the Cook Strait gap (Shepherd et al., 2012). Notably, this became apparent for Kiwi only after inclusion of data from extinct populations, demonstrating that spatial ranges of extant populations resulting from anthropogenic change can mislead understanding of natural spatial diversity (Burbidge, Colbourne, Robertson, & Baker, 2003). Although flying birds might be expected to experience more gene flow and thus less spatial structure than flightless species, other factors appear to influence the frequency of exchange. The small forest dwelling Toutouwai (*Petroica*) robin has relatively deep spatial structure compared to Kererū (*Hemiphaga*) pigeon that lacks geographic division at neutral genetic markers. A classic haplotype signal of population expansion in Kererū suggests recent population recovery, perhaps a response to forest expansion after the last glacial maximum (Goldberg et al., 2011). The aerial predator Kārearea (*Falco*) also has low neutral genetic diversity without prominent spatial partitioning, but nevertheless shows ecologically significant stepped size difference between North Island and South Island populations either side of Cook Strait gap (Trewick & Olley, 2016). Size is likely linked to hunting attributes and suggests ecological adaptation associated with a stepped environmental gradient (Endler, 1977; Trewick & Olley, 2016), confirming that adaptive responses can be faster than genetic drift at neutral loci (Hoffman & Willi, 2008). Shallow genetic differentiation between profoundly size-contrasted eagles has previously been reported from the region (Bunce et al., 2005). Variation in mean genetic distance between north and south lineages in different taxa (Figure 7) might be due to the populations becoming isolated at different times, however, variation in generation time and mutation rate could have the same effect.

Fossil calibrated phylogenetic analysis of rail mtDNA genomes indicates that the Weka lineage arose in New Zealand about 8 million years ago (late Miocene/early Pliocene), probably after colonization by a flying *Gallirallus* ancestor (Garcia-R et al., 2014a,b). At that time, separate northern and southern main islands likely existed and there is no evidence for their physical connection until the late Pleistocene. It is plausible that initial range expansion across these islands by a flying ancestor led to the establishment of separate populations that then evolved independently, as evident in *Gallirallus* more widely in the Pacific (Figure 1) (e.g., Garcia-R et al., 2014a; Trewick, 1997b). The depth of divergence between north and south Weka arising in this manner would depend on how long flight was retained by the founding populations. We found mean sequence divergence at the mtDNA locus of 0.058 (Control Region) and 0.0145 (Cytb). Assuming a rate of molecular divergence of ~2% per million years (Weir & Schluter, 2008), an inference of lineage splitting no more than 3 million years ago can be made. However, for avian Control Region this rate is almost certainly too conservative (Garciá-Moreno, 2004; Garcia-R et al., 2017; Weir & Schluter, 2008), implying a lineage split within the last million years is more likely. Thus, the divergence within Weka mtDNA could represent colonization of one


Buff-banded rail


Toutouwai 10.3%
Weka 4.5%
Kiwi 2.8%
Rowi
NI brown
Whio 2.4%
Ngiru-ngiru – Miromiro 1.8%
Kererū 0.3%
Kaka 0.3%
Kārearea 0.1%

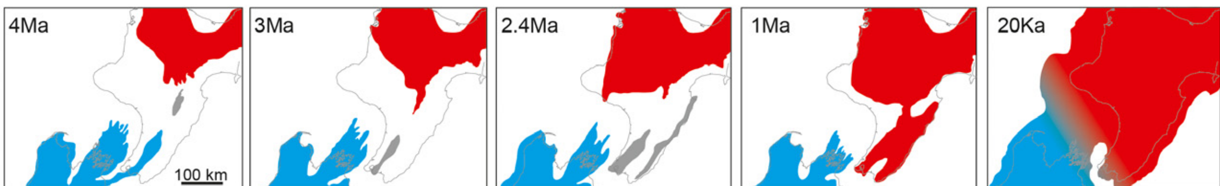

4Ma
100 km
3Ma
2.4Ma
1Ma
20Ka

FIGURE 7 MtDNA Control Region haplotype networks for eight New Zealand birds. Average Jukes-Cantor genetic distances among haplotypes are shown for each. North Island and South Island sampling is shown in red in blue, respectively. Sampling of Buff-banded rail outside New Zealand shown in grey and white. Passeriformes—Toutouwai, *Petroica longipes* and *P. australis* (Miller & Lambert, 2006); Casuariiformes—Kiwi, *Apteryx mantelli* and *A. rowi* (Shepherd et al., 2012); Gruiformes—Weka, *Gallirallus australis* (this study), Buff-banded rail, *Gallirallus philippensis* (Garcia-R et al., 2017); Anseriformes—Whio, *Hymenolaimus malacorhynchos* (Robertson, Steeves, et al., 2007); Ngiru-ngiru/Miromiro—*Petroica macrocephala* (Miller & Lambert, 2006); Columbiformes—Kererū, *Hemiphaga novaeseelandiae* (Goldberg et al., 2011); Psittaciformes—Kaka, *Nestor meridionalis* (Dussex et al., 2015); Falconiformes—Kārearea, *Falco novaeseelandiae* (Trewick & Olley, 2016). Inset maps show approximate palaeogeography of central New Zealand during the last 4 million years including the last glacial maximum (20 thousand years), with present day coastline indicated (redrawn from Trewick & Bland, 2012). Northern and southern islands shown in red and blue, respectively, with areas of uncertain connection in grey

island by Weka from the other during the late Pliocene or even mid-Pleistocene.

It can be presumed that bird ranges expand to fill accessible, suitable habitat as tectonic activity enlarged North Island, southwards. Northern Weka and small forest birds would have occupied the new habitat in a manner routinely evoked when considering expansion from climate refugia (e.g., Graham, VanDerWal, Phillips, Moritz, & Williams, 2010; Hewitt, 1996), and observed after species introduction (e.g., Su, Cassey, Dyer, & Blackburn, 2017). Modern bird range changes in New Zealand confirm this (e.g., Clegg et al., 2002), but bridging the gap between north and south would have required long distance dispersal (Crisp, Trewick, & Cook, 2011). The geographic distance involved is not great, and New Zealand has experienced recent avian colonization from Australia 1500 km away (Trewick, 2011), but a seaway is a significant ecological gap that can reduce the rate of gene flow (Endler, 1973). Such dispersal would be more challenging for Weka and other flightless birds and even small forest birds than it would be for strong flying species (e.g., Kererū pigeon fly between Stewart and South Island across 30 km Foveaux Strait, in search of food; Goldberg et al., 2011). Establishment after long distance dispersal will depend on ecological interactions including intraspecific competition, which is a function of population density (e.g., Lomolino, 2000). Detection of historical gene flow may therfore be further diminished by numerical disadvantage (Petit & Excoffier 2009), so that neutral alleles arriving rarely via long distance dispersal have little long-term impact on local allele frequencies. Similarly, gene flow at neutral loci arising from short-term secondary contact, such as temporary closure of Cook Strait in late Pleistocene time, would be influenced by population density and intrinsic dispersal rate (Barton & Gale, 1993). In Weka, the local mismatch of nuclear alleles from the host and mitochondrial haplotypes from host and ectoparasistes could be an expression of gene flow at a contact zone with differential introgression of markers (Funk & Omland, 2003). As expected, the uniparental haploid mtDNA has narrower clines than the biparental diploid markers (Barton & Gale, 1993; Morgan-Richards, Trewick, & Wallis, 2000).

Details of the interaction between ecology and biogeography remain elusive (Wiens, 2011), as apparently minor impediments to dispersal are concordant with major faunal changes or strong population structure. Indeed, "*looking at the proximity of the islands, we shall feel astonished . . .that. . .a. . . more complete fusion has not taken place*" (Wallace, 1860). This naive expectation is born out in Oceania by species such as the Buff-banded rail that range over widely spaced islands, but by definition, endemic species are geographically restricted. Endemism is a product of evolution commonly associated with allopatry (Mallet, 2008), yet New Zealand examples indicate that ecological and evolutionary priority effects (De Meester, Vanoerverbeke, Kilsdonk, & Urban, 2016) must influence intraspecific evolution. Phylogeographic structure of Weka and their ectoparasites, and several flying birds, coincide with the sea strait between North and South Islands, although this young, narrow seaway is unlikely to have been the direct cause of lineage splits. Rather it likely represents an environmental step where spatial and ecological constraints intersect (Caro, Caycedo-Rosales, Bowie, Slabbekoorn, & Cadena, 2013; Sulloway & Kleindorfer, 2013; Trewick & Olley, 2016). The opening and closing of gaps over geological time creates potential for varied phylogeographic structure among taxa and among loci in the same lineage, with biodiversity outcomes dependent on ecological factors (Warren, Cardillo, Rosauer, & Bolnick, 2014).

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AUTHOR CONTRIBUTION

Steve Trewick did DNA sequencing, genetic analysis and figure preparation, and wrote the manuscript draft. Morgan-Richards did louse sampling and sequencing and supported science writing. Stephen Pilkington developed the microsatellite markers and genotypes Weka population samples. Lara Shepherd sampled museum skins and supported generation of Control Region sequence data with Stephen Pilkington. Gillian Gibb did the ancientDNA sequencing and mtDNA assembly from a Weka fossil bone.

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