IBIS
BOU international journal of avian science
Ibis (2016), doi: 10.1111/ibi.12398

Spatial size dimorphism in New Zealand's last endemic raptor, the Kārearea *Falco novaeseelandiae*, coincides with a narrow sea strait

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Although New Zealand's avifauna includes many unusual birds, species-level diversity within lineages is typically low. There are, however, several instances where different allied forms are recognized in each of the two main islands. Among them is the Kārearea *Falco novaeseelandiae*, which is the only surviving endemic raptor species in New Zealand. Recent analysis confirms it to be a distinct lineage in the global radiation of this genus and most closely related to the Aplomado Falcon *Falco femoralis* of South America. We examined body size metrics and neutral genetic markers in Kārearea sampled across New Zealand to assess subspecific variation within the species. We found strong evidence using linear modelling and Bayesian clustering for two distinct sizes within Kārearea, in addition to the recognized sexual dimorphism. The boundary between the size clusters coincides closely with the Cook Strait, a narrow seaway between the two largest islands. However, analysis of mitochondrial sequence data and nuclear microsatellites showed no compelling partitioning at neutral loci. These data suggest adaptive change along a stepped environmental cline. Lineage splitting in Kārearea has either yet to become apparent in the distribution of neutral genetic variation and/or regional adaptation is proceeding despite gene flow.

Keywords: conservation, falcon, microsatellites, population genetics, raptor.

Before people arrived in New Zealand the native avifauna included representatives of the three bird orders described as raptors (Strigiformes, Accipitriformes, Falconiformes). However, New Zealand diversity in each was limited, with a maximum prehuman fauna of two owls, two eagles/hawks and one falcon. The Kārearea *Falco novaeseelandiae* Gmelin 1788 is the only endemic New Zealand bird of prey species that is still extant. Three other endemic species, Eyles' Harrier *Circus eylesi*, Haast's Eagle *Aquilla moorei* and Laughing Owl *Sceloglaux albifacies* became extinct following human colonization, which occurred about 600 years ago (Worthy & Holdaway 2002). Two native raptors shared with Australia, the Swamp Harrier/Kahu *Circus approximans* and Morepork/Ruru *Ninox novaeseelandiae*, have fared better. The Swamp Harrier, which appears to have established on New Zealand after human settlement and after the extinction of Eyles' Harrier and Haast's Eagle (Worthy & Holdaway 2002), is one of the few native New Zealand birds to have increased in abundance since human colonization (Eakle 2008).

Morphological and molecular analyses indicate the geologically recent ancestry of New Zealand raptors, including Haast's Eagle, the world's largest eagle, which probably shared a common ancestor with Australian *Aquilla* in the Pleistocene (>2.6 Mya) (Bunce *et al.* 2005). Phylogenetic analysis of the Falconiformes indicates the closest living relative of Kārearea is the South American Aplomado Falcon *Falco femoralis* (Fuchs *et al.* 2015), and although geographically distant, these species have similar plumage patterning and behavioural attributes. Time calibration of molecular data using fossil information indicates that the global falcon

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radiation was rapid and associated with an increase in open grassland habitats during the late Miocene/early Pliocene. Analysis of whole genome data from Saker *Falco cherrug* and Peregrine *Falco peregrinus* Falcons support this (Zhan *et al.* 2013). The common ancestor of Kārearea and Aplomado Falcon probably existed in the late Pliocene and the geographical distribution of these two species today on either side of the Pacific suggests an impressive dispersal around the globe.

The inference that global falcon diversification was influenced by open habitats might explain colonization of New Zealand during the Plio-Pleistocene, when mountain building and climate change increased habitat diversity in New Zealand (Trewick & Bland 2012, Heenan & McGlone 2013). However, it has been suggested that Kārearea are well adapted to life in forests (Seaton & Hyde 2013), and certainly during the Holocene, prior to human colonization, the New Zealand landscape was dominated by forest (Trewick & Morgan-Richards 2009). Today, Kārearea use many habitats including bush, coastline and estuary, montane, open tussock land, farmland and exotic pine plantations throughout New Zealand (Bell & Lawrence 2009).

Kārearea vary considerably in size and coloration, over and above the sexual dimorphism typical of raptors (Krüger 2005), and this variability has caused taxonomic confusion since its earliest observation. Several scientific names have been proposed that in part reflect this confusion: *Falco novae-Seelandiae* Gmelin 1788, *Falco brunnea* Gould 1838, *Falco australis* Hombr. et Jacq 1841, *Falco harpe* Forster 1844 and *Falco ferox* Peale 1848 (Medway 1976, Gill *et al.* 2010). William Bayley on board *HMS Resolution* noted two kinds of 'small hawks' at Queen Charlotte Sound (McNab 1914), although whether they were different sexes, ages, morphs or species such as harrier and falcon is unknown. George Gray also reported two types (Dieffenbach 1843), and Smith (1884) referred to two species that used different habitats. When examining museum skins, Sharpe (1873) recognized there may have been two forms or species or a continuum of sizes, but noted uncertainty about the sex of specimens he examined. Buller (1888) recognized larger and smaller forms, and later Moncrieff (1927) found that North Island individuals tended to be smaller than South Island ones. Although currently classified as a single species, three distinct races have been proposed that were predicted to differ in morphology and ecology as well as in their spatial distribution (Fox 1977, 1988). Their geographical ranges and the correlation between morphology, ecology and behaviour remain speculative.

The type of racial variation reported in Kārearea is not uncommon among New Zealand Neoaves despite the general pattern of low species diversity within lineages (Trewick & Gibb 2010). Several taxa are represented by somewhat distinct forms on mainland New Zealand and are generally classified as subspecies, the spatial ranges of which appear to be associated with the two main islands (Buller 1868). The fact that New Zealand forest bird lineages typically comprise only shallow taxon diversity across the country (Trewick & Gibb 2010) suggests that recent geophysical changes in the environment have resulted in taxonomic turnover (Olson *et al.* 2009), but the existence of subspecies, if biologically valid, suggests that diversification is underway.

Differences in size and other attributes among spatially separated populations could represent adaptation to local conditions and may develop where gene flow (dispersal, migration) among populations is limited, ultimately increasing diversity through ecological speciation (Lenormand 2002). However, racial variation is common among recognized species of falcon, and where examined in detail there is varying support for the many subspecies that have been proposed. It is well recognized in avian biology that the designation of subspecies can obscure real patterns of diversity (Zink 2004), and this in turn obscures understanding of evolution.

We examined the evidence for one, two or more races within Kārearea to better understand the relationship between space and variation. We analysed morphological and genetic variation in the context of spatial distribution to determine the scale of putative differences among populations and to assess whether there is compelling evidence for abrupt partitioning that could be suggestive of distinct evolutionary lineages, rather than a continuum of size variation.

METHODS

Sample collection

Standard bird metrics (weight, tail length, wing length, tarsus length) were gathered from Kārearea sampled around New Zealand using all available

sources for this protected species (Fig. 1). In addition, we collated raw metric data from Fox (1977), field research undertaken in Kaingaroa Forest during 2000 and 2011 (including Seaton 2007, Thomas 2008), measurements from captive and rehabilitated birds of known provenance (Wingspan Birds of Prey Trust), and from frozen specimens of Kārearea killed by accidental vehicle collisions, electrocution or poisoning and submitted to Department of Conservation area offices. Preserved skins in the collections of Te Papa Museum of New Zealand, Canterbury Museum and Auckland War Memorial Museum were also examined. Wing length was defined as the distance on the closed wing from the foremost extremity of the carpus to the tip of the longest feather. Tail length was measured from the skin between the deck (central) feathers to the tip of the longest feather (Spencer 1965). Samples of blood, feathers, muscle or toe pads for DNA extraction were obtained from as many Kārearea as possible including some captive birds (Wingspan Birds of Prey Trust), wild birds at Kaingaroa forest and other locations, and preserved museum specimens. Sampling locations were mapped using QUANTUM GIS v2.2 (QGIS 2015) (Fig. 1).

Morphometric variation

Summary statistics, frequency graphs and bivariate plots were generated in R v3.0.2 (R Core Team 2013). Morphometric analyses focused on wing length, which has been shown to be a good predictor of overall body size in falcons and other birds (Grant 1971, Wiklund 1996) and is less sensitive to fluctuations in female reproductive condition. Significant differences between the mean wing lengths of males and females were tested using a *t*-test (IBM SPSS Statistics 20). Hartigans' dip test for unimodality (Hartigan & Hartigan 1985) using the R package Diptest 0.75–6 (Maechler 2013) with 4000 replicates was used to determine whether the frequency of wing lengths, independent of sex differences, had a bimodal or normal distribution. The R project (i386 v3.0.2) package MCLUST v4.3 (Fraley *et al.* 2012) was used to impartially examine distributions of wing length and tail length variation. This model-based clustering analysis estimates data clusters using maximum-likelihood estimation of multivariate mixture models without priors to assign individuals to clusters (Fraley & Raftery 2002). Optimality of alternative models was compared using the Bayesian information criterion (BIC) with each individual being assigned to a group with estimated uncertainty.

Habitat variation

We looked for relationships between Kārearea morphometrics and habitat, latitude and location. Information on habitat was estimated for each

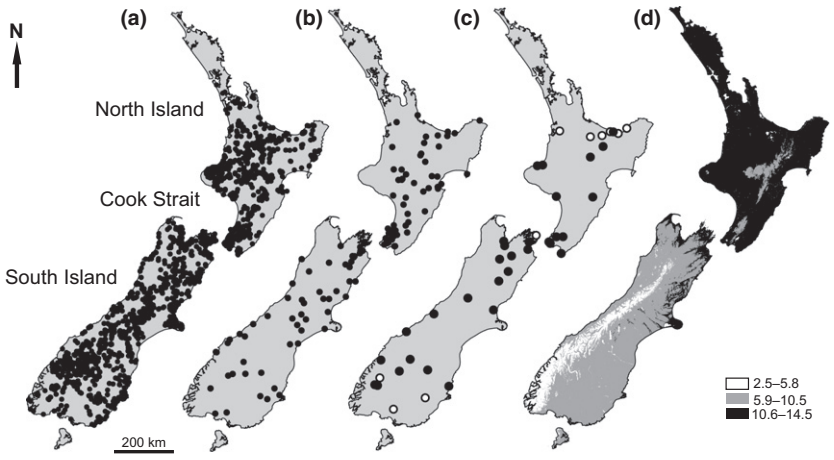

Figure 1. Kārearea *Falco novaeseelandiae* sampling. (a) Sightings of Kārearea during 2010–2015 demonstrate almost continuous occurrence except in the most northern part of the country. The species also occurs on the sub-Antarctic Auckland Islands and many nearshore islands (data courtesy of D. Bell, nzfalcon.org.nz). (b) Locations of Kārearea that provided morphometric data. (c) Locations of Kārearea sampled for genetic analysis (open circles, all samples; filled circles, microsatellites). (d) Annual mean temperatures (°C) across New Zealand. Data were mapped using the Quantum Geographic Information System (QGIS 2015).

individual bird using GIS data. GPS coordinates for each Kārearea sample site were used to estimate primary habitat using ArcMap (ESRI, 2010) to sample environmental data from the Land Environments New Zealand database (LENZ: Leathwick *et al.* 2003). As records of sampling locations for some individuals were poorly defined and Kārearea typically forage widely, an area of 20 km² around each mapped location was used to characterize habitat. Primary habitats across >80% of each location area fell into one of eight categories according to the LENZ database: high producing exotic grassland, low producing exotic grassland, exotic forest, indigenous forest, tall (native) tussock grassland, river, lake and pond, gravel and rock.

ANOVA was used to identify factors associated with the distribution of morphometric variation. Based on the results from the cluster analysis and the habitat and latitude analysis, we used linear modelling (R i386 v3.0.2) to explore the influence of spatial and environmental parameters on variation within the morphometric data.

Genetic variation

DNA extraction used either a phenol/chloroform method or the GenElute kit (Sigma-Aldrich, St Louis, MO, USA). Tissues were finely chopped with sterile scalpel blades and then incubated at 55 °C with Proteinase K (10 ng/μL) and a CTAB buffer (100 mL 1 M Tris, 280 mL 5 M NaCl, 40 mL of 0.5 M EDTA and 20 g of CTAB) with shaking at approximately 200 r.p.m. until digested. This was followed by a combined phenol, chloroform/isoamyl alcohol cleanup using standard methods (Sambrook *et al.* 1989). DNA was precipitated using ice-cold ethanol, mixed via inversion and left at −20 °C overnight. After spinning at 16 060g for 10 min, the ethanol was poured off, and after air-drying the DNA was re-suspended in 40 μL of H_2O for storage. GenElute (Sigma-Aldrich) extractions were performed following the manufacturer's methods.

A fragment of the mitochondrial Control-Region (CR) approximately 525 base pairs in length was amplified using the polymerase chain reaction (PCR). Primer combinations differed depending on DNA quality. PCR with DNA templates from modern tissue used primers L15206 (CTATGTATTACTTTGCAT) and H15856 (GT GAGGAACGGATCGAAG) previously applied to Peregrine Falcon (Talbot *et al.* 2011). An additional primer (CR624, CGACAGCCATCTATACATTCTAGGA) was designed for use with H15856 when amplifying from age-degraded templates. PCR amplifications for all samples were carried out in 10-μL reactions containing 0.05 μM of each primer, 1× manufacturer's buffer, 200 μM each deoxynucleotide, 2 mM $MgCl_2$ and 0.1–0.2 units Taq polymerase. PCR with a Biometra T3000 thermal cycler used an initial denaturing step of 94 °C for 3 min, and 30 cycles of: 94 °C for 15 s, 51 °C for 15 s and a 1-min extension of 72 °C, followed by a 7-min final extension at 72 °C. Amplification products were checked on 1% agarose gels and subjected to Sap/Exo digest before sequencing using Big Dye v3.1 chemistry on an ABI3730 genetic analyser.

Sequences were checked, trimmed and aligned using Geneious v6.1.7 (Biomatters Ltd Auckland, New Zealand). Population statistics were calculated using DnaSP v5 (Librado & Rozas 2009). We constructed networks of CR haplotypes with location traits using PopArt (Leigh & Bryant 2015).

Kārearea were genotyped at six microsatellite loci using primers designed for Peregrine Falcon (Nesje *et al.* 2000): NVH fp82-1, NVH fp46-1, NVH fp5, NVH fp13, NVH fp31 and NVH fp79-4. The forward primer of each pair was labelled with either of the fluorophores HEX or 6-FAM. PCRs in 10-μL volumes contained ~10 ng of genomic DNA with 0.05 μM of each primer, 1× manufacturer's buffer, 200 μM each deoxynucleotide, 2 mM $MgCl_2$ and 0.1–0.2 units Taq polymerase. Thermal cycling used an initial denaturing step of 94 °C for 3 min followed by 35 cycles of 94 °C for 30 s, 50 °C annealing for 15 s and a 72 °C extension for 45 s, followed by 5 min at 72 °C. Amplification products were subsampled and pooled for automated genotyping using combinations of fluorophore and allele size range to maximize efficiency. Automated genotyping used an ABI3730 device with GeneScan-500 LIZ size standard for fragment length calibration.

Microsatellite data were scored using GeneMarker v6.0 (SoftGenetics, State College, PA, USA), and tested for null alleles, stuttering and large allele drop out using Micro-Checker v2.2.3 (van Oosterhout *et al.* 2004). We used Bayesian assignment analysis implemented with Structure v2.3.4 (Pritchard *et al.* 2000) to infer genotype clusters for potential hypothetical clusters (*K*)

between 1 and 15 in separate runs with 10 iterations for each. We did not use location as a prior. The outputs were analysed using the online program STRUCTURE HARVESTER v0.6.93 (Earl & vonHoldt 2012) so that averaged scores for each *K* within the dataset could be compared using Delta-*K* (Evanno *et al.* 2005). Results from STRUCTURE HARVESTER were summarized using CLUMPP v1.1.2 (Jakobsson & Rosenberg 2007), which merged the run data for each individual and each population over the 10 iterations. The output was imported into DISTRUCT v1.1 (Rosenberg 2004) for graphical representation.

To test for any signal of population structure corresponding to the original three-race and a revised two-race hypothesis, we used AMOVA in ARLEQUIN v3.5.1.2 (Excoffier & Lischer 2010). The data were grouped according to a number of alternative parameters reflecting the different hypotheses about population structuring, and the AMOVA repeated with each. A model of isolation by distance was tested using population pairwise F_{ST} values and geographical distances between sampling locations retrieved from Google EARTH v6.0 (Google Inc.). ARLEQUIN v3.5.1.2 was used to implement the Mantel test of the correlation between genetic differentiation and geographical distance using 1000 permutations.

RESULTS

Morphological variation

Size metrics varied considerably among a total of 245 Kārearea (Table 1), although not all metrics were obtained from all individuals examined. Wing lengths, for which there were the most data ($n = 213$), ranged from 123 to 308 mm. If considered for males and females separately, male size (123–268 mm) fell in the lower end of this range compared with females (212–308 mm), as is common in raptors. In fact our analysis revealed an average difference in male and female wing length of 40 mm. A similar degree of variance was encountered among tail lengths ($n = 207$) and tarsus lengths ($n = 211$), and so most analyses were conducted separately for males and females.

Wing length and tail length were significantly positively correlated in both males (Pearson's correlation coefficient, $n = 106$, $\rho = 0.3735$, $P < 0.0001$) and females ($n = 94$, $\rho = 0.5411$, $P < 0.0001$). As expected, weight and wing length were also positively correlated in males ($n = 57$, $\rho = 0.282$, $P < 0.05$) and females ($n = 72$, $\rho = 0.5655$, $P < 0.0001$). A higher variance in weight of females (Table 1), as expected given variation in reproductive condition, was evident in the closer correlation among male metrics than female metrics. Culmen length was also positively correlated with weight ($n = 32$, $\rho = 0.6352$, $P < 0.0001$) and wing length ($n = 32$, $\rho = 0.4723$, $P = 0.0063$) in female Kārearea, but not in males. We also noted that centre toe length and weight were negatively correlated in males ($n = 12$, $\rho = -0.780$, $P = 0.0028$) but positively correlated in females ($n = 18$, $\rho = 0.6226$, $P = 0.0058$), although sample sizes were small. Such allometric differences might reflect differences in hunting behaviour of males and females.

Even when male and female data were treated separately, wing lengths and other metrics did not

Table 1. Means and ranges of morphometric variables from male and female Kārearea *Falco novaeseelandiae* sampled through New Zealand.

	Variable	*N*	Mean	SD	CV	Min.	Max.
Male	Weight (g)	60	257.22	40.27	12.71	170	372
	Wing length (mm)	110	240.57	20.36	7.7	123	268
	Tail length (mm)	109	168.19	9.03	3.71	147	190
	Tarsus (mm)	109	56.37	2.46	3.7	50	62.5
	Centre toe (mm)	51	40.92	3.28	7.9	36	49.5
	Culmen tip (mm)	24	17.81	1.04	5.72	14.8	20.3
Female	Weight (g)	79	488.76	97.27	14.63	245	846
	Wing length (mm)	103	280.53	16.08	3.7	212	308
	Tail length (mm)	98	192.19	15.89	6.24	108	234
	Tarsus (mm)	102	63.4	4.05	5.39	54	74
	Centre toe (mm)	45	48.56	4.87	6.91	41.6	64
	Culmen tip (mm)	34	22.18	1.45	5.24	18.5	27.2

appear to be distributed in a unimodal fashion and Hartigan's dip test (based on 4000 replicates) confirmed this (males D = 0.0909, $P = 0.5232$; females D = 0.1061, $P = 0.4627$). When normal mixture modelling for model-based clustering (MCLUST v4.3) was applied to wing and tail length data of only female Kārearea, two distinct clusters were revealed, predominantly separating North Island and South Island individuals (Fig. 2). MCLUST uses assignment without priors and there is no restriction on the potential number of data clusters, so finding that two groups was optimal for the data and neither one nor three was informative.

We looked to see whether habitat was a predictor of Kārearea size, as proposed by Fox's (1977) three-morph hypothesis, using habitat classifications based on LENZ. We found that male and female Kārearea with the longest wings came from areas of open country dominated by tall tussock grassland and low-producing grassland. Kārearea with the smallest wing lengths were from areas classified as indigenous forest. Sample sizes for several of the habitat types were low (<10) but we found significant differences (ANOVA Tukey's test) between mean wing lengths of Kārearea from indigenous forest and low-producing grassland in males ($P < 0.0001$) and females ($P < 0.01$) (Table S1). This pattern is consistent with the prediction that 'bush' and 'eastern' falcons are partitioned ecologically by habitat type, and may be adapted to them. However, we noted that the spatial distribution of these habitat types was uneven, with most low producing grassland in South Island and most indigenous forest Kārearea sampled in North Island.

Using a generalized linear modelling approach implemented in R we examined which parameters were the best predictors of wing size. A significant influence of habitat type would suggest ecological adaptation consistent with the three-morph hypothesis, whereas correlation with latitude would imply a gradualistic phenotypic response to environmental conditions associated with distance from the equator. A third option was an inter-island effect, with partitioning of populations either side of the Cook Strait (Fig. 1). On their own, each of these parameters appeared to have a significant influence, but the hierarchical analysis showed that the North Island/South Island classification was most influential (Table 2).

We then plotted wing size against latitude to further assess this (Fig. 3). There was a weak correlation between wing length and latitude for the data as a whole and for the males and females separately, but we also observed an abrupt step in sizes at the latitude of the Cook Strait. Slopes of regressions between wing length and latitude for males and females from North Island and South Island were different, rather than having the same trajectory as expected if all were part of the same gradient. Furthermore, when analysed separately, latitude was not indicated as influencing wing length in any of the island/sex sample sets (Table 2). This suggested that the apparent gradient in size traits with latitude was an artefact of fitting a linear model to populations with different trait distributions. North Island Kārearea are smaller than South Island Kārearea, and despite some

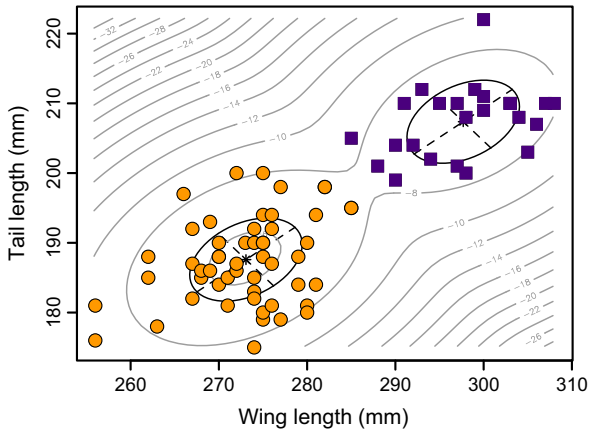

Figure 2. Two groups (squares and circles) identified by Bayesian clustering of female Kārearea wing and tail lengths in MCLUST (BIC −1125.378, log.likelihood −545.2623) with the EES model (ellipsoidal, equal volume, shape and orientation). Component means are shown with an asterisk at the centre of each covariance ellipse. Log density contours were superimposed.

Table 2. Summary results from linear model analysis with latitude, habitat type and main island as predictors of wing size variation in Kārearea.

Coefficients	Estimate	SE	*t* value	Pr(>|*t*|)
(Intercept)	252.2	34.087	7.400	3.52E-11***
Habitat type	0.9	0.812	1.123	0.264
North Is./South Is.	22.2	4.152	5.330	5.66E-07***
Latitude	0.1	0.948	0.140	0.889

***P < 0.001.

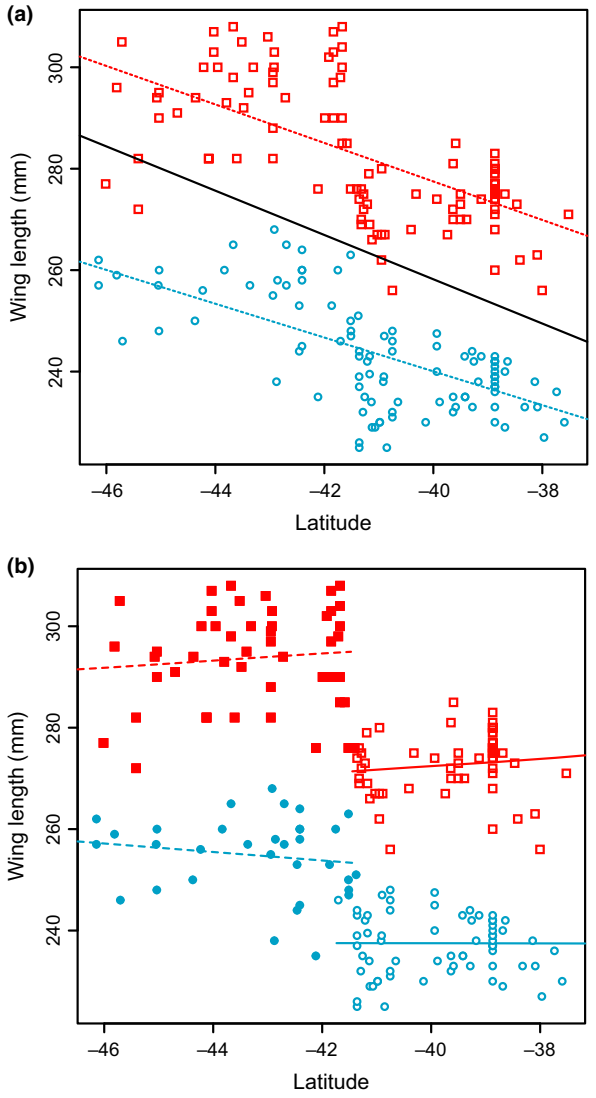

Figure 3. Linear regressions of Kārearea wing length against latitude of sampling site. (a) All Kārearea males (circles) and females (squares). Regression lines fitted to all data (undotted line), male data (lower dotted line) and female data (upper dotted line). (b) North Island Kārearea (open symbols) and South Island Kārearea (filled symbols) with regression lines fitted to each sex/island combination (South Island dashed line, North Island full line).

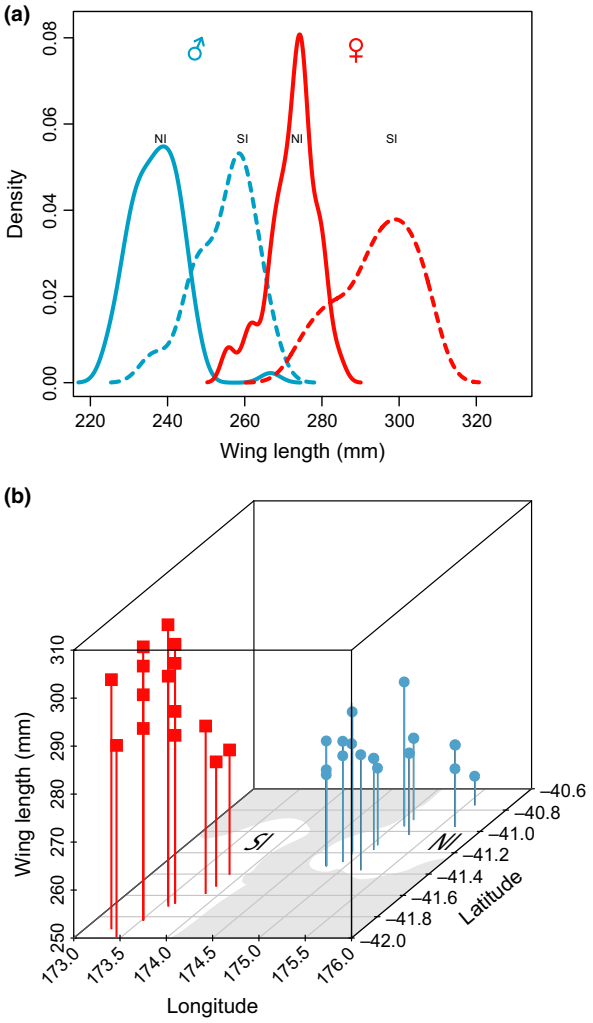

Figure 4. (a) Density distribution of Kārearea wing lengths. Males (left), females (right), North Island (continuous lines) and South Island (dashed lines). (b) Pinplot of female wing lengths in the vicinity of Cook Strait (grey area) between North Island (round heads) and South Island (square heads).

variance that is to be expected from natural variation and measurement error, the abrupt difference in size is striking. The largest female and smallest male Kārearea (based on wing length) in our data came from sites about 0.3° of latitude apart (*c.* 35 km) on either side of Cook Strait.

There was a clear distinction in length of wing among Kārearea of the two islands (Fig. 4). The size distributions of females in particular were skewed slightly to smaller sizes, resulting in a shoulder on the density distribution. This was likely to be due to measurement errors associated with feather condition, which tend to result in slight underestimates in some birds. Plumage condition is typically at its worst during the breeding season, and this is when many Kārearea are measured because they are accessible. Nevertheless, mean wing lengths of female and male falcons were significantly different between the North Island and South Island. Mean wing length for male falcons in the North Island was 237.03 mm

Table 3. Summary of mitochondrial DNA Control-Region sequence diversity among Kārearea from six regions of New Zealand: NNI, northern North Island; CNI, central North Island; CK, Cook Strait; CSI, central South Island; SSI, southern South Island; AK, Auckland Islands. h, number of haplotypes; Hd, haplotype diversity.

Region	*N*	h	Hd	*n*
AK	3	1	0.000	0.0000
SSI	13	1	0.000	0.0000
CSI	6	2	0.533	0.0010
CK	14	3	0.484	0.0015
CNI	5	3	0.800	0.0019
NNI	24	4	0.750	0.0019
ALL	65	5	0.614	0.0015

($n = 69$), whereas South Island birds had a mean wing length of 256 mm ($n = 31$) ($t = -14.599$, $P < 0.0001$). North Island females had a mean wing length of 272.75 mm ($n = 57$) and South Island females had a mean of 293.7 mm ($n = 48$) ($t = -13.29$, $P < 0.0001$). Thus, the ratio of average female to male size in terms of wingspan was the same (at two decimal places) for each island (1.14 or 0.66 as ratio of male/female).

Genetic variation

Mitochondrial CR sequences were obtained from 69 individual Kārearea (Table S2). Genetic diversity was low with just five haplotypes identified throughout New Zealand, and nucleotide diversity (π) of 0.00147 among 65 sequences (excluding four from captive birds) (Table 3). Diversity in the south was zero and gradually increased northwards, where the highest nucleotide diversity ($\pi = 0.00194$) was among Kārearea sequences from northern North Island. The most common haplotype (A) was found throughout New Zealand, whereas B and D were found only in the North Island (Fig. 5). Haplotype C was found only in Kārearea from the northern regions of South Island (Marlborough and Nelson). Four captive falcons had the commonest haplotype (A).

Microsatellite genotypes were obtained for six loci from 47 Kārearea. There was no evidence of unexpected frequency of null alleles or linkage among loci. The number of alleles per locus ranged from 2 to 13 and observed heterozygosity across the entire country was low, ranging from 0.0 to 0.45, whereas expected heterozygosity was between 0.14 and 0.85. Neither the Bayesian assignment (STRUCTURE v2.3.4) nor AMOVA (ARLEQUIN v3.5.1.2) analyses provided convincing evidence of population genetic structure in the microsatellite data among the Kārearea sampled. STRUCTURE HARVESTER showed peaks in the Delta-*K* values for $K = 2$ and $K = 5$ using the Evanno method, but genotype plots showed no compelling support for $K = 2$, $K = 3$ or $K = 5$, and $K = 1$ cannot be rejected for these data (Fig. 5).

A hierarchical analysis of molecular variance of population structure revealed no significant subdivision between samples assigned to three race classes (Bush, Eastern and Southern) on the basis of proposed range boundaries (Fox 1977). Pairwise comparison of population F_{ST} values did, however, show a significant though small departure from zero between the North Island and far south of the South Island. The Wellington sample was significantly different from most Southern populations, Marlborough and Kaingaroa forest. Pairwise comparison of data grouped into four broad latitudinal zones of New Zealand (Table 1, Fig. 5) suggested a significant ($P < 0.05$) but small departure from zero between southern South Island and southern North Island ($F_{ST} = 0.1526$), and between northern South Island and southern South Island ($F_{ST} = 0.1037$). Private alleles present in relatively small samples (Wellington area, Kaingaroa forest, Wanaka and Fiordland) probably explain this. The exact test of population differentiation based on allele frequencies (Raymond & Rouset 1995) found no significant differentiation among regions or zones. A Mantel test revealed no significant correlation between geographical distance and genetic distance ($P = 0.713$), providing no support for an isolation by distance model.

DISCUSSION

We found a degree of morphological variation in Kārearea that is consistent with a proposal of distinct races originating in 19th century records of New Zealand raptors. We used a model-based maximum likelihood approach without priors to estimate clusters in our morphological data from Kārearea, and this indicated an optimal number of two groups for each sex (Fig. 2). Regression analysis of the full data set implied that size variation was structured geographically and a relationship between latitude and wing length (a proxy for other morphological variation) was apparent for males, females and the combined data. We noted a marked step in size rather than a gradation.

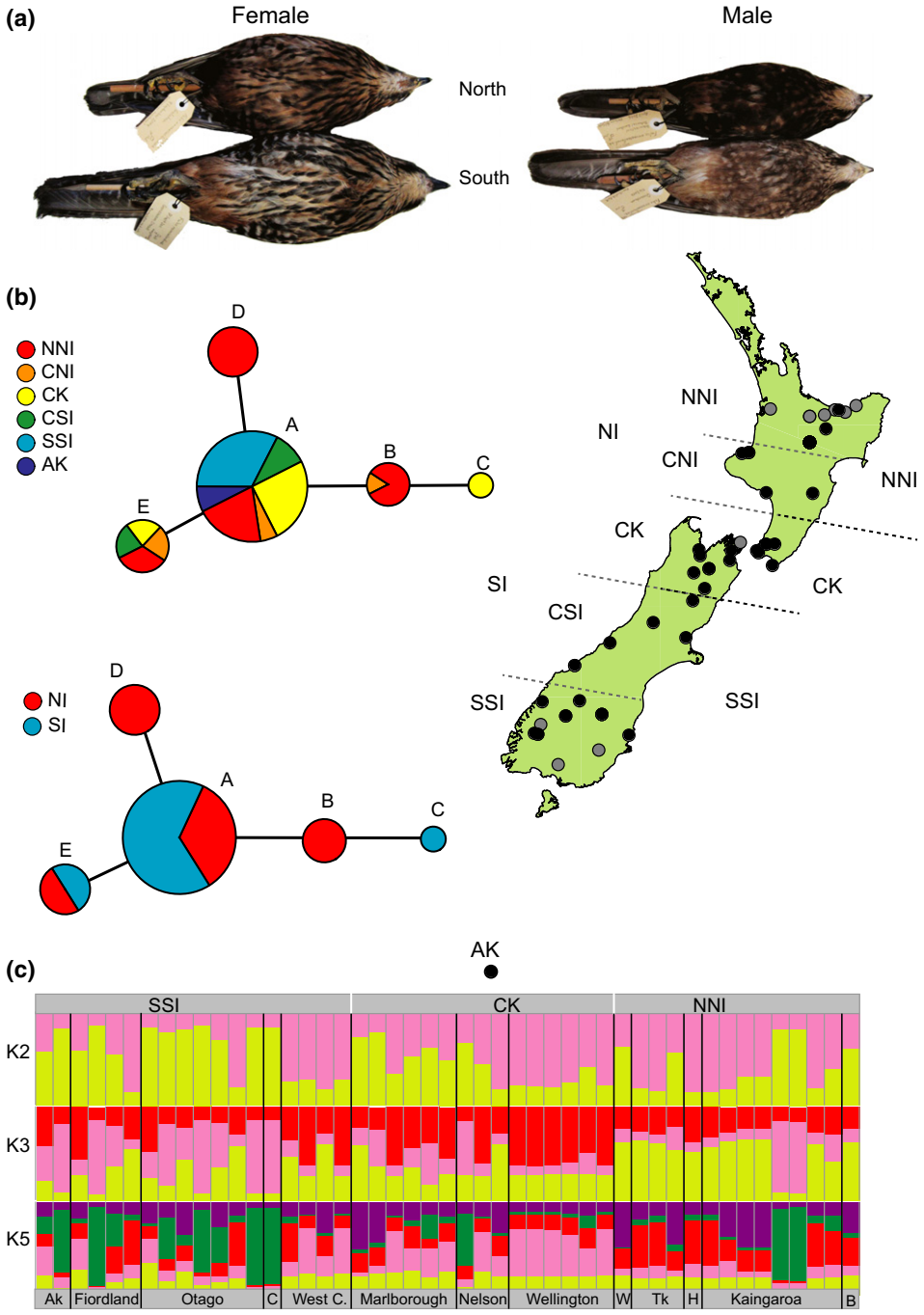

Figure 5. (a) Size disparity of North and South island Kārearea is evident in representative museum skins originally collected from North Island (female Bay of Plenty, male Wellington) and South Island (female and male Otago). (b) The occurrence of five Control-Region mtDNA haplotypes among 69 birds grouped by region (upper) and by island (lower). Node sizes in median joining networks are proportional to sample size of each haplotype. Map shows sample locations for haplotype (circles with grey or black fill) and microsatellite (black fill only) data. Zones used in analysis: NNI, north North Island; CNI, central North Island; CK, Cook Strait; CSI, central South Island; SSI, south South Island; AK, Auckland Islands. (c) Genotypic structure of 47 Kārearea surveyed with six microsatellite loci inferred using Bayesian assignment analysis with hypothesized population number (*K*) of 2, 3 and 5. Graphs show averaged results from 10 iterations at each value of *K*. Map (centre right) shows sampling locations (circles with black fill), and regions. Letter codes at base of bar plot indicate sample localities: Ak, Auckland Islands. C, Canterbury; West C, West Coast South Island; W, Wanganui; Tk, Taranaki; H, Hawkes Bay; B, Bay of Plenty (see Supporting Information Table S1). Photographs courtesy of Andrew Thomas.

When samples from either side of this step were analysed separately, as indicated as appropriate by cluster analysis, they had different characteristics. Regressions of wing length with latitude for males and females from North Island and South Island indicated they had different slopes, rather than having the same trajectory as expected for subsamples of the same population. In fact, when considered separately, latitude was not indicated as influencing wing length in any of the island/sex sample combinations (Fig. 3) and this was confirmed by general linear modelling. We found that North Island Kārearea were significantly smaller than South Island Kārearea, and despite some variance that is to be expected from natural variation and measurement error, the abrupt difference in size was striking. The step in the size distribution coincides closely with the ocean and Cook Strait seaway between the two main islands of New Zealand. The largest female and smallest male Kārearea (on wing length) in our data came from sites about 0.3° of latitude apart (*c.* 35 km) on either side of Cook Strait.

Spatial diversity and polymorphism

In flying birds, the basis of the close relationship between wing size and body size is clear (Videler 2006). Wing length in Kārearea and other birds could therefore provide a direct proxy for body size because more mass without more wing would tend to be disadvantageous. However, wing size could vary for other reasons (e.g. the demands of migration; Hamilton 1961). The most prominent trend in raptor size variation is sexual size dimorphism, thought to be driven by both sexual and ecological demands in species for which hunting on the wing is critical (Krüger 2005, McDonald *et al.* 2005, Pérez-Camacho *et al.* 2015). It has long been recognized that ecological and reproductive demands on male and female animals differ (Darwin 1859). In Kārearea we found some evidence of linkage between morphotype and habitat/prey use; open country habitat was associated with larger Kārearea in South Island (higher latitude), and native forest with smaller Kārearea in North Island. It was not possible to assess whether this is a causal relationship but, if it is, the few instances of relatively small Kārearea in South Island (Fig. 4b) could represent rare migrants into suboptimal habitat.

Despite the difference in average size of each sex on the two islands, the ratio of female/male wing length within islands remained the same (1.14). This is typical of bird-hunting falcons and the high degree of sexual dimorphism could reflect resource partitioning when competition with other aerial predators is low (Newton 1979), but many explanations of sexual dimorphism in raptors in which females are bigger than males have been suggested (McDonald *et al.* 2005). Raising the linear wing length by an exponent gives a more relevant expression of mass (Summers 1988). In Kārearea, the male/female cubed wing length ratio is 0.66 in both populations. This is close to the most extreme size difference seen in falcons around the world, among which ($n = 61$) the mean is approximately 0.85 and reaches near parity (Krüger 2005). Multivariate regression modelling suggests that the most extreme sexual dimorphism in falcons is related to hunting difficulty associated with prey and habitat type (Krüger 2005).

The 25° of latitude spanned by the two main islands of New Zealand influences climatic conditions, but topographic variation generates other environmental gradients within the islands (Fig. 1d). There was a pronounced difference in the availability of open hunting habitat, resulting in an association in our capture-site habitat analysis between low producing grassland and larger Kārearea, and indigenous forest and smaller Kārearea. A larger proportion of the South Island is above the elevational tree line and the dry eastern area mostly lacks tall forest today. For at least the last 5 million years the Southern Alps have generated a rain-shadow to the east of South Island, supporting dry forest and high country grasslands. Natural fires or those set by early human settlers resulted in the loss of forest generally in the east and regeneration is slower than in the wetter west. In North Island this rain-shadow is less pronounced and a smaller proportion of the landscape is above the tree line (Wallis & Trewick 2009). Smaller falcons may be at an advantage in forested habitat, and as male nest provisioning is critical for reproductive success, this suggests that sexual and spatial dimorphism may have the same underlying causes.

Racial partitioning of forest birds between the two main islands of New Zealand is apparent in species with a range of ecologies. In some cases, members of taxon pairs differ in subtle plumage coloration, but there are several instances where South Island races are larger than their North

Island counterparts. Size differences have been reported in the extinct Laughing Owl (Gill 1996) and other species known only from pre- or early human Holocene fossils: adzebills *Aptornis otidiformis* and *Aptornis defossor* (Oliver 1955), New Zealand Owlet Night-jar *Aegotheles novaezeelandiae* (Rich & Scarlett 1977), geese *Cnemiornis gracilis* and *Cnemiornis calcitrans* (Scarlett 1972) and wrens *Pachyplichas jagmi* and *Pachyplichas yaldwyni* (Millener 1988). The extant parrots Kaka *Nestor meridionalis* and Kea *Nestor notabilis* (Holdaway & Worthy 1993, Higgins 1999), the New Zealand Robin *Petroica australis* (Fleming 1950) and Saddleback *Philesturnus carunculatus* (Parker *et al.* 2014) also show size differences. Although most data are from a limited number of locations, the number of examples indicates a general trend that could have a common driver.

This trend in size variation that is demonstrated so clearly in Kārearea accords with the expectations of Bergmann's rule. Bergmann (1847) described the pattern of natural size variation among related vertebrate species, and provided an explanation in terms of thermoregulation and climate: 'body size varies inversely with ambient temperature, so that body size increases with latitude' (Watt *et al.* 2009). Bergmann (1847) considered the distribution of species within genera but Rensch (1938) later reformulated the concept to refer to races (populations) within species. This makes evolutionary sense because populations are the subjects of natural selection and it allows energetic efficiency to be considered as an adaptive trait that responds to environmental conditions. Globally, many birds show a pattern of spatial size variation consistent with Bergmann's rule (e.g. Hamilton 1961, Olson *et al.* 2009) and detailed examples of clinal variation include little if any spatial structure at neutral genetic loci (e.g. Antoniazza *et al.* 2010, Brommer *et al.* 2014). In New Zealand this clinal structure appears to be disrupted by the seaway between the islands, or environmental conditions correlated with this disjunction, in Kārearea at least. One other species, the Kaka, shows a similar step in body weights and wing lengths (Dussex *et al.* 2015) in the same area.

Adaptation and population structure

The difference in size and shape of Kārearea between North Island and South Island predicts that the distribution of neutral genetic variation is partitioned across Cook Strait, resulting in greater homogeneity of genetic variation within these islands than between. However, mitochondrial and microsatellite data were consistent in revealing little genetic structuring in Kārearea. The mtDNA CR showed a small amount of spatial variation with apparently private haplotypes present in the North and South Islands. Bayesian assignment analysis of microsatellite data did not support regional clusters, although comparison of regional populations revealed instances of significant departure of pairwise F_{ST} values from zero. Increased sampling could show more widespread sharing of haplotypes and alleles, but our sampling across New Zealand is likely to have documented the scale of variation. Most genetic variation in the analysis was present within the population samples and not between them. This is in keeping with studies of other falcons using the same genetic markers that revealed limited genetic structure among subspecies of Peregrine, Gyr and Sakar falcons (e.g. Nesje *et al.* 2000, Johnson *et al.* 2007, Nittinger *et al.* 2007, White *et al.* 2013). It is also consistent with genetic structure in Kaka in the same landscape as Kārearea (Dussex *et al.* 2015).

Kārearea may have a genetic signal of recent diversity and dispersal like that of other falcon species, but they differ in having a pronounced step in size over the relatively small spatial scale of New Zealand. Within-population and between-'type' genetic variation exists over a much larger landscape in other species such as Saker Falcon on the Eurasian continent (Eastham *et al.* 2002). This suggests rapid adaptation to local conditions by Kārearea, which is consistent with evidence that phylogenetic diversification of Falconiformes is youthful and dynamic (Fuchs *et al.* 2015). In the New Zealand region, the capacity of raptor morphology to adapt to available resources is spectacularly demonstrated by the giant *Harpagornis* eagle, which shared recent (Pleistocene) ancestry with a much smaller Australian species (Bunce *et al.* 2005). Intense natural selection on morphology and behaviour that tunes hunting ability to local conditions is the likely explanation for species radiation and population adaptation in falcons (Johansson *et al.* 1998, Zhan *et al.* 2013). As reproductive success in falcons is strongly influenced by individual quality (Zabala & Zubergoitia 2014) and has significant fitness outcomes, evolutionary shifts are likely to be rapid.

The geologically young global radiation of falcons including shared ancestry of Kārearea and Aplomado Falcon indicates the capacity of these birds to disperse and colonize over distance and water. Many instances of wide distributions that include islands are known in falcons, with Peregrine Falcon in particular having a near global range. Despite this dispersal potential, spatial effects influence the distribution of neutral alleles in Peregrine Falcon, which shows genetic bottlenecking associated with island colonization (Talbot *et al.* 2011). In Kārearea, the distribution of neutral genetic variation and pattern of size variation together indicate natural selection operating despite current or recent gene flow. Selection on functional loci that result in shifts of metabolic and predatory traits could proceed despite leakage at neutral loci (e.g. Dowle *et al.* 2014, Fitzpatrick *et al.* 2015). Such a process would be enhanced by any degree of gene flow limitation associated with a landscape feature such as the Cook Strait that influences intergenerational dispersal. Intraspecific competition that limits success of dispersing individuals and the habitat discontinuity associated with the Cook Strait seaway that marks a shift in environment (Fig. 1d) could reduce gene flow. Modelling has shown that stepped clines tend to move to areas of low population density (Endler 1977). Biologically significant differences in habitat, even if narrow, have rapid and significant influences on avian population structure (e.g. Steeves *et al.* 2005, Hull *et al.* 2008, Saitoh *et al.* 2015).

Subspecies

In describing what he referred to as the 'new species concept', Ernst Mayr noted that a subspecies was a 'geographically localized subdivision of the species, which differs genetically and taxonomically from other subdivisions' (Mayr 1942, 1956: p. 108). However, he also noted that, away from the museum drawer, most subspecies are rarely separated into definite isolated sections. The existence of morphological races and in particular size variants associated with islands, which by definition comprise isolated sections, was well recognized by Mayr. Modern genomic data are revealing that the dynamics of locus-specific evolution are complex and result, in the short term at least, in mismatch among different types of evidence. The application of haplotype analysis to taxonomy (e.g. Zink 2004) continues to focus attention on neutral genetic markers that can readily be modelled with parameters of population size and mutation rate, but the genetics of adaptation may not correlate with this. In fact, rich multilocus data show that population adaptation (akin to speciation) can proceed when partitioning of neutral genetics is not apparent (e.g. Dowle *et al.* 2014) and gene flow continues (e.g. Feder *et al.* 2012). Thus subspecies classification allows recognition of geographical variation that is likely to be adaptive, even if evidence from neutral loci is equivocal about partitioning. In this way, Kārearea contribute to a more dynamic view of avian evolution in New Zealand, where diversity is dominated by deep taxonomic difference (Trewick & Gibb 2010). Recent scrutiny of a few bird lineages (e.g. Galapagos finches; Lamichhaney *et al.* 2015 and references therein) has revealed evolutionary flux that challenges traditional perceptions of species. Thus explaining widely observed patterns such as relatively low diversity on islands (e.g. Mayr 1956) and the latitude biodiversity gradient (e.g. Dowle *et al.* 2013) requires both evolutionary genetics and ecology (Faria *et al.* 2014).

Formal recognition of distinct subspecies in Kārearea places appropriate emphasis on their different evolutionary potential, and for conservation management supports an existing strategy to avoid translocation and cross-breeding in captivity of falcons from the two islands. We therefore propose *Falco novaeseelandiae novaeseelandiae* as the nominotypical subspecies from the South Island and *Falco novaeseelandiae ferox* for the smaller North Island form. The name *Falco ferox* was proposed in 1848 from material collected during the United States Exploring Expedition (1838–1842) in the Bay of Plenty, North Island, and retained for the smaller North Island 'bush hawk' (Buller 1888).

The New Zealand Department of Conservation supported this work through assistance with sampling and provision of a grant from the Taxonomic Units Fund. Specimens were kindly contributed by Noel Hyde and Andrew Thomas (Wingspan Birds of Prey Trust) and Andrew allowed use of photographs. Colin Miskelly and Alan Tennyson (Te Papa Tongarewa Museum of New Zealand) assisted with access to specimens for measurements. Paul Scofield (Canterbury Museum) assisted with samples and measurements. Chifuyu Hawksby, Richard Seaton, John Holland, Laurence Barea and Tess Embling contributed additional specimens. David Bell (nzfalcon.org.nz) generously provided Kārearea sighting

data for the period from 2010 to 2015. Ed Minot and members of the Phoenix group (evolves.massey.ac.nz) provided support during the research. Ian Henderson and Rod Hitchmough gave feedback on earlier drafts and we appreciate feedback from three anonymous reviewers and editors Lluis Brotons and Rebecca Kimball. Particular thanks to Nick Fox, whose PhD research provided the foundation for this work.

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Received 30 March 2016;
revision accepted 6 July 2016.
Associate Editor: Lluis Brotons.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Tukey HSD test of Kārearea *Falco novaeseelandiae* wing lengths grouped by the dominant habitat type in the vicinity where each bird was sampled.

Table S2. Kārearea *Falco novaeseelandiae* samples used for genetic analysis, including details of location, region, zone mtDNA CR haplotypes identified and specimens genotyped with microsatellites.