

Population structure and biogeography of *Hemiphaga* pigeons (Aves: Columbidae) on islands in the New Zealand region

Julia Goldberg^{1*}, Steven A. Trewick¹ and Ralph G. Powlesland²

¹Ecology Group, Institute of Natural Resources, Massey University, Private Bag 11-222, Palmerston North, New Zealand, ²Science & Research Unit, Department of Conservation, PO Box 10420, Wellington, New Zealand

ABSTRACT

Aim The New Zealand avifauna includes lineages that lack close relatives elsewhere and have low diversity, characteristics sometimes ascribed to long geographic isolation. However, extinction at the population and species levels could yield the same pattern. A prominent example is the ecologically important pigeon genus *Hemiphaga*. In this study, we examined the population structure and phylogeography of *Hemiphaga* across islands in the region.

Location New Zealand, Chatham Islands and Norfolk Island.

Methods Mitochondrial DNA was sequenced for all species of the genus *Hemiphaga*. Sixty-seven individuals from mainland New Zealand (*Hemiphaga novaezeelandiae novaezeelandiae*), six of the Chatham Islands sister species (*Hemiphaga chathamensis*), and three of the extinct Norfolk Island subspecies (*Hemiphaga novaezeelandiae adicea*)

*Correspondence: Julia Goldberg, Ecology Group, Institute of Natural Resources, Massey University, Private Bag 11-222, Palmerston North, New Zealand.
E-mail: J.Goldberg@massey.ac.nz

INTRODUCTION



been isolated there for a comparatively long time, but an alternative explanation is that they arrived more recently and have since been extirpated elsewhere. For example, if *C. amoena* was extinguished in New Caledonia, the genus would be rendered endemic to the New Zealand region (Fig. 2b). Such an inference might be considered less parsimonious because dispersal is often considered to be an unlikely phenomenon (for discussion see Cook & Crisp, 2005). One

way to explore the plausibility of this alternative is to examine the population genetic structure of New Zealand taxa to see if they have retained the capacity for recent exchange. If they do, we cannot exclude the possibility that deeper-level endemism in New Zealand is a result of recent extinction elsewhere.

Therefore, in this study we examined the phylogeography of *Hemi hana* pigeons, which are ecologically important forest birds and endemic to the New Zealand region. The

genus *Hemi haga* is considered to be part of the radiation of

These originated from aviary birds collected in the 1800s. Because *Hemi haka* on the Kermadec Islands is represented by only a single subfossil bone, we were not able to include this extinct species in our study. The *L. an a c i c* (EBU45523M) tissue sample came from the Australian Museum, Sydney.

DNA extraction

For DNA extraction of the modern *Hemi haka* and *Lo hola-im* samples, the GenElute Mammalian Genomic DNA kit (Sigma, Auckland, New Zealand) was used following the manufacturer's protocol. The DNA extractions of the extinct Norfolk Island pigeon samples were undertaken in a dedicated ancient DNA laboratory, remote from modern DNA facilities, using the Qiagen QiAMP DNA Minikit (Qiagen, Auckland, New Zealand), following standard procedures for ancient DNA (Willerslev & Cooper, 2005).

nucleotide differences (k) were calculated using DnaSP v.4.0 (Rozas *e. al.*, 2003). Tajima's D statistic (Tajima, 1989) was developed to distinguish homologous DNA sequences evolving in a non-random manner (i.e. lack of neutrality). However, it

consistently placed the root between *H. cha. hamen i*

Chatham Islands and mainland New Zealand by 0.012, more or less identical to the *c.* 0.01 difference reported by Millener & Powlesland (2001).

likelihood tree because the tree consists almost entirely of sequences linked by no more than a single change, and in such cases the parsimony tree is the maximum likelihood estimator (Steel & Penny, 2000).

DISCUSSION

The large forest pigeon *H. n. no ae eelandiae* is distributed throughout mainland New Zealand where suitable habitat exists today. We found that genetic diversity at the mtDNA D-loop locus lacks spatial structure. The pattern of low diversity, shallow coalescence and high connectivity among populations of *Hemi hoga* within mainland New Zealand is indicative of a recent bottleneck and rapid recent range expansion. The geophysical phenomenon most likely to have resulted in substantial population reductions and thus genetic bottleneck that could yield this pattern is Pleistocene climate

could have occurred at any time after their formation and the establishment of suitable vegetation. These islands are, and have always been, separated from mainland New Zealand by more than 600 km of ocean, yet both have been colonized during their short history by a range of forest birds, including *Chlorocephalus* parakeet, *Neophilae* parrot, *Petroica* robin, *Chalcophaps*, cuckoo, *Geothlypis* warbler and *Zosterornis* silvereyes (Clements, 2007). The Kermadec Islands, which were also once inhabited by *Hemiphysalis*, are even further (> 900 km) from New Zealand, and their general lack of bird endemism has been ascribed to extinction through repeated, violent

of dispersal, colonization and extinction governing its assembly.

ACKNOWLEDGEMENTS

Samples were kindly provided by Otago Museum and we are

- Clout, M.N., Gaze, P.D., Hay, J.R. & Karl, B.J. (1986) Habitat use and spring movements of New Zealand pigeons at Lake Rotoroa, Nelson Lakes National Park. *No. o ni* , **33**, 37–44.
- Clout, M.N., Karl, B.J. & Gaze, P.D. (1991) Seasonal movements of New Zealand pigeons from a lowland forest reserve. *No. o ni* , **38**, 37–47.
- Clout, M.N., Karl, B.J., Pierce, R.J. & Robertson, H.A. (1995) Breeding and survival of New Zealand pigeons *Hemihagnano ae eelandiae*. *Ibi* , **13**, 264–271.
- Cook, L.G. & Crisp, M.D. (2005) Directional asymmetry of long-distance dispersal and colonization could mislead reconstructions of biogeography. *Journal of Biogeography* , **32**, 741–754.
- Cooper, A. & Cooper, R.A. (1995) The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *Proceedings of the Royal Society B: Biological Science* , **261**, 293–302.
- Cowie, R.H. & Holland, B.S. (2006) Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *Journal of Biogeography* , **33**, 193–198.
- Crandall, K.A. & Templeton, A.R. (1993) Empirical tests of some predictions from coalescent theory with applications to intraspecific phylogeny reconstruction. *Genetics* , **134**, 959–969.
- Daugherty, C.H., Gibbs, G.W. & Hitchmough, R.A. (1993) Mega-island or micro-continent? New Zealand and its fauna. *Trends in Ecology and Evolution* , **8**, 437–442.
- Excoffier, L., Laval, G. & Schneider, S. (2005) Arlequin (version 3.0): an integrated software package for population genetics data analysis. *Molecular Bioinformatics Online* , **1**, 47–50.
- Falla, R.A. (1953) The Australian element in the avifauna of New Zealand. *Emu* , **53**, 36–46.
- Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences (with discussion). *Statistical Science* , **7**, 457–472.
- Gibb, G.C. & Penny, D. (2010) Two aspects along the continuum of pigeon evolution: a South-Pacific radiation and the relationship of pigeons within Neoaves. *Molecular Phylogenetics and Evolution* , **56**, 698–706.
- Gibbs, D., Barnes, E. & Cox, J. (2001) *Pigeon and dove: a guide to pigeon and dove of the world*. Yale University Press, New Haven.
- Goldberg, J., Trewick, S.A. & Paterson, A.M. (2008) Evolution of New Zealand's terrestrial fauna: a review of molecular evidence. *Philosophical Transactions of the Royal Society B: Biological Science* , **363**, 3319–3334.
- Goodwin, D. (1960) Taxonomy of the genus *Discala*. *Ibi* ,

Kerr, K.C.R., Lijtmaer, D.A., Barreira, A.S., Hebert, P.D.N. & Tubaro, P.L. (2009) Probing evolutionary patterns in neotropical birds through DNA barcodes. *PLoS ONE*, **4**, e4379.

Landis, C.A., Campbell, H.J., Begg, J.G., Mildenhall, D.C.,

