ORIGINAL ARTICLE

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

Julia Goldberg¹*, Steven A. Trewick¹ and Ralph G. Powlesland²

¹Ecolog G o , In i e of Na al Re o ce, Ma e Uni e i, P i a e Bag 11-222, Palme on No h, Ne Zealand, ²Science & Re ea ch Uni, De a men of Con e a ion, PO Bo, 10420, Welling on, Ne 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 *Hemi haga*. In this study, we examined the population structure and phylogeography of *Hemi haga* across islands in the region.

Location New Zealand, Chatham Islands and Norfolk Island.

Methods Mitochondrial DNA was sequenced for all species of the genus *Hemi haga*. Sixty-seven individuals from mainland New Zealand (*Hemi haga no ae eelandiae no ae eelandiae*), six of the Chatham Islands sister species (*Hemi haga cha hamen i*), and three of the extinct Norfolk Island subspecies (*Hemi haga no ae eelandiae 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 ano am h 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 endemicity in New Zealand is a result of recent extinction elsewhere.

and the second s

Ő.

Therefore, in this study we examined the phylogeography of *Hemi haga* 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 haga* 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. ic* (EBU45523M) tissue sample came from the Australian Museum, Sydney.

DNA extraction

For DNA extraction of the modern *Hemi haga* and *Lo holaim* 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 coalesence and high connectivity among populations of *Hemi haga* 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 *Q* ano am h parakeet, *Ne* o parrot, *Pe_oica* robin, *Ch_occc*, cuckoo, *Ge_gone* warbler and *Zo_eo* silvereyes (Clements, 2007). The Kermadec Islands, which were also once inhabited by *Hemi haga*, are even further (> 900 km) from New Zealand, and their general lack of bird endemicity 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 *Hemi haga no 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. *Jo. nal of Biogeog a l*, **32**, 741–754.
- Cooper, A. & Cooper, R.A. (1995) The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *P. oceeding of the Re al Socie*, *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. *Jo., nal of Biogeog a h*, **33**, 193–198.
- Crandall, K.A. & Templeton, A.R. (1993) Empirical tests of some predictions from coalescent theory with applications to intraspecific phylogeny reconstruction. *Gene ic*, **134**, 959–969.
- Daugherty, C.H., Gibbs, G.W. & Hitchmough, R.A. (1993) Mega-island or micro-continent? New Zealand and its fauna. *T* end in Ecolog and *E* ol ion, **8**, 437–442.
- Excoffier, L., Laval, G. & Schneider, S. (2005) Arlequin (version 3.0): an integrated software package for population genetics data analysis. *E ol iona*, *Bioinfo ma ic Online*, 1, 47–50.
- Falla, R.A. (1953) The Australian element in the avifauna of New Zealand. *Em*, 53, 36–46.
- Gelman, A. & Rubin, D.B. (1992) Inference from iterative simulation using multiple sequences (with discussion). *S. a. i. ical 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. *Molec la Ph logene, ic and E ol ion*, **56**, 698–706.
- Gibbs, D., Barnes, E. & Cox, J. (2001) *Pigeon and do e : a g ide o igeon and do e of he o ld*. 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. *Philo o hical T an ac ion of he Rq al Socie, B: Biological Science*, **363,** 3319–3334.

Goodwin, D. (1960) Taxonomy of the genus D c la. 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.,