A comparison of the pre-human and present isotopic niches of brown teal (*Anas chlorotis*): implications for conservation

RICHARD N. HOLDAWAY*
Palaecol Research Ltd, P.O. Box 16569, Christchurch, New Zealand, and School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

MURRAY WILLIAMS
School of Biological Sciences, Victoria University, Wellington, New Zealand

DAVID J. HAWKE
Christchurch Polytechnic Institute of Technology, Christchurch, New Zealand

Abstract Bone samples from 2 surviving populations of New Zealand's endemic and endangered brown teal (*Anas chlorotis*) had a much smaller distribution of stable isotopic values ($\delta^{13}C$, $\delta^{15}N$) than those from Holocene-age fossil bones of the same species. Comparison with $\delta^{13}C$ and $\delta^{15}N$ values from 2 other taxa of known ecologies indicated that some brown teal were forest floor omnivores. The results indicate that the riparian and estuarine wetlands occupied by present natural populations represent only an extreme, truncated part of the species' potential habitat. To aid present conservation efforts we suggest that brown teal be released into forested areas and islands managed as mammal-free enclaves to test whether modern birds can survive in habitats once occupied by now-extirpated populations. Palaeoecological studies, including stable isotope analyses, can be used to identify conservation options not obvious from research on declining remnant populations in anthropogenic environments.

INTRODUCTION

Brown teal (*Anas chlorotis*), New Zealand's most ubiquitous waterfowl before human settlement (Holdaway *et al*. 2001; Worthy 2002), now persists naturally as 3 small remnant populations in the northern North Island (O'Connor *et al*. 2007; Robertson *et al*. 2007). Two of these populations have experienced significant declines during the past 20 years (Parrish & Williams 2001; Ferreira & Taylor 2003) and the species is listed as endangered by the IUCN (Birdlife International 2013). In response,

the New Zealand Department of Conservation has sought to establish new populations by releasing captive-raised birds in predator-free environments (O'Connor *et al*. 2007).

Evidence of the bird's ubiquity and distribution in pre-human times is derived from bone deposits of Holocene age (10,000 years to present) across North, South, Stewart and Chatham Is. Worthy (2002) recorded 73 sites (excluding Chatham Is) which contained fossil brown teal bones. Of these 73 geographically-separated non-archaeological sites, 53 (72.6%) were sinkholes, caves, or rock shelters, 9 (12.3%) were wetlands (springs, stream beds, lake beds, or swamps), 10 (13.7%) were in coastal

dune systems, and 1 (1.4%) was in dunes between a large shallow lake and the sea. All sites were originally surrounded by forests as diverse as wet and seasonally dry podocarp forests, and montane beech forests up to 800 m altitude.

Historic observations of brown teal, summarised by Dumbell (1986) and Marchant & Higgins (1990), report a more restricted distribution and more limited habitat associations. Observations in the 19th and early 20th centuries were of birds in deep, quiet waterways with abundant overhanging vegetation in lowland swamp forests (Buller 1888), occluded lake margins (Potts 1882; Guthrie-Smith 1927), and tidal reaches of tree-fringed lowland streams (Bell 1959; McKenzie 1971; Weller 1974). However, it is the predominantly pastoral environment occupied by 2 remnant populations (at Mimiwhangata, Northland and Okiwi, Great Barrier I) that informs present conservation management (O'Connor *et al.* 2007; DoC 2011).

Basing conservation responses on existing ecological characteristics of small and declining populations in much-modified biotic landscapes has long bedevilled avian conservation practice in New Zealand. This "what is....is best" perspective has been challenged as needlessly restricting conservation options (Gray & Craig 1991). However, few deliberately experimental translocations of conservation-dependent species to test perceived habitat choices have been made (Miskelly & Powlesland 2013), exceptions being North Island kokako (*Callaeas wilsoni*) to Tiritiri Matangi I (Rimmer 2004), South Island takahe (*Porphyrio hochstetteri*) to pasture-dominated islands (Lee & Jamieson 2001), and rock wren (*Xenicus gilviventris*) to low altitude sites on Anchor and Secretary Is (M. L. Willans, Department of Conservation, *pers. comm*.). If experimental translocations are not favoured as conservation practice, then palaeoecological data, by providing information on past environments, their species assemblages, and species' habitats (Atkinson & Millener 1991; Worthy & Holdaway 2002; Willis *et al.* 2007), may suggest additional conservation choices.

Increasingly, palaeobiology is contributing to conservation and restoration ecology (Chamberlain *et al.* 2005; Dietl 2009; Koch *et al.* 2009; Dietl & Flessa 2011). Among possible approaches for determining historic feeding environments of avifauna, 2 have received some attention in New Zealand: reconstructions of environments at the sites containing palaeobiological materials (*e.g.*, Atkinson & Millener 1991); and reconstructions of diet from C and N isotopic analyses of fossil bones (*e.g.*, Holdaway *et al.* 2002a,b).

Stable isotope analysis bridges the temporal divide between former and present ecosystems and ecologies by generating comparable results for both fossil and modern samples. We use measurements of carbon and nitrogen isotope ratios in fossil and modern bone collagen to reconstruct the isotopic niches of brown teal before and after human-induced habitat change. Bone collagen provides an isotopic signal time-averaged over most of the animal's lifetime (Drucker *et al.* 2008; Holdaway *et al.* 2011) so is an appropriate material on which to compare isotopic niches. The concept of an isotopic niche (Newsome *et al.* 2007) allows elements of an animal's niche to be visualised as an "isotopic niche space" (Schmidt *et al.* 2007), free of subjective interpretation. Isotopic niches are not, *per se*, ecological niches, but for extinct taxa and populations, useful information on possible changes in the use of habitat and resources can be derived from comparisons of isotopic niche spaces. Niche space can be considered as being the area within the envelope containing the data points in 2 or more dimensions. We use our results to suggest additional environments and locations in which conservation of brown teal could be attempted.

METHODS
Samples
Eighteen Holocene fossil bones from 8 localities representing most palaeo-environments in which brown teal occurred (Worthy 2002; Appendix 1) were analysed, including bones of 8 individuals from a single population on Takaka Hill, Nelson (Worthy & Holdaway 1994) to examine within-site variability.

The fossil bones were from a coastal lacustrine and estuarine site (Marfells Beach/Lake Grassmere) and from limestone cave sites in southern beech (*Nothofagus* spp.)-podocarp forest on Takaka Hill (northwest Nelson), in podocarp/tawa (*Beilschmiedia tawa*) forest in the Waitomo area, North Island (Gardeners Gut Cave; Blue Gum Cave), and in the hardwood forest with emergent matai (*Prumnopitys taxifolia*) on the downs of inland Canterbury (Kings Cave; Pyramid Valley) and Southland (McKercher's Cave, Browns) (Worthy 1984; Holdaway & Worthy 1997;1998a, b; Worthy & Holdaway 1996).

Modern bones were from 15 brown teal cadavers, 5 from Mimiwhangata in coastal Northland (35° 25′ S; 174° 25′ E) and 10 from the Okiwi basin-Whangapoua Estuary region on Great Barrier I (36° 08′ S, 175° 24′ E).

Analysis
Bone gelatin samples were prepared and measured at GNS Science (Lower Hutt, New Zealand; fossil samples) according to the protocol in Holdaway *et al.* (1999). For carbon and nitrogen isotopic analysis, *c.* 1.5 mg duplicate sub-samples were combusted to carbon dioxide and nitrogen gas in a ANCA

Table 1. Means, standard deviations, and ranges of $\delta^{13}C$ and $\delta^{15}N$ isotope values from bone collagen of modern and fossil brown teal (*Anas chlorotis*), and comparative values from "anchor" species (*Chenonetta finschi*; *Aegotheles novaezealandiae*, from Holdaway *et al.* 2002a,b).

Population	Sample	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
		Mean ± SD	Range	Mean ± SD	Range
Northland	5	-19.3±1.1	-18.6 to -21.3	8.0±0.7	6.9 to 8.6
Great Barrier I	10	-17.3±2.1	-15.0 to -22.2	8.3±1.2	6.1 to 9.8
All modern	15	-18.0±2.1	-15.0 to -22.2	8.2±1.0	6.1 to 9.8
Takaka Hill	8	-22.3±0.7	-21.4 to -23.4	6.4±1.3	5.1 to 8.0
All fossil	18	-21.8±2.5	-14.6 to -25.7	8.0±2.5	5.1 to 13.5
Finsch's Duck	35	-25.3±1.5	-22.1 to -27.5	5.5±2.4	2.0 to 10.2
Owlet nightjar	12	-20.0±0.8	-18.8 to -21.0	10.8±3.7	5.3 to 14.1

SL elemental analyser coupled to a GEO 20/20 continuous flow isotope ratio mass spectrometer (both Europa Scientific®, Crewe, UK), in series with calibration and control standards. Results are reported as %C and %N by dry mass, molar ratios, and as $\delta^{13}C$ or $\delta^{15}N$ (‰) = $(R_{SAMPLE}/R_{STANDARD} – 1)*1000$ with R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$ number ratios, relative, respectively to the primary standards VPDB (Vienna PeeDee Belemnite) and N_2 gas in air. Calibration to primary standards used the sucrose standard IAEA-C6 (currently accepted $\delta^{13}C$ value -10.45‰), the mineral oil NBS-22 (currently accepted $\delta^{13}C$ value -30.03‰) and the ammonium sulphate standard N-1 (currently accepted $\delta^{15}N$ value +0.4‰). The analytical precision reported by the laboratory, based on repeat analysis of control standards, was ±0.1‰ ($\delta^{13}C$) and ±0.3‰ ($\delta^{15}N$).

These analyses were carried out in 2003-2006. Accepted values for some calibration standards (including NBS-22 and IAEA-C6) changed by up to a few tenths of a part per thousand (‰) during this period (Coplen *et al.* 2006). We have not been able to ascertain the exact calibration values used by the laboratory for our samples, but the uncertainties thus introduced are small in relation to the isotopic shifts that we report.

Interpreting stable isotope measurements
For all analyses and in the figures, carbon isotope values from modern teal bones were adjusted to account for the reduction in the $\delta^{13}C$ of atmospheric CO_2 caused by the burning of fossil fuels with low $\delta^{13}C$ (Suess effect) by adding 1.14‰ (Friedli *et al.* 1986) to the measured $\delta^{13}C$ values for the modern material. The measured values are listed in Table 1 and the Appendix.

The isotope values for brown teal were interpreted by reference to values for 2 extinct "anchor" species, Finsch's duck (*Chenonetta finschi*) and New Zealand owlet-nightjar (*Aegotheles novaezealandiae*), whose diets and ecologies are inferred by analogy with close living relatives. Finsch's duck was a poorly-flighted sister species of the Australian wood duck (*Chenonetta jubata*) (Worthy & Olson 2002). The extant Australian species is primarily a terrestrial herbivore, but consumes some insects (Marchant & Higgins 1990) and the New Zealand species had a similar diet (Holdaway *et al.* 2002b). In contrast, the New Zealand owlet-nightjar (*Aegotheles novaezealandiae*), like all owlet-nightjars (van Tyne & Berger 1976), was an obligate insectivore (Holdaway *et al.* 2002a). This, the largest species of owlet-nightjar, was so poorly flighted (Rich & Scarlett 1977) that it would have foraged on or near the ground.

To quantify the change in the brown teal isotopic niche, we calculated Convex Hull Areas (CHA) (Layman *et al.* 2007). The CHA is the simplest polygon that encompasses the isotopic data set in question. Population-level isotopic niche effects were determined using the distance to centroid (DC; Newsome *et al.* 2012). Calculation of the DC metric for a population involves determining the shortest (Euclidean) distance from each data point to the mean values of $\delta^{13}C$ and $\delta^{15}N$, calculating the means and standard deviations, and comparing the population parameters using 1-way ANOVA.

Current applications of isotopic niche metrics emphasise Bayesian methods, because they allow uncertainty estimates. These estimations require knowledge of the probability distributions of each isotopic endpoint. It was inappropriate to apply Bayesian methodology because the fossil isotopic data were beyond the valid use of the limited data for those populations. Accurate probability distributions were not available for the extremities of each polygon, particularly that enclosing the fossils, which are single points with no further information on how representative or otherwise they are of isotopic values for brown teal in those places.
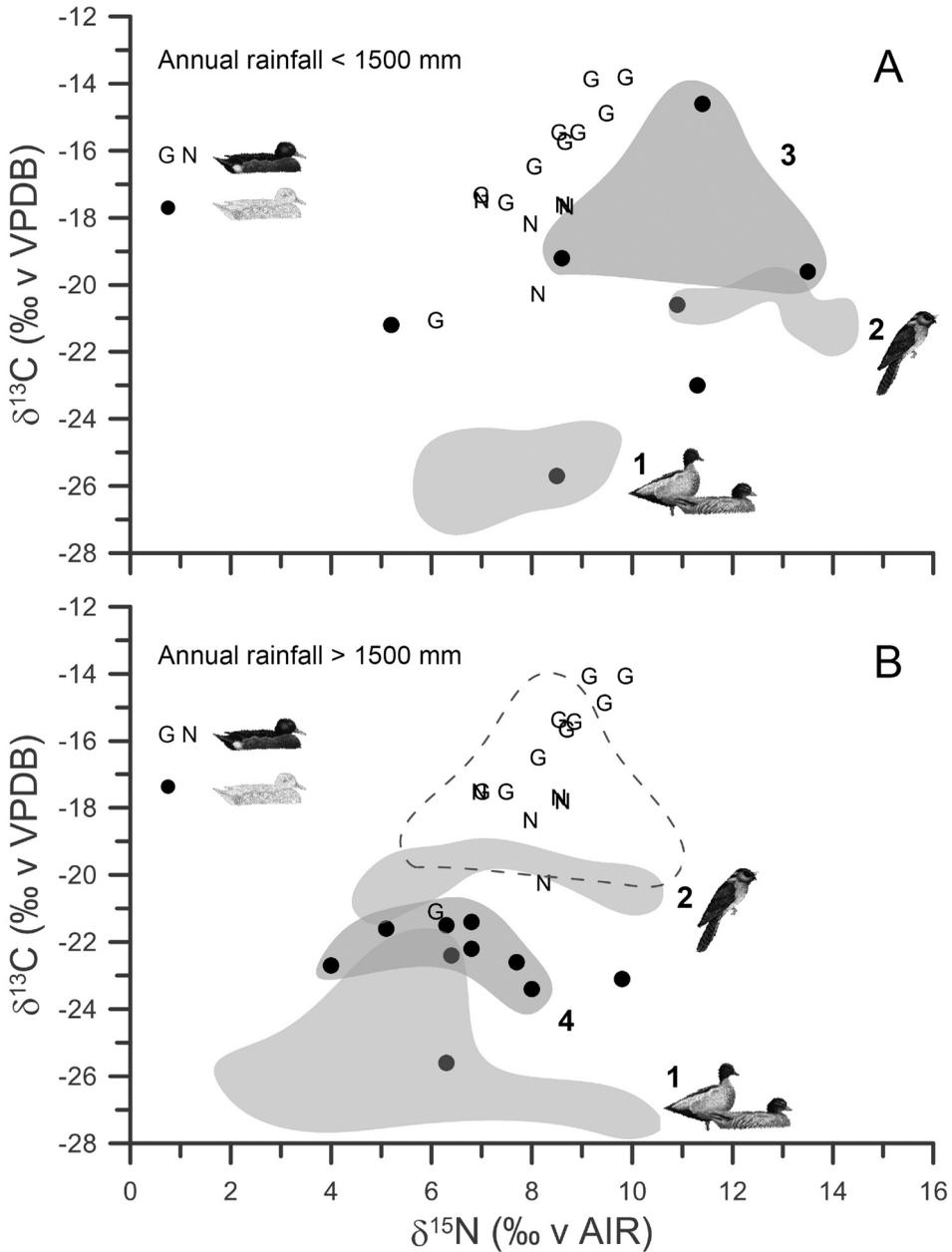
Fig. 1. Isotopic niches as indicated by δ¹³C and δ¹⁵N values of bone gelatin of living and extirpated populations of New Zealand brown teal (*Anas chlorotis*), in comparison with those of 2 "anchor" species whose trophic levels and habitats are based on comparison with surviving congeners.●, fossil brown teal; G, living brown teal, Great Barrier I; N, living brown teal, Northland. Data are presented separately for **A**, sites with annual rainfall < 1500 mm, and **B**, sites with annual rainfall > 1500 mm (Great Barrier I and Northland sites have annual rainfall > 1500 mm). Shaded areas: 1, extinct Finsch's duck (*Chenonetta finschi*) – terrestrial herbivore; 2, extinct New Zealand owlet-nightjar (*Aegotheles novaezealandiae*) – terrestrial insectivore; 3, fossil brown teal from estuarine area (Marfells Beach, Lake Grassmere); 4, fossil brown teal, Takaka Hill. Dashed line in **B** indicates hypothetical position for fossil brown teal in higher rainfall areas (moved to left by difference in δ¹⁵N between Finsch's duck and owlet-nightjar data from high and low rainfall areas (see text for explanation).

RESULTS

Isotope composition of bone gelatin

The large ranges of $\delta^{13}C$ (-14.6 to -25.7‰) and $\delta^{15}N$ (5.1 to 13.5‰) values from fossil bones (Table 1, Appendix 1) indicate the teal lived in a wide range of environments and fed at different trophic levels (Fig. 1A, B). Values for brown teal from Takaka Hill (shaded area 4, Fig. 1B) were tightly clustered and indicate all had a similar diet and fed in similar habitat.

The range of values of both $\delta^{13}C$ (adjusted for Suess effect) and $\delta^{15}N$ was higher in sites with annual rainfalls below 1500 mm (Fig. 1A) than in sites with higher rainfalls (Fig. 1B). In general, the $\delta^{15}N$ values of brown teal, and both comparison species, were lower in high rainfall sites (Fig. 1B). Three fossil samples from a site in an estuarine environment in a low rainfall area (Marfells Beach) had the highest values of $\delta^{13}C$ and high values of $\delta^{15}N$ (shaded area 3, Fig. 1A).

The ranges of $\delta^{15}N$ values from both extant populations (Table 1, Appendix 1) were similar, but the range of $\delta^{13}C$ values from the Great Barrier I population (mean, without Suess effect adjustment -17.2‰, SD = 1.95, $n = 14$) was greater than that from Northland (mean, without Suess effect adjustment = -19.4‰, SD = 1.15, $n = 5$) and the means differed significantly (ANOVA, $F_{1,17}$=5.506, $P = 0.031$). The difference in $\delta^{13}C$ values between the Northland and Great Barrier I samples (Fig. 1A) probably reflects the access of some Great Barrier birds to estuarine food.

The (adjusted) $\delta^{13}C$ and $\delta^{15}N$ values from the extant populations lie adjacent to, and partly within, the values from fossil bones (Fig 1 A, B). The mean (adjusted) $\delta^{13}C$ value (-16.6‰, SD = 2.01 SD, $n = 19$) from the extant populations was significantly higher (ANOVA, $F_{1,36}$= 49.32, $P \ll 0.001$) than that from all the fossil birds (-21.8 ± 2.5‰ SD, $n = 18$). However, although the mean $\delta^{13}C$ values for the 3 (low rainfall area) Marfells Beach birds (-17.9‰) and the extant birds in the high rainfall sites of Northland and Great Barrier I (-16.6‰) were indistinguishable ($F_{1,20}$ = 0.856, n.s.), the $\delta^{15}N$ values (11.2 ‰, 8.3‰, respectively) were significantly different ($F_{1,20}$ = 13.251, $P = 0.0016$). The difference (2.8‰) was of the same order as that between the low and high rainfall area populations of Finsch's duck (3.2‰). The extant populations occupy the isotopic niche space that would be occupied by birds of estuaries in high rainfall areas for which there is no fossil record at present (dashed line, Fig. 1B).

Isotopic values for the extirpated populations of brown teal range from those similar to values from Finsch's duck bone collagen (Holdaway *et al.* 2002b) to those which match values from the owlet-nightjar (Holdaway *et al.* 2002a). The widest isotopic range was for individuals from areas with annual rainfall below 1500 mm (Fig. 1A). Brown teal values for the low – but not the high – rainfall areas include high

$\delta^{13}C$ values consistent with the birds having fed in an estuarine environment where the food chain includes plants which use carbon from dissolved bicarbonate rather than atmospheric CO_2. New Zealand has very few C_4 plants (Wardle 1991), which were unlikely to have contributed significantly, if at all, to the elevated $\delta^{13}C$ values.

The area of the brown teal CHA for the surviving populations was 80% smaller than that for the Holocene populations (Fig. 2), and the CHA of the present populations is displaced to the extreme edge (open environment, low fertility) of the Holocene isotopic niche. However, although the isotopic niche of the living population is *c.* 20% of that occupied by extirpated populations, the isotopic niches did not differ at the population level: distances to the centroids for each population (Northland, Great Barrier I; Takaka Hill in the Holocene) were not significantly different ($F_{2,20}$= 1.190; $P = 0.325$).

DISCUSSION

Brown teal habitats in pre-human New Zealand

The locations at which fossil brown teal bones have been found confirm its widespread presence on all 3 main islands of New Zealand during the Holocene, before human arrival (Worthy 2002). It was also present on Chatham I (Travers 1868) and specimens (in Zoology Museum, Cambridge University, UK) reputedly were obtained from adjacent Southeast I (Rangatira).

The brown teal was the most abundant fossil waterfowl in lacustrine deposits for which there is a fossil record (Worthy 2002), but there are few of these. Most fossil sites containing brown teal were away from lakes and rivers, near the coast and in areas covered by wet and seasonally dry podocarp-hardwood forests, and lower montane beech forests (Worthy 2002).This wider distribution suggests that the bird may have been part of the food webs of a wider range of habitats than that occupied by any other New Zealand waterfowl.

Although forested sites such as Hobsons Tomo and Bone Cave on Takaka Hill (Worthy & Holdaway 1994) and Holocene Hole (on the Mount Cookson Plateau, northern Canterbury) (Worthy & Holdaway 1995) had no standing or flowing water nearby, many other sites were close enough to waterways and wetlands for faunas from there to have been preserved in the sites along with the forest fauna. In particular, cave and rock shelter fossil accumulations include material brought in by predators such as the laughing owl (*Sceloglaux albifacies*) (Holdaway & Worthy 1996), New Zealand falcon (*Falco novaeseelandiae*) (Worthy & Holdaway 1995), and the extinct harriers (*Circus* spp.) (Holdaway 2002), whose hunting ranges could well have included adjacent wetlands as well as forests.
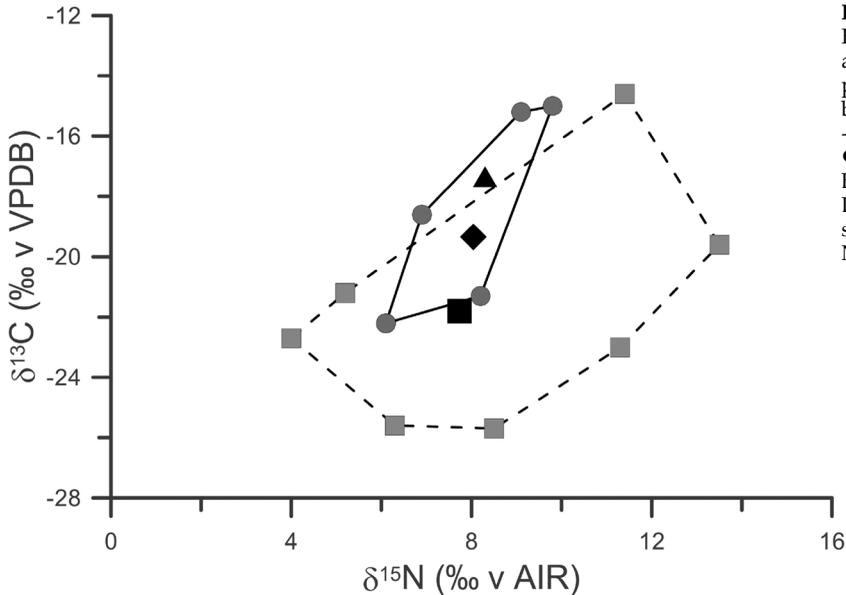
Fig. 2. Comparison of Convex Hull Areas (shaded symbols and lines) for living and extinct populations of New Zealand brown teal (*Anas chlorotis*): ■ --, Holocene fossil individuals; ●, extant Northland and Great Barrier I populations, combined. Locations of centroids (solid symbols): ▲, Great Barrier I; ◆, Northland; ■, Holocene fossils.

The different modes of deposition in each site, including wide-ranging raptors and streams bringing in material from terrestrial as well as wetland sources resulted in fossil faunal assemblages representing the full range of local habitats. Because of the potential for movement of material from elsewhere, species present in sites in heterogeneous environments cannot be assigned to any particular habitat or food web without additional evidence. However, the presence of brown teal remains in areas lacking surface water, such as on Takaka Hill and Mount Cookson, does suggest that the species could inhabit forest and was not confined to pond and stream habitats typical of other duck species (Atkinson & Millener 1991; Worthy & Holdaway 1994; Worthy 2002) and this contention is supported by the stable isotopic measurements presented here.

Former isotopic niche of brown teal – comparisons with "anchor species"

Stable isotope analyses of C and N in fossil bones can contribute to our understanding of the ecology and biology of extirpated populations in the contexts provided by measurements on other taxa with known – or credibly inferred – diets and habitats. The range of isotopic values from the fossil bones show that brown teal originally occupied a wide isotopic niche consistent with their having a varied diet and occupying the habitats implied by the location of their remains.

A potential difficulty for stable isotopic analyses of wetland systems is the wide range of values that can be obtained for members of such a food web,

including values that could be found in adjacent terrestrial food webs. A comparison of the carbon and nitrogen isotope ratios for the Takaka Hill specimens, where the brown teal could have only consumed food from a purely terrestrial food web, with those of the modern birds living in estuaries and freshwater wetlands, supports the contention that the isotopic values for that population, at least, reflect the local food web.

The high $\delta^{15}N$ values in some of the fossil bones might suggest a marine component in the duck's diet even away from the coast. The only coastal birds, the 3 individuals from Marfells Beach, had $\delta^{15}N$ values of 8.6‰, 11.4‰, and 13.5‰. However, the Pyramid Valley bird, which lived on or near a freshwater pond surrounded by seasonally dry forest, had a $\delta^{15}N$ of 11.3‰. In this instance, $\delta^{13}C$ might be a better indicator of a marine component in the diet. The Marfells Beach bird whose $\delta^{15}N$ (11.4‰) most closely matched that of the duck from Pyramid Valley had a $\delta^{13}C$ of -14.6‰, as against -23.0‰ for the Pyramid Valley bird, but the Marfells Beach bird with lowest $\delta^{15}N$ value (8.6‰) had $\delta^{13}C$ value which matched that of the bird from the same site with the highest $\delta^{15}N$ (13.5‰). Clearly, these ducks were living in the same general area but obtaining their carbon and nitrogen from different food webs (reservoirs).

Of the other factors that can lead to enrichment in $\delta^{15}N$, levels of seasonal rainfall (and hence water stress) and soil age are important (Amundson *et al*. 2003; Vitousek 2004). Elevated values of $\delta^{15}N$ are typical of New Zealand ground-feeding forest taxa, including moa and Finsch's duck, in low rainfall

areas with soils at least 10,000 years old (RNH, *unpubl. data*). In this study, bone gelatin δ^{15}N values were relatively high in some birds from Takaka Hill, despite the karst plateau being one of the few hill country areas where seabirds were not present during the Holocene (Worthy & Holdaway 1994). However, the plateau was never glaciated, and the soils have developed under forest there for at least the past 14,000 years (Worthy & Holdaway 1994). Similarly, the soils around Pyramid Valley are at least 10,000 years old, but this site enjoys, at least at present, much lower, and more seasonal, rainfall than does Takaka Hill.

The carbon source in fresh waters can be terrestrial, which might give a terrestrial δ^{13}C signal in a species feeding on freshwater organisms. However, most of the New Zealand waterfowl, living and extinct, show higher values of δ^{13}C (RNH, *unpubl. data*) than those in the fossil brown teal bones, which are themselves consistent with those of terrestrial taxa in New Zealand forests, whose δ^{13}C varies with the density of canopy cover and edge component of the local vegetation (RNH, *unpubl. data*).

Another factor which supports our contention that the isotopic values of the fossil brown teal reflect a wide isotopic niche space for the species in the past is that the carbon and nitrogen isotopic values for brown teal bone gelatin and for that of the 2 "anchor" species (Finsch's duck; owlet-nightjar), all varied consistently in magnitude with respect to rainfall (Fig. 1). The bones of the anchor species analysed were from the same areas as the brown teal fossils, so the baseline food web values will be similar and cover the range of isotopic values for ground-feeding herbivores and insectivores in those areas. The patterns of differences and similarities in the data between taxa were clearer when considered within the isotopic envelopes for these species under the different environmental regimes (Fig. 1). For the extirpated population near Marfells Beach, and the extant Great Barrier I population, the species occupied areas adjacent to estuaries, which are complex isotopic environments. Variations in isotopic values in components of these food webs can exceed those of terrestrial systems, and, as was evident, the carbon and nitrogen isotopes value can vary independently, according to the different reservoirs represented in the individual diets.

Rainfall< 1500 mm
The 3 Marfells Beach fossil brown teal (Fig. 1A) had higher δ^{13}C values than those of the obligate insectivore owlet-nightjar, and their δ^{15}N values were consistent with their having fed, in different combinations in different individuals, on invertebrates (and probably aquatic plants) in the brackish coastal lake and freshwater wetlands.

The Pyramid Valley specimen had isotope values that set it between the owlet-nightjar and Finsch's duck in the lower rainfall areas, which suggests that individual was a forest-floor omnivore under the single-storey canopy which prevailed in that locality.

In contrast, the isotope values for the bird from King's Cave, 200 km to the south, are within the isotopic envelope for the insectivorous owlet-nightjar. Emphasising the variety of trophic levels exploited by Holocene brown teal, the McKerchar's Cave (Southland) example was firmly within the isotopic envelope for the primarily vegetarian Finsch's ducks in low rainfall forest. Indeed, the Holocene Hole (North Canterbury) specimen lived in a low rainfall area that was on a sub-montane plateau and its isotope values were most similar to those from teal in the higher-rainfall but similarly closed-canopy southern beech forest environment of Takaka Hill (Worthy & Holdaway 1994, 1995).

Rainfall >1500 mm
Eight of the 10 birds from higher rainfall areas were from Takaka Hill which was covered until the late 19th century by silver beech (*Nothofagus menziesii*) and Hall's totara (*Podocarpus cunninghamii*) forest (Worthy & Holdaway 1994). These birds were firmly in the "forest omnivore" isotopic niche, with both their δ^{13}C and δ^{15}N values between those of the owlet-nightjar and Finsch's duck. This implies relatively little individual variation in diet amongst birds in a common feeding environment. The marble karst of Takaka Hill is devoid of standing water – and surface streams - over many square kilometres and the teal would have been feeding on the forest floor.

One of the other 2 birds, from Blue Gum Cave in the west-central North Island, had the same δ^{13}C value as the Takaka Hill birds, but its higher δ^{15}N value suggests that it included more invertebrates in its diet. Although Gardiner's Gut Cave is near Blue Gum Cave, and hence the bird inhabited the same wet, multi-story forest, its isotopic values were within the envelope for Finsch's ducks from areas with the same rainfall and was therefore likely mostly vegetarian, but partly insectivorous.

Faunal deposits in coastal areas, including Delaware Bay (Nelson), Northland (Millener 1981), and Native I (Stewart I) (Worthy 2002) are in or near lacustrine or estuarine environments not dissimilar to those used now by brown teal in Northland and on Great Barrier I, or had associated coastal freshwater wetlands typical of those formerly occupied in Northland and Manawatu "sand country" in the early 20th century. Unfortunately, no samples were available for isotopic analysis from these sites, so we estimated the distribution for birds from higher rainfall estuarine areas by subtracting the difference

between mean δ^{15}N values for Finsch's ducks in higher and lower rainfall areas, from the values for birds from Marfells Beach (eastern Marlborough). The resulting distribution (Fig. 1B) is close to that for the extant populations.

Although brown teal have not been recorded as living in the exclusively coastal edge environment exploited by its sister species on the Auckland Is (Williams 1995), they were formerly present on small islands around Stewart I (*e.g.*, Ulva, Codfish, Ruapuke), in Fiordland, and on Hauraki Gulf and Bay of Plenty islands (Dumbell 1986), and also on Te Whanga lagoon on Chatham I (Fleming 1938). In addition, modern records of brown teal foraging at stream mouths and on the littoral on Kapiti I (MW, *pers. obs.*) and on exposed low tidal areas on Great Barrier I (Weller 1974, 1975; Moore *et al.* 2006) support the possibility that some brown teal may have exploited coastal foods as well.

We consider that our isotopic analyses, in conjunction with historic and contemporary accounts of habitat occupied, identify the wide variety of habitats that have been occupied by brown teal. Although an isotopic niche space is not the same as the popularly understood "ecological niche", the differences in isotopic niche spaces represented in the data from fossil and contemporary teal bones indicate that today's remnant populations occupy only a small subset of the habitats occupied before human arrival.

Modern feeding environments

Recently extirpated populations of teal in Fiordland and on Stewart I were last observed on forest-fringed lakes and at stream mouths in sheltered bays (MW, *unpubl. obs.*). The remnant brown teal populations in Northland and on Great Barrier I feed predominantly in anthropogenic, lowland pastoral landscapes. The primary places of breeding and refuge for brown teal on Great Barrier I are in seepage areas and, especially, along watercourses (Barker & Williams 2002), whereas in Northland refuges and territories have extended beyond streams to seepages and ponds with abundant marginal vegetation (Williams 2001). The major difference between the habitats of these 2 populations is that some Great Barrier I birds feed in an estuary (Moore *et al.* 2006), whereas those in Northland are confined to fresh waters, a difference which is reflected in the stable isotope values for the 2 populations.

The lower δ^{13}C values of some Northland and Great Barrier I birds probably reflect a greater use of food obtained from beneath, or at least at the edge of, closed cover. The smaller range of values relative to the fossil birds can be interpreted as reflecting an absence of the original vegetation from the sites occupied. The δ^{15}N values are at the high end of the range for brown teal in wetter areas, which reflects both the enhanced nitrogen supplies in managed farmland, and the birds' use of the estuarine food web, where available.

Habitats of other managed and introduced populations

Captive-reared brown teal released on 3 islands (Kapiti, Titiri Matangi, Mana) and at a fenced mainland enclave (Karori Wildlife Sanctuary, Wellington) have successfully established small (<20 birds) populations and captive releases have successfully supplemented wild birds "lingering" at the tip of Coromandel Peninsula (O'Connor *et al.* 2007). Tiritiri Matangi and Mana birds are confined to small, artificial wetlands, Coromandel birds mostly to pastoral flats near stream mouths, while Kapiti I birds (from a 1968 release of captive-reared and wild birds; Williams 1969) have been observed feeding beneath forest canopy away from the streams in which they take daytime refuge (MW, *pers. obs.*). Attempts at establishing captive-reared teal at 2 other fenced mainland enclaves (Tawharanui, Cape Kidnappers) are on artificial wetlands in pastoral landscapes similar to the landscape occupied by the Northland and Great Barrier I populations (O'Connor *et al.* 2007; DoC 2011).

Pre-human brown teal habitats – implications for conservation choices

The isotopic niche of modern teal is a constricted subset of that of the fossil birds (Fig. 1). Potential conservation options lie in attempting to return brown teal to environments used in pre-human times – if those environments still exist or can be successfully restored, and if they exist where introduced mammalian predators do not.

The principal isotopic difference between fossil and modern birds is characterised by δ^{13}C values of -21‰ and lower for fossil birds, with higher values for fossil individuals being from the eastern, dry area around Marfells Beach, where the birds had access to the brackish Lake Grassmere. We interpret the low values for most of the fossil sample as being characteristic of a range of habitats beneath closed forest canopies, in which different populations fed at trophic levels from herbivory (those whose isotopic values corresponded to those of Finsch's duck), to omnivory (birds on Takaka Hill with an isotopic niche between that of Finsch's duck and the owlet-nightjar), to insectivory (brown teal with isotopic values matching those of the owlet-nightjar). We suggest that forest ecosystems free from key introduced mammalian predators such as cats (*Felis catus*), stoats (*Mustela erminea*), ferrets (*M. putorius*), and rats (*Rattus* spp.) offer additional conservation options.

We are not aware of any site in modern New Zealand, mammalian predator-free Kapiti I and

perhaps Great Barrier I excepted, where brown teal behave as forest floor omnivores or insectivores. On Great Barrier I, few attempts have been made to locate brown teal elsewhere than on the lowlands, but teal are often encountered by trampers and hunters in hill country gullies and seepages and including near the black petrel (*Procellaria parkinsoni*) colony on Mt. Hobson (J. Sim, D. Barker, *pers. comm.*). In the Karori Wildlife Sanctuary, teal have been seen at night within stream furrows beneath forest and at the very heads of catchments (R. Empson, *pers. comm.*).

Predator exclusion fences are now being placed around large areas of forest and wetland throughout New Zealand (Innes *et al.* 2012). These sanctuary areas all offer opportunities to test whether pre-human characteristics and adaptability remain part of the behavioural repertoire of modern teal. As all brown teal re-establishment attempts have been, and are likely to be, sourced from captive bred birds (O'Connor *et al.* 2007), themselves many generations removed from the wild (Bowker-Wright *et al.* 2012), there is no certainty that the birds will retain the responses and search images necessary. Nevertheless, existing sanctuaries such as Orokonui (Dunedin), Maungatautari (Waikato), and Lakes Rotokare (Taranaki) and Opouahi (Hawkes Bay) already offer the opportunity to test this, as does the Tuku reserve on Chatham I.

There are forested island reserves formerly occupied by brown teal but now mammal-free and used for other species conservation projects which could also be used in a similar way. For example, Anchor I (Fiordland) offers lake, forest, and shoreline feeding environments, Codfish I (off Stewart I) offers stream and forest habitat, and Southeast (Rangatira) I (off Chatham I) offers shoreline and forest feeding opportunities. Like Kapiti and Mayor (Tuhua) Is, the latter on which teal have been placed recently, they offer an opportunity for teal to recover lost habitat recognition. The brief period since extinction of populations outside the relict areas, the bird's mobility, and the generally similar climates and environments make it unlikely that the present populations differ physiologically from the extinct ones.

Our study emphasises that conservation options for brown teal are potentially broader than the present focus on pastoral landscapes. Pastoral landscapes have already been identified as fraught with environmental and management challenges (Williams 2001; Barker & Williams 2002; Moore 2003; Moore *et al.* 2006) and are clearly not analogues of the habitats in which brown teal evolved. Introductions to fenced sanctuaries with largely intact forest will also assist more in achieving ecosystem restoration goals than would maintaining the taxon in managed farmland.

Rather than seek more of the same (DoC 2011) we encourage a search for alternatives based on evidence from the past, including historical records, palaeo-ecological information on former distributions, and especially stable isotope analyses. The assumption that the circumstances into which remnant populations of declining species descend are optimal, or even "typical", and so need to be replicated as part of conservation strategies, has long been discredited (Gray & Craig 1991; Lomolino & Channell 1995; Channell & Lomolino 2000). The approach we have employed here seems applicable to other endangered species (*e.g.*, takahe) with struggling remnant populations and for which conservation management remains problematic.

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Appendix 1. Sources of bone samples and isotope values (‰) obtained. Fossil bones were from Canterbury Museum (CM) and Museum of New Zealand (MNZ) collections and their field collection sites given in publications (1,Worthy &Holdaway (1994); 2,Worthy 1997; 3, Worthy (1984); 4, Worthy & Holdaway (1995); 5, Worthy (1998); 6, Holdaway & Worthy (1997)). When comparing modern and fossil bones, carbon isotope ($\delta^{13}C$) values from modern teal bones were adjusted for the modern rise in atmospheric CO_2 (Suess effect) by adding 1.14‰ (Friedli *et al.*1986) to the measured $\delta^{13}C$ values.

Sample no.	Isotope value (‰)		C:N ratio	Source	Location
	$\delta^{13}C$	$\delta^{15}N$			
Modern					
AC1	-17.7	8.1	3.2	Great Barrier I	Okiwi
AC2	-15.2	9.1	3.2	Great Barrier I	Okiwi
AC3	-16.6	8.5	3.2	Great Barrier I	Okiwi
AC4	-18.6	7.0	3.2	Great Barrier I	Okiwi
AC5	-22.2	6.1	3.2	Great Barrier I	Okiwi
AC6	-16.5	8.8	3.2	Great Barrier I	Okiwi
AC7	-18.7	8.6	3.2	Northland	Mimiwhangata
AC8	-21.3	8.2	3.2	Northland	Mimiwhangata
AC9	-18.6	6.9	3.2	Northland	Mimiwhangata
AC10	-19.4	7.9	3.2	Northland	Mimiwhangata
AC11	-18.7	8.6	3.2	Northland	Mimiwhangata
AC12	-15.0	9.8	3.1	Great Barrier I	Okiwi
AC13	-16.1	9.5	3.2	Great Barrier I	Kawa
AC14	-16.8	8.7	3.1	Great Barrier I	Port Fitzroy
AC15	-18.7	7.4	3.1	Great Barrier I	Okiwi
Fossil					
ACSI/1	-21.4	6.8	2.8	CM/Av16708A	Pothole 3, Canaan Rd, Takaka Hill[1]
ACSI/2	-19.6	13.5	2.9	CM/ Av16461	Marfells Beach[5]
ACSI/3	-19.2	8.6	2.8	CM/ Av12931	Marfells Beach[5]
ACSI/4	-23.0	11.3	2.8	CM/ Av5881	Pyramid Valley[6]
ACSI/5	-14.6	11.4	2.8	CM/ Av13177	Marfells Beach[5]
ACSI/6	-20.6	10.9	2.7	CM/ Av23071	Kings Cave[2]
ACSI/7	-25.7	8.5	2.8	CM/ Av32396	McKerchar's Cave, Browns, Southland
ACSI/8	-25.6	6.3	2.8	CM/ Av28208	Gardners Gut Cave, Waitomo[3]
ACSI/9	-23.1	9.8	2.8	CM/ Av21550	Blue Gum Cave, Waitomo[3]
ACF1	-21.2	5.2	2.7	MNZ/ S33362	Holocene Hole, Canterbury[4]
ACF2	-23.4	8.0	2.8	MNZ/ S32427.1	Hobsons Tomo, Takaka Hill[1]
ACF3	-22.4	6.4	2.8	MNZ/ S32427.2	Hobsons Tomo, Takaka Hill[1]
ACF4	-21.5	6.3	2.8	MNZ/ S32427.3	Hobsons Tomo, Takaka Hill[1]
ACF5	-22.6	7.7	2.8	MNZ/ S32427.4	Hobsons Tomo, Takaka Hill[1]
ACF6	-21.6	5.1	2.8	MNZ/ S32427.5	Hobsons Tomo, Takaka Hill[1]
ACF7	-22.7	4.0	2.8	MNZ/ S32427.6	Hobsons Tomo, Takaka Hill[1]
ACF8	-22.2	6.8	2.8	MNZ/ S32427.7	Hobsons Tomo, Takaka Hill[1]
ACF9	-21.4	6.8	2.7	MNZ/ S32427.8	Hobsons Tomo, Takaka Hill[1]