SHORT COMMUNICATION

Bone stable isotopes indicate a high trophic position for New Zealand's extinct South Island adzebill (*Aptornis defossor*) (Gruiformes: Aptornithidae)

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Abstract: The adzebills (Aptornithidae) were an ancient endemic lineage of large flightless Gruiformes that became extinct shortly after Polynesian settlement of New Zealand. The diet and ecology of these enigmatic birds has long been a matter for conjecture, but recent stable isotope analyses of bones of the North Island adzebill (*Aptornis otidiformis*) have indicated that adzebills may have been predatory. Here, we add to our understanding of adzebill ecology by providing the first stable isotope analyses of South Island adzebill (*A. defossor*) bones from two Holocene deposits. We interpret the results within frameworks of stable isotope measurements on bones of faunal species with known diets and from the same deposits (thereby mitigating regional effects on isotope values). Our results strongly support the hypothesis that adzebills had a high trophic position. Considered alongside the unique skeletal adaptations of adzebills and the distribution of the species during the Holocene, we suggest that adzebills were most likely terrestrial predators restricted to dry podocarp forests and may have specialised in dismantling rotting logs to obtain invertebrates and/or excavating burrowing animals such as tuatara or the chicks of burrow-nesting birds.

Keywords: avian herbivores; avian predators; carbon; diet; extinct; Holocene; insectivores; isotopes; nitrogen; omnivores

Introduction

The endemic basal gruiform family Aptornithidae (adzebills), represented by the genus *Aptornis*, remains one of New Zealand's most enigmatic avian lineages. Limited molecular evidence points to an Eocene divergence date for the aptornithid lineage from rails (Houde 2009), and fossil remains show that *Aptornis* has been part of the New Zealand avifauna since at least the early Miocene (Worthy et al. 2011). Two species, the South Island adzebill (*Aptornis defossor*) and North Island adzebill (*A. otidiformis*), were encountered by Polynesian settlers in the 13th Century AD (Wilmshurst et al. 2008). Both species were flightless, stood about 80 cm tall, and ranged from c. 16 kg (*A. otidiformis*) to 19 kg (*A. defossor*) in weight (Worthy & Holdaway 2002). Their bones have been recovered from early midden deposits (Worthy 1999) and it is likely that both species became extinct around the same time as moa (15th Century AD; Perry et al. 2014) via a combination of hunting, habitat loss and possibly predation by the introduced kiore (*Rattus exulans*) (Fleming 1969).

The Aptornithidae get their common name from their most notable morphological feature, a large down-curved bill resembling an adze. This unique bill morphology has long spawned conjecture about the diet and ecology of adzebills. Owen (1871) made the first inferences about adzebill diets based on a detailed morphological analysis, stating that 'the peculiarities of the skull in *Aptornis* may be considered in relation to the food of the bird and the work to which its long adze-like beak was put. I infer this work to have involved frequent strong and deep thrusts into the ground, and that the quest was for animal, not vegetable matters.' In comparing muscle attachments on adzebill skulls with those of kiwi, which have beaks adapted for soil probing, Owen suggested the muscles could generate quadruple the force in thrusting the beak into the ground. Owen also recognised adaptations in the tarsometatarsus for digging or scratching, concluding that 'Everything bespeaks the force with which this massive metatarsal was worked in *Aptornis*.' Owen's hypothesis regarding the animal-based diet of adzebills is supported by Worthy and Holdaway (2002, p. 399), who reported that a set of gizzard stones associated with a well-preserved adzebill skeleton was smaller than would be expected if adzebills had been herbivorous. Worthy and Holdaway (2002, p. 213) also presented bone stable isotope data for two individuals of North Island adzebill. These specimens were shown to be more enriched in ^{15}N than two herbivores (coastal moa, *Euryapteryx curtus*, and Finsch's duck, *Chenonetta finschi*) and an insectivore (New Zealand owlet nightjar, *Aegotheles novaezealandiae*), indicating a higher trophic position, i.e. predator.

Here, we further examine the diet of adzebills by presenting the first bone stable isotope data for the South Island adzebill, assessed within a framework of faunal species with known trophic positions. We constrain our study to site-specific comparisons between faunal species at two localities, as stable isotope values can be strongly influenced by variations

in environmental factors such as aridity (e.g. Rawlence et al. 2012) that can confound interpretations of diet.

Methods

Study sites and specimens

We measured dietary stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) from South Island adzebill bones, as well as bones from other faunal species of known trophic levels, from the same deposits at two locations.

The first study site was Finsch's folly tomo, a c. 5 m deep vertical shaft in limestone on farmland near Kimbell, South Canterbury (44° 2′ S, 170° 43.5′ E) (Fig. 1). A brief description of the site and its sediments was provided by Grealy et al. (2015). Finsch's folly tomo contains rich and diverse late Holocene fauna and the site is the subject of continuing excavation and research. Identical elements were used for each species to ensure different individuals were being sampled, except where clear size variation indicated bones were from different individuals. For isotope analysis, we sampled South Island adzebill (n=2), three avian herbivore species (Finsch's duck, n=4; kakapo, *Strigops habroptilus*, n=5; and South Island goose, *Cnemiornis calcitrans*, n=2), reptilian (tuatara, *Sphenodon punctatus*, n=4) and avian (weka, *Gallirallus australis*, n=2) omnivores, and two avian predators (laughing owl, *Ninox albifacies*, n=1; and Eyles' harrier, *Circus teauteensis*, n=1). A further South Island adzebill bone was sampled for radiocarbon dating but a nitrogen isotope value was not obtained for this specimen. Sampled bones from Finsch's folly were deposited in the collections of Canterbury Museum, Christchurch, New Zealand (Canterbury Museum Accession Number 2013.2).
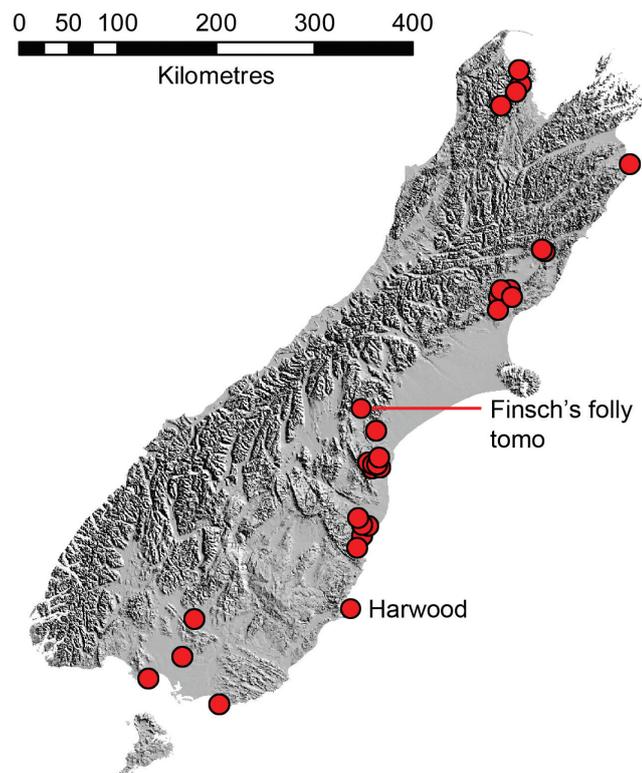
Figure 1. South Island, New Zealand, showing distribution of naturally deposited sites where Holocene remains of South Island adzebill (*Aptornis defossor*) have been recovered (including the sites examined in this study).

The second study site was Harwood, Otago Harbour (45° 46′ S, 170° 40′ E). Bones at Harwood are found ex-situ on intertidal sand flats at low tide (Lalas et al. 2014). The exact origin of the bones has yet to be determined, although they may originate from dunes that formerly covered the site that have since eroded due to shoreline regression. We sampled bones of South Island adzebill (n=1), two avian herbivore species (a phalange belonging to a large moa – either heavy-footed moa, *Pachyornis elephantopus*, or South Island giant moa, *Dinornis robustus* – n=1; and a femoral shaft belonging to a small moa – either little bush moa, *Anomalopteryx didiformis*, or upland moa, *Megalapteryx didinus* – n = 1) and dog, or kurī (*Canis familiaris*; n=2). Radiocarbon and stable isotope measurements were performed on all five bones.

Stable isotope analyses

Bone samples were pre-treated and gelatinized at the Waikato Radiocarbon Dating Laboratory (University of Waikato, Hamilton, New Zealand) and $\delta^{15}N$ and $\delta^{13}C$ values were measured at the Waikato Stable Isotope Laboratory following the methodology outlined by Wood et al. (2014). Measurement precision was ±0.2%.

Radiocarbon dating

Bone samples were submitted to the Waikato Radiocarbon Dating Laboratory for radiocarbon dating. Samples were cleaned, ground to a fine powder and decalcified in 2% HCl, before being rinsed and dried. The residue was then gelatinised at HCl (pH 3.0) at 90°C for 4 hours, ultrafiltered and freeze-dried. Radiocarbon measurements were made using an accelerator mass spectrometer at the Keck Radiocarbon Dating Laboratory (University of California, Irvine, USA). Radiocarbon ages were calibrated using the ShCal13 curve (Hogg et al. 2013) via OxCal 4.2 (Bronk Ramsey 2008).

Results

South Island adzebill had the highest mean $\delta^{15}N$ value from Finsch's folly tomo (9.785) followed by weka (8.87), tuatara (7.89), laughing owl (7.88), Eyles' harrier (7.11), South Island goose (4.18), Finsch's duck (3.86) and kākāpō (2.8) (Table 1; Fig. 2). Eyles' harrier had the highest mean $\delta^{13}C$ value (-19.03) followed by South Island adzebill (-19.61), laughing owl (-19.89), kākāpō (-20.33), tuatara (-20.6), weka (-21.39), South Island goose (-23.44) and Finsch's duck (-26.99) (Table 1; Fig. 2). At Harwood, the South Island adzebill also had a relatively high $\delta^{15}N$ value (13.25) compared with dog (mean = 11.74) and the two moa species (mean = 7.4) (Table 1; Fig. 2). South Island adzebill had the highest mean $\delta^{13}C$ value (-19.51) followed by dog (-20.21) and moa (-23.19) (Table 1; Fig. 2).

The three radiocarbon dates from Finsch's folly tomo were quite tightly spaced (Table 1), suggesting the bones in the tomo may have accumulated relatively rapidly sometime between c. 1000 and 2000 years ago. Four of the bones from Harwood (including the two dogs) have calibrated ages ranging from 716–505 years before present (BP) (corresponding to 1234–1445 AD, or the early settlement period; Table 1). A kiore-gnawed seed from the same site dates to 543 ± 30 years BP (Table 1). The bone of the small moa species from Harwood was earlier (calibrated age of 1521–1350 years BP; Table 1) indicating a prolonged period of deposition for material at this site.
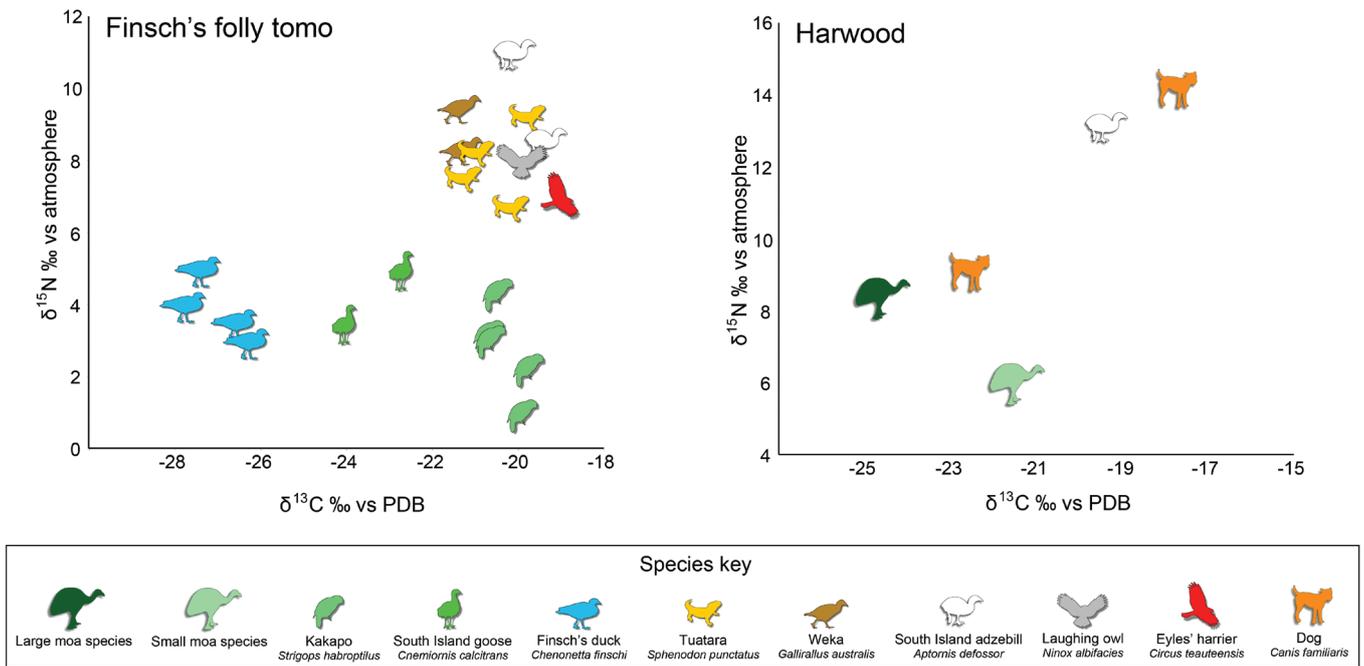
Figure 2. Dietary stable isotopes (δ^{15}N and δ^{13}C) for bones from Finsch's folly tomo (South Canterbury) and Harwood (Otago Harbour), New Zealand. PDB = Pee Dee Belemnite.

Discussion

Trophic positions

The relatively low δ^{15}N values exhibited by Finsch's duck, South Island goose and kākāpō bones from Finsch's folly tomo are typical of herbivores. The partitioning of these three species by their differing δ^{13}C values (Fig. 2) could potentially be due to differences in several environmental factors relating to their microhabitats and diets (Dawson et al. 2002). However, many of these factors (e.g. atmospheric CO_2 concentration, salinity) were controlled for through using a single bone deposit that accumulated over a short temporal span. Moisture (e.g. proportion of aquatic vegetation in diet) and irradiance (e.g. use of open vs. sub-canopy habitats) are the two most likely factors differentiating the δ^{13}C values of these species at Finsch's folly tomo. Holdaway et al. (2002) and Worthy and Holdaway (2002) also reported relatively depleted ^{13}C values for Finsch's duck, the latter authors suggesting this result reflected feeding beneath a dense canopy. However, it can be difficult to attribute any one factor to explaining δ^{13}C values (Dawson et al. 2002).

The relatively enriched ^{15}N signal of South Island adzebill from Finsch's folly tomo (one of the specimens had the most enriched value measured from the deposit) reflects a high trophic position. The enriched ^{15}N relative to the predatory laughing owl and omnivorous weka and tuatara, all of which can consume high proportions of beetles and other large invertebrates in their diets (Carroll 1963; Walls 1981; Worthy 1997), suggests that the South Island adzebill was not strictly an insectivore, but was a predator, as has been inferred for the North Island adzebill.

This interpretation is further supported by the results from Harwood. Here, the South Island adzebill bone was enriched in ^{15}N compared with the two moa specimens. However, the isotopic composition of the two dog bones were quite different (Fig. 2) and this may be due to different diets of the two individuals. In New Zealand, prehistoric dogs are known to have had widely-varied diets that included a wide range of marine (fish, shellfish) and plant components (Wood et al. 2016) and this is reflected by variability in isotope values (Kinaston et al. 2013). Therefore, neither the fact that the isotopic signature of one of the dogs is similar to those of the moa, nor that the other is relatively enriched in ^{15}N is surprising. Fauna with marine components in their diets (such as fish) tend to be more enriched than those with exclusively terrestrial diets (Schoeninger & DeNiro 1984).

Ecological niche of adzebill

Stable isotopes from the South Island adzebill support North Island adzebill data (Worthy & Holdaway 2002) that demonstrate adzebills were predators. In light of this finding, it is interesting to consider whether adzebills were generalist predators, or whether the unique morphological adaptations seen in adzebill skeletons may reflect a particularly specialised niche.

The distribution of Holocene bones shows that adzebills inhabited eastern regions of both islands, which Worthy and Holdaway (2002) interpreted as a preference for shrublands and grasslands. However, the absence of adzebill in any of the abundant, widespread and highly diverse Holocene faunal assemblages from the Central Otago region (Worthy 1998; Wood 2008), a sparsely forested region where the vegetation was dominated by shrublands and grasslands (Wood & Walker 2008), appears to contradict this conclusion. We suggest that the distribution of Holocene adzebill remains (Fig. 1; also see Appendix 4 in Worthy & Holdaway 2002) actually reflects a preference for dry podocarp forest. This preference is supported by more detailed analysis of deposits where both bones and pollen have been analysed. For example, in the graveyard deposit in the Honeycomb Hill Cave System,

Table 1. Results of stable isotope and radiocarbon analyses from Finsch's folly tomo (FF) and Harwood (H) deposits. Bone abbreviations are: cmc (carpometacarpus), fem (femur), hum (humerus), tmt (tarsometatarsus), tt (tibiotarsus), with prefixes denoting L (left) or R (right). CRA = conventional radiocarbon age. *δ^{13}C value indicates some marine carbon, so actual age may be younger.

Site	Species	Bone	Lab no. (Wk)	d^{15}N$_{AIR}$, ‰	Nitrogen % w/w	d^{13}C$_{VPDB}$, ‰	Carbon % w/w	C:N mol ratio	CRA	CRA error	Calibrated age (95.4% confidence)
FF	Tuatara	L hum	34021	8.20	15.04	-21.05	41.94	3.25			
FF	Tuatara	L hum	34022	6.69	15.18	-20.20	42.06	3.23			
FF	Tuatara	L hum	34023	9.19	15.10	-19.85	41.91	3.24			
FF	Tuatara	L hum	34024	7.48	14.79	-21.31	41.03	3.24			
FF	Finsch's duck	L hum	34025	4.98	15.40	-27.38	43.29	3.28			
FF	Finsch's duck	L hum	34026	3.50	15.60	-26.55	43.64	3.26			
FF	Finsch's duck	L hum	34027	2.98	15.25	-26.27	42.82	3.27			
FF	Finsch's duck	L hum	33989	3.99	15.45	-27.76	44.64	3.37	1344	25	1286–1181 years BP
FF	Kakapo	R tmt	34028	2.29	15.46	-19.81	42.65	3.22			
FF	Kakapo	R tmt	34029	3.22	15.49	-20.72	42.92	3.23			
FF	Kakapo	R tmt	34030	4.39	15.35	-20.52	42.65	3.24			
FF	Kakapo	R tt	34037	1.02	15.42	-19.95	42.78	3.24			
FF	Kakapo	R tt	34038	3.10	15.28	-20.66	42.88	3.27			
FF	South Is. goose	L cmc	34031	4.91	15.88	-22.78	43.96	3.23			
FF	South Is. goose	R cmc	33990	3.44	15.66	-24.09	44.39	3.31	1646	25	1560–1418 years BP
FF	South Is. adzebill	R fem	34032	8.56	15.98	-19.45	44.74	3.27			
FF	South Is. adzebill	R fem	33991			-19.20			1645	25	1560–1417 years BP
FF	South Is. adzebill	R fem	34033	11.01	15.63	-20.17	43.78	3.27			
FF	Weka	R hum	34034	9.45	15.74	-21.40	44.63	3.31			
FF	Weka	R hum	34035	8.29	15.34	-21.37	42.76	3.25			
FF	Laughing owl	R tt	34036	7.88	15.33	-19.89	43.00	3.27			
FF	Eyles' harrier	R fem	37403	7.11		-19.03					
H	Dog		23829	14.26	16.2	-17.78	45.5	3.28	740	30	682–564 years BP*
H	Dog		23830	9.21	15.5	-22.63	43.6	3.28	616	30	637–525 years BP
H	Large moa species		23831	8.63	15.8	-24.68	44.3	3.27	567	30	621–505 years BP
H	Small moa species		23832	6.16	15.4	-21.56	44.5	3.37	1572	30	1521–1350 years BP
H	South Is. adzebill		23833	13.25	15.9	-19.51	44.7	3.28	737	35	716–560 years BP
H	Matai (seed)		23834			-24.0			543	30	550–502 years BP

Oparara, adzebill remains were rare (one individual) above a pollen sample indicative of glacial-maximum shrublands, but most abundant (at least 19 individuals) above a pollen sample that reflected a mixed podocarp-beech forest (Worthy & Mildenhall 1989). Such a preference for tall dry forest would explain the relative rarity of Holocene adzebill bones from both Central Otago and the wetter regions of western Southland and the West Coast. Moreover, we found evidence for contemporaneous podocarp forest at both Harwood (pollen assemblage containing diverse podocarps but no beeches; matai, *Prumnopitys taxifolia*, wood and seeds in sediments associated with bones) and Finsch's folly tomo (scarce pollen grains in sediment are almost exclusively podocarp).

Features of adzebill skeletons, including the large robust skull, large muscle attachment points on the skull and cervical vertebrae, and short stout tarsometatarsi (Worthy & Holdaway 2002) suggest that adzebills were well adapted for digging with both beak and feet. Moreover, the large lacrimals, which may have reduced forward vision, and large olfactory capsules of adzebills do not rule out the possibility that they may have been nocturnal or relied partly on smell to detect prey. We suggest that the most plausible ecological niche of adzebill may have been as a terrestrial predator in dry podocarp forests, perhaps specialising in complete dismantling of rotten logs to obtain invertebrates (being somewhat complementary to the surface excavation performed by the kaka, *Nestor meridionalis*, or male huia, *Heteralocha acutirostris*) or excavating burrowing animals such as tuatara or the chicks of burrow-nesting birds such as kiwi. Moreover, prior to the arrival of predatory mammals in New Zealand the density of large invertebrates, frogs and lizards may have been much higher in forests (as is seen now on predator-free islands; Ramsay 1978; Whitaker 1978) and could have provided another possible food source for adzebills. Although none of the adzebill specimens analysed for stable isotopes had a strong ^{13}C enrichment indicative of a significant marine dietary component, this result does not rule out the possibility that adzebills may have occasionally preyed upon seabirds.

Conclusions

Stable isotope ratios from bones of the extinct South Island adzebill, in particular δ^{15}N, indicate that the species had a high trophic level and was most likely a predator. In consideration of morphological characteristics of the skeleton and distribution of Holocene bones of the species, we suggest that the South Island adzebill was likely a predator of terrestrial fauna living on or in the ground of dry podocarp forests. This interpretation supports previous interpretations about the diet of the North Island adzebill.

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