

When the lonely goose? Implications of a revised history of the lake and its surrounding vegetation for a radiocarbon age for the only South Island goose (*Cnemiornis calcitrans*) from the Pyramid Valley lake bed deposit, New Zealand

ALISON G. JOHNSTON

2990 Coaltrack Road, Coalgate, Selwyn 7673, Canterbury, New Zealand

BRENDAN G. DUFFY

School of Geography, Earth and Atmospheric Science, The University of Melbourne, Melbourne Vic 3010, Australia

GHD, 180 Lonsdale Street, Melbourne, Victoria 3000, Australia

RICHARD N. HOLDAWAY*

Palaeocol Research Ltd, PO Box 16 569, Hornby, Christchurch 8042, New Zealand

Abstract: A high resolution chronology of deep water charophyte algal remains in the Pyramid Valley lake deposit, North Canterbury, South Island, New Zealand, records the presence and drainage of a previously unsuspected much larger (c. 50 ha) lake. The larger lake occupied the surrounding basin and the present lake (1 ha) was a semi-isolated embayment at its south-western margin. Fluctuating lake levels and its final drainage drove changes in the vegetation and hence in the habitats available for the avifauna recorded in the rich fossil record. A high precision radiocarbon age on the only South Island goose (*Cnemiornis calcitrans*) in the fauna coincided with the presence of lowland forest and not with the brief period when sedges and grassland colonised the newly exposed former lake bed. This suggests that the South Island goose was able to survive in different habitats through successive glacial-interglacial vegetation cycles. Information from other disciplines can be essential to interpreting both a fossil site and the circumstances surrounding the presence of a particular species in it.

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INTRODUCTION

The extinct flightless South Island goose (*Cnemiornis calcitrans*) is related to the Cape Barren goose (*Cereopsis novaehollandiae*) of southern Australia

(Oliver 1955; Worthy *et al.* 1997; Gill *et al.* 2010). Based on this relationship, the New Zealand bird has been assumed (Holdaway & Worthy 1997; Worthy *et al.* 1997; Worthy & Holdaway 2002) to have required the same short grass swards as its Australian relative, which avoids scrub and forest (Marchant & Higgins 1990). Worthy & Holdaway

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*Correspondence: turnagra@gmail.com

(2002) also assumed, based on the inferred habitat, that it shared the Australian bird's diet of grass and herbs (Marchant & Higgins 1990).

Such phylogenetic analogies can be inappropriate, however, especially when one of the taxa has colonised a different area, with different environments and different suites of potential predators, competitors, and food resources. Local examples are the extinct New Zealand harriers (*Circus* spp.), which had evolved the wing proportions of forest-dwelling, bird-eating, goshawks (*Accipiter* spp.). Despite their different proportions, habitat, and diet, the New Zealand harriers were undoubtedly harriers and not goshawks (Holdaway, in Worthy & Holdaway 2002). Similarly, there is no *a priori* reason why *Cnemiornis* geese should behave in the same way as *Cereopsis* does in its own environment. The relationship between the Australian and New Zealand geese is at generic level or above, not sister species like the harriers, and *Cnemiornis* confronted completely different suites of competitors and predators.

In addition to potential clues from phylogenetic relationships, evidence for the habitats of extinct taxa can be gained by secure association between a species' presence and the contemporary local palaeoenvironment. A glacial climate has prevailed for most of the past million years (Petit *et al.* 1999; Ehlers & Gibbard 2007), interspersed with relatively brief warm interglacials such as the present Holocene. Climatically driven changes in the New Zealand vegetation have been routinely (Worthy & Mildenhall 1989; Worthy & Holdaway 1993, 1994, 1995, 1996, 2000, 2002; Worthy 1994, 1997, 1998a, b, 2000; Worthy & Swabey 2002; Worthy & Grant-Mackie 2003) taken into account in discussions of fossil avifauna.

In broad terms, the Quaternary history of New Zealand's vegetation is regarded as well known, but there are still issues, and local details are sparse. Pollen-based models of the glacial vegetation include extensive grasslands and little forest in the South Island (Newnham *et al.* 2013), despite the diversity of forest birds endemic to the South Island (Gill *et al.* 2010). The prevailing views on past vegetation patterns means that much of the discussion on former habitats in the South Island has been predicated on an implied paucity of forest for most of the past million years. Fleming's (1962, 1979) reconstruction, with its extensive grasslands and ice caps, has become – with recent refinements (e.g. Newnham *et al.* 2013) – canonical. The goose is therefore seen as a relict, glacial grassland species confined to tiny areas of suitable habitat in the forest-dominated Holocene landscape, as has been proposed for the South Island takahe (*Porphyrio hochstetteri*), based on the tiny relict population's Fiordland habitat (Mills *et al.* 1984).

During the Holocene, grassland in New Zealand was limited to riparian strips and river beds, alpine meadows, and drought-prone areas of central Otago (McGlone 1988). If the South Island goose required short grasslands, its fossil remains should be found both where and, importantly, when there were grasslands in an area. However, their fossils are present in areas, such as North and South Canterbury, when and where the dominant Holocene vegetation was forest (Molloy *et al.* 1963; Burrows 1989; Holdaway & Worthy 1997; Wood *et al.* 2017). One such site is the Pyramid Valley lake bed deposit in North Canterbury (42° 58' 22.54" S, 172° 35' 50.12" E) (Fig. 1), whose rich fossil avifauna includes just a single South Island goose (Holdaway & Worthy 1997; Holdaway 2015).

To put its rarity at Pyramid Valley in context, a brief survey of published records of the South Island goose yielded a total of 14 individuals from north of South Canterbury, including the West Coast and Takaka areas (Worthy & Holdaway 1993, 1994, 1995, 1997). There was none among the 137 waterfowl individuals in the large (a total of 770 individuals) natural and archaeological avifaunas at Marfells Beach in Marlborough (Worthy 1998c). Twenty-one have been recorded from South Canterbury (Worthy 1997), 43 from Otago (Worthy 1998b), and only two from Southland (Worthy 1998a).

The presence of a grassland goose at Pyramid Valley is anomalous because the site contains a diverse forest bird fauna (Holdaway 1990; Holdaway & Worthy 1997). Indeed, Holdaway & Worthy (1997) appealed to the unlikely and unsubstantiated presence of grassland and shrubland on the surrounding hills to explain the presence of a known grassland species, the New Zealand quail (*Coturnix novaezelandiae*), in the lake bed. The goose was one of eight species of waterfowl recorded from the deposit (Holdaway & Worthy 1997), including both aquatic and terrestrial species, but of these only the extant New Zealand shelduck (*Tadorna variegata*) is a grazer, known to require grassland (Williams 1971). Its remains from Pyramid Valley have not been radiocarbon dated.

Local events can, while being usually much more difficult to identify, modify the vegetation around a particular site on much shorter time scales than glacial-interglacial cycles. The possibility of significant local changes during the relatively brief history (Gregg 1972; Johnston 2014) of Pyramid Valley has never been considered. The environment around the lake over the past 5,000 years is thought to be one of the best known in New Zealand as a result of decades of analysis of the microfossils in the lake bed sediments (Deevey 1955; Harris 1955; Moar 1970; Gregg 1972; Burrows 1989) and interpretation of the avifauna preserved there (Holdaway & Worthy 1997).

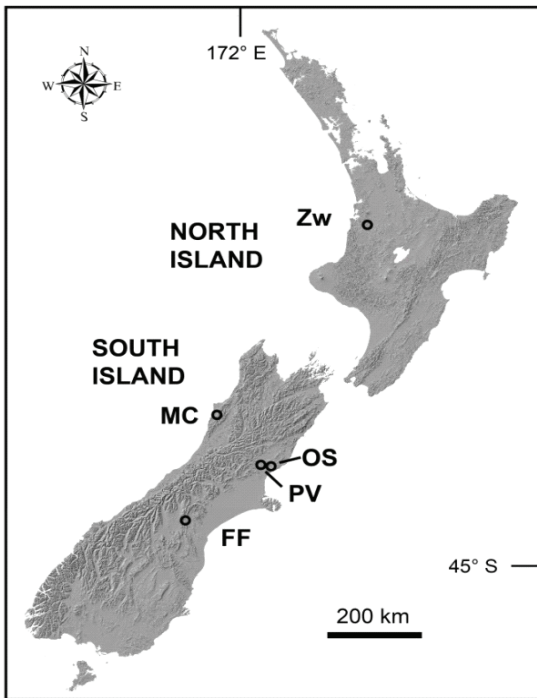


Figure 1. Locations of sites for which radiocarbon ages on New Zealand geese (*Cnemiornis* spp.) are available. *Cnemiornis gracilis*: Zw, Zweiholen Passage, Gardner's Gut Cave. *Cnemiornis calcitrans*: MC, Metro Cave; OS, Omih Stream cutting, State Highway 1; PV, Pyramid Valley; FF, Finsch's Folly pitfall cave.

Results of these studies supported a model in which Pyramid Valley was surrounded by lowland forest, growing to the water's edge (Eyles 1955), throughout the late Holocene (Burrows 1989) before the forest was destroyed by Polynesian fires (Moar 1970). As the 1 ha lake lacks an inlet stream, its maximum depth of *c.* 1 m is sustained by rainfall runoff from the surrounding hills and a few springs at its southern periphery. The springs depend on the local water table, and the outlet stream is small, intermittent, and deeply incised. There was no space for peripheral or riparian grassland. The lake bed now supports a vegetation of pasture grasses during long dry periods.

The lake has always been assumed to have been shallow and confined to its present basin. Moar (1970) suggested that the charophyte algae (Plantae: Charophyceae: Charales) that Deevey (1955) identified by their oospores in distorted cores from Pyramid Valley are typical of shallow, calcareous lakes such as that at Pyramid Valley, but could not provide a chronology because of the core distortion. However, New Zealand charophytes have since been shown to have narrow ecological

ranges within a water body (Schwarz *et al.* 2002). All species require a water depth of at least 1 m over them and are usually found at water depths of 2–12 m (Schwarz *et al.* 2002). These depth requirements pose a problem for current interpretations of how the deposit developed and of its surrounding environment. Investigating the implications of this re-interpretation of the habitat of charophytes, with its attendant requirement for deep water, is important in interpreting the environmental history of the lake basin, and hence of the habitats of birds living there.

The lone Pyramid Valley goose represents a local source population of geese which seems, on the basis of the otherwise abundant large birds in the deposit, to have been small. If it was present at a time when there was grassland in the catchment, then that would support the hypothesis that the South Island goose was restricted to grassland and that "forest was not its preferred habitat" (Holdaway & Worthy 1997). To determine whether the goose's presence coincided with grassland, we developed a new detailed chronology of the lake's history and hence of changes in the surrounding vegetation. We also re-evaluated the local ecosystem in the context of the local topography and its tectonic and seismic history, and obtained a high precision radiocarbon date for the goose to align it with its contemporary habitat.

MATERIALS and METHODS

Radiocarbon ages

Goose

The radiocarbon age for the goose (Canterbury Museum Av5406) was measured at the 14Chrono Laboratory, Queen's University, Belfast, UK, and the conventional age calibrated to calendar years using OxCal4.4 software (Bronk Ramsey 1995, 2001) referenced to the SHCal20 curve (Hogg *et al.* 2020). Bone collagen was extracted using a method based on that of Brown *et al.* (1988), but using a Vivaspin® filter cleaning method introduced by Bronk Ramsey *et al.* (2004).

Deposit age-depth model

AGJ obtained five ¹⁴C ages in addition to ages measured for the excavation in 2008 (Holdaway 2015) and four presented by Gregg (1972) for a total of 14. Using PAST Version 3.26b® (Hammer *et al.* 2001), mean calibrated (SHCal20) calendar dates were regressed against depth (cm) of the sample in the stratigraphy to relate subsurface features with the geologic age. In addition, a Bayesian age-depth model was generated using the same radiocarbon ages via the Deposition option in OxCal4.4 (Bronk Ramsey 2009), as a comparison to the regression models.

Palaeolimnology

Sediment cores

The Pyramid Valley site is protected under a Queen Elizabeth II National Trust Covenant. Permission was obtained from the covenant management committee and the landowners (the Hodgen family) for a 4 × 4 m excavation, which was undertaken in February 2008 (Holdaway 2015). Cores were obtained from the northern and western walls of the excavation pit (Holdaway 2015). The cores were taken by embedding two 100 × 100 mm aluminium angle extrusions into the sediment walls, one overlapping the other so that an almost square section of the sediment column was contained. The cores were cut free using monofilament nylon, depths marked and labelled, then wrapped in two layers of self-adhesive plastic vapour barrier, a layer of aluminium foil and a final outer layer of self-adhesive plastic. Both excisions yielded unbroken 1,500 mm cores with minimum distortion of the stratigraphy. Two supplementary “cores” were cut in the same way, with aluminium angle extrusions sized to make a final 1-cm square section. The cores were wrapped and frozen at -18°C until processing.

Charophyte sampling and analysis

Charophyte oospores in successive 1-cm³ blocks cut from main core were counted in water suspension. The gel-like nature of the sediment made it impossible to sieve the microfossils from the organic lake sediment. Each block was disaggregated in a few drops of distilled water in a Petri dish under a binocular microscope, with the sediment being stirred gently with a paint brush.

The oospores sometimes had to be separated from the remaining amorphous organic matter (AOM) using size 00 and 000 brushes. Identifiable specimens were counted once the disaggregated sediment had dried in the dishes as the AOM tended to obscure some of the oospores. Most samples contained only 5–10% inorganic material, mainly as individual quartz grains. Three 1-cm³ samples were taken for each lineal centimetre of the core, and the individual totals of oospores of *Chara globularis* and *C. australis* were recorded and averaged.

Each species was counted by dividing the sediment in the Petri dish into pie-segments with a brush and rotating the dish under the microscope until each section had been counted and the totals recorded. The larger charophyte oospores floated and were relatively straightforward to count. The much smaller *Nitella* oospores were difficult to remove from the sediment gel and were not included in the analyses. Totals for the two species were plotted against depth in the core and against the age-depth model dates for each sample.

Topography

A digital elevation model (DEM) at 5-cm resolution was generated from high resolution aerial photogrammetry, collected using a DJI Phantom Pro® quadcopter. The photogrammetry survey was flown by M. Cockcroft and A. Wandres, Department of Geology (now School of Earth and Environment), University of Canterbury, and the DEM was generated by Dr Wandres using Agisoft Photoscan® (now Metashape®). Ground control points for the photogrammetry survey were collected with a real-time-kinematic (RTK) GPS survey (Trimble R8 GNSS®) relative to a site benchmark at northern end of the present lake. The DEM was further cross-checked against an earlier roving RTK survey of the site collected by BD using the same RTK equipment. The site's lack of forest cover provided a relatively favourable GPS environment and horizontal accuracies are likely to be entirely within 2 cm, with minor variation depending on the detailed satellite geometry during the surveys.

Tectonic setting

An appreciation of the tectonic setting is fundamental to understanding the history of the Pyramid Valley lake site. The North Canterbury Fault and Fold Belt (NCFFB) is an area of intense deformation within the Pacific Plate of the New Zealand Plate Boundary, south of the Hope Fault (Pettinga *et al.* 2001; Litchfield *et al.* 2003). A key feature of the NCFFB is the Culverden Basin, which is appressed between the Hurunui Bluff Fault and the foothill ranges of the Southern Alps (Fig. 2). Pyramid Valley lies in an area of, generally, north and northwest-trending faults that mark the southwestern end of the Culverden Basin and where shortening rates may reach 3–5 m / 1,000 years (Nicol 1991; Nicol *et al.* 1994). Pettinga *et al.* (2001) referred to the westernmost, range front elements of this north-striking fault system as the West Culverden Fault Zone. At the southern end of the West Culverden Fault Zone, the Culverden Basin terminates at the Doctor's Dome, a domal uplift that exhumes basement greywackes of the Pahau subterrane of the Torlesse Supergroup (Nicol 1991; Nicol & Campbell 2001; Campbell *et al.* 2003; Rattenbury *et al.* 2006).

Along the western edge of Doctor's Dome, the Early Cenozoic rocks of the Eyre Group are partially truncated by westward thrusting on the Karetu thrust, forming the MacDonald Syncline. The Karetu Fault probably ruptured most recently 350 ± 60 yrs B.P., near simultaneously with linked faults further south, and as part of a centuries-long episode of uplift of the dome (Nicol & Campbell 2001).

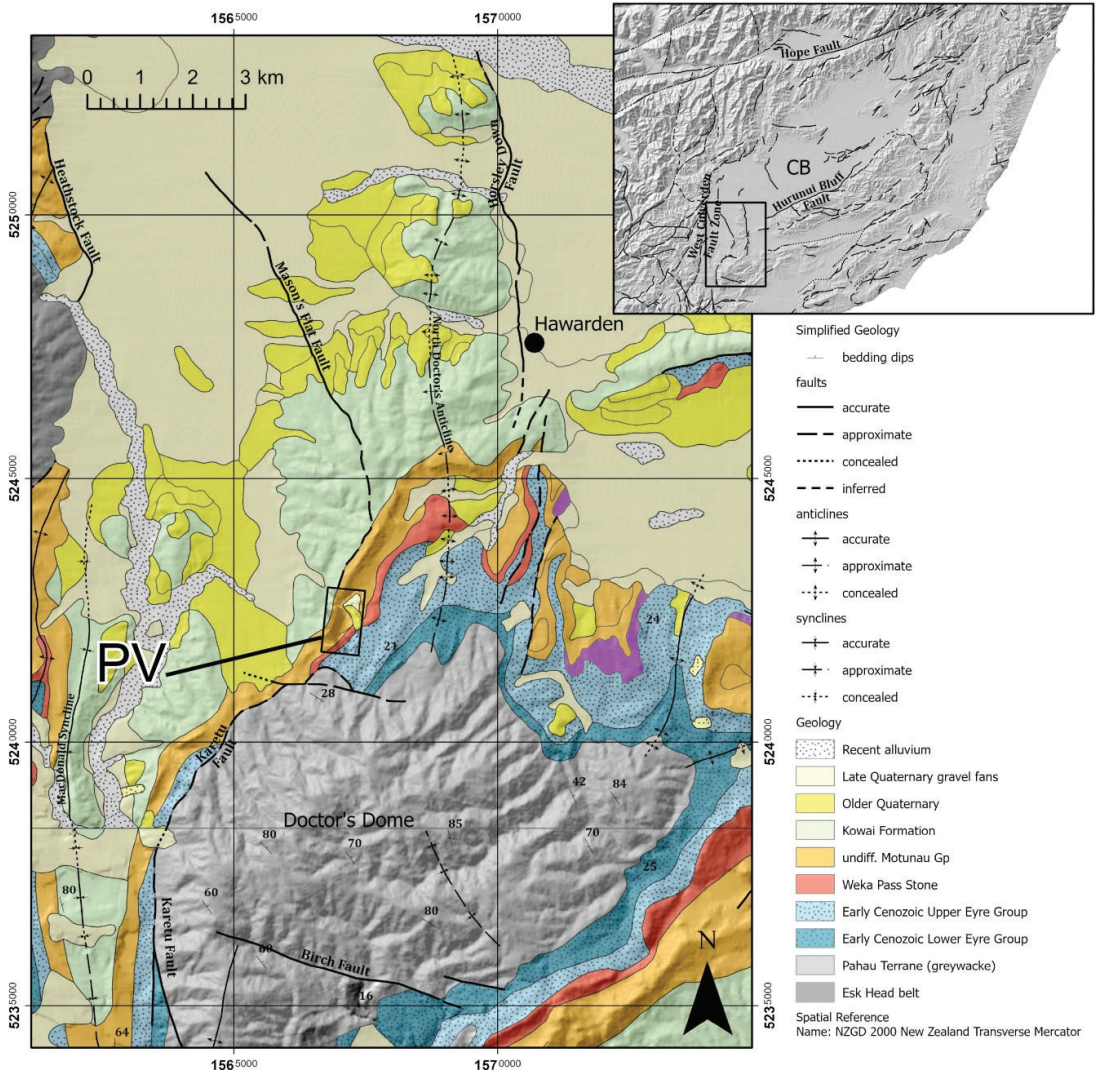


Figure 2. Geology of the study area based on the Kaikoura and Christchurch 1:50,000 geological map sheets (Rattenbury *et al.* 2006; Forsyth *et al.* 2008). Inset shows the regional context of the study area at the southwest end of the Culverden Basin (CB).

North of Pyramid Valley, the left-lateral reverse Mason's Flat Fault forms as a footwall splay of the West Culverden Fault Zone. A Holocene earthquake on the Mason's Flat Fault has thrust Late Pleistocene and Holocene gravel fans eastward along a complex NW-striking fault trace. The timing of that earthquake is unknown (Barrell & Townsend 2012). The northward change from westward thrusting on the Kareru Fault to eastward thrusting on the Mason's Flat Fault is probably at least partially accommodated by

the un-named east-west fault that truncates the Cenozoic stratigraphy on the northern edge of the Doctor's Dome and which is analogous to multiple east-west faults further south, including the Birch Fault (Campbell *et al.* 2012). East of Pyramid Valley, north-striking faults and folds repeat much of the Cenozoic stratigraphy, forming prominent ridges of the Weka Pass limestone and resulting in eastward thrusting on the Horsley Down Fault system. The southward extension of this fault system south of Hawarden is unclear (Barrell & Townsend 2012).

North Canterbury is an active seismic area and the complex tectonic system, with its several known faults, has controlled the drainage patterns and the development of basins such as that which formerly contained Pyramid Lake. Individual earthquakes on the local fault lines may therefore have controlled the distribution of local vegetation by determining the presence and fates of impoundments, and hence of habitats for moa and other birds.

Pyramid Valley geology

Within all this complexity, Pyramid Valley is a lithologically controlled, north-trending valley on the western limb of a north-trending anticline, referred to here informally as the North Doctor's Anticline. The valley is developed between strike ridges of the Oligocene Weka Pass Formation to the east and the Miocene Mount Brown Formation of the Motunau Group to the west (Rattenbury *et al.* 2006). Although relatively simple at first glance, several aspects of the geomorphology are remarkable.

The Motunau Group underlying the Mt Brown Formation limestone doubles in thickness between the southern and northern parts of the study area at a location that coincides with a possible north-side-upthrown, northeast-striking, thrust fault. The fault bounds the northern edge of Pyramid Valley lake and is so interpreted because its trace displaces a small, northwest-plunging valley and ridge a few tens of metres northeast of the lake. The trace is parallel to the Weka Pass Limestone and thus may represent bedding-parallel slip. The divergence of the Motunau group from the Weka Pass stone may be caused by depositional

thickening against a presently west-dipping unconformity, which is locally reactivated as a bedding-plane fault. Alternatively, it may represent localised thickening of the Motunau Group to accommodate the variable wavelength of folding between weaker and stronger elements of the Cenozoic stratigraphy. Either way, the Pyramid Lake scarp, which is parallel to bedding in the Weka Pass Limestone, probably developed by faulting parallel to the bedding.

Another possible tectonic feature is suggested by the presence of a NW-striking, cross-valley scarp of indeterminate origin that aligns with the course of the stream that now drains the valley through the gap in the Mt Brown limestone. The elevated area is mapped as alluvium (Rattenbury *et al.* 2006). However, the Mt Brown Limestone south of the river dips much less steeply than it does north of the river and is apparently displaced westwards on the north side of the river by several meters, consistent with the expected effect of south-westward thrusting on a northeast dipping fault. If this feature is a fault, it does not appear to displace the Weka Pass Limestone and thus may merge with the same bedding plane that forms the Pyramid Lake Scarp.

RESULTS

Radiocarbon ages

Goose

The Pyramid Valley goose's conventional radiocarbon age (UBA42951) of 928 ± 34 years B.P. (Before Present, Present = 1950 CE) is equivalent to a calendar date 1σ range of 1062 ± 23 CE. This age is listed, along with other radiocarbon ages available for *Cnemiornis* spp., in Table 1.

Table 1. Radiocarbon ages for New Zealand geese (*Cnemiornis* spp.). Calibrated dates and date ranges from OxCal4.4, using the SHCal20 curve (Hogg *et al.* 2020). Sources: 1, this paper; 2, Wood *et al.* (2017); 3, Worthy & Holdaway (2002); 4, Worthy & Swabey (2002). Locations are shown in Fig. 1. The South Island birds constitute 5% of the recorded individuals (see text). Museum accession codes: Av, Canterbury Museum, Christchurch; AU, Auckland University Department of Geology; WO, Caves Museum, Waitomo. The Omih Stream specimen will be lodged with the Museum of New Zealand Te Papa Tongarewa.

Site	Museum	Lab. no.	CRA	SD	$\delta^{13}\text{C}$	Calibrated dates B.P.			
						Mean	SD	Median	Source
Pyramid Valley	Av5406	UBA42951	1,062	23	-25.4	928	34	935	1
Omih Stream, SH#1	RNH colln	NZA24925	18,954	75	-21.9	22,817	124	22,846	1
Finsch's Folly	2013.2	Wk33990	1,646	25	-24.09	1,486	38	1,488	2
Metro Cave	AU9789	NZA2141	15,260	140	?	18,507	152	18,493	3
Zweiholen	WO446	NZA9071	22,630	130	?	26,879	226	26,946	4

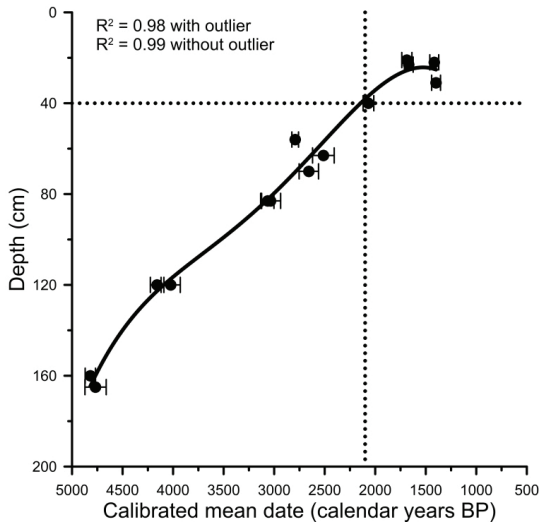


Figure 3. Quartic age-depth model for sediment deposition in the Pyramid Valley lake bed. Dotted lines indicate depth and date of the increase in grass and sedge pollen interpreted by Moar (1970) as marking Polynesian arrival. Equation is: Y (date) = $2.469E-6X$ (depth)⁴ - $0.002007 * X^3 + 0.4387 * X^2 - 2.886 * X + 1426$; $n = 14$. Linear $R^2 = 0.98212$; quadratic $R^2 = 0.98438$; cubic $R^2 = 0.98963$; quartic $R^2 = 0.98964$. See Appendix for age-depth model analyses.

Age-depth model

Radiocarbon ages available for the development of a depth-age model for the Pyramid Valley deposit are shown in Appendix Table T1. The calibrated ages in Johnston (2014) were recalculated using the later SHCal20 Southern Hemisphere calibration curve (Hogg *et al.* 2020), via OxCal4.4 (Bronk Ramsey 2009).

After comparing polynomial regressions of mean dates against depth with the Bayesian model (Appendix Fig. A1), the quartic regression (Fig. 3) was chosen as the best model for the changes in the deposition rate through time and for the dates of significant events in lake history (Fig. 3). Modelled probability distributions for the calibrated calendar age ranges are shown in Appendix Fig. A2.

Charophytes

Proceeding upwards from the bottom, charophyte oospores were recorded first at 95 cm (*c.* 3,400 years B.P.) (Fig. 4), then again at 89 cm (*c.* 3,300 years B.P.) after which they were present in every sample up to 71 cm depth (*c.* 2,900 years B.P.). The absence of oospores near the bottom of the core is associated with the lowest levels being within a well-preserved *Carex* sedge vegetation indicating low water levels.

Highest oospore counts were from 57 to 49 cm (*c.* 2,450–2,250 B.P.), in which interval both *Chara australis* (which grows in deeper water) (Schwarz *et al.* 2002) and *C. globularis* were present. No oospores were recovered from the 70 or 69 cm samples (*c.* 280 years B.P.), and they were also absent from the 59 to 57 cm samples (*c.* 2,550–2,450 years B.P.). No oospores were recorded from samples above 51 cm depth (*c.* 2,100 years B.P.) (Fig. 4).

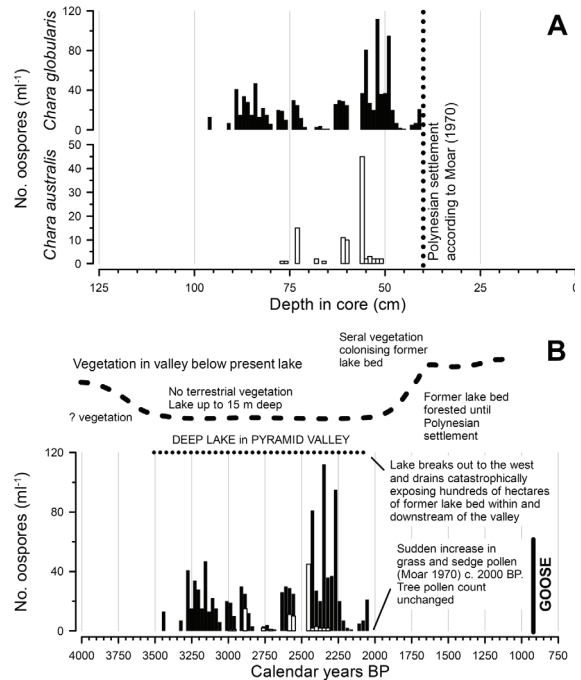


Figure 4. Counts of black (*Chara globularis*) and white (deep water) (*C. australis*) charophyte oospores in contiguous 1 cm samples of the Pyramid Valley sediment core in relation to revised model of lake history and surrounding vegetation. **A**, mean counts of charophyte oospores versus depth on core. **B**, mean counts versus modelled date for sample depth. Dates derived from age-depth model (relationship in Fig. 3).

Topography

The extent of flooding of the southern arm of Pyramid Valley with even a small (≥ 25 cm) increase in water depth in the present lake is shown in a contour map (Fig. 5) generated from the GPS data. Profiles across and along the southern arm of the valley are located on the Digital Elevation Model with contours drawn at 1 m intervals above mean sea level (Fig. 6).

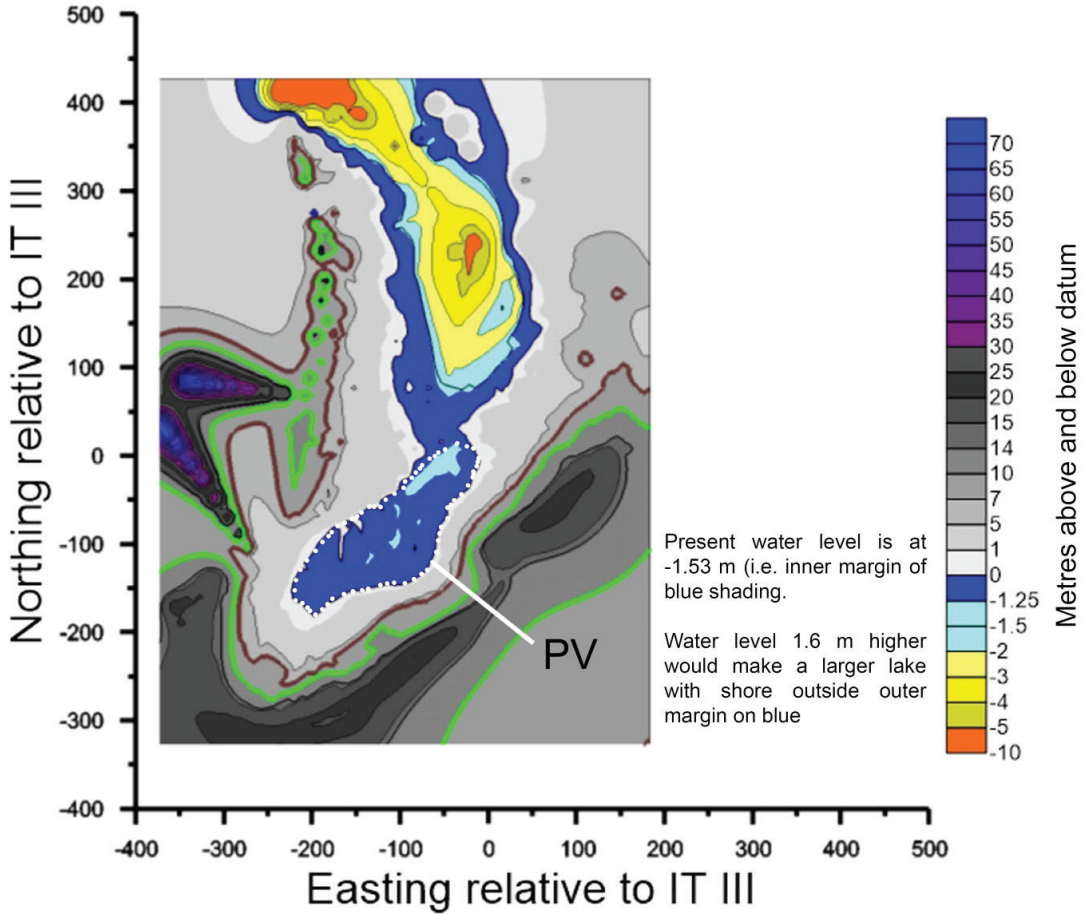


Figure 5. Contour map of southern arm of Pyramid Valley *sensu lato*. Note that the present lake (PV) is an enclave offset from the rest of the valley, and that a minimal increase in water depth entails the lake extending throughout the valley (dark blue). Map generated from GPS traverse data. Traverses and mapping by BD. IT III is a survey tube just outside the north-eastern corner of the boundary fence of the Queen Elizabeth II Covenant (Plan LT43834, "Proposed Open Space Covenant over Lot 2 D.P. 4721, Block X, Waipara Survey District". It is 18.36 m south-east of the Bench Mark referred to in Topology section above).

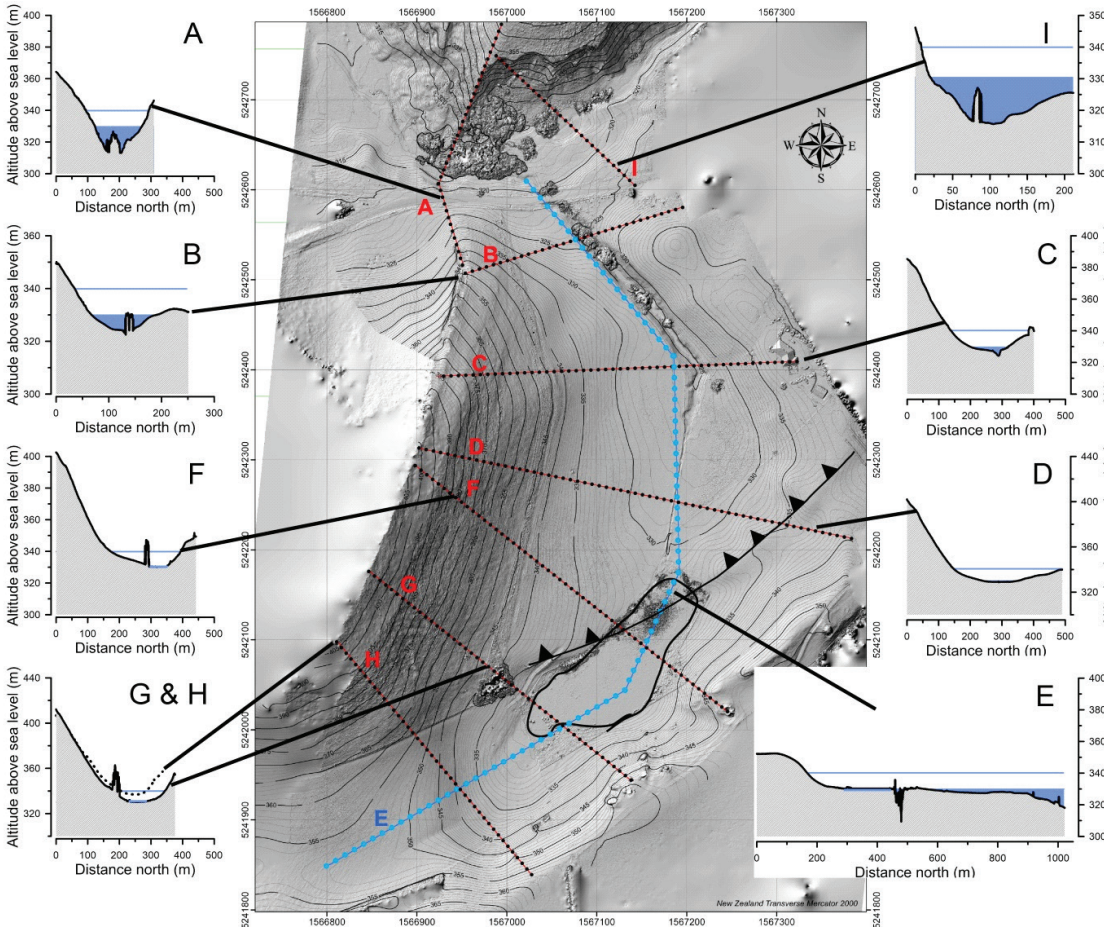


Figure 6. Digital elevation model of the southern arm of Pyramid Valley *sensu lato*, with valley profiles and profile of breakout gap (A). Maximum water level in the present (1 ha) lake outlined at southern end of valley is shown as blue shading in profile panels. Tall “structures” in profiles A, B, F, G, and I are trees; pattern at northern end of present lake and “deep” point in profile E are artefacts of reflection from the lake in the photogrammetry. Grid in main image is New Zealand Transverse Mercator 2000. In the present lake, excavations have been concentrated along the north-western shoreline and in the middle of the northern basin. Low cliffs at northern ends of lines of profiles A and I are shown in Fig. 7. Grey line enhanced by line with triangles indicating side of uplift passing diagonally southwest along north-western shore of lake is a fault trace: the present lake has been offset from the rest of the valley by oblique movement of this fault.

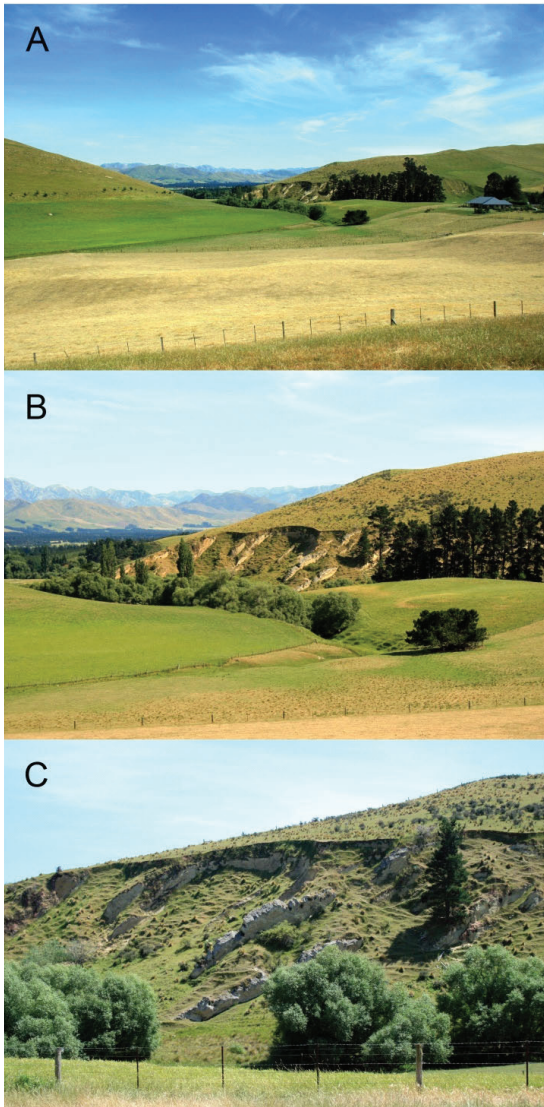


Figure 7. Southern arm of Pyramid Valley. **A**, View northwest from above northern end of present lake, showing breakout gap in ridge of Mt Brown sandy limestone (central distance) and dry outlet stream. **B**, Enlarged central section of view in A showing the near 90° turn in the outlet stream bed towards the northwest, deepening as it does so. **C**, Detail of cliffs on northern side of breakout gap. Strata of brittle Mt Brown limestone stand proud of the surface, where soft clay has been eroded from between them. The willow (*Salix* sp.) trees stand in a deeply cut channel at the entrance to a narrow valley leading to the Waipara River flats beyond.

DISCUSSION

In contrast to the present view of a static environment around Pyramid Valley, with forest surrounding a small, possibly ephemeral, lake, the charophyte fossil record shows that the present 1 ha lake is a small remnant, in a high level enclave, of a much larger and deeper water body. For 1,500 years, oospores of deep water algae were deposited in fluctuating numbers in the accumulating sediment. They were shed by plants both growing within the small enclave when the lake was deep enough and drifted in from plants in the larger lake when the water bodies were still linked. The enclave itself was too shallow to support charophyte growth (Schwarz *et al.* 2002).

Gaps in the deposition record when the level of the main lake was below the lip of the enclave. In the strongly seasonal North Canterbury climate (Worthy & Holdaway 1996; Holdaway & Worthy 1997), lake levels would have fluctuated seasonally as well, but for most of its existence the large lake was deep enough in summer for the charophytes to grow and reproduce.

Recognition of a larger lake in the valley encompassing the smaller water body and deposit known for many years as “Pyramid Valley” creates a problem of nomenclature to distinguish one from the other despite their being aspects of the same structure. Hereafter, to maintain continuity of usage, the 1 ha enclave that contains the fossil deposit is Pyramid Valley (PV) and the larger lake is Pyramid Valley Lake (PVL).

Pollen records (Harris 1955; Moar 1970) set against the new age-depth model shows that until c. 2,050 B.P. (50 BCE) the area supported a forest of hardwoods with emergent matai (*Prumnopitys taxifolia*) podocarps. The lake margins fluctuated, with emergent wetland vegetation (Moar 1970). Sometime around 2050 B.P. (50–100 BCE), the Mt Brown limestone ridge failed at a point on the line of a much earlier west-east drainage feature (Fig. 7) and the PVL avulsed westwards down the old dry valley across the adjacent plain and into the upper Waipara River.

Why the ridge collapsed is under investigation. The presently favoured mechanism is based on the underlying structure revealed in the still-eroding cliffs on the northern side of the ridge break. Here brittle limestone strata are separated by soft, mobile clays. High lake levels along the ridge could mobilise the clay (as it is still eroding on the western side) causing it to slump and cease to support the limestone plates. Those in turn could then break away under their own weight: once water was flowing through the gap, the flow would have shaken and flexed them until they failed and fragmented in turn as further supporting clay was washed away. A catastrophic rate of flow is

supported by the presence of a 10-m deep gouge in the valley floor at the break, below the cliffs, and the absence of limestone blocks of the Mt Brown strata in or beyond the gap. The ridge failure may have been triggered by an intense rainfall event which overflowed the PVL, or by a major earthquake caused by the rupture of one or more faults, including the Mason's Flat Fault which lies along the western foot of the enclosing ridge (Fig. 2).

The deep gully of the lower outlet stream, cut in indurated sediment is far deeper than could be cut in those sediments by any stream outflow from the present lake. However, it could have been cut by base flow during a catastrophic breakout. The tectonic structure of the valley itself may itself be responsible for the partial isolation and raised position of Pyramid Valley, as it is bounded on the outlet side by a fault trace (Fig. 6).

Regardless of the mechanism of the ridge failure, its timing is clearly shown by both the permanent cessation of deposition of charophyte oospores and the sudden appearance of abundant sedge and grass pollen. Draining of PVL would have left nearly 50 ha of bare lake bed within the valley itself and perhaps several square kilometres of flattened forest in the outlet valley and on the plain beyond.

At the onset of the high grass and pollen at 40 cm depth, in a "transition layer", Harris (1955) recorded the terrestrial hounds tongue fern (listed as *Microsorium*, now *Zealandia pustulata*). Although it grows in forest, the fern also colonises open ground: it is drought tolerant and can be found in open, dry environments (New Zealand Plant Conservation Network 2021). Moar (1970) did not mention its presence, and the sudden abundance of hounds tongue fern may signal the appearance of bare ground near the lake as it was not a feature of the record before or for long after the lake drained. The fern would have been replaced rapidly by grasses, sedges, and bracken fern (*Pteridium esculentum*). Moar (1970) suggested that the increase in grasses and other seral vegetation at 40 cm resulted from deforestation by Polynesian fires, but his figure does not show any contemporary reduction in tree pollen.

Contrary to Moar's (1970) interpretation, the new age-depth model shows that the sudden increase in grass and sedge pollen at 40 cm depth occurred at c. 2,100 yrs B.P., predating by at least 1,400 years the removal of the local forest by Polynesian fires, but contemporary with the abrupt end of charophyte deposition in the PV sediments. Hence, the changes in the pollen profile can now be confidently attributed to the sequence of seral vegetation colonising the newly vacated bed of the PVL. The likely extent of that area is shown in Figures 6 & 8. The forest surrounding the PVL

and its fauna was unaffected and over the next few centuries spread across the former lake bed.

For a brief period, perhaps less than a century, after the PVL drained, there was grassland near Pyramid Valley. Holdaway & Worthy (1997) appealed to the unlikely presence of shrubland on the surrounding hills to explain the presence of a New Zealand quail (*Coturnix novaezelandiae*) in the deposit. The presence of seral vegetation following the lake drainage now offers an alternative explanation. The quail bones were not located in the Canterbury Museum collections during an intensive search (Holdaway & Worthy 1997), but if they can be found an AMS radiocarbon age could resolve that issue.

The presence of grassland near the deposit for a significant period, if only for a few decades, means that the goose's assumed habitat was present, as was an avenue for its colonisation from the Waipara River plain via the newly cleared outwash valley. However, there is no evidence that South Island geese reached Pyramid Valley then. The lone goose died in the 11th century CE, 1,000 years after the PVL drained, more than enough time for forest to have spread right across the former lake bed. There is no corridor of open country where water could flow into the larger lake. It was and is a closed basin whose saddles are above the levels of adjacent valleys. Any drought that could have changed the vegetation to replace forest with grassland would have had to have been protracted and would have been clearly visible in the pollen record. There is no such record. The rarity of other grassland species in the deposit (Holdaway & Worthy 1997) supports the brevity of the presence of grassland at Pyramid Valley.

The radiocarbon age for the Pyramid Valley goose brings the number of ages available for the genus to five, four for the South Island goose and one for the North Island species. The sample is too small to reveal detailed trends in distribution, but some patterns are apparent. The North Island goose lived near Waitomo just before the Oruanui super eruption of Taupo Volcano (Vandergoes *et al.* 2013). The local vegetation at that time was probably lowland rain forest judging from the contemporary presence of the moa *Anomalopteryx didiformis* (Millener 1981), a rainforest indicator species (Worthy & Holdaway 2002).

In the South Island, forest birds were preserved with the geese in Finsch's Folly Cave (Wood *et al.* 2017). According to the environmental reconstruction developed here, the goose at Pyramid Valley co-existed with forest birds. However, the other two radiocarbon dated South Island geese are much older. The goose from Metro Cave on the Nile River near Charleston on the West Coast (Fig. 1) lived there as the climate was

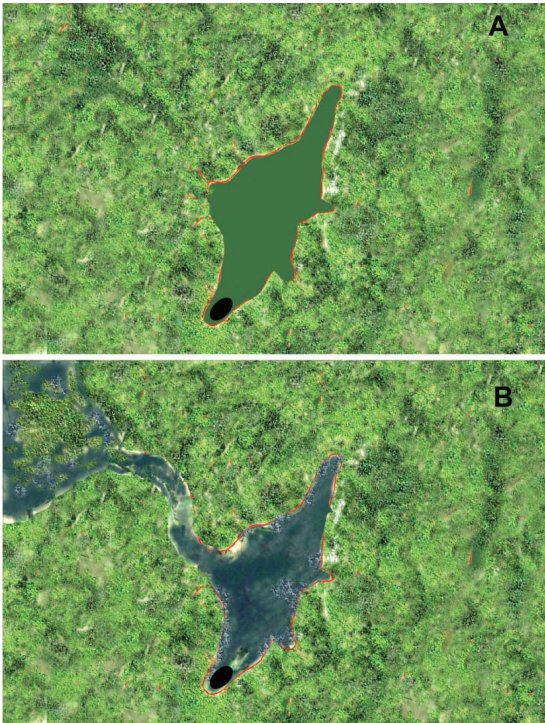


Figure 8. Reconstruction of the former extent and breakout path of Pyramid Lake, in relation to the position and extent of the present lake. **A**, Extent of lake with depth of 8 m at present lake; faint shoreline terraces on slopes to west of present lake indicate a possible maximum depth of *c.* 16 m. **B**, Position of valley wall failure and breakout stream down old drainage valley to west, with approximate extent of newly exposed lake floor and that cleared of vegetation by breakout flow.

warming after the most recent (Otiran-Weichselian) glaciation so would have occupied glacial low forest and shrubland (Newnham *et al.* 2013). The Omihi Stream goose from North Canterbury, 18 km from Pyramid Valley, lived there during the coldest part of the glaciation. The dated bone, a well-preserved tarsometatarsus whose sharp edges had not been worn by post-mortem transport, was recovered from clean sands that had accumulated in a stream delta in a wetland at a time when the local vegetation was indeed dominated by grassland.

What emerges, therefore, is that, far from being an obligate inhabitant of short turf grassland like its Australian relative, the South Island goose was able to occupy different habitats. Far more so than *Cereopsis*, the New Zealand birds were confronted with a landscape dominated by woody vegetation throughout their post-colonisation evolutionary history. During that time they lost entirely the power of flight.

Like the harriers, they retained their ancestral bill form. It is easier for waterfowl (and rails) than for other birds to become flightless when there is no selection pressure from predators. Unlike other birds, duck and rail wings develop later than their legs, so any selection for flightlessness would not be compromised by development processes in which wings developed before the legs (Olson 1973; Slikas *et al.* 2002). Bills adapted to cropping vegetation can cope easily with tree leaves as well as grass. Similar-sized goose-like birds (*moanalo*, whose ancestors were *Anas* ducks) occupied forest in pre-human Hawaii (Olson & James 1991). One species, *Thambetochen cauliodous*, at least, was folivorous and perhaps even a pteridivore (James & Burney 1997). Even the Hawaiian goose *Branta sandwichensis*, a true goose, can, despite its “normal goose bill”, browse tree foliage (Fig. 9).



Figure 9. Goose bills adapted to cropping grass can also be used to browse tree foliage. Juvenile Hawaiian geese (*Branta sandwichensis*) foraging on tree leaves while their parents graze the grass below. Note that some of the lower branches have already been stripped bare. Photo: RNH, Regent's Park (London) Zoological Gardens, May 1988.

Our results show that the habitat and biology of species in the rich fossil avifauna of Pyramid Valley must be interpreted in relation to a changing local environment. Access to the site, and hence possibility of being incorporated in the deposit, would have been governed by the lake level, as well as defining when a species was “made available” by the local presence of its habitat. The implications of the presence of any species in a fossil deposit must be assessed therefore on the basis of detailed

chronologies of both that species and of the local environment. On that basis, the presence of the South Island goose at Pyramid Valley in the 11th century CE when the area was forested and not during the brief period when grassland and an avenue of approach were available provides further evidence of the adaptability of these flightless birds. One important conclusion from the study is that, to understand the dynamics of an extinct system and the biology of an extinct species, even to explain the presence of a single individual of a species in an otherwise rich fossil avifauna, it is necessary to employ information from other, apparently unrelated, disciplines.

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APPENDIX. Age-depth model ages and Bayesian age-depth model for the Pyramid Valley lake bed deposit

Table A1. Radiocarbon ages for organic materials from the Pyramid Valley lake bed: shaded, ages used in age-depth model. Sources: *AJG; this study; ²Holdaway *et al.* (2014); ³Gregg (1972). Dated materials: G, gyttja; BG, bone gelatin; PM, unidentified fossil plant material; Peat, lower black peat; *Carex*, leaf of fossil *Carex secta* in growth position at base of excavation, **samples from same depths dated independently.**

OxCal4.4		Unmodelled B.P. (Before 1950 CE)										Unmodelled BCE/CE					
SHCal20		68.3% CI					95.4% CI					68.3% CI			95.4% CI		
Laboratory number	CRA	SD	$\delta^{13}\text{C}$	From	To	From	To	Mean	SD	Median	Depth (cm)	From	To	Mean	SD	Median	Material
*Direct AMS-PV 31	1558	30	-11.9	1424	1352	1513	1314	1398	44	1393	31	526	598	552	44	557	G
*Direct AMS-PV 22	1572	27	-19.8	1453	1362	1518	1352	1416	44	1407	22	497	588	534	44	543	G
¹ NZA29769	1824	25	-21.4	1730	1619	1810	1610	1687	50	1700	21	220	332	263	50	250	BG
¹ NZA29766	1812	25	-19.0	1722	1615	1745	1590	1668	43	1657	23	229	336	282	43	294	BG
Direct AMS-PV 40	2137	29	-19.8	2095	2015	2288	2000	2067	53	2062	40	-146	-66	-118	53	-113	G
Direct AMS-PV 63	2473	29	-15.4	2681	2364	2703	2353	2513	107	2485	63	-732	-415	-564	107	-536	G
³ NZ619	2620	49	NA	2762	2522	2844	2488	2657	96	2700	70	-813	-573	-708	96	-751	PM
Direct AMS-PV 56	2714	23	-13.4	2844	2752	2851	2746	2792	33	2781	56	-895	-803	-843	33	-832	G
³ NZ620	2930	63	NA	3151	2946	3227	2851	3035	99	3032	83	-1202	-997	-1086	99	-1083	PM
¹ NZA29785	2954	25	-25.0	3146	2997	3171	2956	3063	61	3061	83	-1197	-1048	-1114	61	-1112	PM
³ NZ621	3720	60	NA	4143	3922	4231	3840	4024	95	4023	120	-2194	-1973	-2282	95	-2074	PM
¹ NZA29791	3818	25	-27.3	4234	4091	4289	3993	4158	67	4157	120	-2285	-2142	-2209	67	-2208	PM
³ NZ622	4280	62	NA	4869	4628	4967	4573	4767	105	4758	165	-2920	-2679	-2818	105	-2809	Peat
¹ NZA29811	4293	20	-25.5	4858	4825	4870	4652	4819	51	4838	160	-2909	-2876	-2873	51	-2889	<i>Carex</i>
¹ NZA29765	3359	25	-21.0	3570	3487	3680	3456	3538	46	3531	U	-1621	-1538	-1589	46	-1582	BG
¹ NZA29819	3892	20	-23.1	4399	4159	4407	4155	4280	71	4278	U	-2450	-2210	-2331	71	-2329	Wood

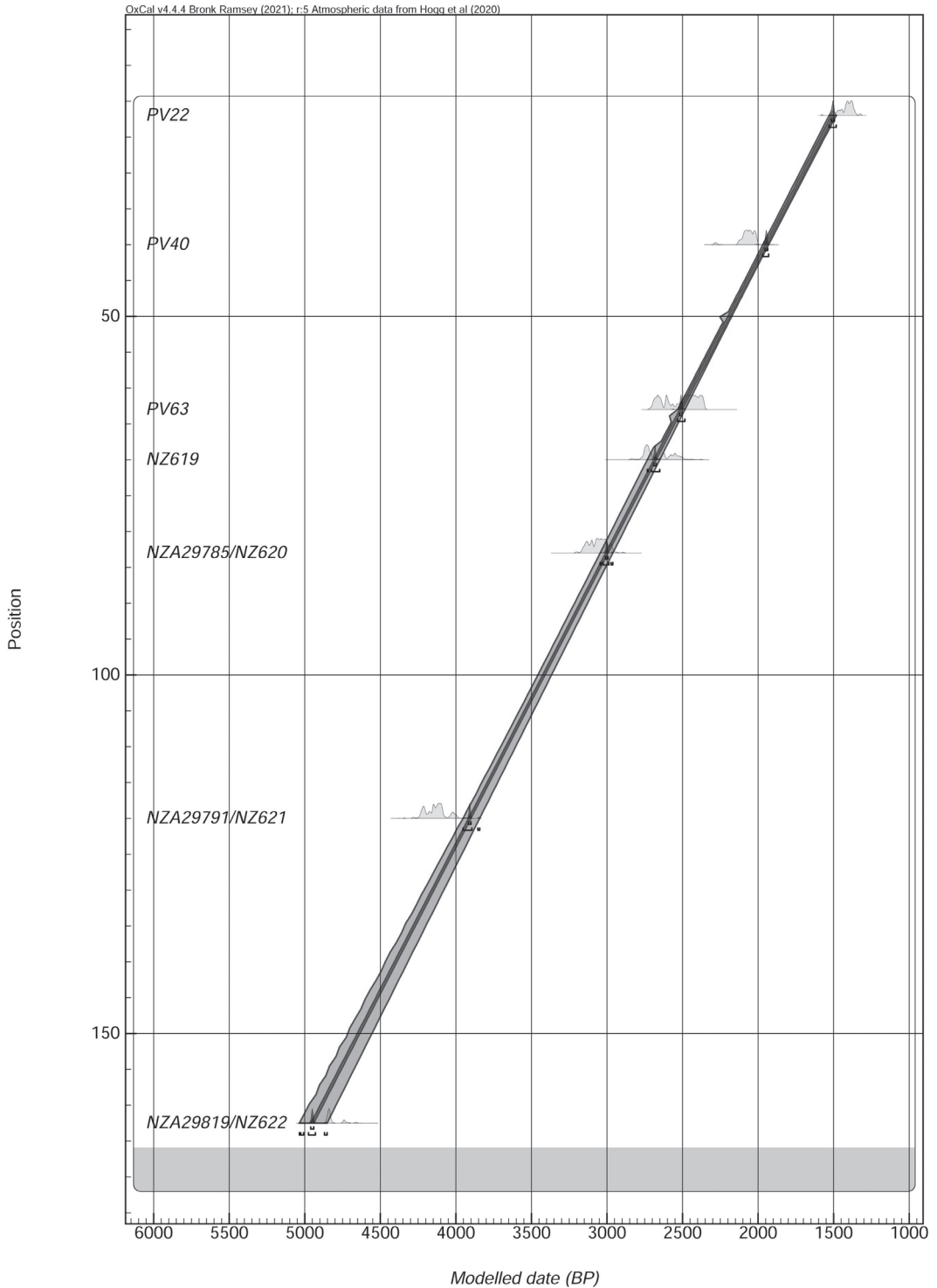


Figure A1. Bayesian age-depth model (OxCal 4.4, Deposition Model, SHCal20 curve (Hogg *et al.* 2020) for Pyramid Valley lake bed deposit.

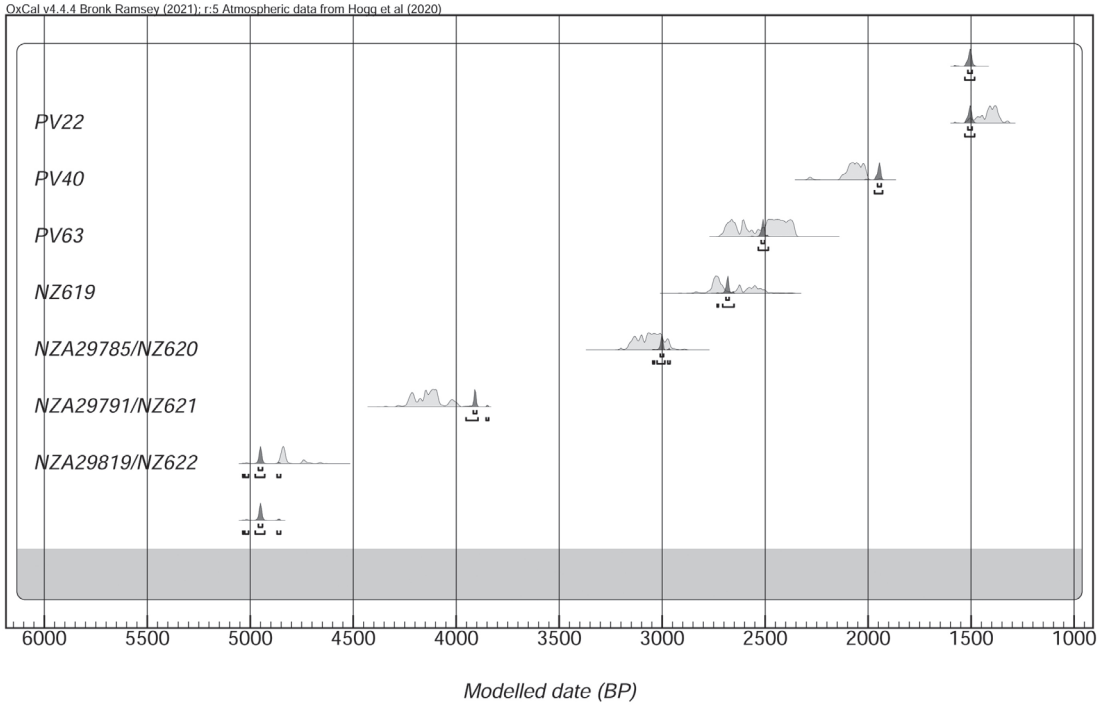


Figure A2. Bayesian modelled calibrated date distributions (OxCal 4.4, Deposition Model, SHCal20 curve) (Hogg *et al.* 2020) for the radiocarbon ages used to generate the Pyramid Valley lake bed deposit age-depth model, with date probability distributions for the start and end of the sequence.