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SHORT NOTE

A Holocene fossil South Island takahē (*Porphyrio hochstetteri*) in a high-altitude north-west Nelson cave

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South Island takahē (Porphyrio hochstetteri) is one of New Zealand's most critically endangered endemic bird species (NZ threat classification system A (1/1), "nationally vulnerable") (Robertson et al. 2017). Maori lore, and as few as 4 recorded sightings during the 19th Century suggest that takahē occurred only in high Fiordland valleys and possibly the Nelson region in recent history (Williams 1960; Reid 1974). The birds were so infrequently seen that they were assumed extinct until a population of ~250-500 was discovered in the Murchison Mountains, Fiordland, in 1948 (Reid & Stack 1974). This population sharply declined until intensive conservation commenced in 1981 (since fluctuating between ~100-180 birds) (Crouchley 1994). Takahē have also been moved to predator-free offshore islands, "mainland islands", and captive breeding centres across New Zealand, and the total population is gradually increasing (presently ~300 birds). Additionally, there is now an initiative to relocate takahe to areas they occurred in prehistory, and 18 takahē were recently released into the subalpine tussock habitats of Gouland Downs, north-west Nelson, in March 2018. However, selecting appropriate localities for takahē reintroductions depends on understanding the bird's natural ecology and distribution prior to human settlement in New Zealand.

The fossil record confirms that takahē was once widespread across the South Island from sea-level

to the alpine zone (Beauchamp & Worthy 1988; Worthy & Holdaway 2002). A related species, the North Island takahē or "moho" (P. mantelli) became extinct before the 20th Century and is primarily known from fossils, although a live bird may have been caught in 1894 ("takahē" in this article will refer to P. hochstetteri only) (Phillipps 1959; Trewick 1996; Worthy & Holdaway 2002). It has been argued that takahē are a specialist tussock-feeding "glacial-relict" species, and thus most lowland takahē subfossils date from the glacial period when grasslands and herbfields were more extensive (Mills et al. 1984). However, subsequent surveys of takahē subfossil data suggest that takahē occurred at low altitudes during the Holocene, and also lived in forest and wetlands as well as grasslands (Beauchamp & Worthy 1988). Furthermore, takahē remains in archaeological middens across the South Island (including coastal sites) confirms that the species was widely hunted by early Maori (e.g. Barber 1994; Scofield et al. 2003). It is now generally accepted that takahe numbers contracted due to human activity and introduced mammals, and the Murchison Mountains region was the last takahē stronghold due to its isolation rather than a preference for this subalpine habitat (Bunin & Jamieson 1995). It has even been suggested that a subalpine habitat may be suboptimal for takahē (Beauchamp & Worthy 1988; Worthy & Holdaway 2002; Hegg et al. 2012).

Although archaeological or fossil remains of takahē are widely distributed throughout the South Island,

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very few originate from high altitudes (Trewick & Worthy 2001). Only 1 takahē fossil specimen (Museum of New Zealand accession MNZ S35514) has been found above the present-day tree-line (Farriers Cave, Mt Arthur, Nelson at 1,270 m) (Trewick & Worthy 2001). The next highest takahē fossils are Pleistocene-aged specimens from Hodges Creek at ~900 m near Mt Arthur, which is currently in tall silver beech (*Lophozonia menziesii*) forest but would have likely been in alpine tussock/herbfields during the Pleistocene (Worthy 1997).

During an expedition in the subalpine (~1,000 m) Euphrates Cave (Rowe et al. 1994; Wood et al. 2012), North-west Nelson, Kahurangi National Park, in March 2017, our team observed a previously unrecorded takahē skull (Fig. 1), the first known from this cave system and the second highest-altitude takahē subfossil known (Trewick & Worthy 2001). The fossil was positively identified as P. hochstetteri by an expert on New Zealand's fossil bird species (Trevor Worthy, *pers. comm.*). Euphrates Cave runs within the limestone Garibaldi Plateau, of which the eastern edge terminates in a short buttress cliff (<100 m) where the main cave entrance and several smaller side-entrances occur. The vegetation communities of the Garibaldi region are described in detail by Druce et al. (1987).

The Euphrates Cave takahē subfossil comprises a complete cranium and upper mandible, found lying on the surface of the cave sediment. Other bone fragments were seen nearby partially embedded in silt and cave sediment, however these were not excavated, and their identity remains unknown. As the purpose of our expedition and our permit was not to excavate or collect osteological subfossils, we left the skull in-situ. The skull was found within a small side passage, which was accessed by traversing over 200 m into the system from the main entrance. However, this small passage and 2 adjacent passages terminate near a small entrance opening into the buttress cliff (~10 m distance from the takahē skull) which may represent the source of origin for the subfossils. As this entrance is relatively inaccessible from the forest below, these subfossils likely fell from the alpine plateau above and were rolled or washed into their present position.

As we left the takahē skull *in situ*, its age could not be determined with radiocarbon dating. However, during the Last Glacial Maximum (LGM), *c*. 26.5– 19 ka, mountainous regions of the South Island including North-west Nelson were extensively glaciated, and Garibaldi Plateau is shown covered in ice in recent simulations (Barrell 2011). Snowlines also lowered by ~800–1,000 m in New Zealand during the LGM (Putnam *et al.* 2013), thus the Garibaldi Plateau would have had an environment like that found at 1,900–2,300 m, which is close to or above the elevation limit of tussock in other parts



Figure 1. The identified takahē (*Porphyrio hochstetteri*) skull *in-situ*. The plastic container nearby, but not directly next to skull and thus providing an approximate scale only, measures roughly 60 mm length.

of the South Island (Mark *et al.* 2013). Therefore, the Garibaldi Plateau was either very sparsely vegetated or inhospitable for takahē during the peak of the LGM. In addition, no Pleistocene-aged subfossils of other alpine-dwelling birds, such as upland moa (*Megalapteryx didinus*) or kea (*Nestor notabilis*), are known from >950 m (which may be due to a lack of dated materials) (Worthy 1997; Worthy & Holdaway 2002). As a result, the takahē skull from Euphrates Cave is most likely Holocene in age, suggesting that the birds were present in the area when humans arrived in New Zealand.

The Euphrates Cave takahē skull provides additional support to the hypothesis that takahē were widespread across the South Island's subalpine habitats and lowland areas at the time of human arrival in New Zealand (Trewick & Worthy 2001). This inference also suggests that takahē are not a glacial-relict taxon or intolerant of forest habitats. The subalpine habitats where takahē subfossils have been found (Garibaldi Plateau and Mt. Arthur), as well as in the valleys of the Murchison Mountains where takahē still live, all occur in areas surrounded by dense beech forest. These "islands" of tussock habitat are probably far too small to have supported stable, isolated takahē populations since the last glaciation. Instead, this distribution better supports takahē having a high mobility and diverse habitat tolerance, and alpine populations of the birds were unlikely to have been isolated from one another. Overall, conservation initiatives can consider subalpine tussock or herbfields, as well as lowland areas, to be appropriate habitats for takahē. There is thus no prehistoric evidence to support suggestions that higher altitudes were preferred by takahē.

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