

A FOSSIL RECORD OF THE BLACK STILT *HIMANTOPUS NOVAEZELANDIAE* GOULD, 1841

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ABSTRACT

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A fossil black stilt (*Himantopus novaehollandiae* Gould, 1841) is reported from Pyramid Valley swamp, North Canterbury, New Zealand. The proportions of the long bones of the fossil wing and leg are similar, but not identical, to those of a small sample of recent black stilts. The proportions differ markedly from those of pied stilts from both New Zealand and Australia. Long bone dimensions of New Zealand pied and recent black stilts are intermediate between those of Australian pied stilts and of the fossil. Both species of stilt in New Zealand appear to have diverged morphologically from their parent populations.

KEYWORDS: fossil - bird - New Zealand - pied stilt - black stilt - *Himantopus novaehollandiae* - *Himantopus leucocephalus* - evolution - hybridisation.

INTRODUCTION

Pyramid Valley Swamp, near Waikari, North Canterbury, New Zealand (42°59'30"S 172°35'50"E), contains one of the best-known deposits of Holocene vertebrates in New Zealand (Falla 1941, Duff 1949, 1951, Scarlett 1955, 1969, Gregg 1972, Burrows 1989, Holdaway & Worthy submitted). The fossils collected from 1939 to 1973 include a range of water birds, mainly ducks and rails, but only one species of wading bird (Charadriiformes) (Falla 1941, Scarlett 1955, 1969, Holdaway & Worthy submitted).

Scarlett (1955) referred the charadriiform material to *Himantopus himantopus* but used the non-committal "stilt" for the vernacular name. The two authoritative lists current at the time adopted different nomenclatures for the New Zealand pied stilts. The New Zealand checklist (Fleming 1953) listed the pied stilt as subspecies *leucocephalus* of *H. himantopus*. Oliver (1930, 1955) followed Gould in treating it as a separate species (*Himantopus leucocephalus*).

Fleming (1953) and Oliver (1930) agreed that the black stilt was a separate species, but differed in their spelling of the epithet; Fleming used *novaezealandiae*, whereas Oliver used *novae-zealandiae*, but changed it later to *novaezealandiae* (Oliver 1955). Therefore, although the Pyramid Valley bird material was not listed as such, the use of *himantopus*, under which species it is currently listed (Turbott 1990), means that Scarlett's record was of the pied and not the black stilt.

The reluctance to identify the material to species was understandable. A lack of comparative material meant that potential differences between the two taxa could not be tested. In any event, "stilt" was probably a sufficient name because the two species were regarded as being very closely related. Indeed, Oliver (1930: 320) regarded the black as "merely a mutant of the white-headed species" even though he listed the two forms separately. Stead (1932) did not discuss the black stilt separately, but discussed Oliver's views and his own observations briefly in a section on the pied stilt. Stead's own conclusion, that

the variation in plumage pattern of the pied stilt in New Zealand resulted from a long history of interbreeding with black stilts, was prescient (Pierce 1982, 1984).

At present, the black stilt is accepted as a distinct, endemic, and endangered species under the name as originally spelled (*Himantopus novaeseelandiae*) by Gould. The species has declined as a result of predation by introduced mammals, loss of habitat, and introgressive hybridisation (Pierce 1982). At the same time, the pied stilt has increased to be one of the most abundant wading birds in New Zealand.

The almost complete replacement of one taxon by the other means that the identity of the original stilt population of New Zealand is important to an understanding of the processes affecting the taxa, and the history of their interactions.

In this paper, the Pyramid Valley stilt bones are identified as being the first fossil record of the black stilt *H. novaeseelandiae* on the basis of limb bone length proportions. Limb bone lengths and intermembral proportions of the fossil are compared with those of recent birds of both species.

MATERIAL AND METHODS

The fossil material was identified by comparison of morphological features and measurements of the fossil bones with features and measurements of bones from recent skeletons of *Himantopus novaeseelandiae* Gould, 1841 and *H. himantopus leucocephalus* (Gould, 1837).

Tarsometatarsus lengths for the fossil and for recent skeletal material were compared with data from live birds. Tarsometatarsus length is the only skeletal measurement which corresponds with a 'standard' skin or live bird measurement. Live-bird measurements for *H. novaeseelandiae* (present population) and New Zealand and Australian populations of *H. himantopus leucocephalus* are from Pierce (1982).

Bones were measured with vernier calipers, to 0.1 mm. Lengths were measured over element extremities, except for the proximal tibiotarsus, where the cnemial crest length was not included, and the length taken to the articular surface.

The term fossil is used as defined in Worthy & Holdaway (1993) and according to current

palaeontological usage, for example, by Olson & James (1991).

MATERIAL EXAMINED

All Canterbury Museum, Christchurch, New Zealand.

Fossil

All from Pyramid Valley, North Canterbury, New Zealand: NZMS 260M33/772038; 42°59'30"S 172°35'50"E. Av6124 1/1; sternum, left and right tarsometatarsi, right tibiotarsus, left and right humerus, furcula, left ulna, left radius, right carpometacarpus, pedal phalanx; collected from Square 69 (Scarlett 1955) on 10 March 1949 by J R Eyles, R J Scarlett, R C Murphy. Av7290 1/1; left femur, Square 62. Av7433 1/1; left ilioischial plate and pubis [may belong with Av6124 (Scarlett 1955)]. Av15130 1/1; immature left coracoid, Square 107. Av 7267, a right carpometacarpus collected from Square 69, was catalogued but has not been located.

Recent complete or substantially complete skeletons (New Zealand)

H. novaeseelandiae Av5188, no data. *H. himantopus leucocephalus*: Av10222, Lake Grassmere, 26 Sep 1951, R Britton; Av12733, Hornby, Christchurch, 1954, Mrs Nosworthy; Av22439, no data; Av28361, Kaituna, Lake Ellesmere, 16 Nov 1973, G A Tunnicliffe; Av36961, Greenpark Sands, Lake Ellesmere, 1987, R N Holdaway.

RESULTS

The part skeleton (Av 6124) from Pyramid Valley differed from those of recent pied stilts in lengths, relative lengths, and shaft widths of the long bones of wing and leg (Table 1). Humeri and ulnae of the fossil were longer than the corresponding elements in the single available skeleton of a recent black stilt (Av5188).

Femur length was similar in pied, black, and fossil skeletons, but the tibiotarsi of the recent black and fossil specimens were shorter than all but one of the recent peds. The tarsometatarsus of the recent black stilt was as long as that of the smallest pied stilt, but the fossil tarsometatarsus was 9.5 mm shorter (Table 1).

The bone length ratios for the major bones of the wing and leg of the black stilt differed from those of the pied stilts, and the ratios for the fossil differed from both (Table 1). The humerus-femur length ratio was similar in the black, piers, and the fossil, but the humerus-tibiotarsus ratio was higher in the fossil and black stilt than in the piers. The tibiotarsus was shorter in proportion to femur length in black and fossil stilts than in the piers. Femur length is one of the better linear correlates of body size (e.g., Alexander 1983).

The femur/tarsometatarsus length ratio of the fossil was markedly different from that of either of

the recent taxa (Table 1). The ratio for the recent black was intermediate between that of the fossil and the New Zealand piers stilts.

The sum of the lengths of the exposed leg element lengths - tibiotarsus plus tarsometatarsus - was slightly less in the black than in the smallest pier, but more than 10 mm (6.9%) less in the fossil than in the black stilt. In the pier stilts, the combined tibiotarsus-tarsometatarsus length was bimodally distributed.

In general, the bones of the black and fossil stilts were stouter, as measured by shaft or terminal widths, than those of pier stilts (Table 1).

Table 1. Lengths (mm) and selected ratios of lengths of major limb bones of recent black and pier stilts, and fossil stilt material from Pyramid Valley. Possible sex of individuals was based on limb proportions. TBT=tibiotarsus, TMT=tarsometatarsus, HUM= humerus, FEM=femur, M= male, F=female.

Element or ratio	Specimen (Taxon plus Av no.)						
	Pier					Fossil	Black
	10222	12733	22439	28361	36961	6124/7290	5188
Humerus length	59.5	53.6	55.9	58.2	57.5	62.0	61.1
Humerus width	3.99	3.54	3.65	3.78	3.70	4.15	4.06
Ulna length	63.5	56.8	61.4	64.6	62.5	67.4	66.3
Ulna width	3.0	2.92	2.96	2.90	3.0	3.11	3.18
Radius	61.2	55.0	58.6	61.7	59.3	64.3	63.3
Carpometacarpus	36.2	31.4	33.3	35.0	34.9	36.9	36.9
Femur length	36.6	31.3	34.3	32.6	33.7	36.5	35.2
Femur width	3.08	2.97	3.08	2.95	3.06	3.30	3.42
TBT length	115.5	95.9	112.9	104.8	109.8	95.3	98.5
TBT shaft width	2.96	2.74	2.85	2.78	2.87	2.93	2.92
TBT distal width	5.81	5.22	5.44	5.43	5.56	6.08	7.42
TMT length	104.3	92.1	102.3	87.4	100.3	78.0	87.5
TMT shaft width	2.45	2.45	2.70	2.15	2.36	2.61	2.61
TMT distal width	6.88	6.61	6.37	6.64	6.65	7.26	7.42
HUM/FEM ratio	1.63	1.71	1.63	1.79	1.71	1.70	1.74
HUM/TBT ratio	0.52	0.55	0.50	0.56	0.58	0.65	0.62
FEM/TBT ratio	0.32	0.33	0.30	0.31	0.31	0.38	0.36
FEM/TMT ratio	0.35	0.34	0.34	0.37	0.34	0.47	0.40
TBT+TMT	219.8	188.0	215.2	192.2	210.1	173.2	185.9
Sex	M?	F?	M?	F?	M?		

None of the skeletons was sexed on its label or in the catalogue. The magnitude of the differences in tarsometatarsus length between groups of peds matched those for live birds (Table 2, data from Pierce 1982), so the skeletons were assigned tentatively to sex *a posteriori*. Tarsometatarsus length in the black stilt skeleton (Av5188) was intermediate between those of the two sexes for the live black sample, and hence the individual was of indeterminate sex (Table 2).

The distinction between the black and pied and identification of the fossil were made on morphometric grounds: no structural distinguishing features were found. The tibiotarsus was much thicker proximally in *H. novaeseelandiae* and in the fossil than in *H. himantopus leucocephalus*. The femur was correspondingly broader distally in the black and fossil stilts than in the peds. With pied stilt material at hand, black and fossil material could be distinguished visually on robustness alone.

The fossil skeleton (Av6124) was identified as a black stilt *Himantopus novaeseelandiae* Gould, 1841 on the basis of the measurements and length ratios. The fossil differed sufficiently in absolute size and proportion from the recent material, in particular the length of the tarsometatarsus, to indicate that more than sexual differences were involved.

The immature coracoid could not be definitely attributed to either taxon. Its robustness suggests that is probably referable to *H. novaeseelandiae*.

DISCUSSION

Contrary to expectation with such similar species, the differences in proportion of the pied and black stilt limb skeletons proved to be sufficient to allow them to be separated with confidence. Some elements, such as the tarsometatarsus, were diagnostic in isolation. The fossil material agreed with the dimensions of the recent black stilt in size and proportions sufficiently to be recognised as the first fossil record of the black stilt *Himantopus novaeseelandiae*. Although the black stilt skeleton was unlocalised, all except one of the pied stilts used for comparison are known to have come from the northeastern or eastern South Island. Given the mobility of stilts, it is unlikely that geographic variation was a factor in the differences noted.

If the immature bone (Av15130) is, as is likely, from the same taxon as the adult skeleton, it demonstrates that the black stilt bred at Pyramid Valley. At the time of deposition, the stilts would have been living on the shore of a small, isolated lowland lake set in forested valley (Burrows 1989). The Pyramid Valley deposits were laid down in the mid to late Holocene. Fossils preserved after the deposition of peat at 1.60 m - 1.70 m have been dated at 4280±62 years BP and before twigs and seeds dated at 2620±49 years BP were deposited at 0.68 m - 0.73 m (Gregg 1972).

The presence of black stilts at Pyramid Valley (Holdaway & Worthy submitted) does not, of course,

Table 2. Comparison of bone dimension with live dimension for tarsometatarsus of Australian and New Zealand pied stilts, black stilts, and the Pyramid Valley fossil stilt. NZP, New Zealand pied; AP, Australian pied. Data for live birds from Pierce (1982).

	Taxon and sex							
	NZP male	NZP female	AP male	AP female	Black male	Black female	AV 5188	Fossil
Live birds								
Mean	100.3	93.0	114.3	109.0	90.8	85.6		
SD	6.4	3.8	6.3	7.8	2.3	5.8		
CMNZ specimens	102.3 104.3	87.4 92.1					87.5	78.0

prove that the black was the only species of stilt in New Zealand when the deposit was laid down. The differences in length and proportions of the limb bones between the fossil and recent black stilts support the contention that the black stilt was the only stilt in New Zealand 3000-4000 years ago. The intermediate position of recent black stilts, between the fossil and the peds, may indicate that the black stilt has converged in proportions to the ped because of long-term introgression between the populations.

If introgression caused the changes in the black stilts, then it might be expected that the present ped stilt has diverged from its parent stock (the Australian population) in the reverse direction. The recent ped stilts from New Zealand do indeed differ in limb bone proportions from the parent Australian stock (Pierce 1982) in the direction of those of the black stilt. The present New Zealand ped has been affected almost as much by the introgression as has the black.

For ped stilts, the sum of the lengths of the tibiotarsus and tarsometatarsus, and tarsometatarsus length itself, seem to be useful indicators of sex. Pierce (1982) found that New Zealand ped stilts were significantly smaller than Australian birds (Pierce 1982 Table 2.1). He also found that in both ped and black stilts, the male had a significantly longer 'tarsus', as measured on live birds. This was confirmed by the bimodal distribution of the small sample presented here.

Pierce (1982) also showed that the tarsus of male and female ped stilts was significantly longer than the corresponding sex in the black stilt. A much larger fossil sample will be necessary before there is sufficient evidence for sexual dimorphism in recent or fossil blacks, or the rate of evolutionary change in the black and ped populations in New Zealand.

The magnitude of the difference between the tarsometatarsus length of the fossil stilt and that of the recent black, suggest that if the former had received 'ped' genes from an immigrant population, the extent of the interbreeding that had occurred at that time was much lower than at present. If ped stilts had been present in numbers in New Zealand much before 4000 years ago, the proportions of the Pyramid Valley stilt would have been closer to those of the present blacks.

Introgression may well have been significant at two stages in the history of peds in New Zealand. At

first, when the immigrant population of peds was small, ped stilts may have had to resort to interspecific matings because of a shortage of conspecific mates. If, as seems likely, the two species occupied different breeding habitats, the degree of interbreeding would have been quite low.

After human-induced changes in the vegetation had forced the two species to occupy the same habitat and the population of the black had been reduced drastically by predation, black stilts would have found it both increasingly difficult to find conspecific mates. The celibate birds would also have been more and more likely to have been near ped stilts. The incidence of matings with peds increased (Pierce 1982).

Several species present or common in New Zealand when Europeans arrived may have colonised within the past 1000 years. There is no fossil evidence for shoveler duck (*Anas rhynchos*), Australasian Harrier (*Circus approximans*), or Pukeko (*Porphyrio melanotus*) in New Zealand more than 1000 years ago (Holdaway & Worthy submitted). These taxa were all represented in the indigenous fauna by congeneric species (Harrier and Pukeko) or an ecological equivalent (Shoveler) that became very rare or extinct after humans arrived.

Recent black stilts are heavier (>200 g) than ped stilts (<200 g) (Pierce 1982). Pierce found no sexual dimorphism in weight in the ped stilt, and the sample size of black stilts was too small to detect any possible differences. Black stilts had significantly longer wings than peds. Male ped stilts had significantly longer wings than the females. In both instances, the longer wing may be a response in increased wing area to the higher mass to be lifted.

The longer wings in blacks was reflected in the long proximal wing elements of both the fossil specimen (Av6124), and of Av5188. The longer wing was best shown by the higher ratio of humerus to tibiotarsus lengths in Av5188 and Av6124 than in either male or female ped stilts.

Pierce (1982) pointed out that the black stilt has the shortest legs of any stilt, and is the heaviest of the four stilts for which he had data. He found that the New Zealand ped stilt has the second shortest 'tarsus' of any *Himantopus*, and that it was significantly shorter in New Zealand than in Australian birds. The New Zealand ped stilt is also more varied

in its markings, and heavier than the Australian pied stilt.

The larger body size, longer wings, and colour of the black stilt suggest that it diverged from a pied ancestor in response to the colder, windier environments of the successive Pleistocene glaciations. Increased body size, dark plumage, shorter legs, and better flying ability would have enhanced survival through better heat retention, quicker warming, and greater power of movement in a windier environment, respectively. The shorter tarsometatarsus of the black stilt would have made for a "lower geared" gait suited to wading in swift streams.

The dimensions of the fossil from Pyramid Valley support the contention that the pied stilt has hybridised extensively with the black stilt in New Zealand, and that both the pied stilt and the black stilt have now sufficient admixtures of the others genes that both differ significantly in proportions from their respective parent populations (Pierce 1982). The parent population of the pied stilt, that in Australia, is still abundant. Unfortunately, the present sample of the parent population of the black stilt appears to be the unique fossil from Pyramid Valley.

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REFERENCES

Alexander, R. McN. (1983). Allometry of the leg bones of moas (Dinornithes) and other birds. *Journal of Zoology, London* 200: 215-231.

Burrows, C.J. (1989). Moa browsing: evidence from the Pyramid Valley mire. *New Zealand Journal of Ecology* 12 (Supplement): 51-56.

Duff, R. (1949). *Pyramid Valley*. 48 pp. Friends of the Canterbury Museum, Christchurch.

Duff, R. (1951). *Moas and Moa-hunters*. 36 pp.

Government Printer, Wellington.

Falla, R.A. (1941). Report on excavations at Pyramid Valley swamp: The avian remains. *Records of the Canterbury Museum* 4(7): 339-353.

Fleming, C.A. (Convener) (1953). *Checklist of New Zealand birds*. 80 pp. A.H. & A.W. Reed, Wellington.

Gregg, D.R. (1972). Holocene stratigraphy and moas at Pyramid Valley, North Canterbury, New Zealand. *Records of the Canterbury Museum* 9: 151-158.

Holdaway, R.N. & Worthy, T.H. (submitted). A reappraisal of the Late Quaternary vertebrate fossil fauna of Pyramid Valley Swamp, North Canterbury, New Zealand. *New Zealand Journal of Zoology*.

Oliver, W.R.B. (1930). *New Zealand Birds*. 541 pp. Fine Arts, Wellington.

Oliver, W.R.B. (1955). *New Zealand Birds*, 2nd ed. 661 pp. A.H. & A.W. Reed, Wellington.

Olson, S.L. & James, H.F. (1991). Descriptions of thirty-two new species of birds from the Hawaiian Islands Part I. Non-Passerines. *Ornithological Monographs* 45: 1-88.

Pierce, R.J. (1982). A comparative ecological study of Pied and Black Stilts in South Canterbury. Unpublished PhD thesis, Department of Zoology, University of Otago, Dunedin.

Pierce, R.J. (1984). Plumage, morphology and hybridisation of New Zealand stilts *Himantopus* spp. *Notornis* 31(2): 106-130.

Scarlett, R.J. (1955). Further report on bird remains from Pyramid Valley. *Records of the Canterbury Museum* 6(4): 261-264.

Scarlett, R.J. (1969). Moas and other extinct birds. pp. 565-568 In: Knox, G.A. (ed.) *The Natural History of Canterbury*. 620 pp. A.H. & A.W. Reed, Wellington.

Stead, E.F. (1932). *The life histories of New Zealand birds*. Search Publishing Co., London.

Turbott, E.G. (Convener) (1990). *Checklist of the birds of New Zealand and the Ross Dependency, Antarctica*. Random Century and the Ornithological Society of New Zealand, Auckland.

Worthy, T.H. & Holdaway, R.N. (1993). Quaternary fossil faunas from caves in the Punakaiki area, West Coast, South Island, New Zealand. *Journal of the Royal Society of New Zealand* 23(3): 147-254.