Bernacchi, L., 1901 — To the South Polar Regions. London: Hurst and Blackett. Brown, R. N. R., 1915 — The life and habits of Penguins. Rep. Sci. Res. Scot. Nat. Antarct. Exped. 1902.4, 4 (14): 249-253.

Levick, G. M., 1915 — Natural History of the Adelie Penguin. Brit. Antarct. Terra Nova Exped., 1910. Zoology 1: 55-84.

Murphy, R. C., 1936 — Oceanic Birds of South America. New York: Macmillan. Murray, J., 1909 — Biology. Appendix I. In Shackleton, E. H., 'The Heart of the Antarctic.' London: Heinemann.

Sapin-Jaloustre, J., 1960 — Ecologie du Manchot Adelie. Paris: Herman. Shackleton, E. H., 1909 — The Heart of the Antarctic. London: Heinemann. Sladen, W. J. L., 1958 — The Pygoscelid Penguins. 1 — Methods of study. 2 — The Adelie Penguin. F.I.D.S. Sci. Reports 17: 1-97.

Sladen, W. J. L., & Ostenso, N. A., 1960 — Penguin tracks far inland in the Antarctic. Auk, 77: 466-469.

Taylor, R. H., 1962 — The Adelie Penguin Pygoscelis adeliae at Cape Royds. Ibis, 104: 176-204.

Wilson, E., 1907 — Aves. Brit. Nat. Antarct. Exped. 1901-4, Nat. Hist. 2: 1-121.

THE EXTINCTION OF MOAS AND OTHER ANIMALS DURING THE HOLOCENE PERIOD

... ***** _

By C. A. FLEMING, N.Z. Geological Survey

The Holocene Period comprises in round figures the last ten thousand years, and is equated with the post-glacial. During the Pleistocene (i.e. the previous one or two million years) world climate underwent severe fluctuations. In New Zealand a large number of plants and animals with more or less long histories in the Tertiary became extinct during the Pleistocene, and the Holocene began with an impoverished biota which lacked organisms sensitive to the types of environmental changes that had characterised the ice ages. Any such stenothermal organisms had disappeared long before during the earlier Pleistocene climatic catastrophes. Among marine organisms, for instance, most of the Pleistocene extinctions took place in the first two glaciations.

The early post-glacial time of warming climate and rising sealevel, from ten thousand to six thousand years ago, is not characterised by extinction, but on the contrary by faunal diversification and active Thus, a recent analysis of the likely age of mainly Australian derivatives among New Zealand birds (Fleming 1962), suggests a considerable number of immigrations and some speciation during the early Holocene. The Holocene culmination of post-glacial warming, often termed the Climatic Optimum or Thermal Maximum, apparently during the interval from 6000 to 4000 years ago, was followed by minor cooling that could have led to extinctions, but I can only think of one that falls in that period. The "Sydney cockle," Anadara, came to New Zealand during at least one of the early inter-glacials, and returned to Northland for a brief interval in post-glacial time, judged by its occurrence as fresh shells near present sea level at Hokianga, in shallow wells at Marsden Point and elsewhere. Its absence as a living animal suggests the only known post-glacial extinction among marine invertebrates.

The Late Holocene, i.e. the last 4000 years, has been characterised by building out of coasts, advance of dunes, ponding of streams to produce coastal peat swamps, and moderate alluviation of many inland valley bottoms after the interval of early Holocene down-cutting that followed the Last Glaciation. The deposits formed in this late Holocene phase are the main sources of bones of the moa, of extinct birds of

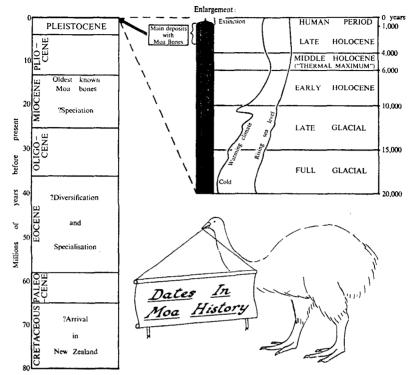


FIG. 1 — Although the Dinornithiformes probably had a long history in New Zealand (time-scale left) the oldest fossil bones are Upper Miocene and the main sources are late Holocene. The enlargement (right) shows their extinction in the human period, thousands of years after the climatic changes to which it has sometimes been attributed.

other groups, and shells of locally-extinct land mollusca. Though it would be rash to be dogmatic, it is doubtful if any major source of extinct bird bones so far known in New Zealand is as old as early or even mid Holocene in age, let alone Pleistocene. The older moa deposits (and there are many) have generally yielded only a few bones, poor in preservation. Fig. 1 shows some dates in Moa history plotted on a scale of absolute time. The dates of their arrival, diversification, specialisation, and speciation are not supported by fossil evidence and are thus speculative.

For some years, the conventional view on the extinction of the moa, held by Duff and Falla after their classic studies of Pyramid Valley swamp and Wairau Bar (1941; 1942), was "that the moas were dying out naturally — from climatic change leading to restriction of grasslands . . . or from the delayed effects of increasing insularity on a continental avifauna, and that man found only smaller genera, notably Euryapteryx, surviving sporadically on the east coast of the South Island" (Duff, 1956, p. 280).

Evidence on the late persistence and human association of moas is scattered and has not previously been brought together as part of the problem of the date and cause of extinction of the whole moa fauna. Fig. 2 shows data compiled mainly from published sources for the complete list of 27 species of moas recognised by Oliver (1949). The doubtful fossil species (Anomalopteryx antiquus) is omitted. Five species are known from undoubtedly late Holocene deposits but not in human association. Twenty-two species, representing all genera, are known in well-documented human culture sites. Three species, representing two genera, have been directly dated by 14C analyses of their bones or stomach contents (Lockerbie; Deevey) as between 1280 A.D. and 1670 A.D. (shown by black circles). Three additional species (two additional genera) have been dated by the close association of their bones with charcoal or tussock bedding that has itself been dated by 14C (shown by crosses). Ten additional species occur in sites that have been dated (Papatowai, Wairau Bar, Pyramid Valley), but are not so closely tied to the dated material as to establish their ages (shown by queries on Fig. 2).

The five species not yet demonstrated to have lived in the human period include four species that are described as unique, rare or sparingly distributed (in dune, swamp or cave deposits), and another (Euryapteryx tane) confined to the North Island. A review of their localities and the deposits where they were found gives no reason to suspect that they are any older than the species known in human association, and they probably survived into the human period.

		7 genera 7 genera			ra -			1
		27 species	22 species	7 genera 16 species				
		MAINLY LATE HOLOCENE (undated)	14 C DATES (AD)					
PACH YORNIS	septentrionalis		Service and the service of the servi	—	T	1		П
	mappini	4.h				X		П
	murihiku				$\overline{}$			
	australis							П
	elephantopus			?	?			П
EMEUS	huttoni			? '	?	?		
	crassus	N	2.7. 4.1.1.1	7	?	?		П
<i>EUR YAPTER Y X</i>	curtus							
	tane							
	geranoides	2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	T_{i} , S_{i} , S_{i}			?		\Box
	gravis	390 N. L. B. W.	J x 150 5 4 5 1 5 1		?	45 2	8	П
ZELORNIS	exilis		Section 1 and the second		Γ.	Ι		П
	haasti	14. 17. 14. 14. 14. 14. 14. 14. 14. 14. 14. 14	SERVICE STATE OF THE SERVICE S					П
ANOMALOPTER YX	oweni		96 k 40 c		1			П
	parvus	(中) (1) 不) (1) (1) (1)	Company of the second of the second	1	1			П
	didiformis			?		\Box		\sqcap
<i>MEGALAPTERYX</i>	hectori	を行うまで、一般など	ti kingi sahba a fili berasi t	?				П
	didinis	4.7	M 160 E.A. I C				X	П
	benhami			7				П
DINORNIS	gazella	1,4 1600,44.0		_	1			П
	struthioides				$\overline{\mathbf{x}}$			П
	torosus						0	П
	novaezelandiae	7 (513) OVEC 11	e of Mary after		T-		-	П
	robustus	\$ 1 kg 1 * 1		?	?	T		П
	hercules	N/ 464 / 19 5		×				М
	giganteus	A Strain		T`	×			П
	maximus	and the second of the second	25 Y 1 37 K			•		ᆏ

FIG. 2 — 27 species of moa recognised by Oliver all occur in Late Holocene deposits, 22 of them associated with human culture-sites, 16 of them in sites that have been dated with different degrees of precision.

A considerable list of carinate birds — rails, ducks, goose, swan, eagle, crow and others — became extinct in the same general period as the moas, and analysis of their subfossil occurrence (not here presented), shows that approximately 50% of them have been found in cultural association, i.e. that they survived into the human period. In addition, a number of bird species or genera became extinct over part of their range, apparently in the same pre-European period of human culture. Among them are the Takahe, the New Zealand Snipe, Kakapo and Merganser. The Tuatara (Sphenodon) also became greatly restricted, apparently during the early part of human occupation of New Zealand. The extinction of further bird species during the European period has recently been reviewed by Gordon Williams (1962).

There is some evidence for extinction of land and fresh-water invertebrates during approximately the same period as the more conspicuous extinction of birds. Two species of fresh-water Ostracoda and a tendipedid midge from the Pyramid Valley deposits have not yet been listed as living animals; they belong, however, to little-studied groups and it would be unwise to infer their extinction in the Holocene. Two extinct forms of fresh-water gastropods described by Cumber (1941), are members of genera and species-groups still surviving, with a bewildering amount of variability (Dell, 1956). Such forms, in plastic evolving lineages, are extinct through modification, and their extinction differs fundamentally in origin and significance from extinction through extermination.

At least two species of marine mollusca used as food by man seem to have changed to a minor degree (at least in some districts) in the interval since the pre-European accumulation of shell middens. The pipi (Amphidesma australe) is appreciably larger in Wairau moahunter middens than in nearby harbours to-day and subfossil toheroa (Amphidesma ventricosa) 1030 years old, have been described by R. M. Cassie as larger than contemporary shells, possibly belonging to an extinct race (Ferguson and Rafter, 1959, p. 217). Bones of fur-seal pups as far north as Tairua (Coromandel Peninsula) suggest that marine mammals suffered local extinction before the arrival of European sealers.

Some terrestrial mollusca, like land birds, suffered restriction of range, or partial extinction, in the Late Holocene. Rhytida greenwoodi, a forest snail now ranging into Nelson, formerly extended to Waipara (Allan, 1937) and Hurunui (D. R. Gregg coll.) at a late Holocene date (see also Hartree on its restriction in Hawke's Bay). Extinct populations of Paryphanta have been recorded from shells in caves and swamps far from the localities of remaining disjunct relict populations (Dell, 1955). Similar restrictions of ranges have affected Placostylus and Succinea in Northland (Powell, several papers). Such restriction has been attributed to desiccation, but could be explained by human burning and sand-dune rejuvenation without meteorological desiccation. The changes wrought by early man in New Zealand have certainly been underestimated (see Cumberland, 1962).

Summarising, there is little evidence of early and mid-Holocene extinction, except in the case of a marine bivalve that disappeared after the Thermal Maximum. In the late Holocene, on the other hand, partial or complete extinction was a widespread phenomenon, most conspicuous in terrestial animals, affecting both vertebrate and invertebrates, but doubtful in fresh-water organisms, unknown in invertebrates

in the sea, where however some stunting of shallow water bivalves was contemporaneous and might conceivably be due to the same causes.

At the 7th New Zealand Science Congress, held in Christchurch in May, 1951, I ventured to maintain on theoretical grounds (before there were any radiocarbon dates) that the most outstanding faunal change of the Holocene, extinction of moas and their companion species, must be attributed to the greatest ecological change in the post-glacial period _ man's arrival in New Zealand (Fleming 1953). During the past decade this thesis (not by any means original but unpopular at that time) has been supported by studies of archaeologists backed by results of 14C dating. On the other hand the view that effects of climatic changes, either post-glacial restriction of grassland by forest (Archey 1941) or the opposite tendency, "significant periods of drought" (Falla 1955), had more to do with their decline than human interference had persisted. Moreover, Oliver (1949) implied that orthogenetic trends contributed to their extinction, and Williams (1962) has stated that "the process could well have been going on independently of either hunting or habitat destruction." It seems we are reluctant to blame our fellow men for a pre-historic offence against modern con-servation ideals and would rather blame climate or the animals them-The simplest explanation is to attribute all late Holocene extinction to the profound ecological changes brought about by the arrival of man with fire, rats and dogs. So far as we know, our incomplete data are not inconsistent with this conclusion.

This paper was presented at the Tenth New Zealand Science Congress (Christchurch 1962). I am grateful to Ron Scarlett, Roger Green, Colin Smart and John Yaldwyn for unpublished data.

REFERENCES

Allan, R. S., 1937 — A note on the Distribution of Rhytida greenwoodi (Gray) in the South Island. Rec. Cant. Mus. 4 (3): 167.

Archey, G., 1941 — The Moa: A study of the Dinornithiformes Auck. Inst. Mus. Bull. 1.

Cumber, R. A., 1941 — Two new species of fresh water molluses from the Waikari moa swamp. Rec. Cant. Mus. 4: 359-360.

Cumberland, K. B., 1962 — Climatic Change or Cultural Interference? New Zealand in Moahunter Times. Pp. 87-142 in Land and Livelihood (Christchurch).

Deevey, E. S., 1955 — Paleolimnology of the Upper Swamp Deposit, Pyramid Valley. Rec. Cant. Mus. 6 (4): 291-344.

Dell, R. K., 1955 — Some New Zealand Subfossil Land Mollusca. Rec. Dom. Mus. 2 (3): 135-144.

- 1956 — The Fresh-Water Mollusca of New Zealand, Parts II and III. Trans. Roy, Soc. N.Z. 84 (1): 71-90. Duff, R., 1941 — Notes on Moa excavations at Pyramid Valley, Waikari. Rec. Cant. Mus. 4: 330-338.

1956 - The Moa-hunter Period of Maori Culture (ed. 2). Cant. Mus.

Bull. 1. Falla, R. A., 1942 — Bird remains from moa-hunter camps. Rec. Cant. Mus. 5: 43-49.

1955 — New Zealand Bird Life Past and Present. Cawthron Lecture Series No. 29 (Nelson).

Ferguson, G. J., and Rafter, R. A., 1959 — New Zealand 14C Measurements - 4. N.Z. Jr. Geol. Geophys. 2 (1): 208-241.

A., 1953 — Materials for a Recent Geochronology of New Zealand. Rep. 7th Sci. Congr. Roy, Soc. N.Z.: 114-123.

1962 — History of the New Zealand Land Bird Fauna. Notornis, 9 (8): Fleming, C.

270-274.

Hartree, W. H., 1960 — A brief note on the Stratigraphy of Bird and Human Material in Hawke's Bay. N.Z. Archaeological Assn. Newsletter, 3 (4):28. Lockerbie, L., 1959 — From Moa-Hunter to Classic Maori in Southern New Zealand, Pp. 75-110, in Anthropology in the South Seas (Thos. Avery & Sons).

Oliver, W. R. B., 1949 — The Moas of New Zealand and Australia. Dom. Mus. Bull. 15.

Williams, G. R., 1962 — Extinction and the Land and Freshwater-Inhabiting Birds of New Zealand. Notornis, 10 (1): 15-32.