

Biological effects of ghosts

Jared M. Diamond

BIG vertebrates have big effects on other species. About one-fifth of the world's bird species and half of its large mammals have become extinct since the late Pleistocene, and many biological features of extant species are likely to have arisen originally as evolutionary responses to them. Recent studies¹⁻⁴ of New Zealand's surviving plants and birds have identified many such legacies of 'ghosts' — in this case, the ghosts of recently extinct large birds. These studies support the growing recognition that modern biology cannot necessarily be understood in terms of modern conditions⁵.

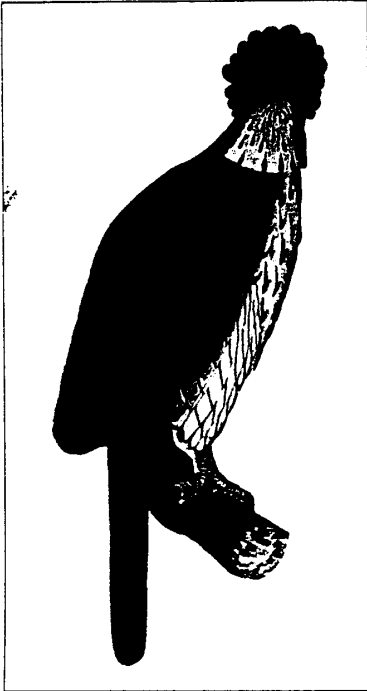
When Europeans reached New Zealand, they found numerous species of plants and small vertebrates, but no terrestrial mammals and no large herbivores or carnivores of any type except humans (Maoris). The subsequent destruction of

New Zealand's native biota by introduced mammals reinforced the view that the biota had failed to evolve defences against large herbivores or carnivores. Closer scrutiny of the flora, however, reveals features known to function elsewhere in the world as anti-herbivore defences: toxic or unpalatable chemicals⁶, mimicry of unpalatable plants or of dead twigs, cryptic coloration, and especially a peculiar growth form termed divarication (branching at a wide angle)^{6,7}.

This form of growth is rare elsewhere in the world but characterizes 10 per cent of woody plant species in New Zealand, where it appears in at least 17 plant families and has thus evolved repeatedly. Divaricating plants have interlaced branches that are difficult to tug or break, tough stems, and few and small leaves on the outside: most large leaves are rele-

gated to the inaccessible interior of the plant, which thus presents an unrewarding woody exterior to herbivores. Divaricating plants also tend to have high nutrient content, as one would expect if divarication evolved to deter large herbivores of a sort absent elsewhere in the world and now extinct in New Zealand. What could those ghost herbivores be?

Pictures courtesy of Richard Holdaway.



Giant predator — reconstruction of Haast's eagle (top) and its huge skull (bottom) compared to that of one of the world's largest living eagles, the wedge-tailed eagle of Australia.

Among the clues are the concentration of divaricating species on fertile alluvial soils and their absence or rarity among plants of cliffs, the alpine zone or canopy epiphytes. It is especially striking that several plant species that are divaricating on the New Zealand mainland are not so on offshore islands, and that nine species divaricating as juveniles cease to be so when they exceed about 3 m in height. As recognized by Atkinson and Greenwood⁷, these clues strongly suggest that divarication evolved as a response to

browsing by New Zealand's moas.

There were about 12 species of these giant, flightless, ostrich-like birds, all of which became extinct soon after arrival of Maoris 1,000 years ago. Preserved moa crops contain the remains of at least 38 plant species³. Weighing up to 200 kg, moas could devour a plant at one bite and must have exerted a considerable selective force. Spines, the usual anti-herbivore device of plants exposed to soft-nosed mammalian browsers elsewhere in the world, would have offered little protection against the heavy, horny head-shields of moas, but divarication would tend to make plants uneconomic fodder.

Abundant fossils show that moas were concentrated on fertile alluvial soils, and were absent from offshore islands and rare in the alpine zone. Moas could not have climbed cliffs or into canopies of trees. The correlation between distribution of moas and of divarication is therefore good. The largest moas were about 3 m tall, nicely matching the height above which plants divaricating only as juveniles cease to be so as adults.

Similarly, among New Zealand's surviving bird species Holdaway² has noted features known to function as antipredator devices elsewhere, despite the absence of large predators among surviving species native to New Zealand. Most of New Zealand's largest extant terrestrial birds — kiwis, kakapo, kea and kaka — are nocturnal or cryptically coloured, or both. The ghosts responsible were two remarkable extinct predatory birds. One was a very large (3 kg) hawk originally described as a harrier but now recognized as the largest of the world's goshawks, a group of bird-hunting specialists. The other was the giant Haast's eagle, at up to 13 kg by far the world's largest predatory bird known from recent times. The eagle would have been the sole New Zealand predator capable of killing an adult moa. One can only speculate what this powerful specialist at attacking tall bipedal prey did when it saw the first arriving Maoris.

Unfortunately, introduced species such as deer and possums browse in ways very different from moas, just as introduced cats and dogs hunt differently from goshawks and eagles. Hence adaptations of New Zealand's plants and small vertebrates to ghosts of large birds failed to protect them against the onslaught of introduced mammals. □

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1. Caughley, G. *N.Z. J. Ecol.* **12** (suppl.), 3–10 (1989).
2. Holdaway, R.N. *N.Z. J. Ecol.* **12** (suppl.), 11–25 (1989).
3. Burrows, C.J. *N.Z. J. Ecol.* **12** (suppl.), 51–56 (1989).
4. Batchelor, C.L. *N.Z. J. Ecol.* **12** (suppl.), 57–65 (1989).
5. Atkinson, I.A.E. & Greenwood, R.M. *N.Z. J. Ecol.* **12** (suppl.), 67–96 (1989).
6. Janzen, D.H. & Martin, P.S. *Science* **215**, 19–27 (1989).
7. Greenwood, R.M. & Atkinson, I.A.E. *Proc. N.Z. ecol. Soc.* **24**, 21–33 (1977).