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Adaptive Evolution: The Legacy of Past Giants

The wire syndrome shared by plants in New Zealand and Madagascar appears to have evolved convergently as a defence against herbivory from now extinct avian giants.

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Evolutionary biologists are often accused of adaptive story telling, in which adaptive explanations are developed to account for particular organismal features or behaviour. While some of these have been validated by rigorous evolutionary study, in many instances they remain untested, 'just-so' stories [1]. Evolutionary psychologists have been especially imaginative, explaining rape, for example, as an adaptation of lower status males to guarantee their reproductive success [2], the killing of newborns as a means for managing limited parental resources [3], and depression as a mechanism of conflict avoidance for individuals in lower social classes [4,5]. Most spectacularly, 20 adaptive and one non-adaptive explanations have been offered for female orgasm [6].

Plant evolutionists have put forward some ingenious hypotheses as well. For example, a shift from a high-browsing to low-browsing dinosaur fauna in the Early Cretaceous is correlated with the emergence of angiosperms. This observation spawned a line of adaptive reasoning in which the low-browsing dinosaurs with sophisticated jaw structures are speculated to have decimated slow growing gymnosperm saplings, thereby creating a favourable environment for the origin and diversification of smaller, weedier early angiosperms [7,8]. That these adaptive stories survived peer review is a testament both to the charisma of dinosaurs (how else are we to interest our offspring in botany?) and to the difficulty of disproving hypotheses about events that took place 130 million years ago (but see [9]). However, an adaptive story linking modifications in plant architecture with herbivory by giant avian dinosaurs — elephant birds and moas — has been validated by a recent study [10]. At least in this case, the legacy of past giants is clear.

Elephant birds and giant moas, which were native to Madascar and New Zealand, respectively, are believed to have been the world's largest 'modern dinosaurs' (birds). Giant moas reached 3.6 m in height and elephant birds could exceed 500 kg in weight — about twice the weight of a grizzly bear. Both giant birds were driven to extinction by humans within the past six hundred years, so if they had a major impact on plant form, it should still be apparent. Indeed,

Figure 1. Artist's impression of an elephant bird that is attempting to feed on a plant with the 'wire syndrome' (drawing by Anya E. Gangaeva).

scientists have speculated that the divaricate plant architecture — wide-angled branches, small leaves, thin, wiry branches, and few or no leaves in the outer canopy — which is common in the New Zealand flora, evolved as a defence against herbivory by giant Moas [11]. This hypothesis is supported by results from feeding experiments with emus and ostriches, in which divaricate architecture, particularly high tensile strength of stems, deters browsing by large flightless birds [12]. Ecophysiological experiments, however, suggest that this architecture might instead be an adaptation to cold climates [13].

To distinguish between these hypotheses, Bond and Silander [10] searched for plants with a divaricate architecture in Madagascar, the former home of giant elephant birds. Madagascar has a very different climate than New Zealand, so convergence in plant architecture, if observed, could be attributed to parallel selection pressure from giant flightless birds. They report species from 25 families and 36 genera that share a suite of traits — the so-called wire-syndrome — with divaricate plants from New Zealand. The 'wire syndrome' includes wide-angled branches, small leaves, and thin, wiry branches (Figure 1). Unlike divaricate plants from New Zealand, however, the leaves of Malagasy wire plants are not clustered inside the plant. Thus, while the wire syndrome appears to have evolved as a defense against giant flightless birds, the paucity of leaves in the outer canopy of New Zealand plants may well represent an adaptation to cold.

Although this combination of experimental and comparative analyses makes for a convincing argument, the evidence is correlative only and based on a single comparison. What if some other ecological or phylogenetic factor was responsible for the convergent wire syndrome? To minimize this possibility, Bond and Silander [10] also compared the architecture of South African plants with Malagasy species from similar habitats and/or close phylogenetic relationships. The wire plant syndrome offers little defense against the kinds of large ungulate browsers responsible for the bulk of herbivory in South Africa. As predicted, South African plants fail to exhibit the wire plant syndrome, even when ostriches are present. Thus, both the absence of terrestrial ungulates in New Zealand and Madagascar, and the presence of avian giants, may be required for the evolution of the wire plant syndrome. The proverbial 'fly in the ointment' is the presence of divaricate plants in Patagonia [14], where both flightless birds (rheas) and terrestrial ungulates roam.

The wire plants of New Zealand and Madagascar should be added to the pantheon of examples of adaptive convergence in plants, such as the evolution of spiny, succulent stems in Cactaceae in the Americas and Euphorbiaceae in Africa and the multiple independent evolution of arborescence on islands. While rigorous tests of adaptive hypotheses remain far too infrequent, they have the potential to transform the image of evolutionary biologists from adaptive storytellers to expert witnesses.

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