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# The Hunters Did It

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To address these issues, Christie *et al.* combined x-ray diffraction and other biophysical approaches to characterize UVR8 structure and function. The crystal structure of UVR8 showed that in the dark-state dimer of this protein, two seven-bladed β-propeller monomers are packed face-to-face onto each other. This arrangement, validated in solution with x-ray scattering, orients loops from each monomer into the dimeric interface. A number of aromatic side chains point from these loops into the interface, including several of the tryptophan residues implicated in UV-B sensing (*8*). The rest of the interface involves multiple salt bridges, with charged residues instead of the hydrophobic contacts among side chains typically found between protein subunits (*9*). These salt bridges are essential for stabilizing the dark-state dimer; their disruption by point mutation leads to constitutive UVR8 monomerization.

How does the detection of a UV-B photon switch UVR8 from dimer to monomer? Christie *et al.* propose an excitonic coupling mechanism (see the figure) like that used by plants in photosynthetic light harvesting (*10*). In this case, the close packing of multiple aromatic residues at the dimer interface (termed a tryptophan pyramid by the authors) facilitates orbital overlap among these chromophores, producing a distinct signature in the far-UV circular dichroism spectrum of wild-type UVR8 (*11*). Mutating residues in the pyramid affects both excitonic coupling and light-dependent conformational changes, reinforcing the linkage between photon absorption and structure change. Replacement of one member of the tryptophan pyramid (Trp 285) with phenylalanine sensitizes UVR8 to shorter-wavelength UV-C irradiation, consistent with the change in absorption characteristics of these two residue types.

Christie *et al.* note that the pyramid does not stand alone: Several salt-bridged residues are within or adjacent to it, including a critical arginine. The authors hypothesize that electron transfer from the excitonically coupled tryptophan pyramid to these salt-bridged residues is essential for the photosignaling process (see the figure).

UVR8 is fundamentally different from other photoreceptors in its use of standard amino acid side chains instead of specialized chromophores for the initial photochemical event. However, this critical difference belies several similarities, including the spontaneous (albeit slow) recovery of the dimeric form with extended dark-state incubation after illumination. Furthermore, UVR8 allosterically converts photosensing to control protein-protein interactions, as seen among the flavin-based blue light photoreceptors (*12*), among others.

Coupled with similar structure/function studies of UVR8 by Wu *et al.* (*13*), the studies by Rizzini *et al.* (*8*) and Christie *et al.* (*1*) address key questions of UV-B photosensing while opening up new directions for research. Based on homologies with other β-propeller proteins, there are clear predictions as to how COP1 (or other partners) will bind the newly freed UVR8 monomer that await testing. Further mechanistic studies of the UVR8 photochemistry and dark state reversion are needed to understand how the sensitivity and timing of the system are set. Finally, the simplicity of UVR8 light-controlled partner switching may also enable this new photochemistry to be harnessed for new biotechnological applications (*14*).

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PALEONTOLOGY

# The Hunters Did It

**Matt McGlone**

Human hunting was responsible for the extinction of large mammal species in tropical Australia.

In the past 100,000 years, many of the largest animals on Earth became extinct. The reasons for these megafaunal extinctions remain contentious (*1*, *2*). In 1967, Martin suggested that within a few hundred years of their arrival, fast-moving bands of hunters eliminated the big game by overkill (*3*). Similarly, Flannery claimed in the 1990s that the current fire-swept Australian landscape with its impoverished soils was created by human elimination of massive marsupial browsers and grazers (*4*, *5*). However, a diverse array of counter-hypotheses has been proposed; the leading argument is that habitat loss through climate change or fire was the critical blow to many large animals (*6*). The loss of 55 large mammal species in Australia (see the figure), shortly after humans arrived ~45,000 years ago (*7*), provides a key test case. On page 1483 of this issue, Rule *et al.* (*8*) present new results from tropical Australia supporting the idea that hunting alone was responsible.

The sparse distribution and poor dating of megafaunal sites have been the greatest obstacles to resolving the late Pleistocene extinction controversy. In recent years, the problem of how to track megaherbivore change has been addressed by use of the coprophilous fungus *Sporormiella*. These fungi grow in herbivore dung; high percentages of their spores in lake or peat deposits show that megaherbivores are abundant nearby (*9*).

Rule *et al.* have generated a 130,000-year record of *Sporormiella* spores, pollen, and charcoal from Lynch's Crater, a volcanic maar in Queensland, Australia, that was surrounded by tropical rainforest until European settlement. From 130,000 to 41,000 years ago, rainforest and sclerophyll forest dominated, with a steady input of *Sporormiella* spores and very low charcoal levels. About 41,000 years ago, *Sporormiella* dropped abruptly to low values, indicating the absence of megaherbivores. At the same time, incidence of fire increased, as evidenced by a steep rise in charcoal fragments. The pollen record shows that these changes were followed by expansion of grassy, eucalypt-dominant sclerophyll forest and eventual loss of rainforest conifers.

Habitat change cannot have been responsible for the loss of the large marsupials, because the grassy sclerophyll forest expanded only after the *Sporormiella* decline. Furthermore, both climate and veg-

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**Extinct after human arrival.** Australia once had a diverse range of large marsupial browsers, such as this 150-kg kangaroo *Sthenurus*. Along with 54 other mammal species 10 kg or more in weight, it became extinct shortly after the arrival of humans ~45,000 years ago. Rule *et al*. show that these extinctions can be attributed to human hunting alone.

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etation had been stable for the previous five millennia. It is thus difficult to argue, as some have (*2*), that progressive drying of the climate was largely responsible for the megaherbivore collapse.

The argument can, however, be made that the initial hunting of large, keystone herbivores increased the fuel load, thus permitting more severe fires and leading to extinctions through habitat loss. Did megaherbivore decline lead to more fire in Queensland as Rule *et al*. suggest?

The best evidence for fire and megaherbivore interactions comes from savannah ecosystems, where the loss of elephants, rhinoceroses, and other large browsers and grazers leads to elimination of forest glades and spread of tall, fire-promoting grasslands (*10*). In a dense tropical forest like that in Queensland, it is unlikely that a similar sequence of events could follow megaherbivore elimination. Such forests have little leaf biomass within terrestrial herbivore reach, and thus regrowth of the understory would have little effect on fire potential (*7*). Similar rainforests in Fiji and other Pacific islands that had no megaherbivores persisted even under low rainfall until the arrival of humans (*11*). The documented extinction of a rainforest conifer and the severe restriction of conifer-dominated rainforest after human arrival suggests that the Queensland forests were hypersensitive to fire and had been little exposed to it until then (*12*). Human-lit fires, which are often targeted in space and time to have the greatest effect on vegetation, were most likely the key factor in the subsequent switch to sclerophyll.

The Australasian megafaunal extinction story now seems clear. Shortly after their arrival, small bands of hunters had a devastating effect on large animals, whether it was ~41,000 years ago in Australia or ~750 years ago in New Zealand (*13*). Any climate change at those times was modest and highly unlikely to affect the outcome. Fire and massive biome disruption followed human arrival in regions where there had previously been little or no fire, such as wet tropical Queensland and eastern New Zealand. But large animals were eliminated just as efficiently from regions with dense, untouched rainforests, such as New Guinea and western Tasmania (*7*). Human hunting was a new, more intense form of predation that was particularly dangerous for large, slow-breeding animals. Human-lit fire, deliberately targeted in space and time and an order of magnitude more frequent than natural lightning ignitions, had a devastating effect on plants hitherto protected by climate and location.

What happened in Australia and adjacent island groups has implications for North America and Eurasia. No fewer than 13 separate hypotheses have been distinguished for the North American extinctions (*14*). Most current work has been cautiously interpreted to allow a role for climate change or ecosystem change in the extinction of megaherbivores (*6*, *15*). A recent modeling study of global megafaunal extinctions follows this trend by arguing for near equivalence of climate and human factors (*16*). However, the coarse resolution of the study and lack of local climate or vegetation factors make it of questionable relevance. The Australasian records clearly show that human hunting alone, on a continental scale at a time of only slight climate and vegetation change, is sufficient to eliminate megaherbivores. Contemporaneous substantial climate and vegetation changes could have sped up or slowed the rate at which the megaherbivores were eliminated in other regions, but are unlikely to have altered the final outcome.

The central question now shifts to the ecosystem effects of eliminating large herbivores while increasing targeted, more frequent fire (*17*). Large herbivores are more efficient than fire at recycling nutrients. They encourage some fast-growing or well-defended plants and disadvantage others. They disperse seeds and spores. To what extent were these functions picked up by other, smaller herbivores? Do global ecosystems function differently now that megaherbivores are gone and human-lit fires are common? New results strongly suggest that they do. Human-lit fires removed drought-adapted Australian woodlands and grasslands, replacing them with fire-adapted chenopod/desert scrub and grassland (*18*). In North America, broadleaf forests of a composition not seen before, and not matched in the present-day vegetation, sprang up shortly after the megafaunal decline, and reduced herbivory has been implicated in this change (*15*). More results are needed from South America, Asia, and Europe to elucidate the effects of megaherbivore declines in different settings and at different times.

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