ation can be approximated by $3.3 \times 10^6$ gallons per year between 1957 and 1976, and by $2 \times 10^6$ gallons per year from 1976 to 1982 (figure I-1). Calculated $^{90}Sr$ activities for 1976 and 1982 take into account radioactive decay.

11. *Draft Environmental Statement: Waste Management Operations, Idaho National Engineering Laboratory, Idaho* (ERDA-1536, Energy Research and Development Administration, Washington, D.C., 1976). Waste volumes are derived from information on pp. I-3 and I-4. Inventories of $^{90}Sr$ have been calculated as follows: the 300,000 gallons of liquid waste calcined in 1974 had a fission product concentration of 6.3 curies per gallon before calcination (figure II-18). If we make the conservative (high) assumption that this fission product activity is exclusively due to the isotope pairs $^{90}Sr/^{90}Y$ and $^{137}Cs/^{137}Ba$, then $^{90}Sr$ would be responsible for one quarter of this activity, that is, about 1.6 curies per gallon. Further assumptions are a high-level waste generation of $0.24 \times 10^6$ gallons per year between 1956 and 1976, and $0.34 \times 10^6$ gallons per year from 1976 to 1982 (pp. I-3 and I-4). Radioactive decay is also accounted for.
12. *Statistical Abstract of the United States, 1975* (Department of Commerce, Washington, D.C., 1975), table 886; Department of Interior, Bureau of Mines, News Release, "Annual U.S. energy use drops again" (5 April 1976), table 2.
13. *Electr. World* **186** (No. 6), 43 (15 September 1976).
14. J. A. Lieberman, W. A. Rodger, F. P. Baranowski, "High-Level Waste Management," prepared testimony presented to the California Energy Resources Conservation and Development Commission, 21 March 1977. We would like to thank T. Lash for bringing this testimony to our attention.
15. This work was supported by grants from the Max and Anna Levinson Foundation and the Ford Foundation.

22 February 1977; revised 26 April 1977

## Plant-Animal Mutualism: Coevolution with Dodo Leads to Near Extinction of Plant

Abstract. *An endemic sapotaceous tree* Calvaria major *found on the island of Mauritius is nearly extinct because its seeds apparently required passage through the digestive tract of the now-extinct dodo* Raphus cucullatus *to overcome persistent seed coat dormancy caused by a specially thickened endocarp.*

Coevolution can lead to mutualism in plant-animal systems, and occasionally one or both of two mutualistic species develops a considerable degree of dependence on the other member of the pair (*1*). Sometimes the elimination of a particular plant species can result in a marked numerical response in an associated animal population (*2*). However, there seem to be no documented examples of the reverse situation, in which a plant declines in abundance as a result of the extirpation of an associated animal, even though such an occurrence is obviously possible (*3*). In this report, I present evidence that the near extinction of a plant species may have been the direct result of the extinction of an animal with which that plant had coevolved. The two species in this example of obligatory mutualism are a now nearly extinct tree *Calvaria major* and the extinct dodo *Raphus cucullatus*, each of which is or was endemic to the island of Mauritius in the western Indian Ocean.

*Calvaria major* is a large monoecious tree in the family Sapotaceae (*4*). Historical forestry records indicate that *Calvaria* was formerly common and frequently exploited for lumber on Mauritius (*5*). However, by 1973, only 13 old, overmature, and dying trees were known to survive in the remnant native forests of the island. The age of each of these trees was estimated to be more than 300 years by experienced Mauritian foresters (*6*). No younger specimens are known to exist despite the fact that the surviving trees produce well-formed, apparently fertile seeds each year. None of these seeds now germinate naturally, and if the total absence of young plants is a valid indication, there has been no germination of *Calvaria* seeds for hundreds of years. Even when planted under nursery conditions, the seeds remain dormant (*6*). Low seed germination rates are not uncommon among tropical island plants (*7*), but the extraordinarily long period of time during which no *Calvaria* seeds have apparently germinated seems too excessive to be normal.

The fruits of *Calvaria* are large, single-seeded drupes about 50 mm in diameter. Anatomically, the fruit is composed of a thin exocarp; a pulpy, succulent mesocarp; and a hard, woody, thick-walled endocarp. The seed is depresso-globulose in shape and is completely enclosed in a stone or pit formed by the walls of the endocarp, which can be as thick as 15 mm. Some other sapotaceous plants also have relatively thick endocarps covering their seeds, but the endocarp surrounding a *Calvaria* seed is extraordinarily thick even for this family. Apparently, *Calvaria* seeds fail to germinate because the thick endocarp mechanically resists the expansion of the embryo within.

At the time of its discovery, Mauritius supported a remarkable endemic avifauna which has subsequently been decimated through the direct or indirect activities of man (*8*). Perhaps the most unusual of the original endemic birds was the dodo. We know disappointingly little of the biology of this fascinating bird; it became extinct by 1681, less than two centuries after it was discovered. We do know that the dodo was a huge, flightless bird that attained an estimated body weight of at least 12 kg. It had a large, strong beak, and the reports of early explorers indicate that dodos fed on fruits and seeds, especially seeds of palms and large forest trees. The dodo possessed a well-developed gizzard that contained large stones, which were used to crush tough food items (*8*).

The temporal coincidence between the extinction of the dodo 300 years ago and the last evidence of natural germination of *Calvaria* seeds led me to hypothesize the following mutualistic relationship between *Calvaria* and the dodo. In response to intense exploitation of its fruits by dodos, *Calvaria* evolved an extremely thick endocarp as a protection for its seeds; seeds surrounded by thin-walled pits would have been destroyed in the dodo's gizzard. These specialized, thick-walled pits could withstand ingestion by dodos, but the seeds within were unable to germinate without first being abraded and scarified in the gizzard of a dodo.

Fossil *Calvaria* pits have been found among skeletal remains of dodos in the mud of the Mare aux Songes marsh, which suggests that dodos ate the fallen fruits of *Calvaria*. Even today the fruits are frequently consumed by endemic frugivorous animals like the Mauritius parakeet *Psittacula echo* and the Mauritius flying fox *Pteropus niger*. Unlike these smaller surviving animals that eat only the fleshy mesocarp and leave the large pit untouched, the dodo was large enough to have swallowed the entire fruit. Many birds will retain in their digestive tract hard objects that the gizzard cannot readily crush; after a period of time, these objects are subsequently either regurgitated or reduced in size and passed through the intestinal tract (*9*). The hard pits of *Calvaria* may have similarly been regurgitated or excreted by dodos.

Germination rates in some plant species that show seed-coat dormancy can be increased significantly by passage through the digestive tracts of animals (*10*). In this way, animals can play an important role in overcoming seed-coat dormancy and in dispersing the consequently germinable seeds. Although there seem to be no recorded instances in which passage through an animal's gut is an absolute necessity for seed germination, in many cases germination rates are extremely low without such treatment (*10*).

If the *Calvaria*-dodo coevolution hypothesis is correct, *Calvaria* pits must have been able to withstand the crushing forces that were presumably generated by a dodo's gizzard. Measurements of

the forces generated by the gizzards of granivorous birds from several taxonomic groups ranging in body weight from 0.8 to 3.2 kg (*11*) reveal the following linear relationship between a bird's body weight and the force generated by its gizzard:

$$y = 843x + 1210, r = .97$$

where $y$ is the force generated by the gizzard (in kilograms per square meter) and $x$ is the bird's body weight (in kilograms). According to the equation, a 12-kg dodo could have produced forces of about $1.13 \times 10^4$ kg/m$^2$ in its gizzard. Intact nuts of hickory (*Carya ovata*), which fracture under point loads of 152 kg or less, are barely within the crushing capacity of a turkey's (*Meleagris gallapavo*) gizzard, which can generate forces of about 3700 kg/m$^2$ (*12*). If the dodo had a similar ratio of gizzard force to the maximum load capacity of objects that could be crushed, intact *Calvaria* pits would have been more than strong enough to withstand the forces in a dodo's gizzard. A sample of fresh, intact *Calvaria* pits ($N = 3$) withstood loads averaging 623 kg before fracturing (*13*).

However, if *Calvaria* pits were retained in a dodo's gizzard for extended periods of time, the endocarp could have been progressively abraded until it was thin enough to be crushed. I have estimated that a typical *Calvaria* pit with a maximum diameter of 30 mm would need to be reduced in size by nearly 30 percent before it could be crushed in a dodo's gizzard (*14*). A bird the size of a dodo would almost certainly have passed an object of this size or larger through its intestinal tract. Turkeys readily void through their intestinal tracts uncrushable objects smaller than about 8 mm in diameter (*15*). A dodo would certainly have passed proportionately larger objects, but there is no way to deduce exactly how large.

Perhaps the most convincing evidence that seed-coat dormancy in *Calvaria* can only be overcome naturally by passage through a bird's digestive tract comes from experiments in which I force-fed single, fresh *Calvaria* pits to turkeys. Some of these pits were retained in the turkey's digestive tract for as long as 6 days, and seven of 17 ingested pits were eventually crushed by the bird's gizzard. The remaining ten pits were either regurgitated or passed in the feces after being reduced in size through abrasion in the gizzard. I planted the ten recovered seeds under nursery conditions, and three subsequently germinated. These may well have been the first *Calvaria* seeds to germinate in more than 300 years.

These observations provide empirical support for the hypothesis that the fruits of *Calvaria* had become highly specialized through coevolution with the dodo. After the dodo became extinct, no other animal on Mauritius was capable of ingesting the large pits. As a result, *C. major* has apparently been unable to reproduce for 300 years and nearly became extinct. The findings presented in this report may provide a basis for preserving the species through propagation of artificially abraded seeds.

STANLEY A. TEMPLE
*Department of Wildlife Ecology, University of Wisconsin, Madison 53706*

### References and Notes

1. D. H. Janzen, *Evolution* **20**, 249 (1966); *Univ. Kans. Sci. Bull.* **47**, 315 (1967); C. H. Dodson, R. L. Dressler, H. G. Hill, R. M. Adams, N. H. Williams, *Science* **164**, 1243 (1969).
2. J. Moffit and C. Cottam, *U.S. Fish Wildl. Serv. Leaflet 204* (1941).
3. D. H. Janzen, personal communication.
4. J. G. Baker, *Flora of Mauritius and the Seychelles* (Reeve, London, 1877); R. E. Vaughan and P. O. Wiehe, *J. Ecol.* **25**, 289 (1937); P. Aubréville, *Adansonia* **12**, 337 (1972); F. Friedmann, personal communication. Aubréville and Friedmann proposed that *Calvaria major* should be considered synonymous with *Sideroxylon grandiflorum*. *Sideroxylon majus* and *S. galeatus* occur, respectively, on the Mascarene Islands of Réunion and Rodrigues, each of which formerly had large flightless birds of the family Raphidae. The seeds of these species have thickened endocarps, but they are not nearly so thick as in *C. major*. The nearest relatives outside of the Mascarene Islands, the ten species of *Sideroxylon* on Madagascar, do not have seeds with thickened endocarps.
5. N. R. Brouard, *A History of the Woods and Forests of Mauritius* (Government Printer, Mauritius, 1963).
6. L. F. Edgerley and P. O. Wiehe, personal communication.
7. S. Carlquist, *Island Biology* (Columbia Univ. Press, New York, 1974), pp. 541–542.
8. M. Hachisuka, *The Dodo and Kindred Birds* (Witherby, London, 1953).
9. J. P. Hillerman *et al.*, *Poultry Sci.* **32**, 332 (1953); D. F. Farner, in *Biology and Comparative Physiology of Birds*, A. J. Marshall, Ed. (Academic Press, New York, 1960), p. 411.
10. W. C. Swank, *J. Wildl. Manage.* **8**, 223 (1944); L. W. Krefting and E. L. Roe, *Ecol. Monogr.* **19**, 269 (1949); C. M. Rick, in *The Galápagos*, R. I. Bowman, Ed. (Univ. of California Press, Berkeley, 1966), p. 215.
11. E. Mangold, *Sitzungsber. Ges. Naturforsch. Freunde Berlin* (1929), p. 286; T. Kato, *Pfluegers Arch. Gesamte Physiol. Menschen Tiere* **159**, 9 (1914).
12. A. W. Schorger, *Auk* **77**, 337 (1960).
13. *Calvaria* pits were subjected to point-loading between two parallel, flat plates of a closed-loop, servo, hydraulic testing machine. A compressive force was applied at a linear rate of loading (226.5 kg/min) until the pits fractured. Loads at fracture were consistent, ranging from 616 to 627 kg.
14. *Calvaria* pits were artificially abraded in a gem tumbler until their maximum diameters were reduced by 10, 20, or 30 percent. They were then subjected to point-loading tests. A 30 percent reduction in diameter reduced the load at fracture by about 50 percent to 310 kg. Extrapolating from the data on turkeys fed hickory nuts, I estimated that any object that fractured under loads of 353 kg or less would have been crushed in a dodo's gizzard.
15. B. C. Wentworth, personal communication.
16. Supported by grants from the International Council for Bird Preservation, the World Wildlife Fund, and the New York Zoological Society. I thank L. F. Edgerley and the late P. O. Wiehe for pointing out the plight of *Calvaria* and J. W. Dreger for performing point-loading tests.

18 April 1977; revised 16 May 1977

## Solar Proton Event: Influence on Stratospheric Ozone

Abstract. *Large-scale reductions in the ozone content of the middle and upper stratosphere over the polar cap regions were associated with the major solar proton event of 4 August 1972. This reduction, which was determined from measurements with the backscattered ultraviolet experiment on the Nimbus 4 satellite, is interpreted as being due to the catalytic destruction of ozone by odd-nitrogen compounds ($NO_x$) produced by the event.*

It is thought that atmospheric $O_3$ is destroyed in the stratosphere and mesosphere by catalytic agents and also as a result of reactions with oxygen allotropes. The relative contributions to the destruction of $O_3$ caused by catalysts are predicted to be altitude-dependent, with odd-hydrogen components ($HO_x$) dominant in the mesosphere and troposphere and odd-nitrogen compounds ($NO_x$) and halogens dominant in the stratosphere.

A measurement of changes in the mesospheric $O_3$ content associated with the solar proton event of 2 November 1969 was reported by Weeks *et al.* (*1*). The first of two rockets carrying ultraviolet $O_3$ photometers was fired into the initial phase of the event at Fort Churchill, Manitoba; the second rocket was launched 2 days later under quieter conditions. The $O_3$ concentration was lower during the initial phase of the event by a factor of 2 at an altitude of 54 km and by a factor of 4 at 67 km than it was 2 days later. The changes and the rapid recovery are consistent with the $HO_x$ chemistry in the mesosphere.

Experiments that could confirm the catalytic reaction cycles in the stratosphere have been difficult to carry out and analyze. The effects of the gradual introduction of contaminants can be determined only if the natural variations in the $O_3$ content are known over appropriate time periods. Transient injections with well-defined spatial and temporal signatures, however, remove the ambi-