

27 | Nature's Odd Couples

From Nature's chain whatever link you strike,
Tenth, or ten thousandth, breaks the chain alike.

Alexander Pope,
An Essay on Man (1733)

POPE'S COUPLET EXPRESSES a common, if exaggerated, concept of connection among organisms in an ecosystem. But ecosystems are not so precariously balanced that the extirpation of one species must act like the first domino in that colorful metaphor of the cold war. Indeed, it could not be, for extinction is the common fate of all species—and they cannot all take their ecosystems with them. Species often have as much dependence upon each other as Longfellow's "Ships that pass in the night." New York City might even survive without its dogs (I'm not so sure about the cockroaches, but I'd chance it).

Shorter chains of dependence are more common. Odd couplings between dissimilar organisms form a stock in trade for popularizers of natural history. An alga and a fungus make lichen; photosynthetic microorganisms live in the tissue of reef-building corals. Natural selection is opportunistic; it fashions organisms for their current environments and cannot anticipate the future. One species often evolves an unbreakable dependency upon another species; in an inconstant world, this fruitful tie may seal its fate.

I wrote my doctoral dissertation on the fossil land snails of Bermuda. Along the shores, I would often encounter large hermit crabs incongruously stuffed—big claw protruding—into the small shell of a neritid snail (nerites include the familiar "bleeding tooth"). Why, I wondered, didn't these crabs trade their cramped quarters for more commodious lodgings? After all, hermit crabs are exceeded only by modern executives in their frequency of entry into the real estate market. Then, one day, I saw a hermit crab with proper accommodations—a shell of the "whelk" *Cittarium pica*, a large snail and major food item throughout the West Indies. But the *Cittarium* shell was a fossil, washed out of an ancient sand dune to which it had been carried 120,000 years before by an ancestor of its current occupant. I watched carefully during the ensuing months. Most hermits had squeezed into nerites, but a few inhabited whelk shells and the shells were always fossils.

I began to put the story together, only to find that I had been scooped in 1907 by Addison E. Verrill, master taxonomist, Yale professor, protégé of Louis Agassiz, and diligent recorder of Bermuda's natural history. Verrill searched the records of Bermudian history for references to living whelks and found that they had been abundant during the first years of human habitation. Captain John Smith, for example, recorded the fate of one crew member during the great famine of 1614–15: "One amongst the rest hid himself in the woods, and lived only on Wilkes and Land Crabs, fat and lusty, many months." Another crew member stated that they made cement for the seams of their vessels by mixing lime from burned whelk shells with turtle oil. Verrill's last record of living *Cittarium* came from kitchen middens of British soldiers stationed on Bermuda during the war of 1812. None, he reported, had been seen in recent times, "nor could I learn that any had been taken within the memory of the oldest inhabitants." No observations during the past seventy years have revised Verrill's conclusion that *Cittarium* is extinct in Bermuda.

As I read Verrill's account, the plight of *Cenobita diogenes* (proper name of the large hermit crab) struck me with that

anthropocentric twinge of pain often invested, perhaps improperly, in other creatures. For I realized that nature had condemned *Cenobita* to slow elimination on Bermuda. The neritid shells are too small; only juvenile and very young adult crabs fit inside them—and very badly at that. No other modern snail seems to suit them and a successful adult life requires the discovery and possession (often through conquest) of a most precious and dwindling commodity—a *Cittarium* shell. But *Cittarium*, to borrow the jargon of recent years, has become a “nonrenewable resource” on Bermuda, and crabs are still recycling the shells of previous centuries. These shells are thick and strong, but they cannot resist the waves and rocks forever—and the supply constantly diminishes. A few “new” shells tumble down from the fossil dunes each year—a precious legacy from ancestral crabs that carried them up the hills ages ago—but these cannot meet the demand. *Cenobita* seems destined to fulfill the pessimistic vision of many futuristic films and scenarios: depleted survivors fighting to the death for a last morsel. The scientist who named this large hermit chose well. Diogenes the Cynic lit his lantern and searched the streets of Athens for an honest man; none could he find. *C. diogenes* will perish looking for a decent shell.

This poignant story of *Cenobita* emerged from deep storage in my mind when I heard a strikingly similar tale recently. Crabs and snails forged an evolutionary interdependence in the first story. A more unlikely combination—seeds and dodos—provides the second, but this one has a happy ending.

William Buckland, a leading catastrophist among nineteenth-century geologists, summarized the history of life on a large chart, folded several times to fit in the pages of his popular work *Geology and Mineralogy Considered With Reference to Natural Theology*. The chart depicts victims of mass extinctions grouped by the time of their extirpation. The great animals are crowded together: ichthyosaurs, dinosaurs, ammonites, and pterosaurs in one cluster; mammoths, woolly rhinos, and giant cave bears in another. At the far right, representing modern animals, the dodo stands alone, the

first recorded extinction of our era. The dodo, a giant flightless pigeon (twenty-five pounds or more in weight), lived in fair abundance on the island of Mauritius. Within 200 years of its discovery in the fifteenth century, it had been wiped out—by men who prized its tasty eggs and by the hogs that early sailors had transported to Mauritius. No living dodos have been seen since 1681.

In August, 1977, Stanley A. Temple, a wildlife ecologist at the University of Wisconsin, reported the following remarkable story (but see postscript for a subsequent challenge). He, and others before him, had noted that a large tree, *Calvaria major*, seemed to be near the verge of extinction on Mauritius. In 1973, he could find only thirteen “old, overmature, and dying trees” in the remnant native forests. Experienced Mauritian foresters estimated the trees’ ages at more than 300 years. These trees produce well-formed, apparently fertile seeds each year, but none germinate and no young plants are known. Attempts to induce germination in the controlled and favorable climate of a nursery have failed. Yet *Calvaria* was once common on Mauritius; old forestry records indicate that it had been lumbered extensively.

Calvaria’s large fruits, about two inches in diameter, consist of a seed enclosed in a hard pit nearly half an inch thick. This pit is surrounded by a layer of pulpy, succulent material covered by a thin outer skin. Temple concluded that *Calvaria* seeds fail to germinate because the thick pit “mechanically resists the expansion of the embryo within.” How, then, did it germinate in previous centuries?

Temple put two facts together. Early explorers reported that the dodo fed on fruits and seeds of large forest trees; in fact, fossil *Calvaria* pits have been found among skeletal remains of the dodo. The dodo had a strong gizzard filled with large stones that could crush tough bits of food. Secondly, the age of surviving *Calvaria* trees matches the demise of the dodo. None has sprouted since the dodo disappeared almost 300 years ago.

Temple therefore argues that *Calvaria* evolved its unusually thick pit as an adaptation to resist destruction by crush-

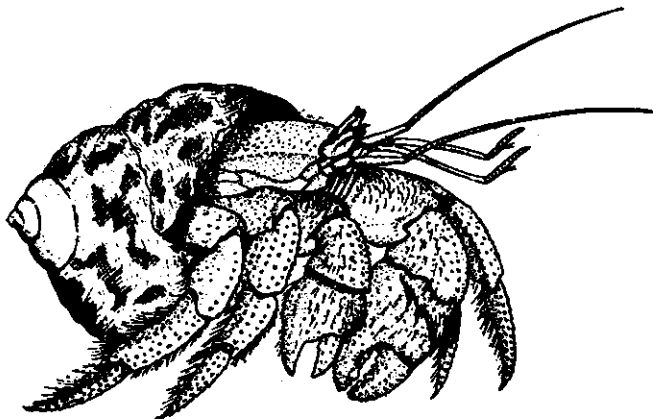
ing in a dodo's gizzard. But, in so doing, they became dependent upon dodos for their own reproduction. Tit for tat. A pit thick enough to survive in a dodo's gizzard is a pit too thick for an embryo to burst by its own resources. Thus, the gizzard that once threatened the seed had become its necessary accomplice. The thick pit must be abraded and scratched before it can germinate.

Several small animals eat the fruit of *Calvaria* today, but they merely nibble away the succulent middle and leave the internal pit untouched. The dodo was big enough to swallow the fruit whole. After consuming the middle, dodos would have abraded the pit in their gizzards before regurgitating it or passing it in their feces. Temple cites many analogous cases of greatly increased germination rates for seeds after passage through the digestive tracts of various animals.

Temple then tried to estimate the crushing force of a dodo's gizzard by making a plot of body weight versus force generated by the gizzard in several modern birds. Extrapolating the curve up to a dodo's size, he estimates that *Calvaria* pits were thick enough to resist crushing; in fact, the thickest pits could not be crushed until they had been reduced nearly 30 percent by abrasion. Dodos might well have regurgitated the pits or passed them along before subjecting them to such an extended treatment. Temple took turkeys—the closest modern analogue to dodos—and force-fed them *Calvaria* pits, one at a time. Seven of seventeen pits were crushed by the turkey's gizzard, but the other ten were regurgitated or passed in feces after considerable abrasion. Temple planted these seeds and three of them germinated. He writes: "These may well have been the first *Calvaria* seeds to germinate in more than 300 years." *Calvaria* can probably be saved from the brink of extinction by the propagation of artificially abraded seeds. For once, an astute observation, combined with imaginative thought and experiment, may lead to preservation rather than destruction.

I wrote this essay to begin the fifth year of my regular column in *Natural History* magazine. I said to myself at the

beginning that I would depart from a long tradition of popular writing in natural history. I would not tell the fascinating tales of nature merely for their own sake. I would tie any particular story to a general principle of evolutionary theory: pandas and sea turtles to imperfection as the proof of evolution, magnetic bacteria to principles of scaling, mites that eat their mother from inside to Fisher's theory of sex ratio. But this column has no message beyond the evident homily that things are connected to other things in our complex world—and that local disruptions have wider consequences. I have only recounted these two, related stories because they touched me—one bitterly, the other with sweetness.



Coenobita diogenes in the shell of *Cistarium*. Drawn from life by A. Verrill in 1900.

Postscript

Some stories in natural history are too beautiful and complex to win general acceptance. Temple's report received

immediate publicity in the popular press (*New York Times* and other major newspapers, followed two months later by my article). A year later (March 30, 1979), Dr. Owadally of the Mauritian Forestry Service raised some important doubts in a technical comment published in the professional journal *Science* (where Temple's original article had appeared). I reproduce below, verbatim, both Owadally's comment and Temple's response:

I do not dispute that coevolution between plant and animal exists and that the germination of some seeds may be assisted by their passing through the gut of animals. However, that "mutualism" of the famous dodo and *Calvaria major* (tambalacoque) is an example (1) of coevolution is untenable for the following reasons.

1) *Calvaria major* grows in the upland rain forest of Mauritius with a rainfall of 2500 to 3800 mm per annum. The dodo according to Dutch sources roamed over the northern plains and the eastern hills in the Grand Port area—that is, in a drier forest—where the Dutch established their first settlement. Thus it is highly improbable that the dodo and the tambalacoque occurred in the same ecological niche. Indeed, extensive excavations in the uplands for reservoirs, drainage canals, and the like have failed to reveal any dodo remains.

2) Some writers have mentioned the small woody seeds found in Mare aux Songes and the possibility that their germination was assisted by the dodo or other birds. But we now know that these seeds are not tambalacoque but belong to another species of lowland tree recently identified as *Sideroxylon longifolium*.

3) The Forestry Service has for some years been studying and effecting the germination of tambalacoque seeds without avian intervention (2). The germination rate is low but not more so than that of many other indigenous species which have, of recent decades, showed a marked deterioration in reproduc-

tion. This deterioration is due to various factors too complex to be discussed in this comment. The main factors have been the depredations caused by monkeys and the invasion by exotic plants.

4) A survey of the climax rain forest of the uplands made in 1941 by Vaughan and Wiehe (3) showed that there was quite a significant population of young tambalacoque plants certainly less than 75 to 100 years old. The dodo became extinct around 1675!

5) The manner in which the tambalacoque seed germinates was described by Hill (4), who demonstrated how the embryo is able to emerge from the hard woody endocarp. This is effected by the swollen embryo breaking off the bottom half of the seed along a well-defined fracture zone.

It is necessary to dispel the tambalacoque-dodo "myth" and recognize the efforts of the Forestry Service of Mauritius to propagate this magnificent tree of the upland plateau.

A. W. OWADALLY

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References and Notes

1. S. Temple, *Science* 197, 885 (1977).
2. Young *Calvaria major* plants that are 9 months old or more can be seen at the Forest Nursery in Curepipe.
3. R. E. Vaughan and P. O. Wiehe, *J. Ecol.* 19, 127 (1941).
4. A. W. Hill, *Ann. Bot.* 5, 587 (1941).

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The plant-animal mutualism that may have existed between the dodo and *Calvaria major* became impossible to prove experimentally after the dodo's extinction. What I pointed out (1) was the possibility that such a relation may have occurred, thus providing an explanation for the extraordinarily poor germination rate in *Calvaria*. I acknowledge the potential for error in historical reconstructions.

I disagree, however, with the conclusion of Owadally

(2) that the dodo and *Calvaria* were geographically separated. There have been virtually no bones of dodos or any other animals found in the uplands of Mauritius not because the animals were never there, but because the island's topography does not cause alluvial deposits there. Catchment basins in certain lowland areas accumulated many bones of animals that were washed into these areas from the surrounding uplands. Accounts of early explorers, summarized by Hachisuka (3, p. 85), definitely refer to dodos occurring in the uplands, and Hachisuka makes a point of clarifying the misconception that dodos were strictly coastal birds. Early forestry records from Mauritius (4) indicate that *Calvaria* was found in the lowlands as well as on the upland plateau. Although native forests only occur in the uplands today, one of the surviving *Calvaria* trees is located at an elevation of only 150 m. Thus, the dodo and *Calvaria* may have been sympatric, making a mutualistic relation possible.

Taxonomic authorities on sapotaceous plants of the Indian Ocean region recognize seeds of *Calvaria major*, as well as the smaller seeds of *Sideroxylon longifolium*, from alluvial deposits of the Mare aux Songes marsh (5), but this has little relevance to the question of mutualism. Mutualistic species will not necessarily be fossilized together.

The Mauritius Forestry Service has only recently succeeded in propagating *Calvaria* seeds, and the unmentioned reason for their recent success strengthens the case for mutualism. Success was achieved when the seeds were mechanically abraded before planting (6). A dodo's digestive tract merely abraded the endocarp naturally the same way the staff of the Mauritius Forestry Service does artificially before the seeds are planted.

The reference Owadally cites (7) is equivocal about the age of the surviving *Calvaria* trees because there is no easy way to accurately date them. Coincidentally, Wiehe, the coauthor of the paper Owadally cites, was

also my source of the estimated age of over 300 years for the surviving trees. I agree that there were more trees surviving in the 1930's than today, which further supports the notion that *Calvaria major* is a declining species and may have been so since 1681.

I erred in not citing Hill (8). However, Hill does not describe how and under what conditions he induced a seed to germinate. Without these details, his description is of little relevance to the question of mutualism.

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References and Notes

1. S.A. Temple, *Science* **197**, 885 (1977).
2. A. W. Owadally, *ibid.* **203**, 1363 (1979).
3. M. Hachisuka, *The Dodo and Kindred Birds* (Witherby, London, 1953).
4. N. R. Brouard, *A History of the Woods and Forests of Mauritius* (Government Printer, Mauritius, 1963).
5. F. Friedmann, personal communication.
6. A. M. Gardner, personal communication.
7. R. E. Vaughan and P. O. Wiehe, *J. Ecol.* **19**, 127 (1941).
8. A. W. Hill, *Ann. Bot.* **5**, 587 (1941).

I think that Temple has responded adequately (even triumphantly) to Owadally's first three points. As a paleontologist, I can certainly affirm his arguments about the rarity of upland fossils. Our fossil record of upland faunas is exceedingly spotty; the specimens we do possess are generally found in lowland deposits, well worn and washed in from higher ground. Owadally was certainly remiss in not mentioning (point 3) that the Forestry Service abrades its *Calvaria* seeds before they germinate; for the necessity of abrasion lies at the heart of Temple's hypothesis. But Temple was equally remiss in not citing the local Mauritian efforts, which, apparently, predate his own discovery.

Owadally's fourth point, however, represents the potential disproof of Temple's claim. If "quite a significant popu-

lation" of *Calvaria* trees were less than 100 years old in 1941, then dodos cannot have assisted their germination. Temple denies that so young an age has been demonstrated, and I certainly have no additional insight that can resolve this crucial question.

This exchange highlights a disturbing issue in the transmission of news about science to the public. Many sources cited Temple's original story. I did not find a single mention of the subsequent doubts. Most "good" stories turn out to be false, or at least overextended, but debunking doesn't match the fascination of a clever hypothesis. Most of the "classic" stories of natural history are wrong, but nothing is so resistant to expurgation as textbook dogma.

The debate between Owadally and Temple is too close to call at the moment. I'm rooting for Temple, but if Owadally's fourth point is correct, then the dodo hypothesis will become, in Thomas Henry Huxley's inimitable words, "a beautiful theory, killed by a nasty, ugly little fact."

28 | Sticking Up for Marsupials

I AM ANNOYED that the rapacious ways of my own species have irrevocably prevented me from seeing the dodo in action, for a pigeon as large as a turkey must have been something else, and stuffed, moldy specimens just don't carry conviction. We who revel in nature's diversity and feel instructed by every animal tend to brand *Homo sapiens* as the greatest catastrophe since the Cretaceous extinction. Yet I would argue that the rise of the Isthmus of Panama a mere two to three million years ago must rank as the most devastating biological tragedy of recent times.

South America had been an island continent throughout the Tertiary period (for seventy million years before the onset of continental glaciation). Like Australia, it housed a unique suite of mammals. But Australia was a backwater compared with the range and variety of South American forms. Many survived the onslaught of North American species after the isthmus rose. Some spread and prospered: the opossum moved as far as Canada; the armadillo is still making its way north.

Despite the success of a few, extirpation of the most dramatically different South American forms must be ranked as the dominant effect of contact between mammals of the two continents. Two entire orders perished (we group all modern mammals into about twenty-five orders). Think how our zoos would have been enriched with a liberal