
The dodo and the tambalacoque tree: an obligate mutualism reconsidered

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Mauritian folklore held that the seed of the tambalacoque (Sapotaceae: *Sideroxylon grandiflorum* [formerly *Calvaria major*]) needed to pass through a dodo's gut before it could germinate (see Durrell 1977), apparently because of the difficulty in germinating this seed, the seed's thick endocarp, and the rarity of the tree. This primary forest tree, like much of the native flora of Mauritius, is now seriously threatened (Cheke 1987). Vaughan and Wiehe (1941) had suggested that dispersal and germination of this tree might have been assisted by the dodo. Temple (1977) went further and formalized the folk notion to propose a coevolved obligate mutualism between the dodo and the tambalacoque. He argued that the seeds of the tambalacoque tree were unable to germinate naturally without abrasion in the gut of a dodo; his arguments for this obligate mutualism appealed to ecologists and have become textbook dogma (Futuyma 1979, Crawley 1983, Feinsinger 1983, Myers 1985, Gilpin and Soule 1986, Faaborg 1988, Abrahamson 1989, Stiles 1989, McNaughton 1989, Begon et al. 1990). However, there have been strong arguments against such an obligate mutualism by many biologists who have worked in Mauritius (Horn 1978, Owadally 1979, Cheke et al. 1984, Vaughan 1984, Cheke 1987). In spite of the serious doubts cast by these discussions, the notion that the seeds of the tambalacoque required treatment by a dodo's gizzard before they could germinate has thrived in the ecological literature (Pijl 1982, Wheelwright and Orians 1982, Armstrong 1985, Howe 1985, Murray 1988, Wheelwright 1988, as well as the previously cited texts). The hypothetical dodo/tambalacoque obligate mutualism is often used as an example of tight interdependence of species in ecology courses (pers. obs. MCW). As noted by Gould (1980) and Cheke (1987), attractive ideas, once entrenched, are difficult to change even in the face of

contradictory evidence. In this note we review the evidence relevant to the hypothesized dodo/tambalacoque mutualism, discuss the natural history of the dodo and the tambalacoque, and review the literature on seed germination to assess what the ecological relationship between the extinct dodo and the endangered tambalacoque may have been. We conclude that there is little evidence that tambalacoque seeds required treatment by dodo guts to germinate.

The obligate mutualism hypothesis

The dodo/tambalacoque obligate mutualism hypothesis was based on two premises: 1) that abrasion of tambalacoque seeds in birds' gizzards allowed germination, and 2) that no seeds have germinated since the dodo's demise 300 years ago. Both of these premises appear to be erroneous. Temple (1977) germinated 3 of 10 seeds that survived passage through turkey guts and argued that these were the first tambalacoque seeds to germinate since the dodo's extinction. This germination experiment suffered from a very low sample size and the lack of a control; Temple assumed no germination of cleaned, unabraded seeds. The tambalacoque fruit, termed a drupe, consists of a large stone (a single seed encased in a hard endocarp) covered with a 5 mm thick layer of tenacious fleshy pulp (Jackson et al. 1988). The endocarp of this ovoid drupe (about 40 × 50 × 50 mm) is as thick as 15 mm, thinning to about 5 mm (Temple 1977, Cheke et al. 1984, Friedmann 1981, Jackson et al. 1988). This protective covering is extremely strong; tambalacoque stones can withstand 4–5 times the force required to crush almonds (Temple 1977, Jackson et al. 1988). The fruit matures over an extended period (18

months for one tree noted by Friedmann 1981) and ripe fruits are green. King (1946), who established a nursery for tambalacoque and other native Mauritian trees around 1940, first reported germination of tambalacoque seeds. He and others have reported germination percentages of from 2.5 to 20% (see Cheke 1987). Although Temple's 30% germination is higher than reported by others, the low sample size in his trial could have produced this result by sampling error. It is also possible that there was an effect of gizzard treatment on germination rate, but germination of unabraded seeds by other workers seriously undermines the obligate mutualism hypothesis. Hill (1941) described germination of the seed in which the endocarp ruptures along a distinct circular line producing a cap which splits off. Hill (1941) and Friedmann (1981) clearly depicted this in illustrations of germinating tambalacoque seeds. No author before Temple (1977) mentioned preparing tambalacoque seeds for germination by abrading them. It is difficult to believe that Hill would have failed to mention abrading the seeds had he done so, given his interest in the mechanisms of germination of seeds enclosed in hard endocarps (Hill 1933, 1937, 1941). The only account of natural germination of a tambalacoque seed was observed in 1983 by G. Souchon, owner of the Curepipe garden where Temple collected his seeds (pers. comm. to ASC). Over several years of watching fruits fall and seeds summarily rot under the parent tree, she noted one seedling emerge which died after a short time. Several other Mauritian tree fruits share the tambalacoque's fruit structure of a seed enclosed in a hard endocarp surrounded with a fleshy mesocarp; the hard endocarp of *Canarium paniculatum* (Bursaceae) splits readily along a comparable fracture zone upon germination (W. Strahm pers. comm., pers. obs. ASC), although natural regeneration in the forest is as infrequent as it is for tambalacoques (Cheke 1987). The Mauritian Forestry Service has found no difference between the germination percentages of abraded and unabraded seeds (Owadally 1979), contrary to Temple's (1977, 1979) claims, although the results of such trials remain unpublished.

Temple (1977) reported that by 1973 only 13 trees remained, all more than 300 years old. Vaughan and Wiehe (1941) surveyed populations of trees in the native forest and recorded size classes. In their 1 ha of sample plots they recorded 33 tambalacoque trees; 3 of these were in the size class 10–14 cm diameter-at-breast-height (DBH), while the others were spread more-or-less evenly (2 to 5 individuals per 5 cm DBH size class) among the larger size classes up to a DBH of 59 cm. While it is difficult to determine the ages of rain forest trees, it seems doubtful that Vaughan and Wiehe's tambalacoques in the smaller size classes were 270 years old. Friedmann (1981) observed a tree 10 cm in diameter and 6–7 m in height which he estimated to be 30–50 years old. Finally, although the tambalacoque is rare and declining (Friedmann 1981), current estimates of

tambalacoque population size are of several hundred trees (W. Strahm per C. Jones, in Cheke 1987).

Natural history of the dodo and the tambalacoque tree

The dodo (Raphidae: *Raphus cucullatus*) was one of three species in the family Raphidae, considered to be derived from pigeons and doves (Columbiformes) (Hachisuka 1953, Cheke 1985). All were large, flightless birds found in the Mascarene Islands in the Indian Ocean to the east of Madagascar. All three species became extinct subsequent to the arrival of Europeans, most likely because of hunting and introduced predators, such as cats, rats, pigs, and monkeys (Hachisuka 1953, Cheke 1987). The dodo occupied Mauritius and was extinct there by the 1660s.

The only direct statement from navigators' journals on the diet of the dodo noted that the bird ate fruit (Hachisuka 1953). The dodo was distinctive in having a large bill, the stout upper bill decurved over the tip of the lower bill, and naked skin on its face and chin. Perhaps the dodo tore into large succulent fruits or may have even been quite omnivorous, including carrion in its diet. The ease with which dodos could be taken on long sea-journeys and kept for years in captivity (Hachisuka 1953, Cheke 1987) suggests that they would accept a very generalized diet. Reports of early explorers and naturalists indicated that the gizzard of the dodo contained one to several large stones, as did the gizzard of the closely related and morphologically similar solitaire (Raphidae: *Pezophaps solitaria*) of Rodrigues Island (Hachisuka 1953). These stones no doubt functioned to grind food in the gizzard. The dodo may have consumed fallen fruits and digested both fruit pulp and seeds, as do seed-eating pigeons to which it is considered related (Hachisuka 1953, Cowles and Goodwin 1959, Lambert 1989). Hachisuka suggested that fallen palm fruits may have comprised a major portion of the dodo's diet; the original Mauritian forests were rich in palm species, notably large-seeded *Latania* spp. in the lowland palm savannah (Vaughan and Wiehe 1937). Interestingly, the better documented Rodrigues solitaire fed on seeds, including whole palm fruits (*Latania* spp.), and foliage (Hachisuka 1953, Cheke 1985). This kind of diet is similar to that of some galliform and pigeon diets; these and other avian granivores digest most of the seeds they eat (Roessler 1936, Swank 1944, Krefting and Roe 1949, Schorger 1960, Rick and Bowman 1961, Janzen 1981a). If dodos were primarily granivorous, they probably destroyed most of the tambalacoque seeds they consumed. Indeed, Temple (1977) found that turkeys (*Meleagris gallopavo*), which are smaller than dodos and so, presumably, have weaker gizzards, destroyed 7 of the 17 tambalacoque seeds he fed them. Although dodos probably dispersed some of the tambalacoque

seeds they ate, the crux of the issue is whether or not tambalacoque seeds require abrasion in order to germinate.

Jackson et al. (1988) conducted germination trials on tambalacoque and makak (Sapotaceae: *Mimusops petiolaris*) seeds, another endemic Mauritian forest tree in which seedlings and saplings are now rare. The pulp on all of their tambalacoque fruits had begun to rot before they could clean the seeds; all of the tambalacoque seeds were killed by fungal and bacterial infections. Friedmann (1981) also noted the susceptibility of tambalacoque seeds to fungal attack. Makak seeds from unripe fruits (the pulp retains latex which presumably prevents microbial attack) germinated very well (79.1%, 89.7%, and 93.3%), seeds from ripe fruits germinated relatively poorly (46.2%), and seeds from rotted fruits failed to germinate at all (Jackson et al. 1988). These results and the observation of wholesale seed spoilage by G. Souchon suggest that thorough cleaning of tambalacoque seeds before the pulp rots may be crucial for successful germination. This could explain Temple's (1977) relatively good germination results with freshly collected turkey-passed seeds and the spotty results of others who made no mention of abrading seeds.

It is likely that dodos dispersed some of the tambalacoque seeds they consumed, but other extinct vertebrates could have been important dispersers; large-billed parrots (*Lophopsittacus mauritianus*), and two endemic giant tortoises (*Geochelone* spp.) may have eaten and dispersed these seeds (Cheke 1987, Iverson 1987). A giant skink (*Leiopisma mauritiana*) may also have eaten the pulp off of fallen fruits (Cheke 1987, Jackson et al. 1988). Introduced monkeys and pigs may disperse some seeds, but they may not clean seeds adequately and they destroy seeds and seedlings of many endemic plants (Cheke 1987). The tambalacoque and other endemic Mauritian forest trees very likely have difficulty in establishment because of a lack of competent seed dispersers which can clean and disseminate the seeds of fleshy-fruited plants. The requirement of thorough pulp removal for successful germination of the seeds of rain forest trees is well documented (Friedmann 1981, Howe and Vande Kerckhove 1981, Ng 1983, Jackson et al. 1988). In addition, establishment of seedlings is impeded by the depredations of introduced animals, habitat degradation, and competition from exotics (Vaughan and Wiehe 1941, Owadally 1978, Cheke et al. 1984, Cheke 1987).

Germination of vertebrate-dispersed seeds

Many plants produce fruits in which the seeds are surrounded by a thick, hard covering; these seeds germinate without abrasion of their protective coats. In many of these, like peach and cherry (*Prunus* spp.), walnut

(*Juglans* spp.), and hickory (*Carya* spp.), the bony endocarp splits along a zone of weakness upon germination (USDA, Forest Service 1974). *Spondias mombin* (Anacardiaceae) seeds are encased in a tough nut and the germinating seedling emerges through a germination canal (Janzen 1985). Hard seeds of large, thick-husked fruits consumed by large mammals with grinding molars and long gut-retention times are not prevented from germinating by their protective coverings. Dinerstein and Wemmer (1988) studied the dispersal of *Trewia nudiflora* (Euphorbiaceae) seeds by *Rhinoceros* in Nepal. *Trewia* seed passage was slow (46–172 h transit times, with most seeds passing in 64–88 h in one trial) and there was significant seed mortality in the alimentary canal of the *Rhinoceros* (26.7 and 47.7% mortality in two trials). Although these animals were important in removing the fruit pulp from these seeds and dispersing them, there was no effect of gut treatment on germination success. Similarly, Janzen (1981b) found no enhancement of germination of seeds of a neotropical tree (Leguminosae: *Enterolobium cyclocarpum*) after passage through horses, although the seeds required scarification (a nick in the seed coat) to germinate. Jicaro (Bignoniaceae: *Crescentia alata*) seeds removed from their fruit pulp germinated as well as seeds passed through horses (Janzen and Martin 1982). While there are exceptional reports of strong effects of gut treatment on germination rate (Rick and Bowman 1961, Noble 1975), most work shows variable and small effects (Krefting and Roe 1949, Lieberman and Lieberman 1986). Delayed germination may be advantageous to many plants.

These examples call into question the implicit assumption in the hypothesized obligate mutualism between the dodo and the tambalacoque that there is a simple tradeoff between the thickness of a seed's protective covering and its ability to germinate.

Summary

The dodo/tambalacoque obligate mutualism notion is not supported by the evidence. Reports of 1) germination of unabraded seeds in which the seed coat ruptures along a natural zone of weakness, and 2) living trees less than 300 years old, undermine the hypothesis that tambalacoque seeds required abrasion in a dodo's gizzard before they could germinate. It is likely that the tambalacoque evolved a thick, tough seed coat in response to consumption by its dispersers, but there is no evidence that the seeds require abrasion before they can germinate. Gut treatment may influence the rate of tambalacoque seed germination, but there is no sound evidence for this. Extinct frugivores were no doubt critical in cleaning and dispersing tambalacoque and other endemic Mauritian forest tree seeds. We emphasize that several endemic primary forest trees of Mauritius now

fail to recruit young trees (Vaughan and Weihe 1941, Cheke 1987, Jackson et al. 1988). In cases where pulp removal from fleshy fruits and seed dissemination by dispersers are essential for successful reproduction the ecological relationship would be an obligate mutualism, but not defined as a one-on-one relationship and not operating by a requirement for seed coat abrasion. This kind of relationship is not unique to the tambalacoque and its dispersers and may be common, at least for fleshy-fruited tropical plants (Howe and Vande Kerckhove 1981, Ng 1983, Dinerstein and Wemmer 1988, Jackson et al. 1988). This view of the ecology of the dodo and the tambalacoque is similar to our understanding of the ecology of other fruiting-plant/disperser communities; rather than exemplifying an exceptional biological phenomenon, what we know about the dodo/tambalacoque relationship is consistent with the non-specific nature of most other seed-dispersal systems which have been studied (Wheelwright and Orians 1982, Herrera 1985). The difference between this system and others is that the interacting plant and frugivore communities were much smaller, as would be expected for island communities.

Although the dodo is gone forever, the germination requirements of the tambalacoque can still be clarified with rigorous germination trials with seeds produced by surviving tambalacoques.

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References

- Abrahamson, W. G. 1989. Plant-animal interactions: An overview. – In: Abrahamson, W. G. (ed.), *Plant-animal interactions*. McGraw-Hill, NY, pp. 1–20.
- Armstrong, P. 1985. The dodo and the tree. – *Geographical Magazine* 57: 541–543.
- Begon, M., Harper, J. L. and Townsend, C. R. 1990. *Ecology: Individuals, populations and communities*. – Blackwell, Oxford.
- Cheke, A. S. 1985. Dodo. – In: Campbell, B. and Lack, E. (eds), *Dictionary of birds*. Buteo Books, Vermillion, SD, p. 152.
- 1987. An ecological history of the Mascarene Islands, with particular reference to extinctions and introductions of land vertebrates. – In: Diamond, A. W. (ed.), *Studies of Mascarene Island birds*. Cambridge Univ. Press, Cambridge, pp. 5–89.
- , Gardner, T., Jones, C. G., Owadally, A. W., and Staub, F. 1984. Did the dodo do it? – *Animal Kingdom* 87: 4–6.
- Cowles, G. S. and Goodwin, D. 1959. Seed digestion by the fruit-eating pigeon *Treron*. – *Ibis* 101: 253–254.
- Crawley, M. J. 1983. *Herbivory: The dynamics of animal-plant interactions*. – Univ. California Press, Berkeley, CA.
- Dinerstein, E. and Wemmer, C. M. 1988. Fruits *Rhinoceros* eat: dispersal of *Trewia nudiflora* (Euphorbiaceae) in lowland Nepal. – *Ecology* 69: 1768–1774.
- Durrell, G. 1977. Golden bats and pink pigeons: A journey to the flora and fauna of a unique island. – Simon and Schuster, NY.
- Faaborg, J. 1988. *Ornithology: An ecological approach*. – Prentice-Hall, NJ.
- Feinsinger, P. 1983. Coevolution and pollination. – In: Futuyma, D. J. and Slatkin, M. (eds), *Coevolution*. Sinauer, Sunderland, MA, pp. 282–308.
- Friedmann, F. 1981. Sapotaceae. – *Flore des Mascareignes* 116: 1–27.
- Futuyma, D. J. 1979. *Evolutionary biology*. – Sinauer, Sunderland, MA.
- Gilpin, M. E. and Soule, M. E. 1986. Minimum viable populations: processes of species extinction. – Sinauer, Sunderland, MA.
- Gould, S. J. 1980. *The Panda's thumb*. – Norton and Co., NY and London.
- Hachisuka, M. 1953. *The dodo and kindred birds*. – Witherby, London.
- Herrera, C. M. 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. – *Oikos* 44: 132–141.
- Hill, A. W. 1933. The method of germination of seeds enclosed in a stony endocarp. – *Ann. Bot.* 47: 873–887.
- 1937. The method of germination of seeds enclosed in a stony endocarp, II. – *Ann. Bot. New Series* 1: 239–256.
- 1941. The genus *Calvaria*, with an account of the stony endocarp and germination of the seed, and description of a new species. – *Ann. Bot. New Series* 5: 587–606.
- Horn, B. K. P. 1978. Dodo apocrypha. – *Science News* 113: 19.
- Howe, H. F. 1985. Gompothere fruits: a critique. – *Am. Nat.* 125: 853–865.
- and Vande Kerckhove, G. A. 1981. Removal of wild nutmeg (*Viola surinamensis*) crops by birds. – *Ecology* 62: 1093–1106.
- Iverson, J. B. 1987. Tortoises, not dodos, and the tambalacoque tree. – *J. Herpetol.* 21: 229–230.
- Jackson, P. S. W., Cronk, Q. C. B. and Parnell, J. A. N. 1988. Notes on the regeneration of two rare Mauritian endemic trees. – *Trop. Ecol.* 29: 98–106.
- Janzen, D. H. 1981a. *Ficus ovalis* seed predation by an orange-chinned parakeet (*Brotogeris jugularis*) in Costa Rica. – *Auk* 98: 841–844.
- 1981b. *Enterolobium cyclocarpum* seed passage rate and survival in horses, Costa Rican Pleistocene seed dispersal agents. – *Ecology* 62: 593–601.
- 1985. *Spondias mombin* is culturally deprived in megafauna-free forest. – *J. Trop. Ecol.* 1: 131–155.
- and Martin, P. S. 1981. Neotropical anachronisms: The fruits the Gompothere ate. – *Science* 215: 19–27.
- King, H. C. 1946. Interim report on indigenous species in Mauritius. – Government Printer, Port Louis, Mauritius.
- Krefting, L. W. and Roe, E. I. 1949. The role of some birds and mammals in seed germination. – *Ecol. Monogr.* 19: 271–286.
- Lambert, F. R. 1989. Pigeons as seed predators and dispersers of figs in a Malaysian lowland forest. – *Ibis* 131: 521–527.
- Lieberman, M. and Lieberman, D. 1986. An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. – *J. Trop. Ecol.* 2: 113–126.
- McNaughton, S. J. 1989. Ecosystems and conservation in the twenty-first century. – In: Western, D. and Pearl, M. (eds), *Conservation for the twenty-first century*. Oxford Univ. Press, Oxford, pp. 109–120.
- Murray, K. G. 1988. Avian seed dispersal of three neotropical gap-dependent plants. – *Ecol. Monogr.* 58: 271–298.
- Myers, N. (ed.). 1985. *The Gaia atlas of planet management*. – Pan Books, London.
- Noble, J. C. 1975. The effects of emus (*Dromaius novaehollandiae* Latham) on the distribution of the nitre bush (*Nitratia billardieri* DC.). – *J. Ecol.* 63: 979–984.
- Ng, F. S. P. 1983. Ecological principles of tropical lowland rain forest conservation. – In: Sutton, S. L., Whitmore, T. C.,

- and Chadwick, A. C. (eds), Tropical rain forest: ecology and management. Blackwell, Oxford. pp 359–375.
- Owadally, A. W. 1979. The dodo and the tambalacoque tree. – *Science* 203: 1363–64.
- Pijl, L. van der 1982. Principles of dispersal in higher plants. – Springer, Berlin.
- Rick, C. M. and Bowman, R. I. 1961. Galapagos tomatoes and tortoises. – *Evolution* 15: 407–417.
- Roessler, E. S. 1936. Viability of weed seeds after ingestion by California linnets. – *Condor* 38: 62–65.
- Schorger, A. W. 1960. The crushing of *Carya* nuts in the gizzard of the turkey. – *Auk* 77: 337–340.
- Stiles, E. W. 1989. Fruits, seeds, and dispersal agents. – In: Abrahamson, W. G. (ed.), Plant-animal interactions. McGraw-Hill, NY, pp. 87–113.
- Swank, W. G. 1944. Germination of seeds after ingestion by ring-necked pheasants. – *J. Wildl. Mgmt* 8: 223–231.
- Temple, S. A. 1977. Plant-animal mutualism: co-evolution with dodo leads to near extinction of plant. – *Science* 197: 885–886.
- 1979. Reply to Owadally. – *Science* 203: 1364.
- USDA, Forest Service. 1974. Seeds of woody plants in the United States. – U. S. Dept Agric., Agric. Handb. 450.
- Vaughan, R. E. and Wiehe, P. O. 1937. Studies on the vegetation of Mauritius. I. A preliminary survey of the plant communities. – *J. Ecol.* 25: 289–343.
- and Wiehe, P. O. 1941. Studies on the vegetation of Mauritius. III. The structure and development of the upland climax forest. – *J. Ecol.* 29: 127–160.
- 1984. [untitled letter]. – *Animal Kingdom* 87: 6–7.
- Wheelwright, N. T. 1988. Fruit-eating birds and bird-dispersed plants in the tropics and temperate zone. – *Trends Ecol. Evol.* 3: 270–274.
- and Orians, G. H. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. – *Am. Nat.* 119: 402–413.