The Dodo: from extinction to the fossil record

The dodo, Raphus cucullatus (Aves, Columbidae), has become one of the most famous birds in the world, a true icon of extinction. Known from a few contemporary illustrations and accounts, probably more has been written about it than any other species, yet we know practically nothing about the bird in life. Recent excavations on Mauritius are now revealing the ecology and habitat of this iconic bird, and providing new information as to why it was so vulnerable to human interference.

Discovery of the Mascarenes

The Mascarene Islands, comprising Mauritius, Réunion and Rodrigues, are isolated volcanic islands situated in the south-western Indian Ocean (Fig. 1). They lie approximately 665 km east of Madagascar, the nearest large land mass. It was Arab traders who first discovered the Mascarene Islands during the thirteenth century, followed by the Portuguese in the sixteenth century, but there is no evidence that either the Arabs or Portuguese settled there. Mauritius was claimed for the Netherlands by the Dutch East India Company (VOC) in September 1598, and was used thereafter as a port of call for provisioning and careening ships, including those from other European maritime nations. During this time, vague accounts were made in ships’ logs and journals about the original fauna, some of which described the dodo. Although inadequate, these accounts have proved invaluable in helping determine the faunal composition of Mauritius before it was irreversibly destroyed by humans and their commensal animals. It was during the century of Dutch occupation that the dodo became extinct.

Written and pictorial evidence

It was VOC company policy that daily records were kept concerning all aspects of the voyages. These included topographical maps, safe shipping routes and potential harbours, as well as written descriptions. Just occasionally, a member of the fleet would describe or illustrate the animals he encountered. Upon the return of the fleets, the journals became important source material for artists, scientists and book publishers (Fig. 2). These publications, which were regularly expanded and illustrated long after the voyage itself, became the source material for scholarly study, but were also plagiarized on numerous occasions. This is why the contemporary accounts and illustrations of the dodo are often contradictory, and have resulted in a wealth of scientific myths and misconceptions.

Transportation of specimens

Besides the transportation of trade goods from the Far East, exotic animals were also brought back to Europe as novelties. These curiosities, many new to
science, caused quite a sensation, and were illustrated in works of art and popular books. Among these imports appeared the dodo, but such were the variations in detail that it is now impossible to know how many specimens were involved. That dodos arrived in Europe and the Far East is without question, but some arrived as partial specimens, and perhaps as few as three or four actually made the journey alive. Only one of these unequivocally arrived in Europe. This individual was exhibited live in a shop somewhere in London in 1638 and may have been the same individual whose remains ended up preserved in the Ashmolean Museum (now University Museum), Oxford. The head, which still retains soft tissue (Fig. 3), and bony core of the foot of this specimen still survive in Oxford; other than this, a foot, with integuments now perished, that is or was in London (whereabouts currently unknown) and a mummified head in Denmark are the only relics of these transported specimens still extant.

**Extinction**

Once humans arrived on Mauritius the dodo was doomed. A number of mariners’ accounts variously describe the capturing and eating of dodos, but hunting by humans cannot alone have caused the bird’s extinction. Hunting was probably restricted to the coastal areas and extremely limited because of the small human population: the population on Mauritius was never more than 50 people during the seventeenth century. It was almost certainly competition and predation by introduced animals, such as rats, monkeys, pigs, goats and deer, which was to blame. Dodos, like many island bird species, were probably long-lived with slow reproductive rates and vulnerable eggs and chicks. Predation and competition of limited food sources must have had a significant effect on the survival of dodo adults and their ability to successfully reproduce. As a result, at some point during the second half of the seventeenth century the dodo became extinct.

**Affinities**

By the beginning of the nineteenth century, such was the scarcity of dodo physical remains that some authorities considered the dodo to be a mythical species. However, the aforementioned dodo remains in Oxford and London formed the basis for the now classic dodo monograph by Hugh Strickland and Alexander Melville in 1848. More importantly, Strickland and Melville confirmed that the dodo was a giant pigeon, an idea that had been met with ridicule when first proposed by Danish Professor, J.T. Reinhardt in 1842. However, most of the dodo’s anatomy still remained unknown, and Strickland and Melville’s monograph initiated a surge of interest from the scientific community; especially to the need to discover fossil material on Mauritius.

**Race to find the first fossil evidence**

George Clark, an amateur naturalist and Master of the Diocesan School at Mahebourg, Mauritius, spent two decades in the mid-nineteenth century searching the island hoping to discover dodo fossil material. By chance, Harry Higginson, a railway engineer, was constructing a railway embankment alongside a marsh called the Mare aux Songes, situated about 1 km from the surrounding lagoon in southeast Mauritius (Fig. 4). In October 1865, Higginson noted that the labourers were stockpiling bones from the marsh, so he immediately informed Clark. By comparing some of the bones with the illustrative plates in Strickland and Melville’s dodo monograph, Clark confirmed that dodo remains were present, after which he immediately monopolized the site. News of the discovery did not take long to circulate on Mauritius, and attracted a host of interested parties, most notably Colonial Secretary Edward Newton, brother of Alfred Newton, a renowned zoologist who was to become the first Professor of Zoology and Compara-

![Fig. 2. Dutch on Mauritius, 1598. Notice the dodo (centre, left), the first time it was illustrated. From Strickland & Melville, 1848.](image)

![Fig. 3. The Oxford dodo. This specimen, along with some skin from a foot, constitutes the only surviving soft tissues.](image)
tive Anatomy at Cambridge. Also interested was the Bishop of Mauritius, Vincent Ryan, who was closely associated with Richard Owen, the superintendent and comparative anatomist at the then British Museum (now the Natural History Museum). Both Alfred Newton and Richard Owen were eager to get any dodo material first.

**Academic blackmail and rivalry**

Clark, via Edward Newton, struck a small monetary deal with Alfred, and agreed to send a consignment of material to him, along with another collection for Richard Owen. The UK intermediaries were George Clark’s brother, Samuel Clark, and one Captain Mylius, Clark’s brother-in-law. However, unbeknown to Clark and Alfred Newton, Mylius set up a new deal with Richard Owen, who offered £100 for a hundred bones. Owen not only received the first dodo material but also claimed the consignment promised to Alfred. This resulted in a bitter feud between the two men, and as a result of Owen’s ungentlemanly behaviour, Alfred intended to make a formal complaint to the Royal Society. However, Alfred had applied to become the first professor of Zoology and Comparative Anatomy at Cambridge, but, unfortunately for him, Owen was one of the main supporters, even writing a testimonial in his favour. By threatening to fail Alfred’s application as professor, Owen forced Alfred to withdraw his complaint and refrain from publishing anything on the dodo’s anatomy. Owen, who was now in complete control, wasted no time in formally describing and illustrating the dodo’s anatomy in his memoir in 1866 (Fig. 5), amidst a commotion of high-profile public lectures and engagements.

**Aftermath**

Such was the intensity of excitement surrounding the dodo remains that relatively little else also found with them in the Mare aux Songes was written up. Owen described a new, extinct parrot, *Lophopsittacus mauritianus*, from a jaw sent by Clark in the first dodo consignment. From collections made in the 1870s, Albert Günther described two species of extinct giant tortoise *Cylindraspis* sp., and a giant skink *Leiolopisma mauritianana*. The Mare aux Songes marsh was reworked more intensively in 1879 by Théodore Sauzier, from which six fossil birds were described in 1893 by Alfred and Hans Gadow. The family of the amateur naturalist Paul Carrière inherited the Mare aux Songes site in 1902, so he was able to send more material to Paris in the early 1900s. This resulted in the retrieval of many more dodo bones and the discovery of new species of reptile. Such was the abundance of dodo...
material collected from the marsh—albeit a composite of many different individuals—that almost all dodo remains held in museum collections today are derived from this one site. Due to an epidemic of malaria on Mauritius in the 1940s, the Mare aux Songes was infilled with dolerite gravels, after which the site fell into neglect and was all but forgotten.

Other discoveries

At the turn of the nineteenth century, Louis Etienne Thirioux, a hairdresser by trade, discovered a complete, well-preserved, associated dodo skeleton and a second partial dodo skeleton in undisclosed caves near Le Pouce Mountain and the Vallée du Prêt. The former is unique and by far the most important fossil dodo discovery made. A second complete, but badly degraded specimen, affectionately known as ‘Dodo Fred’, was discovered in a cave in the highlands near Beau Cherie in a 2007 (Fig. 6), confirming that dodos once occurred in the wet Mauritius highlands as well as dry lowland, coastal regions.

Return to the Mare aux Songes

In 2005, a Dutch expedition discovered fresh fossil material at the Mare aux Songes, beneath the dolerite gravels. This resulted in full scale annual excavations from 2006 by an international multidisciplinary team, and thousands more bones were recovered. More importantly, contextual data was obtained and the genesis of the fossil locality could be ascertained. The Mare aux Songes was created from the collapse of a large lava tunnel system. It comprises three basins (Fig. 7) fed by underground streams, and with the basin ground water influenced by tidal movement. A late Holocene sea level high stand created a seasonal lake 10 kya, acting as an oasis situated in an otherwise comparatively dry, leeward part of the island. The erosion of the coral reef surrounding the lagoon resulted in the accumulation of wind-blown coral sands in the Mare aux Songes basins (Fig. 8), raising the pH to almost neutral. Over the next few millennia, the fall of sea levels desiccated the lake, producing a marshy environment, which acted as a miring trap or catchment area of fossil remains. The neutral pH, rapid burial of skeletal elements, and anaerobic conditions of the sediment resulted in their exceptional preservation.

The fossil layer averages 300–500 mm in thickness and contains seeds, tree trunks and branches, leaves, insects, land snails and even fungi (Fig. 9). The fossil remains are dominated by extinct giant tortoises Cylindraspis sp. (>90 per cent), but they also include a suite of vertebrate and invertebrate species that once also occurred on the island. Dodo fossil remains are the commonest bird component (>7 per cent). Minimum number counts (based on the most common element, i.e. tarsometatarsus) show that at least 300–400 individual dodos have to date been retrieved from the marsh, but only a small percentage of the Mare aux Songes basin has so far been excavated.

Because of the exceptional quality of the fossil material, DNA sampling has been attempted, but exposure to high temperature has affected the preservation of amplifiable DNA; thus this has so far proved unsuccessful. A further attempt at obtaining DNA
from Dodo Fred, whose remains were situated in a humid, highly alkaline cave, also failed. Relatively poor quality DNA had previously been obtained from the skin remnants of the Oxford dodo, from which it was suggested that the dodo and closely related solitaire Pezophaps solitaria of neighbouring Rodrigues are a sister clade nested within the family Columbidae and derived from the same ancestor as the southeast Asian Nicobar pigeon Caloenas nicobarica; however, this has been disputed and the dodo’s precise relationships need to be independently verified.

Discussion

As a result of this new physical evidence, it is now possible to make scientifically informed conclusions about the dodo’s ecology and the reasons why it disappeared so rapidly. Fossil evidence has shown that the dodo was commonly found in the lowlands and close to the coast on the leeward side of the island, but probably less so in the highlands, occupying dry and wet forest zones and feeding on fallen fruits and seeds. The lowland palaeo-environment comprised at least four species of palm (Hyophorbe, Dictyosperma and Latania (two species) screw pines (Pandanus), canopy trees such as tambulacoque Sideroxylon grandiflorum and ebony Diospyros sp., and a host of smaller plant species (Fig. 10). All of these forest species now only occur on a few mountain tops of Mauritius or on off-shore islets. Without exception, coastal and lowland forests on oceanic islands are the first to be exploited by humans, especially if they are dry and easily burnt-off. The dodo, being restricted in range, would have been extremely susceptible to human interference, especially combined with the introduction of potential predatory and competitive exotic animals. Once humans settled on Mauritius, these negative factors combined to drive the dodo to extinction in less than 100 years.

Suggestions for further reading