

Dead as a dodo: the fortuitous rise to fame of an extinction icon

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Today, the Dodo is the most famous species known to have been driven to extinction through human activity. However, it disappeared over a century before Cuvier demonstrated the reality of extinction, and was only one of a huge number of species that died out following early European expansion around the globe. Unlike many other now-extinct Mascarene species, the Dodo's decline and disappearance was not documented by contemporary observers. Repeated settlement changes on Mauritius during the seventeenth century led to protracted 'cultural amnesia' over its very existence, and it was widely regarded as mythical by European scientists into the nineteenth century. A series of scientific and socio-cultural hurdles, which all had to be overcome before a given species could be widely appreciated by the general public as an icon of human-caused extinction, are identified and assessed in order to understand how the Dodo returned from scientific death and achieved its tremendous posthumous celebrity. This review indicates that although some ecological and evolutionary factors may have given the Dodo an increased chance of becoming famous, these factors are offset by a much greater series of serendipitous events, emphasising the importance of contingency and the fundamental lack of inevitability in historical processes.

The dodo was (perverse distinction)
Immortalized by his extinction

[Lucie-Smith E. (1970). *Six more beasts*, p. 16]

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Introduction

The Dodo *Raphus cucullatus*, a large, flightless pigeon [Columbiformes: Columbidae (formerly Raphidae)] found on the island of Mauritius until the seventeenth century, is probably today's greatest icon of extinction. Its very name is synonymous with the extinction process, and this single species is rivalled in its unenviable position only by the dinosaurs, which instead represent an entire superorder of several hundred known species (Weishampel et al. 2004). As one of the earliest species to be identified as extinct, the Dodo gained tremendous celebrity throughout the nineteenth and twentieth centuries, and continues to represent a source of considerable fascination and interest in popular culture today (e.g. Fuller 2002; Pinto-Correia 2002; den Hengst 2003; Grihault 2005).

Public appreciation of the Dodo's extinction through human activity is increasingly relevant in light of the escalating anthropogenically-driven global biodiversity crisis. Whereas the perpetrators of prehistoric human-caused extinctions are presumed not to have understood the wider-scale ecological impacts of their actions, in the Dodo's case it is frequently also popularly assumed that those who were responsible for its extinction were aware of what they had done or even (Day 1981) deliberately

exterminated the bird. For example, to quote Carl Jones (Quammen 1996, p. 277):

There were extinctions before and there's been lots of extinctions since, but it was an important extinction because for the first time, the first time in the whole of man's history, that he actually realised *he* had caused the disappearance of a species ... / And it was at that moment – or in that era – when he realized the Dodo was gone, that he realized the world was an exhaustible place. That he couldn't go on pillaging and raping. So it signified a very profound moment.

However, this *post hoc* interpretation of the origin of the Dodo's celebrity is contradicted by a series of historical facts. Not only did the Dodo die out over a century before extinction became generally accepted as a real process, but a series of additional contingent historical factors further confused any meaningful scientific understanding of its status and demise before the nineteenth century.

Barriers to historical recognition of Dodo extinction

The European scientific community did not become widely convinced of the reality of extinction before Georges Cuvier demonstrated conclusively at the end of

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the eighteenth century that many fossil quadrupeds such as mammoths and mastodons were distinct from living species (Cuvier 1796; Rudwick 1997). Although extinction had been debated during the eighteenth century by authorities such as LeClerc de Buffon ((1749–1767); see also Roger (1997)), early misperceptions of evolutionary and geological processes led to a general denial of its reality by important contemporary thinkers such as Lamarck (Burkhardt 1977; Gould 1987). In fact, several extinctions and extirpations occurring in the Mediterranean region c. 2000 years ago were recognised by Classical writers, but these were not absorbed into the body of Western scientific thought until their recent ‘rediscovery’ or reinterpretation following the current concerns over human-driven biodiversity loss (Parejko 2003).

However, the Dodo died out almost a century and a half before Cuvier’s demonstration of the reality of extinction, primarily due to predation of eggs and nestlings by introduced rats and pigs (Cheke 1987). Its extinction date remains the subject of debate (Roberts and Solow 2003; Cheke 2004, 2006; Hume et al. 2004; Mlíkovský 2004), with additional confusion arising from the suggestion that the Dutch name ‘dodaersen’ was transferred to a now equally extinct large flightless Mauritian rail, the Red Hen *Aphanapteryx bonasia* (see Cheke 2006). However, the Dodo was undoubtedly extinct by the close of the seventeenth century. The dominant European paradigm for interpreting the natural world during this period and for much of the eighteenth century remained the Enlightenment version of the Classical and medieval *scala naturae*, or Great Chain of Being, a world-view that held Creation to be a rigid and strictly ordered hierarchy encompassing all known plant and animal diversity (Grayson 1984; Lovejoy 2005). The Great Chain of Being was fundamentally perfect, unbroken and unchanging, and extinction was impossible under this paradigm because God’s benevolence and plenitude would not permit the disappearance of any links in the chain. Whereas LeClerc de Buffon was criticised by both church and establishment for his ideas in the mid-eighteenth century (Roger 1997), due to the anti-clericalism of the French Revolution, by whose government he was appointed to the museum in 1795, ‘extinction held no philosophical or religious terrors for Cuvier’ (Young 1992).

The Dodo was also only one of a large – and increasing (e.g. Turvey et al. 2007) – number of species known to have become extinct through anthropogenic impacts (direct overhunting, habitat destruction, introduction of exotic species) in the historical interval between the expansion of European exploration, trade and sea-power around the globe from the late fifteenth century onwards, and the scientific validation of extinction by Cuvier at the end of the eighteenth century. For example, for mammals alone, MacPhee and Flemming (1999) listed 40 species known or believed to have died out between 1500 and

1800. Indeed, the Dodo was only one of at least 48 endemic species of terrestrial vertebrates that became extinct before 1800 (with a further 6 + local extinctions) on the Mascarene Islands of Mauritius, Rodrigues and Réunion following European contact and subsequent colonisation in the sixteenth and seventeenth centuries (Cheke 1987; Mourer-Chauviré et al. 1999; Cheke and Hume 2008).

Several of these extinct Mascarene species were small-bodied birds and reptiles which in some cases were not recorded in early historical accounts and are only known from subfossil remains. However, many larger-bodied members of the extinct endemic Mascarene faunas (e.g. giant tortoises *Cylindraspis* spp., Raven Parrots *Lophosittacus mauritianus*, endemic ducks and sheldgeese (*Anas theodori*, *Alopochen* spp.), Red Hens, pigeons and parakeets) were well-known to the early colonists, and were often also actively overexploited through unrestrained hunting as recorded in many of the same historical documents that refer to Dodos (Soeteboom 1648; Strickland and Melville 1848; Cheke 1987, 2006; Hume et al. 2004; Cheke and Hume 2008). Non-endemic species that became locally extinct over the same time period, such as the Green Turtle *Chelonia mydas*, Dugong *Dugong dugon*, Greater Flamingo *Phoenicopterus roseus* and Reed Cormorant *Phalacrocorax africanus*, were also described in the early accounts. Most notably, Rodrigues also supported its own endemic large, flightless pigeon, the Solitaire *Pezophaps solitaria*, which was last reliably reported in 1755 (Cheke 1987) and which was described extensively in life and recorded as being hunted for food (Leguat 1707; Tafforet 1726; Charpentier de Cossigny 1732–1755; Genes de la Chancelière 1735).

Although several historical records document the exploitation of Dodos by sailors (Soeteboom 1648; Strickland and Melville 1848; Fuller 2002), the only contemporary report that might acknowledge the decline and rarity of the species during the early colonial period is Governor Hugo’s enquiry in 1674 of a recaptured slave as to whether he had seen any Dodos while free in the forest – the captive claimed to have seen Dodos just twice between 1663 and 1674 (Pitot 1905), but given that the name transferred to Red Hens in the 1660s, we cannot be sure that either Hugo or the slave were using ‘dodaersen’ in its original sense (Cheke 2006). This lack of interest stands in marked contrast to contemporary awareness by local observers of the decline and/or disappearance of several other now-extinct Mascarene species, and even of the direct and indirect human involvement in these events. Slaughter of giant tortoises elicited comment from numerous observers, and protective legislation on Réunion in 1671 (Bour 1981; Cheke 1987; Cheke and Hume 2008), and declines in other species were also reported. For example, in 1698 Governor Deodati lamented the extinction of the Mauritian Sheldgoose *Alopochen*

mauritanus (see Barnwell 1948), and flamingos, wildfowl and native pigeons were reported to be extinct on Réunion by Feuilley (1705) and Boucher (1710) respectively. Hunting by settlers and fugitive slaves was blamed for observed eighteenth-century declines of the flying-foxes *Pteropus niger* and *P. subniger* (Lanux 1772), the Pigeon Hollandais *Alectroenas nitidissima*, and Thirioux's Grey Parrot *Psittacula bensoni* (Charpentier de Cossigny 1732–1755, 1764; Hume 2007; Cheke and Hume 2008). There was also very early recognition of exotic mammal persecution impacting native Mascarene species; some bird species were noted to be confined to islets by the 1690s due to rat predation on the mainland of Rodrigues (Leguat 1707), and already by the mid-1600s, Dutch colonists on Mauritius were blaming feral pigs for drastically reducing tortoise and turtle clutches (Cheke 1987; Pitot 1905). Borghesi (1703, in Lounnon 1970) and Feuilley (1705) attributed the disappearance of the Réunion Pigeon *Alectroenas duboisi* to cats, and Pingré (1763) also blamed cats for the disappearance of the Rodrigues Night Heron *Nycticorax megacephalus* and Leguat's Rail *Erythromachus leguati*. Other eighteenth-century authors blamed the near disappearance of tortoises on Rodrigues to cats eating their eggs and young (Charpentier de Cossigny 1799; Marragon in Dupon 1969), and Charpentier de Cossigny (1732–1755) was told that feral cats were responsible for the decline of the Solitaire, although he blamed overhunting.

Furthermore, during the Dodo's decline and extinction, Mauritius was settled, abandoned and then reoccupied by settlers with no knowledge of the species. Although the Dodo appears to have been common before colonisation of Mauritius up to the 1630s, with large numbers reported by visiting mariners (Strickland and Melville 1848; Wissen 1995), Dodo records were already sparse by the time the Dutch first settled in 1638 (Cheke 1987). The colony was abandoned in 1658, and the island was then uninhabited until the Dutch re-established a station, with different personnel, in 1664 (Moree 1998). The last Dodo record generally accepted as being reliable (e.g. Cheke 1987, 2004, 2006; Wissen 1995; Ziswiler 1996; Moree 1998; den Hengst 2003; Grihault 2005), made by the shipwrecked sailor Volkert Evertsz on an offshore islet in 1662, occurred during this interval. The island was then permanently evacuated by the Dutch in 1710, and not recolonised until 1721 by the French. Contemporary French records (see Cheke and Hume 2008) do not mention the Dodo, and it is equally absent from popular French accounts of Mauritius from the mid-eighteenth century (e.g. La Caille 1763; Bernardin 1773).

This pattern of colonial history, together with a lack of available specimens, led many late eighteenth- and early nineteenth-century scientists in the colonial power, France – including Cuvier – to regard the former existence of the Dodo as very doubtful (e.g. Lamouroux

and Desmarest 1824–1830). Strickland and Melville (1848) later recorded that

the vague descriptions given of them by early navigators were long regarded as fabulous or exaggerated, and these birds, almost contemporaries of our great-grandfathers, became associated in the minds of many persons with the Griffin and the Phoenix of mythological antiquity.

Leguat's well-known account of his two-year stay on Rodrigues, including his detailed observations of Solitaires, was also long dismissed in Europe as romantic fiction (see discussion in North-Coombes (1991) and Racault (1995)), and despite subfossil and documentary evidence of Leguat's veracity emerging in the nineteenth century (e.g. Günther and Newton 1879; Leibbrandt 1887), this view has persisted in literary circles (e.g. Atkinson 1922; Adams 1983; Severin 2002). In France, LeClerc de Buffon's (1770–1783) confused and partial use of sources in relation to Dodos and Solitaires probably also contributed to the disbelief in these species that prevailed towards the end of the eighteenth century. He relied heavily on Cauche's (1651) chimaera 'oiseau de Nazareth' (combining features of Dodos and Cassowaries), assumed that the Rodrigues Solitaire and Réunion 'Solitaire' (the facultatively flightless ibis *Threskiornis solitarius*) were the same kind of bird (see Hume and Cheke 2004), and believed (for no obvious reason) that Réunion had a Dodo as well as its 'Solitaire'.

Although the Dodo was reported to be locally extinct by Mauritian writer Morel (1778), and considered both a valid species and probably totally extinct by French encyclopaedist Mauduyt (1784) and French explorer Bory (1804), the alternative interpretation of the species as an imaginary creature became the dominant viewpoint amongst French scientists until several decades after Cuvier's validation of the process of extinction. Morel, secretary of the hospital in Port Louis, was responding to LeClerc de Buffon's plea for more data on the large flightless birds reported in the past, but of which, despite the French colonies on the Mascarenes, nothing had recently been heard:

It is certain that for nearly a century, no animal of this species had been seen here. However it appears that before they (= these islands) were settled, one was able to find some species of very large, heavy birds incapable of flight, and that the first mariners that spent time here soon destroyed them because of these ease with which they could be caught. (ASC's translation)

Morel was wrong about Rodrigues, as Solitaires had survived until about 20 years earlier (Cheke 1987); and furthermore he did not interpret the Dodo's disappearance as a *species* extinction, as he thought the birds would have been 'emus, cassowaries or even rheas'. Mauduyt (1784), probably picking up on Morel's paper and aware of doubts over the Dodo's reality, wrote that

it appears, *either because the species has been totally destroyed* (our italics), or because the species consists only

of a very small number of individuals pushed back into little frequented places, that one no longer finds the Dodo in the same spots where those who first landed discovered them. But one should not suppose that this bird never existed, as certain modern travellers believe (just) because all their researches and efforts have failed to find it in these populated and cultivated islands, where it was observed in the times when they were desert.

Cuvier himself was only convinced of the Dodo's reality when the Mauritian naturalist Julien Desjardins sent him subfossil Solitaire (not Dodo) bones in 1830 (Strickland and Melville 1848). In Britain, disbelief in Dodos never really took hold because of limited input from the Mascarenes (due to near-permanent war with France) and the presence of physical Dodo remains lacking in France – a head and foot in the Ashmolean Museum, Oxford, from the Tradescants' seventeenth-century collections, and a foot in the British Museum (Ovenell 1992; Hume et al. 2006). Edwards (1760), Latham (1785) and Shaw (1792) recycled old accounts and referred to these Dodo remains, although Stephens (1819–1826) suspected Savery's famous Dodo paintings were from imagination and the Oxford head and foot belonged to different unidentified species. Prior (1819), with the British force invading Mauritius in 1810, reported matter-of-factly that 'the *Dodo*, a large clumsy and singular bird, which like the ostrich could not fly, was formerly found here according to naturalists, but is extinct'.

Nonetheless, wider recognition of the Dodo as a real animal only followed Duncan's (1828) redescription of the London and Oxford specimens, although this physical evidence was nonetheless rejected by René-Primevère Lesson (1828, 1831). The Oxford specimens were later described more substantially by Strickland and Melville (1848), and further skeletal material was rediscovered in Copenhagen and Prague in the 1840s (Wissen 1995). No further physical remains became available until the discovery of extensive subfossil Dodo remains in the Mare aux Songes swamp in 1865 (Clark 1866).

This flightless pigeon from a remote Indian Ocean island was only one of the numerous other extinctions now known from the historical period, and was largely forgotten and even considered fictional during the period when extinction was first formally studied. How, therefore, did the Dodo manage to overcome these major obstacles, and become a global flagship for this ecological process?

Factors determining contemporary appreciation of human-caused extinction

In order to understand how the Dodo achieved its posthumous celebrity, it is necessary to identify the scientific and socio-cultural hurdles that had to be overcome before a given species could be widely recognised by the general public as an icon of human-caused extinction. The scientific information available in the nineteenth

century on species that died out during the historical and recent prehistoric periods must, therefore, be reassessed in light of these different hurdles. This provides new insights into the process by which the Dodo – instead of any other recently extinct species – managed to become a household name, as well as warning against simplistic teleological interpretations of history and demonstrating the significant role played by contingency in the Dodo's rise to fame.

Did historical observers know that the species existed?

Although the Dodo's reality was in dispute by the close of the eighteenth century, it had once been familiar to both visitors to Mauritius and European commentators (e.g. Herbert 1634; Ray 1678; LeClerc de Buffon 1770–1783). Therefore, although subsequently forgotten in Mauritius, later scientific debate, in England at least, was based on a largely consistent understanding of what kind of animal was being referred to. Although Dodos were mistakenly illustrated using Cassowaries and King Penguins in popular seventeenth-century accounts (Strickland and Melville 1848; Hume 2006), and Lesson (1828, 1831) also confused the Dodo with a Cassowary despite knowledge of the British Dodo specimens (Duncan 1828), these errors were not followed by other contemporary zoologists. Likewise, zoologists did not pick up the name change to Red Hens until the mid-nineteenth century (Newton 1868; Cheke 2006), so the only real confusion over the identity (rather than reality) of the Dodo during the seventeenth and eighteenth centuries resulted from LeClerc de Buffon (1770–1783) confounding the species with the Rodrigues Solitaire and Réunion Ibis. However, as Dodo, Solitaire, Réunion Ibis and Red Hen were all relatively large flightless birds from the same island group, which became extinct as a result of similar anthropogenic pressures during the same 100-year interval, this did not detract significantly from a general contemporary scientific understanding of the species.

This contrasts with the generally poor contemporary knowledge of many other taxa which became extinct during the seventeenth or eighteenth centuries in different geographical regions, because the history of the Mascarenes made these islands a disproportionately important source of historical data on recently extinct species. Although island systems across the globe have experienced a massive series of anthropogenically-mediated extinctions, most of these events (e.g. Mediterranean islands and Pacific region) took place before historical-era European expansion (e.g. Alcover et al. 1999; Steadman 2006), and were not recorded by the peoples involved. The existence of prehistoric extinction events was not generally appreciated by European scientists until the mid-nineteenth century onwards, and their magnitude, dynamics, timing and

causation are still the focus of considerable research. Furthermore, although most of these islands also experienced further extinctions following first contact and colonisation by Europeans and their associated invasive mammals (primarily rats, cats, dogs and pigs), many regions were discovered before the Enlightenment increased European scientific interest in systematic studies of the natural world. In general, Spanish and Portuguese explorers were also much less inclined to record the island wildlife than their later rivals the Dutch, English and French. For example, although Columbus carried a naturalist with him on his second voyage to Hispaniola in 1493 to assess the potential value of plants in the newly discovered West Indies (Moscoso 1943), the region's extensive early historical-era land mammal extinctions, which represent almost 40% of all post-AD 1500 mammalian species losses (MacPhee and Flemming 1999; Turvey et al. 2007), went effectively unrecorded until the twentieth century. The only well-known contemporary European account that mentions some of these now-extinct species is that of Gonzalo Fernández de Oviedo (see Miller 1929), and they remain known almost entirely from palaeontological and pre-Columbian zooarchaeological specimens (see MacPhee and Flemming 1999). Similarly, although the Portuguese discovered both St Helena and the Mascarenes, they left few accounts of the former (Ashmole and Ashmole 2000), and only one very minimal description of a landing on the latter: Réunion in 1528 (North-Coombes 1980).

The Mascarenes are also significant because they were almost the only large but still relatively accessible tropical islands that remained uninhabited until the sixteenth century, because of their remote oceanic location, and so retained a substantial fauna to be reported by interested contemporary observers. Other tropical islands first reached by humans equally late tended to be smaller (e.g. St Helena, Christmas Island), with consequently less spectacular or visibly unique faunas. Only the Galápagos group (whose largest island Isabela/Albemarle is much larger than any of the Mascarenes), home to giant tortoises, land and marine iguanas, flightless cormorants, and generally very tame wildlife, can be said to match the Mascarenes in terms of its charismatic biota. However, instead of fascinating and delighting their discoverers, the Catholic bishop who made the first landfall in 1535 'pronounced them cursed of God. Thereafter pious Spaniards generally avoided them' (Larson 2001). Unlike the Mascarenes, the Galápagos lacked readily available fresh water, and after a disastrous second visit in 1546, the Spanish sent no other explorers or settlers for another 150 years (Larson 2001). Even adventurer William Dampier (1697), the first to discuss the islands' wildlife in any detail, found these lands of 'dildo trees' (cactus) and tortoises unfit for human habitation (Larson 2001).

Furthermore the wildlife there, although spectacular, was not unique in the eyes of sixteenth- and seventeenth-century travellers, as similar species were also already known from other parts of the world – unlike Dodos, which were recognised as being unique to Mauritius as early as the 1630s (Herbert 1634; Mundy 1608–1664).

Although some larger islands also retained many now-extinct species into the historical era, the geographical and ecological heterogeneity that permitted their late survival also restricted early European colonists from travelling widely and finding these animals. In particular, it is now known that several members of the Malagasy megafauna survived beyond initial European interaction with Madagascar, with some species persisting into the recent historical period (Burney et al. 2004). However, these were almost completely unrecorded by early European visitors (mostly slave and cattle traders), presumably because the animals were reduced to relict populations in the largely inaccessible interior of the island, and European trading posts were coastal and generally temporary (due to malaria and Malagasy resistance) until the late nineteenth century. The only well-known contemporary European records of these Malagasy megafauna are the brief, almost certainly second-hand descriptions of elephant birds and large mammals given by Flacourt (1658) (see Simons 1997; Burney and Ramilisonina 1998; Goodman et al. 2004), which were largely ignored by eighteenth-century naturalists such as LeClerc de Buffon (1749–1767, 1770–1783) and only reinterpreted after subfossil material of large mammals and birds was found in Madagascar from the mid-nineteenth century onwards.

Was the species interesting enough to report?

Of the subset of historically extinct species that were encountered or known about by contemporary European commentators, only those that were considered 'interesting', typically because they were good eating or their appearance seemed unusual, striking, or exotic to the largely non-scientific observers of the period, were likely to be reported or exhibited. This subjective bias prevented a large number of particularly smaller terrestrial vertebrates encountered by early travellers from being made known to a wider audience.

Large-bodied vertebrates are usually the first species to become extinct following human arrival on islands, either through selective targeting by hunters (Duncan et al. 2002) or because size-dependent scaling of ecological and life-history traits increases their vulnerability to anthropogenic disturbance (Cardillo et al. 2005), hence the massive series of prehistoric insular extinctions removed the great majority of these charismatic species before they could be recorded by interested European observers. The Dodo, one of the few unusual large flightless island birds

to survive into the historical era due to the late human colonisation of the Mascarenes, was clearly considered by early visitors to Mauritius to be sufficiently charismatic to be of popular and commercial interest in Europe. Flightlessness in birds was seen as a peculiar and even oxymoronic character, and the absence of functional wings is invariably mentioned in early accounts of Dodos (e.g. Strickland and Melville 1848), whereas in other birds wings were rarely commented on. Several live individuals were exhibited during the seventeenth century in England, the Netherlands, Prague, India, Jakarta and Japan (Fuller 2002; Hume 2006; Cheke and Hume 2008). Invaluable preserved soft tissue material from these captive birds featured in various catalogues and lists (e.g. McGregor 1983), and was available for study in Oxford and London by Ray (1678) onwards through to the nineteenth century. The only other Mascarene species to be exhibited in Europe in the 1600s were the Red Hen and the Black-Spined Flying-Fox *Pteropus niger*, both exhibited in Prague c. 1605 (Haupt et al. 1990; Cheke 2007; Cheke and Hume 2008), and a Réunion Giant Tortoise *Cylindraspis indica* exhibited in Paris in 1676 (Bour 2004). There was also an unsuccessful attempt to transport two Réunion Ibises to France in 1667, but 'as soon as they were in the vessel they died of melancholy, not wanting to eat or drink' (Valledor de Lozoya 2003; Hume and Cheke 2004). Although after a considerable interval other Mascarene species were exhibited in Europe in the mid to late eighteenth century, including several that are now extinct (e.g. Pigeon Hollandais, Mascarin Parrot *Mascarinus mascarinus*, Hoopoe Starling *Fregilupus varius*, Rougette Flying-fox *Pteropus subniger*, and giant tortoises *Cylindraspis* spp. from all three Mascarene Islands), these did not die out until the late eighteenth or the nineteenth century, and were not recognised as extinct (or even considered endemic in the case of the tortoises) until the mid-nineteenth century or later.

Among the Mascarene species brought to Europe, only the Dodo caught the imagination enough to be widely illustrated. Although several other species featured occasionally in books (e.g. *Het Tweede Boeck* 1601; Herbert 1634), or were illustrated for special purposes (e.g. Emperor Rudolf's *Kunstammer*; Haupt et al. 1990), only the Dodo was illustrated by a popular and famous painter. Between 1611 and 1628, Roelant Savery included the Dodo in at least 10 paintings (den Hengst 2003; Hume and Cheke 2004), which over the next two centuries had become dispersed into most western European countries. The Dodo images subsequently published in natural histories well into the nineteenth century are almost all based on Savery's standard Dodo (Ziswiler 1996). While the equally unique Red Hen and Raven Parrot faded from memory until rediscovered in the mid-nineteenth century, the Dodo lived on through Savery's illustrations and their derivatives (Figure 1).



Figure 1. 'The Dodo, and the Guiney pig' by George Edwards, from *Gleanings of natural history, exhibiting figures of quadrupeds, birds, insects, etc.* (Edwards (1760), p. 294).

Was the species recognised as distinct?

Taxonomic confusion hindered the early recognition of many now-extinct species, with seventeenth and eighteenth-century observers not appreciating that they were distinct from related or morphologically similar taxa known from other parts of the world. This confusion affected the majority of the more poorly known recently extinct small terrestrial vertebrates (e.g. insular lizards and bats), but also many larger, more charismatic species. Most notably, the extinct Irish Elk *Megaloceros giganteus* was considered conspecific with the extant North American Moose *Alces alces* by Molyneux (1697), a view followed by Goldsmith (1774) and Catton (1788). Similarly, the South African Bluebuck or Blaauwbok *Hippotragus leucophaeus*, one of only two large-bodied (>100 kg) continental mammal species to die out between 1500 and the early nineteenth century (the last individual was seen around 1800), was only one of many rather similar large ungulates encountered in South Africa by the early Dutch and British colonists, and although its extinction was rapidly recognised, it was widely considered to be merely a subspecies of the extant Roan Antelope *H. equinus* by many nineteenth-century and some early twentieth-century authors (Klein 1974).

The various giant tortoise species present in the Mascarenes during the historical period, which had all

become extinct by the 1840s, were not recognised as distinct until the late nineteenth century, with the only surviving Indian Ocean giant tortoise population on Aldabra long considered to be conspecific with the geographically and taxonomically distinct Galápagos tortoises (Chambers 2004). Similarly, flying-foxes were widely mentioned by most visitors to the Mascarene Islands, but were generally not distinguished by contemporary observers from each other or those in Asia. *Pteropus subniger*, which survived until c. 1870 (Cheke and Dahl 1981), was only recognised as a distinct species by Brisson (1756), and *P. niger* was still confused with Asian species well into the nineteenth century (see Andersen 1912). Therefore, although *P. subniger*, the Rodrigues giant tortoises *Cylindraspis vosmaeri* and *C. peltastes*, and the Réunion Giant Tortoise *C. indica* were all exhibited in Europe during the eighteenth century (Brisson 1756; LeClerc de Buffon 1776; Austin et al. 2002), contemporary observers did not attribute any greater significance to their subsequent disappearance beyond economic constraints resulting from a lack of bats and tortoises for exploitation (Charpentier de Cossigny 1732–1755; Lanux 1772; Billiard 1822). Many historically extinct birds were also not recognised as distinct species by the taxonomic standards of contemporary scientists, and contemporary observers in the Mascarenes and other regions referred to endemic ducks, geese, herons, parrots, pigeons and other taxa in very generic terms. A greater confusion resulted from the seventeenth-century Dutch and French use of the name 'Indiaensche/Indische Raven' and equivalents to describe not only large Asian hornbills *Buceros* spp. (the 'standard' usage of the time; e.g. Ray 1678) but also South American macaws *Ara/Anodorhynchus* spp., as well as the now-extinct large endemic Raven Parrot (Cheke 2006). LeClerc de Buffon (1770–1783) mistakenly thought that all of these references described corvids, and Strickland (in Strickland and Melville (1848)), who wrote before Raven Parrot bones had been found, assumed that hornbills had formerly occurred on Mauritius (Cheke 2006).

Recognition of the taxonomic uniqueness of insular species, extinct or otherwise, is essential for appreciating the concept of endemism. Many historical island extinctions were, therefore, often interpreted as merely regional disappearances (extirpation of local populations) rather than global extinction events, because European scientists had a very poor understanding of range restriction or its implications until the nineteenth century. This may partly reflect the fact that the fauna of Britain, the large island most familiar to the contemporary European scientific community, is composed almost entirely of continental species as a result of being repeatedly connected to mainland Europe during Quaternary glacial cycles. Although the extinctions of several large mammals (Wild Boar *Sus scrofa*, European Beaver

Castor fiber, Brown Bear *Ursus arctos*, Grey Wolf *Canis lupus*) had been recorded throughout the British historical period (see Yalden 1999), all these species survived elsewhere in Europe. However, the Dodo's distinctive appearance led early travellers to the Mascarenes to recognise it as being range-restricted as early as 1629 (Herbert 1634), and soon afterwards consideration of the Dodo and the Red Hen led Peter Mundy (1608–1667) to display tremendous foresight in 1638 by speculating on the autochthonous evolution of flightless birds on islands (Grihault 2005; Cheke and Hume 2008).

Was the species known to be extinct?

Mauduyt's (1784) pronouncement on the Dodo was, as far as we can tell, the first time that a recently living species was considered to possibly be extinct at a global scale – in this case, as discussed above, the doubts of others came not from any supposition that it survived, but from scepticism that it had ever existed. A large number of other species recorded by early naturalists are now known to have also died out during the historical period, but were not recognised as being extinct by nineteenth-century observers or scientists. This is partly because the final extinction of any species is typically preceded by a period of increasing rarity, when declining remnant populations are infrequently encountered or completely missed even by the trained observers, and may be restricted to suboptimal habitat types in marginal parts of their former range (e.g. Channell and Lomolino 2000). Confusion over whether species that have not been observed for extended time periods have actually died out remains a continuing problem today for understanding true levels of extinction (Diamond 1987; Butchart et al. 2006). Many tropical regions and island groups were also only visited very infrequently by Europeans before the nineteenth and twentieth centuries, and so the most recent information was often many decades old.

Other extinct species known only from the recent palaeontological record were also initially often thought to still survive. For example, the first scientific description of subfossil moa bones by Owen (1840) was soon followed by numerous stories of supposed European encounters with moa, leading to general optimism that the birds might soon be 'seen striding among the emus and ostriches in the Regent's Park' (Anderson 1989). It is instead now considered that all moa species became extinct soon after the arrival of Polynesian colonists in New Zealand about 700 years ago, several centuries before European arrival (Holdaway and Jacomb 2000). The most famous example of this misperception is Thomas Jefferson's eighteenth-century belief that the remains of mammoths and ground sloths known from eastern North America were evidence of living megafauna in the then-unexplored western part of the continent (Grayson 1984; Martin

2005). More recently, Aurochs *Bos primigenius* (European wild cattle) are documented as having died out in a Polish royal hunting reserve in 1627 (van Vuure 2005). Although this disappearance was locally recognised and reported, there is no evidence that there was a wider contemporary awareness of the former distribution of the species, nor whether it still survived elsewhere. As it was in fact long gone from the rest of its range, this first recorded historical extinction effectively went unnoticed by scientific commentators until the nineteenth century. As with the Bluebuck, the Aurochs was also not widely recognised as being significantly distinct from similar taxa, in this case domestic cattle.

The problems involved with determining that a species had definitely died out also appear to have limited wider appreciation of the historical-era extinctions of two marine vertebrates, Steller's Sea Cow *Hydrodamalis gigas* and the Great Auk *Pinguinus impennis*. Both species were well-known to science by the early nineteenth century and were also known to have been heavily persecuted by direct hunting, with the mining engineer Petr Yakovlev, who overwintered on Bering Island in 1754–1755, displaying unusual awareness of extinction by anticipating the Sea Cow's disappearance through wasteful overexploitation (Domning 1978). The last Sea Cow is now known to have been killed c. 1768 on Bering Island, with prehistoric human hunting elsewhere having restricted the species to shallow waters around the uninhabited Commander Islands by the late Holocene (Stejneger 1887; Domning 1978). However, this relictual distribution was not readily apparent in the nineteenth century, and the possibility of its continued survival in other remote parts of the North Pacific, a region well away from familiar Western European trading or whaling routes, was suggested by several scientists during this period, notably Nordenskiöld (1885). Indeed, Leonhard Stejneger spent 18 months on Bering Island during 1882–1883 partly to assess Nordenskiöld's claims (Stejneger 1887, 1936), and even more recently, the status of Steller's Sea Cow was still regarded as 'inadequately known – survey required or data sought' in the precursor to the present-day IUCN Red List (Scott 1965).

The Great Auk was known to have had a much wider distribution across the boreal and low-Arctic regions of the north Atlantic, with historical colonies off Newfoundland, Iceland, the British Isles, and possibly Greenland and Norway (Montevocchi and Kirk 1996). The bird's great rarity by the early nineteenth century made it the subject of considerable interest from scientists and collectors, but although the last definite record is of two birds killed off Iceland in June 1844, before the major scientific revival of the Dodo brought about by Strickland and Melville (1848), credible but unsubstantiated reports continued to be made throughout the middle years of the nineteenth century. The first suggestion that the species might be extinct was

made as early as 1837 by William Proctor after he failed to find surviving breeding birds in Iceland, but many researchers continued to believe for several decades that it still survived in undiscovered colonies elsewhere in the remote north Atlantic. It was not until the 1860s or 1870s that nearly all commentators accepted that the species had disappeared (Gaskell 2000).

Were humans identified as being responsible for the extinction event?

Any candidate to become an icon of anthropogenically-mediated extinction must not only have been identified as a real extinct species by nineteenth-century scientists, but also required early recognition that human (and in particular, European) activity had driven the extinction event. The negative effects of human hunting and introduced predators on native island biotas were recognised very early on in the Mascarenes, as noted above. Local appreciation of the potential for human activities to drive extirpation or extinction of native species did occur relatively early in some other island systems, such as St Helena, where overexploitation of seabirds and their eggs led to restrictions being imposed by the British East India Company before 1707: the island's pre-human avifauna (bar one species) had been exterminated before 1600 by rats, cats and pigs introduced by the Portuguese before the Dutch and British mariners arrived (Ashmole and Ashmole 2000). However, anthropogenic involvement in the extinctions of many other insular species remained controversial well into the twentieth century. In particular, the idea that human activity (overhunting, introduction of the Pacific Rat *Rattus exulans*, and widespread deforestation) drove both prehistoric moa extinction and also many historical and even modern-day extinctions in New Zealand was widely countered until relatively recently by the suggestions of 'genetic senescence' and subtle but natural modern-day environmental changes (Fleming 1962; Worthy and Holdaway 2002).

The need for recognition and acceptance of human involvement precluded the iconisation of any prehistoric species as human-caused extinctions, even for megafaunal species that died out in the Late Pleistocene such as mammoth and mastodon, which were amongst the first species to be identified as extinct by Cuvier. Prehistoric human culpability in Quaternary megafaunal extinctions was widely suggested and discussed during the nineteenth century (Grayson 1984), but the relative impact on terrestrial faunas of early subsistence hunters, climatic changes associated with glacial cycles, and other factors has still not been resolved and remains the subject of extensive ongoing debate (e.g. Grayson 2001; Barnosky et al. 2004; Wroe et al. 2004).

Was scientific awareness of recent extinction disseminated to a wider non-scientific audience?

The Dodo's popular iconisation took place during the mid-nineteenth century. It was first used as the prime example of a species wiped out by recent human activity in the *Penny Magazine* (Broderip 1833; reprinted in the *Penny Cyclopaedia*), where the author wrote that

The agency of man, in limiting the increase of the inferior animals, and in extirpating certain races, was perhaps never more strikingly exemplified than in the case of the Dodo. That a species so remarkable in its character should become extinct, within little more than two centuries, so that the fact of its existence at all has been doubted, is a circumstance which may well excite our surprise, and lead us to a consideration of similar changes which are still going on from the same cause.

Soon afterwards in the popular and widely read account of the Beagle voyage, Darwin (1839) (presumably using Duncan (1828), Blainville (1829) or Broderip (1833) as his source material), described the decline of the now-extinct Falkland Islands Fox or Warrah *Dusicyon australis* in the following terms: 'Within a very few years after these islands shall have become regularly settled, in all probability this fox will be classed with the Dodo, as an animal which has perished from the face of the earth'.

While popular articles also appeared in the *Literary Gazette* (Forbes 1847), much greater public awareness of the Dodo's demise followed publication of the monograph *The Dodo and Its Kindred* (Strickland and Melville 1848). Strickland's previous work (1844) and the book generated follow-up notes from natural scientists all over Europe (Hachisuka 1953, pp. 238–239), but it was the substantial and positive review in the widely read *Blackwood's Edinburgh Magazine* ([Review] 1849) that not only alerted an extensive interested Victorian readership to the Dodo's extinction, but emphasised the fact, clearly still not common knowledge, that species extinction could occur at all. After discussing local extinctions in the UK, the reviewer (probably Broderip, *contra* Hachisuka 1953) went on to say that 'the death of the Dodo and its kindred is a more affecting fact, as involving the extinction of an entire race, root and branch, and proving that death is a law of the *species*, as well as of the individuals that compose it'. He emphasised the point by drawing attention to other apparently impending extinctions (European Bison *Bison bonasus*, Norfolk Island Kaka *Nestor productus*, Kakapo *Strigops habroptilus*, kiwis *Apteryx* spp.; of these only the kaka in fact became extinct (Tennyson and Martinson 2006), and the Great Auk is notably absent from the list). In relation to the Dodo, he also indulged his readers in childhood nostalgia, citing the *Three Hundred Animals*, a book of illustrated information for children (Boreman 1730) which had been in print in various editions until c. 1820 and with which he expected they were all familiar

(although it was not Boreham's book but the similar, indeed plagiaristic, Macloc (1813) that included the Dodo). It was thus not *any* animal that had become extinct, but an old friend from favourite childhood books.

Shortly after publication and review of Strickland and Melville (1848), a life-size reconstruction of a Dodo was displayed in 1851 at the Great Exhibition in London (visited by six million people; Auerbach 1999) and later exhibited at the Crystal Palace at Sydenham (Bartlett 1898). In the newly built Oxford University Museum of Natural History, the Dodo remains were also brought together in the main public gallery in 1860 (Nowak-Kemp, personal communication 2006) with an outside 1651 painting of a Dodo by Roelant Savery's nephew Jan/Hans Savery (Strickland and Melville 1848). Charles Dodgson (better known by his pen-name Lewis Carroll) was a frequent museum visitor and became familiar with the species (Batey 1980), leading him to feature it as a character in *Alice's Adventures in Wonderland* (Carroll 1865).

Full recognition of the Dodo's extinction was still patchy in the 1860s; the editors of the *National Encyclopaedia* (1866/1867) wrote that 'we only know that it does not now exist in the islands which abundant testimony proves it to have once inhabited ... / It is in fact extinct; or if it indeed survive (*sic*), Madagascar is the most likely spot in which it lingers'. Similarly, the section on the Great Auk is written entirely in the present tense ('it breeds.../'; 'the female lays.../'), with an apparent afterthought noting unconvincingly that 'it is now held to be extinct', and only Steller's Sea Cow is accepted as having become extinct. However, *Alice's Adventures in Wonderland* included two memorable illustrations of the Dodo by Sir John Tenniel (Figure 2), and firmly established the bird as a popular figure in Victorian culture, the attraction coincidentally emphasised by the publicity surrounding the discovery of subfossil Dodo bones in Mauritius in the same year as the book first appeared in print, and the consequent publication of Richard Owen's famous osteological monograph the year after (Owen 1866). Therefore, although Mark Twain joked in 1896 that 'Apparently, there has only been one prominent event in the history of Mauritius, and that one didn't happen', referring to the storyline of the romantic novel *Paul et Virginie* (Bernardin 1789; see Wilson 2002), the Dodo had by then already gained its major international reputation as an extinction icon. Indeed, Twain's fellow countryman and raconteur Nicholas Pike (1873) deliberately chose the Red Hen rather than the Dodo to front his book on Mauritius, because the latter had already become too hackneyed! He commented in his preface that 'Everyone has heard all about the Dodo, once existent in Mauritius, but many are not aware of the very beautiful bird the *Aphanapteryx imperialis*, coexistent with it'.

The Dodo's popular appeal was also magnified by its comic-sounding, wonderfully alliterative and highly

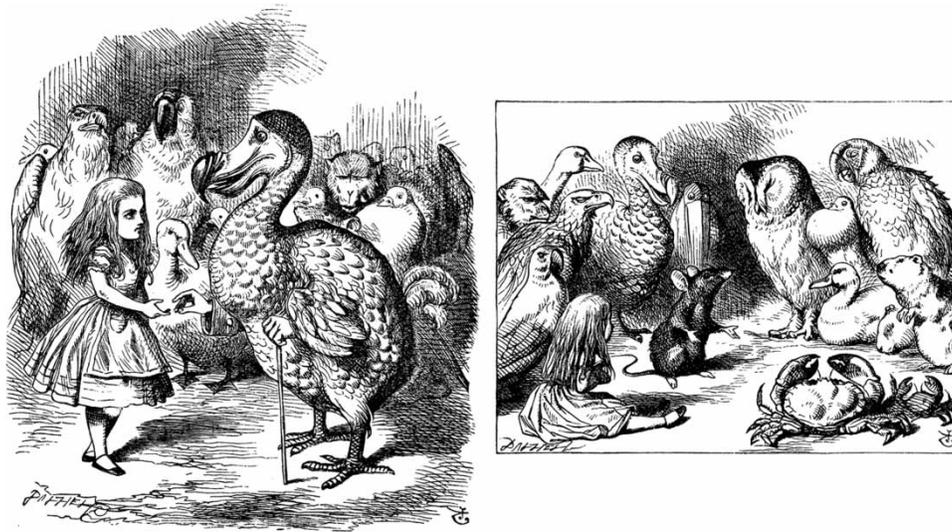


Figure 2. Illustrations of the Dodo by Sir John Tenniel in *Alice's Adventures in Wonderland* (Carroll 1865).

memorable name, which in English was also an easy play on the pre-existing expression 'dead as a doornail', thus further establishing it in the public consciousness. Although probably of Victorian origin, 'dead as the Dodo' is attested only from 1904 (Oxford English Dictionary, accessed online January 2006). The less catchy 'extinct as the Dodo' may have been coined earlier; this was already in use in a non-zoological context by 1870 (Huxley 1870), and by 1887 it was current enough to be used by Marxist philosopher Belfort Bax (1887). The Dodo's grip on popular imagination was further aided by an enduring belief in its supposed gross obesity and lack of intelligence, which was widely held in the nineteenth century to have contributed to its extinction – a deeply entrenched misperception about the species (Kitchener 1993; Gould 1996). Back in the seventeenth century, Bontius, not himself an eye-witness, described the Dodo as 'a slow-paced and stupid bird and which easily becomes a prey to fowlers' (Ray 1678). LeClerc de Buffon (1770–1773) devoted a whole paragraph to the Dodo's supposed misshapen clumsiness, which formed the basis for most subsequent opinion and descriptions in both France and England prior to the publication of Strickland and Melville (1848). Smith (1807) provided what might be the most prejudiced and miserly outlook of all in her description of the species:

The Dodo, *Didus*, is a bird that inhabits some of the islands of the East Indies. Its history is little known; but if the representation of it be at all just, this is the ugliest and most disgusting of birds, resembling in its appearance one of those bloated and unwieldy persons who by a long course of vicious and gross indulgences are become a libel on the human figure.

The well-known junior synonym for the species erected by Linnaeus in 1766, *Didus ineptus*, is clearly based on such an interpretation.

Unexpected and fortuitous associations with these factors were also instrumental in making the Dodo a desirable subject for contemporary artists, which ultimately provided a major basis for its dissemination into the cultural mainstream. Charles Dodgson included the Dodo in *Alice's Adventures in Wonderland* largely because he identified himself with the bird; he had adopted 'Dodo' as a nickname for himself that reflected his stammer ('Do-Do-Dodgson'; Gardner 2000), and its appearance in the book is self-referential and apparently quite unrelated to the scientific interest in the species. Similarly, Roelandt Savery was overweight and never married, and the fat, solitary Dodos juxtaposed with paired representatives of other animal species included in many of his works have been interpreted as a signature image (Valledor de Lozoya 2003), the Dodo generally placed adjacent to his colophon. Although Strickland and Melville (1848) also discussed the Solitaire, which was better studied in life than the Dodo and noted to be in decline by contemporary observers, the limited skeletal material available in the early nineteenth century, and lack of any soft tissue specimens, paintings, or depictions in popular books, meant that this species was largely ignored in favour of the Dodo by non-scientists. Of the few other species that fell victim to historical-era extinction events that were also recognised by the contemporary scientific community, only the Great Auk became the focus of anything like a comparable degree of public appreciation and iconisation in Great Britain (see Fuller 1999). However, popular accounts of Great Auks in nineteenth- and twentieth-century fiction typically

portrayed romanticised last survivors eking out a solitary existence on remote islands, rather than acknowledging that the species was extinct (e.g. Kingsley 1863; Blyton 1944), following persistent ideas in nineteenth-century scientific circles that a few birds might indeed have survived. For the same reason, although Steller's Sea Cows were also presented as major characters in *The White Seal*, a short story which formed part of the widely-read collection in *The Jungle Book* (Kipling 1894), they were also depicted as still around but hiding from humans, having found a safe refuge from hunters in the North Pacific.

Conclusion

This assessment of the series of stages required for a historically extinct species to become widely appreciated by the general public suggests that both chance and necessity played a part in the Dodo's rise to fame, but also provides an illuminating illustration of the importance of contingency and the fundamental lack of inevitability in historical processes (*cf.* Gould 1989).

Certainly, some ecological and evolutionary factors may be interpreted as 'predetermined' to have given the Dodo an increased chance of becoming well-known as an extinct species. The avifauna of the Mascarenes displayed evolutionary innovations characteristic of island systems such as gigantism and flightlessness, interesting to scientists and non-scientists alike, as well as being vulnerable to extinction due to evolution in the absence of native mammalian predators. Indeed, the role of islands as 'natural laboratories', and the key insights they provided during the development of evolutionary thinking during the nineteenth century, makes it no surprise that these systems also promoted an early understanding of the extinction process. The geographical felicity provided by the Mascarenes' remote location far from the nearest continent also meant that they were not settled during prehistory, so that their charismatic 'weird and wonderful' island faunas were still extant upon European arrival – hence both these species and the inevitable extinctions which followed colonisation could be documented and reported back in Europe by literate observers.

However, these factors are offset by a greater series of contingent, serendipitous historical events, which emphasise that the Dodo just happened to be in the wrong place at the right time. For example, although the Mascarenes were not discovered by European explorers until *c.* AD 1500, they are also shown on older maps of Arab navigators (North-Coombes 1980). Had the discovery of the Mascarenes by both Arabian and Portuguese sailors been anything more than superficial, the Dodo would probably have been driven to extinction before the subsequent arrival of the Dutch. More importantly, the fortunate survival of the head and foot of the Oxford Dodo into the nineteenth

century, despite the destruction of the remainder of the specimen by Ashmolean Museum staff in 1755 (Ovenell 1992), formed the basis for most of the scientific interest in the species during the nineteenth century before the discovery of Dodo subfossil material at the Mare aux Songes in 1865. The former existence of two other Dodo specimens in Oxford, long since vanished (Ovenell 1992), and the relatively recent disappearance of the London Dodo foot (Fuller 2002; Hume et al. 2006), further emphasise the tremendous good fortune that any contemporary Dodo material has survived at all. The personal reasons that led Charles Dodgson and possibly also Roelandt Savery, the two people most influential in popularising the Dodo to a wider audience, to identify with the species are also clearly a matter of complete chance. Altogether, the Dodo represents not only an icon of extinction but also a prime example of the vagaries of fame.

Finally, it is also important to recognise that scientific and public appreciation of human culpability in the Dodo's extinction did not automatically generate any conservation concerns during the nineteenth century. Instead, extinction at the hand of man was regarded as an unfortunate but inevitable consequence of human superiority over nature (and European superiority over non-European peoples), an attitude based on contemporary religious and social philosophies which led to misinterpretation of Darwin's 'survival of the fittest' and prompted the development of acclimatisation societies rather than conservation organisations during the later part of the nineteenth century (e.g. McDowall 1994). Strickland and Melville (1848), after recognising that the Dodo and Solitaire 'furnish the first clearly attested examples of the extinction of organic species through human agency', went on to write that 'our consolation must be found in the reflection, that Man is destined by his Creator to "be fruitful and multiply and replenish the Earth and subdue it"'. Their main concern was not that conservation efforts should be established to prevent further extinctions, but instead that it is

the duty of the naturalist to preserve to the stores of Science the knowledge of these extinct or expiring organisms ... / so that our acquaintance with the marvels of Animal and Vegetable existence may suffer no detriment by the losses which the organic creation *seems destined to sustain.* (our italics).

The concept of preventing further extinctions only began to surface as the nineteenth century wore on, and in the UK, it was the debate around the demise of the Great Auk rather than that of the Dodo which led to the first bird protection legislation in Europe in 1869 promoted by zoology professor Alfred Newton (for seabirds; Barclay-Smith 1964; Gaskell 2000). However, the first straightforward and inclusive bird protection legislation anywhere in the world specifically aimed at conserving endemic species was fittingly initiated in Mauritius in 1878

by Alfred's colonial-administrator brother Edward (Newton 1878 [enacted in 1880]; Cheke and Hume 2008).

Although the route taken by the Dodo to become a global icon was tortuous and unpredictable, it has now developed into an invaluable flagship species, warning of the fragility of global ecosystems and the vulnerability of the world's biota to anthropogenically-mediated extinction. In this era of increasing biodiversity loss, as charismatic species such as the Yangtze River Dolphin *Lipotes vexillifer* and the Ivory-Billed Woodpecker *Campephilus principalis* continue to slip towards extinction, we can only hope that there will not be many other such icons in the future.

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