in dispersal mortality unexpectedly selects for increasing mobility. Decreasing patch size and holding dispersal mortality constant also selects for increasing mobility. Concurrent changes in dispersal mortality and fragment size thus result in complex patterns of dispersal evolution as fragmentation proceeds through complex interactions between kin competition intensity and extinction-recolonization dynamics. Nevertheless, in wolf spiders, ballooning propensities were found to decrease both with decreasing salt marsh size and connectivity. Spatially explicit simulations have explored how spatial variation in the cost of dispersal would affect spatial distribution of dispersal genotypes. Isolated habitat fragments are expected to contain more dispersive genotypes than would well-connected fragments when they had just been recolonized, but the reverse trend holds for fragments colonized for a longer time. Similarly, species and/or genotypes with a larger propensity or ability to disperse are more likely to colonize new islands, or “Darwinian islands,” whereas “fragment islands” are increasingly isolated one from another, and only those philopatric species or genotypes are likely found on these fragments. Along the same lines, dispersal has also been found to decrease during ecological succession, whereas it increases during biological invasions or range expansions.

SEE ALSO THE FOLLOWING ARTICLES
Flightlessness / Fragmentation / Inbreeding / Invasion Biology / Metapopulations / Succession

FURTHER READING

DODO

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The dodo, Raphus cucullatus (family Columbidae), has become one of the most famous birds in the world, a true icon of extinction, with probably more written about it than any other species, yet we know practically nothing about the bird in life. Contemporary accounts and illustrations are often contradictory, plagiarized from earlier sources or simply manufactured from pure imagination. This has resulted in a wealth of scientific myths and misconceptions based on totally inadequate source material.

DISCOVERY OF THE MASCARENES
The volcanic and isolated Mascarenes Islands, comprising Mauritius, Réunion, and Rodrigues, are situated in the western Indian Ocean. Mauritius, the home of the dodo, lies 829 km east of Madagascar, the nearest large land mass. Arab traders probably discovered the Mascarene Islands as early as the thirteenth century, followed by the Portuguese in the early sixteenth century, but neither the Arabs nor Portuguese, as far as it is known, settled there. Following the acquisition of Mauritius by the Dutch East India Company (VOC) in 1598, the islands were used as ports of call for provisioning ships. For a short period thereafter, the Dutch and other European nations recorded in ships’ logs and journals vague and inadequate references to the original fauna and flora, including the dodo. These early accounts are invaluable in determining the island’s original ecological composition, because by the end of the seventeenth century, Mauritius had been altered beyond recognition due to the ravages of humans and their commensal animals. It was during this century of human occupation on Mauritius that the dodo became extinct.

WRITTEN EVIDENCE
It was standard practice for VOC fleets to record in ships’ logs and journals all details concerning their voyages, including shipping routes and safe harbors for ship refurbishment. Upon the return of the fleets, the journals became important source material for future VOC voyages, artists, scientists, and book publishers. It was these publications, often expanded and illustrated long after the voyage itself, that have become the source material for scientific study. Except in the case of the skilled artist
Joris Joostensz Laerle, who accompanied the Gelderland fleet to Mauritius in 1601–1603, most observers were not trained naturalists. The observations of contemporary voyagers, therefore, are based primarily on the culinary aspect of the fauna and only secondarily on its appearance or habits. Researchers have used these drawings and accounts as a basis for determining the ecology and morphology of species now extinct, notably the dodo, and as a result, a continuous series of misinterpretations has been made. Despite the wealth of material that has been written based on the contemporary accounts, very little is reliable and based on actual observation.

It was during the voyage of Admiral Jacob Cornelisz van Neck in 1598 that Mauritius was claimed for the Netherlands, although van Neck never actually visited the island. The discovery was made by Vice Admiral Wybrandt Warwijck, who had been separated from van Neck during a storm. While anchored in Vieux Grand Port, southeast Mauritius, Warwijck sent a reconnaissance party on shore including ship’s mate Heyndrick Dircksz Jolinck, who saw and described the dodo for the first time. Upon the return of the fleet to the Netherlands in 1599–1600, the dodo was mentioned in a small publication entitled “A True Report,” which also gave an account of the voyage. Enlarged and expanded editions were published in 1600 and 1601, which included a copper engraving, illustrating not only Dutch activities on shore but also, for the first time, the dodo and other animals (Fig. 1). Van Neck’s account has been plagiarized more than any other.

For the next few decades, Dutch fleets called at Mauritius, either on the way to or from the East Indies. Only a few accounts mentioned the fauna; the last detailed description was made in 1631. Despite visiting Mauritius, the Englishmen Peter Mundy in 1628 and Thomas Herbert in 1639 made further observations, but these were from captive dodos in Surat, India. The Frenchman Francois Cauche visited Mauritius in 1638 but did not publish his account until 1641. Furthermore, his account is untrustworthy. He is the only observer to record the call, nest, and egg of the dodo, but he appears to have mingled these descriptions with that of the cassowary *Casuarius casuarius.* In 1662, ship-wrecked Dutch sailor Volkert Evertszen saw living dodos on an islet off Mauritius and managed to catch some after a chase. Two Dutch governors of Mauritius, Commander Hubert Gerritsz Hugo between 1673 and 1677 and Opperhoofd Isaac Joan Lamotius between 1677 and 1692, recorded dodos. Unfortunately, they gave no descriptions other than the Dutch name “Dodaersen,” which has resulted in some confusion, as another species of flightless bird, the red rail *Aphanapteryx bonaia,* which survived until around 1700, was similarly named. It may have been the dodo or the rail to which they referred. According to Lamotius, who mentions the dodo for the last time in 1688, the dodo had become extremely rare by this time and presumably died out shortly after.

PICTORIAL EVIDENCE

Very few images of dodos derived from ships’ journals exist, and only one observer, the aforementioned Joris Joostensz Laerle, drew a dodo on Mauritian soil. How many of the other illustrations were based on live birds is not known, as most were plagiarized from other sources or derived by artists from mariners’ verbal accounts to illustrate popular books. These attempts at illustration, although charming in their own way, leave much to be desired and can only be used as rough interpretations of the living bird. Furthermore, some illustrations were made from memory and not published until many years later, so it is inevitable that inconsistencies exist. Living or stuffed dodos made the journey to the Far East and Europe, particularly the Netherlands, and these specimens formed the basis for numerous paintings, all differing to varying degrees in posture and coloration. Despite the lack of scientific credibility, some authorities continue to erect new species based on this illustrative and written evidence. The existence of the supposed white dodo from Réunion was based entirely on four white dodo paintings and contemporary accounts. However, recent work has shown that the accounts are referable to a white ibis *Threskiornis solitaria,* not a dodo, and the paintings are based on an albinistic dodo from Mauritius.

The most famous and prolific dodo artist was Roelandt Savery (1576–1639), who drew and painted the bird at least ten times, but nearly always in the same pose. It is
not known whether the model was a live or stuffed bird, but variations in his renditions imply that some were based on memory and others created purely for artistic composition. Much scientific speculation has been founded on these variations, including seasonal fat and thin cycles, sexual dimorphism, and age, without taking into account the abilities or intentions of the artists involved. Therefore, it is impossible to obtain any scientific credence from them. This is certainly not the case with a dodo portrayal by Ustad Mansur from around 1625. This specimen was part of a menagerie kept by Emperor Jahangir in Surat, and is illustrated among other accurately portrayed species of birds. It is almost certainly the most reliable colored rendition of the dodo that has survived.

TRANSPORTATION OF SPECIMENS, LIVING OR DEAD

Because of the minor variations in dodo illustrations, it has been postulated by some authorities that each image represents a different individual. Based on this assumption, at least 17 dodos must have been transported to Europe. However, physical and documentary evidence suggests that as few as two or three dodos made the journey alive to Europe, and a similar number survived the journey east. One specimen, the only dodo to have unequivocally reached Europe alive, was exhibited in a shop somewhere in London in 1638. This individual may have been the one that ended up in the Ashmolean Museum (now University Museum), Oxford. Despite popular belief, this unique stuffed specimen was not thrown onto a fire to be burned. After examining the disintegrating specimen in 1755, the trustees could save only the head and one foot, disposing of the rest. The head, which still retains soft tissue, and the bony core of the foot still reside in Oxford today, whereas all other dodo skin remnants have long since decayed.

EXTINCTION

Inferences made from the few accounts of dodos on Mauritius indicate that the birds disappeared on the mainland concomitant with ever-increasing encroachment by humans and their commensal animals. Hunting was probably restricted to the coastal areas and extremely limited because of the small human population; therefore, it was almost certainly competition and predation by introduced animals, such as rats, monkeys, pigs, goats, and deer, that were responsible for the dodo’s demise. Although still a matter of debate, dodos may have survived until at least 1688, but they had probably ceased to breed long before, with the last aged survivors hanging on in just a few remote places.

RACE TO FIND THE FIRST FOSSIL EVIDENCE

Until the discovery of dodo bones in 1865, virtually no physical remains existed, leading some authorities to doubt that the dodo had ever existed. However, the stuffed Oxford remnants, a foot in London and a skull in Copenhagen, still survived. The British elements formed the basis for the first anatomical study by Hugh Strickland and Alexander Melville in 1848, after which scientific interest in procuring dodo specimens intensified—in particular, the need to discover fossil material on Mauritius.

George Clark, Master of the Diocesan School at Mahebourg, Mauritius, spent some years searching the island hoping to discover dodo fossil material. At the same time, Harry Higginson, a railway engineer, was constructing a railway embankment alongside a marsh called the Mare aux Songes, near the spot where the Dutch first landed. In October 1865, Higginson noted that the laborers were stockpiling bones from the marsh. Informing Clark of the discovery, preliminary excavations revealed the first dodo bones, after which Clark immediately monopolized the site. He sent the first consignment of material in late October to Richard Owen, comparative anatomist at the then British Museum (now the Natural History Museum) and was paid £100 for 100 bones. Owen wasted no time in formally describing and illustrating the dodo’s anatomy the following year (Fig. 2).

Figure 2 Richard Owen’s reconstruction of the dodo in 1869. After illustrating a stout, squat dodo in 1866, Owen, upon obtaining more fossil material, had the bird redrawn in 1869, producing a much more accurate reconstruction. Reprinted from Hume, 2006.
amidst a commotion of high-profile public lectures and engagements.

The Mare aux Songes marsh was reworked more intensively in 1889 by Théodore Sauzier and again by Paul Carié in the early 1900s, resulting in the retrieval of many more dodo bones. 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. Around 1904, Louis Etienne Thirioux, a hairdresser by trade, discovered a complete dodo in a cave near Le Pouce Mountain. It can still be seen in the Mauritius Institute, Port Louis. Until 2007, this was by far the most important fossil dodo discovery made.

AFFINITIES

The affinities of the dodo were explored by numerous authors, and it was often preposterously placed within a large assortment of bird orders—for example, a miniature ostrich, a rail, or even a vulture. After examining a skull in Copenhagen, Professor J.T. Rheinhardt proposed that the dodo was related to Columbiformes (pigeons and doves). This assertion was initially met with ridicule, but after Strickland and Melville confirmed his theory by examination of the Oxford dodo head, the idea became universally accepted. DNA studies have now concluded that the dodo and closely related solitaire *Pezophaps solitaria* of Rodrigues are a sister clade nested within the family Columbidae and derived from the same ancestor as the southeast Asian Nicobar pigeon *Caleonan Nicobarica*.

RECENT DISCOVERIES

In 2005, a Dutch expedition discovered fresh fossil material at the Mare aux Songes. This resulted in a full scale excavation in 2006 and 2007, which revealed thousands of bones beneath a layer of rubble, put in place by the British Army during the 1940s to prevent malaria. The fossil layer also contained seeds, tree trunks and branches, leaves, insects, land snails, and even fungi, deposited long before humans arrived on the island. The fossil remains are dominated by extinct giant tortoises *Cylindraspis* sp., but they also include snakes, lizards, owls, hawks, rails, parrots, pigeons, and songbirds. The flora comprised palms, canopy trees such as tamarind *Sideroxylon grandiflorum* and ebony *Diospyros* sp., and a host of smaller plant species, enabling scientists to reconstruct the dodo’s habitat in a pristine state.

In 2007, more important discoveries were made. A complete but degraded dodo skeleton, “Dodo Fred,” was discovered in a cave in the highlands, with further fossil discoveries made in lowland caves, which increased not only the known distribution of the dodo, but also the chances of obtaining good quality DNA.

As a result of this new physical evidence, it is now possible to make scientifically valid conclusions about the dodo’s ecology. The dodo was found close to the coast as well as in the mountains, occupying dry and wet forest zones, and feeding on fallen fruits and seeds. Judging by the number of individuals preserved, it was abundant in the lowlands at least, and it coexisted with vast numbers of giant tortoises and other animals. The seasonal lake/marsh environment at the Mare aux Songes not only abounded with fruiting trees and shrubs but probably acted as an oasis on the otherwise dry leeward side of the island, thus attracting numerous birds (Fig. 3). However, there are still uncertainties about the dodo’s morphology, and no doubt, more interpretation will be made from the few images and contemporary accounts. What is certain is that the dodo was unable to cope with the rapid changes brought about by anthropogenic agencies and died out less than a century after being discovered.

SEE ALSO THE FOLLOWING ARTICLES

- Extinction
- Flightlessness
- Fossil Birds
- Mascarene Islands, Biology

FURTHER READING


DROSOPHILA

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The genus *Drosophila* provides excellent opportunities to study evolution on island systems. The endemic Hawaiian *Drosophila* are a classic example of adaptive radiation and rapid speciation in nature evolving in situ over the course of the past 25 million years. Other groups of *Drosophila*, found on true islands or in island-like systems (e.g., the Madrean Archipelago), are invaluable tools to understanding evolutionary biology and have served as theoretical and empirical model systems for over 50 years.

HAWAIIAN DROSOPHILA

The endemic Hawaiian Drosophilidae, with an estimated 1000 species, consists of two major lineages, the Hawaiian *Drosophila* and the genus *Scaptomyza*. The high degree of species diversity in Hawai‘i is extraordinary, with about one-sixth of the world’s known Drosophilidae being endemic to this small archipelago. Phylogenetic analyses indicate that the family colonized the Hawaiian Islands only once, roughly 25 million years ago. The genus *Scaptomyza*, which also contains a large number of mainland taxa, seems to have escaped from Hawai‘i and undergone subsequent diversification on the mainland (see below).

There are currently 411 described species of Hawaiian *Drosophila*, with an additional ~150 awaiting description. These species have been divided into eight species groups (picture wing, nudidrosophila, ateledrosophila, antocerocerus, modified tarsus, modified mouthpart, haleakalae, rustica) based largely upon sexually dimorphic characters possessed by males and thought to be used mainly in courtship and mating. These characters range from elaborately pigmented wings to elongate setae, cilia, and bristles on the forelegs to unique structures on the mouthparts and forelegs (Fig. 1). The wide variety of secondary sexual characters possessed by males of the various species groups suggests that sexual selection may have played an important role in the diversification of this group.

Approximately 85% of Hawaiian *Drosophila* are single-island endemics, possibly owing to their relatively poor flight abilities and low tolerance for desiccation. These physiological constraints, coupled with the unique geological history of the Hawaiian Islands, have led to a spatially distributed pattern of diversification referred to as the progression rule, where older species are found on older islands, and younger species are found on younger islands (Fig. 1).

One explanation for the large numbers of drosophilid species in the Hawaiian Islands involves adaptation to so-called empty niches. This atmosphere of reduced competition allowed these species to experiment with novel life history strategies, and thus to diversify. Several adaptations unique to the Hawaiian Drosophilidae seem to bear this out. For example, the small group of ~15 species placed in the *Scaptomyza* subgenus *Titanochaeta* have specialized to oviposit in spider egg sacs. Larvae develop and parasitize the spider eggs while they are being guarded by adult spiders. Sixty-seven percent of Hawaiian *Drosophila* for which data is available breed on only a single host plant family, whereas 79% are specific to a single host substrate, such as leaves, bark, or sap flux (Magnacca *et al.*, 2008).

Hawaiian *Drosophila* have served as a model system to address a number of evolutionary phenomena, including how founder events and mating asymmetries can drive species formation (Fig. 2). Throughout their evolutionary history, Hawaiian *Drosophila* have repeatedly undergone founder events, either as they colonize new islands or when populations are subdivided (e.g., by lava flows or erosional processes). Hampton Carson utilized Hawaiian *Drosophila* to illustrate his founder flush theory, a type of founder effect speciation that proposes a reduction in intraspecific competition and an increase in population size following a colonizing event. Once the population size becomes large again, selection is reasserted, and the population may constitute a new species (Fig. 2).

Alan Templeton also used Hawaiian *Drosophila* to explain his transilience founder effect theory. Templeton