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The changing face of the dodo (Aves: Columbidae:*Raphus cucullatus*): iconography of the Walghvogel of Mauritius

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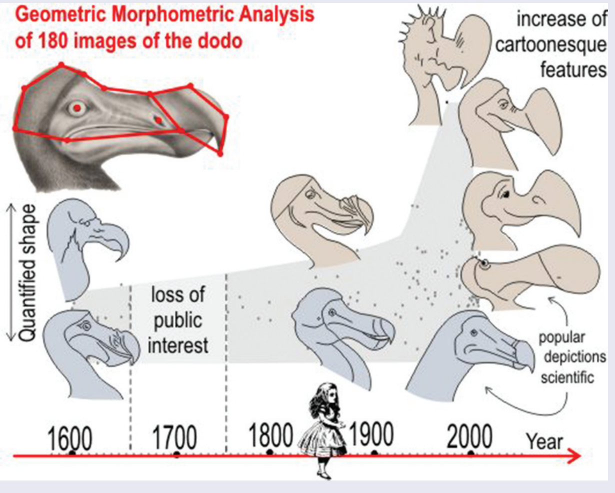
ABSTRACT
The dodo (*Raphus cucullatus*) was a large, flightless pigeon endemic to the island of Mauritius (Indian Ocean). Its unusual appearance was recorded in several 17th-century depictions of live or recently killed birds. It became extinct at the end of the 17th century, and in some subsequent accounts, it was even considered as non-existent. Dodo images became rare from the mid-17th century, but its inclusion in Lewis Carroll's *Alice's Adventures in Wonderland* initiated a change, establishing it as an icon to a much wider public. Since then, illustrations of dodos have been used in all kinds of media, arguably making it the most iconic extinct bird. Here we analyse how the dodo image evolved from 1600 to 2013, using 2D-geometric morphometrics. Our results show that in particular cartoons, animations and logos tend to put an extreme emphasis on the bulging anterior part of the beak, and that the beak is strongly hooked. The variation in dodo images has increased since 1865, culminating in an explosion of shapes during the past decades. The often exaggerated, cartoonesque depiction of the dodo is in line with the long-held but incorrect popular belief that it was a clumsy, tragic bird destined for extinction.



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Introduction

The dodo (*Raphus cucullatus*, Linnaeus 1758), or Walghvogel as originally termed by the Dutch, was a giant pigeon, endemic to the island of Mauritius (Indian Ocean). It has become an icon of human-induced extinction and the most-cited example of an insular species that lost the ability to fly. Since its discovery at the end of the 16th century by sailors and traders, its unusual appearance caught the public interest, and there are several contemporaneous depictions of dodos (Figure 1a-e). Live specimens have been reported to have been exhibited during the 17th century in Europe, India, Jakarta and Japan (Fuller 2002; Hume 2006; Cheke and Hume 2008; Winters and Hume 2015). One or more of these may have suffered from obesity due to incorrect diet and lack of physical action (Kitchener 1993), which theoretically could have led to a pathological bulgy appearance in drawings. Pictures of 'fat' dodos may also have been based on male individuals exhibiting a sexual display behaviour with puffed-out feathers, as most pigeons do, as suggested by Angst et al. (2011a, 2011b; this should be treated with caution, as few reliable descriptions of dodo behaviour are available; Hume, 2006). In less than a century after its discovery, the dodo silently went extinct, and in some subsequent accounts, it was considered fictional or even mythical (Turvey and Cheke 2008). Naturalists remained, however, interested in this enigmatic flightless bird. With very few remains of the dodo preserved, they had little to work with and limited knowledge of the dodo's

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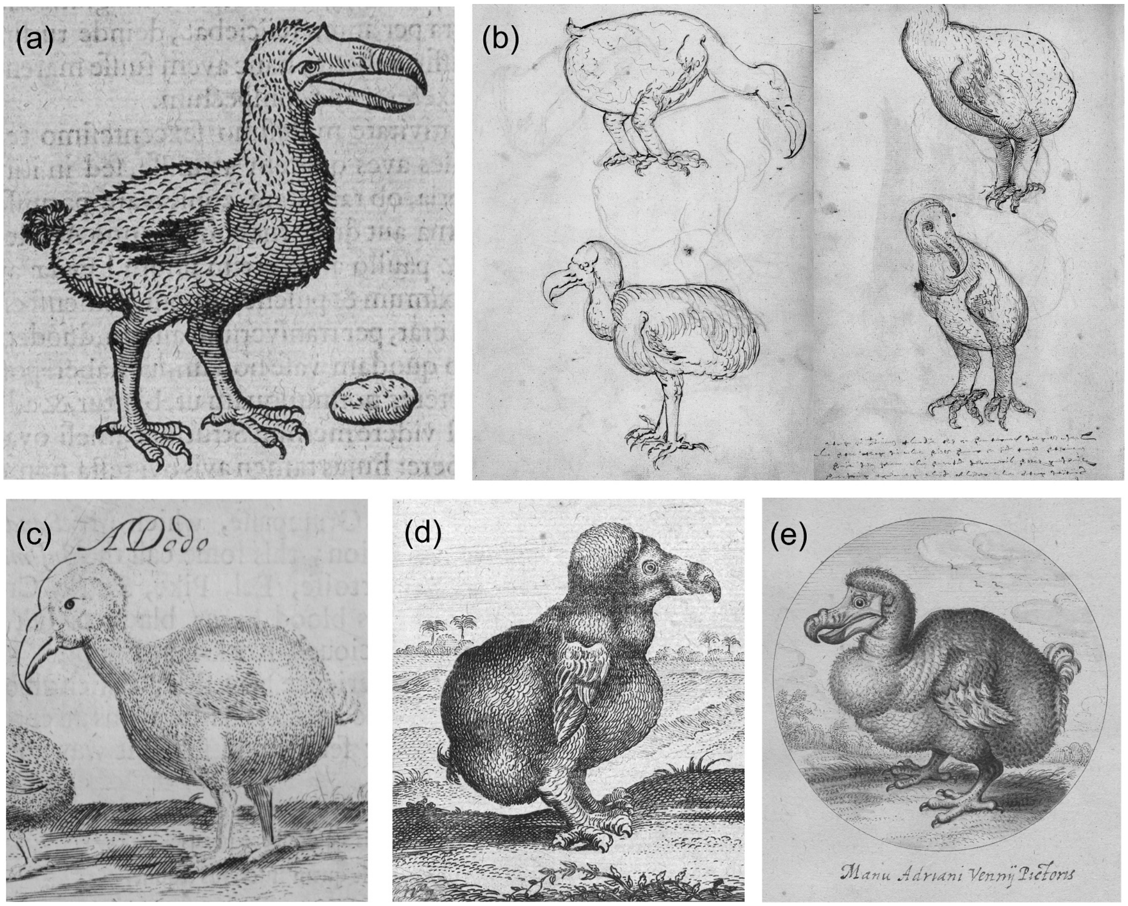

Figure 1. (a) Dodo with gizzard stone in Carolus Clusius' (1605) *Exoticorum*, after a sketch from Van Neck's travel journal Het Tweede Boeck (1601). (b) Compilation of dodo sketches made during the voyage of the VOC Gelderland in 1601, attributed to Joris Joostensz Laerle. (c) Fragment from 'A Dodo, A Hen, A Cacato' by Thomas Herbert (1634). (d) Drawing of a Dodo by Pieter van den Broecke (1634). (e) Illustration of the dodo in the revision of Clusius' *Exoticorum* (book 10; 1626) by Adriaen van de Venne, after Roeland Savery's sketches and paintings. Five early 17th-century illustrations of a dodo from travel accounts and natural history books by Clusius (1605), Laerle (1601), Herbert (1634), van den Broecke (1634) and van de Venne (1626).

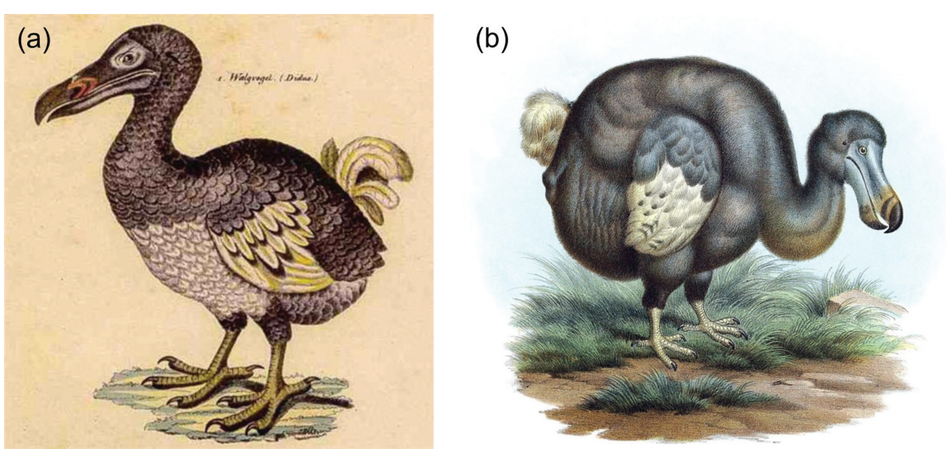

Figure 2. (a) The dodo figured in Lorenz' Oken *Allgemeine Naturgeschichte für alle Stände* (1839) by Johann Susemihl. (b) The upper dodo as figured in Richard Owen's *Memoir of the Dodo* (1866) by James Erxleben. Two dodo illustrations, one by Susemihl in Oken's natural history book (1839) and one by Erxleben in Owen's memoir of the dodo (1866).

relationships (e.g., Buffon 1770; De Blainville 1829; Oken 1837; Owen and Broderip 1866) (Figure 2a, b), placing it in different taxonomic groups, considered related to, or members of, chickens, swans, ratites, penguins, vultures, waders and rails (extensive review in Parish 2012). A turning point in the popular image of the dodo was the publication of *Alice's Adventures in Wonderland* (1865) (Figure 3a). The author, Lewis Carroll, pen-name of Charles Lutwidge Dodgson, presumably used the dodo as a caricature of himself, with the alliterate name 'dodo' mocking his stutter (Gardner 2000). This set the stage for the dodo to be a personality, and not just a product of natural history. Although an image of the dodo was circulating in the scientific community of

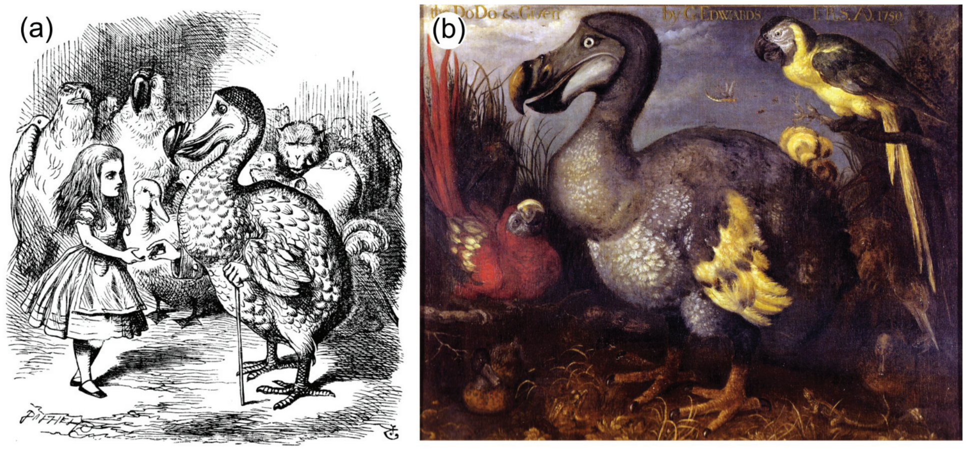

Figure 3. (a) The dodo of Lewis Carroll's *Alice's Adventures in Wonderland* (1865) by John Tenniel. (b) 'Edward's dodo' by Roelant Savery (1626); one of the most famous and often-copied paintings of a dodo. The portrait came into the possession of the ornithologist George Edwards, who later donated it to the British Museum, hence the name. Tenniel's dodo in Carroll's Alice's Adventures in Wonderland (1865) (top) drawn after Savery's Edward's dodo (below).

the late 19th century, its inclusion in the blockbuster *Alice's Adventures in Wonderland*, drawn by illustrator John Tenniel, established the dodo as an icon to a much wider public (Fuller 2002). Tenniel based his illustration on the painting of a dodo by the Golden Age painter Roelant Savery (1576–1639; also spelt Roelandt), now held in the Natural History Museum, London (Hume 2006). Since then, illustrations of the dodo have been used in all kinds of media (e.g., book illustrations, cinema, logos), arguably making it the most iconic extinct bird.

Here, we analyse 1) if, and if so how, the popular image of the dodo changed through time, and 2) to what extent these images approximate the preserved specimens: the 'Oxford dodo' (see below). Our focus here is on illustrations of the dodo's head. To trace morphological variation in the shape of the head of the dodo as illustrated or modelled, we quantified shape using 2D-geometric morphometrics. Application of geometric morphometrics to solve issues in art history is well established (e.g., Cobden et al. 2017; Nelson et al. 2017; Hayes and van den Bergh 2018), and is a powerful tool to analyse and quantify differences in shape. We explored head shape variation in correlation with year of creation of the image and the main purpose of the illustration, which we categorise as naturalistic (with the intent to approximate the form of the 'living' dodo, acknowledging obvious differences in skills and accuracy of the artist) or non-naturalistic (fantasy, logos, and sketches).

Materials & methods

We surveyed the literature and online resources for images through time of dodos (*Raphus cucullatus*) showing the head in lateral profile and without substantial covering by hats, veils or other objects. Our wide-range survey included sketches, paintings, scientific illustrations, story illustrations, cartoons, decorations, souvenirs, logos and photographs of models and statues of dodos. We categorise these as naturalistic versus non-naturalistic, where we subdivide the latter into fantasies, logos and sketches. We acknowledge that especially for the early images, it is generally not possible to indicate if, and if so to what extent, images were intentionally copied, embellished on purpose, suffered from the artist's inability to draw or incorrect memory, or drawn without motivation to approach the reality. We treat them therefore on an equal basis and mutually compare them and with the known preserved specimens, ignoring the inferred artistic background (as in Van der Geer 2008).

In total 179 images ranging from 1601 to 2014 met the required conditions. The requirement of lateral profile unfortunately but unavoidably excluded a number of famous illustrations, among which is the one by Cornelis Saftleven (1638), which is perhaps the most reliable painting of a dodo from life. Its head is, however, shown in three-quarter profile and therefore not suitable for our analysis. For the same reason, we had to exclude a drawing of a recently killed dodo from the Gelderland journal (1601), made in Mauritius, but were able to include the image of a live bird from the same journal. Although the excluded Gelderland image is arguably the most accurate contemporary illustration of the dodo's bill available, we were fortunate to be able to include the drawing in the middle of the same illustration, where the head is shown in profile view. This image reproduces the same features of the dodo's bill as in the excluded image.

Our dataset includes the perhaps most famous Dodo painting, known as 'George Edwards' Dodo' (Figure 3b), painted by Roelant Savery in circa 1626 (now kept in the library of the Natural History Museum, London). Before moving to London, Savery was a court painter at the court of the Holy Roman Emperor Rudolf II in Prague, who had an aviary. It is speculated that the imperial aviary held a living dodo, which after its death was stuffed with hay and cloth as was custom in the 17th century, and drawn as such by Savery and his predecessor at the court, Jacob Hoefnagel (Hume 2006). Notwithstanding its history, when Savery painted his first complete dodo in 'Landscape with Orpheus in the Underworld' with animals (1611 or post-1614, see Parish and Cheke 2019), a stuffed dodo was present at the imperial collection (Hume and Cheke 2004). His earliest depiction of a dodo is that of the head only, figuring in 'The Temptation of Saint Anthony' (c. 1611–1613), based upon a dried specimen (Parish and Cheke 2019). Savery subsequently painted several dodos, using the drawings of this dodo as an archetype, including in his majestic painting 'The Paradise' in 1626 and several new versions of Orpheus. His source, likely at least in part based on the congested taxidermy specimen in Prague, might explain the stiffness and bulkiness depicted by Savery's dodos, leading to artificial protrusions and distortions in the body and a wrinkled, desiccated beak (Van Wissen 1995; Hume and Cheke 2004, p. 305). Roelant Savery's nephew Hans (or Jan) II (or Hans Savery the Younger) also painted a dodo with extreme distortions in circa 1651, included in our dataset. Likely, he copied the dodo from his nephew, but distorted the bulky features of the dodo's body even more as an artistic exaggeration.

We also included the drawing of the 'Oxford dodo', published by Strickland and Melville (1848) in their book on the extinct birds of Mauritius, Rodriguez and Réunion (=Bourbon) (Figure 4). The Oxford dodo was first listed in 1656 in a catalogue of the collection of horticulturist John Tradescant as 'Dodar, from the Island Mauritius; it is not able to flie, being so big' (Nowak-Kemp and Hume 2017a). How and when it ended up in that collection remains unknown, but it may have been the dodo from a London shop mentioned by L'Estrange (see Hume 2006). Later, when the collection moved to the Ashmolean Museum, it was exhibited there (Hachisuka 1953), still as a complete bird (Nowak-Kemp and Hume 2017a). When in 1755 it was considered unfit for display due to decay, it was discarded, and only the desiccated head and left foot were kept (Ovenell 1992; probably both feet at the time, see Nowak-Kemp and Hume 2017a). The remaining soft tissue of the head's left side was dissected by Acland to reveal its anatomy and illustrated by Strickland and Melville (1848) in order to clarify its taxonomic position and confirm its placement with pigeons and doves (Nowak-Kemp and Hume 2017b). The remains were eventually transferred to the Oxford University Museum in the 1850s. According to Hume et al. (2006), the Oxford specimen belonged to a female and was adult, as inferred from the fully fused growth plates of the tarsometatarsus (lower leg) and its small size.

On each image, 13 landmarks on the skull and beak (upper mandible) were placed (Figure 5). The (lower) mandible was excluded to allow for the inclusion of images of dodos with their beak (wide) open as occurring in illustrations where they talk, shout or sing. Landmarks were digitised in tpsDig2 (Rohlf 2006), version 2.32, for all specimens. Images were mirrored where needed to ensure identical orientation, with the head facing to the right. Skull shape was then quantified with geometric morphometrics. A key advantage of this method is that shape variation can be visualised directly (Rohlf and Marcus 1993). Shape is defined as the resulting geometry after the size, location and orientation has been removed from the landmark data (Kendall 1984). To achieve this, a full generalised Procrustes analysis (Dryden and Mardia 2008) was performed on the collected coordinates using the software MorphoJ (Klingenberg 2011). Principal components are calculated in order of the amount of variation they cover, where PC1 captures the most variation, PC2 the second most and so on. Eigenvalues of each component that explained about 10% or more of the total shape variation were considered significant for further interpretation.

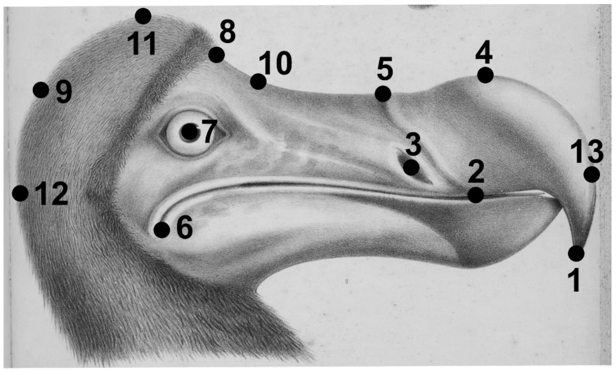

Figure 5. Geometric landmarks and their placement in illustrations of the dodo, depicted in profile. Landmark definitions: 1, tip of the beak; 2, posterior border of rhinotheca along the tomial edge; 3, nostril; 4, dorsalmost point of the beak; 5, posterior border of the rhinotheca along the dorsal edge of the beak; 6, posteriormost point of the mouth; 7, pupil; 8, anteriormost point of the plumage along the dorsal midline of the skull; 9, highest point of the curvature of the back of the head; 10, anterior point of the forehead; 12, posterior end of the head; 13, anteriormost extension of the beak. The position of geometric landmarks (red dots) on a drawing of the head of a dodo.

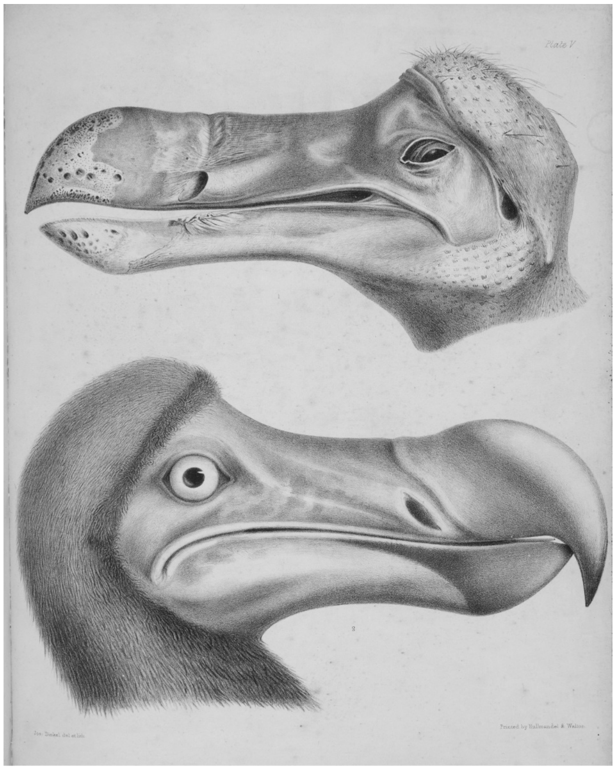

Figure 4. Study of the dodo in Hugh Edwin Strickland and Alexander Gordon Melville's *The Dodo and Its Kindred* (1847), probably by Mr. Ford. Reconstruction of the head of the dodo in Strickland and Melville's monograph on the dodo (1847).

Canonical variate analysis (CVA) was performed to maximise differences between groups by producing weighted variables, referred to as canonical variates (Pietrusewsky 2008). Generally, the first few canonical variates describe most of the variations present, analogous to principal component analysis. We here use the function Canonical Variate Analysis in MorphoJ to visually represent the differences among pre-assigned groups. For PCA and CVA, the eigenvalues of each component or variate that explained about 10% or more of the total shape variation were considered significant for further interpretation. Shape changes for each principal component and canonical variate were visualised using the warped wireframe function in MorphoJ.

A multivariate regression was performed with MorphoJ on the dataset to examine the influence of year of creation of the image on the shape variation as shown in the Procrustes coordinates. Year of creation of models generally follows Parish (2015). For a few images lacking a precise date, we used the lower limit of the age range. For images with a broad age range, e.g., mid-19th century, we used the median. A permutation test with 10,000 randomisation rounds was performed on the regression to test for independence. Significance level for the tests $p = 0.05$.

Results

For raw data, see Table S2. Note: all tests are significant at the 0.01–0.0001 level based on 1000 permutations unless specified otherwise.

Principal component analysis

The main variation described by the first principal component, PC1, explains 18% of the total shape variation (Table 1, Table 2). PC1 captures the relative size of the front part of the beak, which in extreme cases bears a conspicuous bulging part (Figure 6a). Dodos depicted with such extreme bulging beaks (high PC1 values) also have a proportionally higher and shorter skull. The main variation described by the second component (PC2) explains 15% of the total shape variation. PC2 captures the downward bending of the tip of the beak. Dodos with high PC2 values have a straighter beak and a somewhat more posteriorly placed eye.

The depiction of the natural specimen kept at Oxford (the 'Oxford dodo', previously at Ashmolean) is found in the PC1-PC2 scatter plot in the upper left quadrant (ID 178). Interestingly, the vast majority of dodo images has a lower PC2 score than these, meaning that they have a more curved, or less straight, beak than the former (Figure 6a). This also applies to Edward's Dodo (c. 1626; ID 9).

The bivariate plot shows that the morphological variation among non-naturalistic images exceeds that among naturalistic images, captured in both PCs and in all directions. Significant outliers (outside the 95% confidence ellipse) are ID 70 (1980, cartoon; Figure 7a) and ID 160 (2013 animation; Figure 7b) (highest PC1, average PC2), ID 87 (2001, cartoon; Figure 7h) (high PC1, low PC2), ID 89 (2002, animation; Figure 7c) (high PC1, highest PC2) and ID 125 (2010, cartoon; Figure 7d) (lowest PC2, average PC1). Logos vary in shape similar to fantastic images.

The main variation captured by the third principal component (PC3) explains 12% of the total shape variation. PC3 captures the size and shape of the skull relative to the beak. Dodos with high PC3 values have a proportionally larger and rounder skull and a shorter beak with a conspicuous hooked tip (Figure 6b). Their eyes are placed more anteriorly, while the nostrils are placed more posteriorly. Significant outliers (outside the 95% confidence ellipse of the PC1-PC3 plot; Figure 6b) with the lowest PC3 scores are ID 118 (2009, cartoon; Figure 7e) and ID 71 (1981, decoration) (average PC1) and ID 86 (2001, cartoon) (lowest PC1). These have elongated beaks with the tip hardly bending downwards.

The position of the border between the featherless face and feathered back of the skull remains practically constant in all considered PCs, and cannot be used as a discriminator between images.

Table 1. Principal component analysis and canonical variate analysis of illustrations of the head of the dodo, based on 13 geometric landmarks.

Principal component	Eigenvalue	% Variance	Cumulative %
1	0.00504745	18.078	18.078
2	0.00427567	15.314	33.392
3	0.00338526	12.125	45.517
4	0.00253363	9.075	54.592
5	0.00197365	7.069	61.661
6	0.00176584	6.325	67.985
7	0.00128569	4.605	72.590
8	0.00124271	4.451	77.041
9	0.00112964	4.046	81.087
10	0.00088934	3.185	84.273
11	0.00080366	2.878	87.151
12	0.00067218	2.408	89.559
13	0.00056417	2.021	91.579
14	0.00041800	1.497	93.076
15	0.00038885	1.393	94.469
16	0.00035245	1.262	95.732
17	0.00029484	1.056	96.788
18	0.00025651	0.919	97.706
19	0.00022271	0.798	98.504
20	0.00017828	0.639	99.142
21	0.00013499	0.483	99.626
22	0.00010443	0.374	100.000
Canonical Variate			
1	0.56703581	57.381	57.381
2	0.26979038	27.301	84.682
3	0.1513670	15.318	100.000

Table 2. Statistics of performed tests. *P*-values are obtained from permutation tests (10,000 permutation rounds). Significant *p*-values (<0.05) are indicated with an asterisk. For the regression on the effect of year on total shape (Procrustes coordinates), a permutation test against the null hypothesis of independence was performed.

Canonical Variate Analysis			
Mahalanobis distance among groups (*p*-value)			
	Logo	Naturalistic	Phantasy
Naturalistic	1.9073 (0.0001*)		
Phantasy	1.6544 (0.1986)	1.5751 (<.0001*)	
Sketch	2.8666 (0.1039)	2.7945 (0.0002*)	3.0272 (0.0137*)
Procrustes distances among groups (*p*-value)			
	Logo	Naturalistic	Phantasy
Naturalistic	0.0690 (0.0012*)		
Phantasy	0.0477 (0.6050)	0.0634 (<.0001*)	
Sketch	0.1207 (0.0288*)	0.1126 (0.0004*)	0.1260 (0.0100*)
Regression over year of creation			
Total SS	4.99527259		
Predicted SS	0.11000406		
Residual SS	4.88526854		
% predicted	2.2		
p-value (1000 rounds)	0.0001*		

Multivariate analysis

A canonical variate analysis on main purpose, where we assigned the images each to one of four (sub)categories (naturalistic, fantasy, logo or sketch), shows a considerable overlap in total shape between the categories with about half the images falling in this shared area (Figure 8) (see Table 2 for statistics). CV1 (57% of the total variance) mainly describes the shape of the tip of the beak, varying from narrow and small, relative to the rest of the skull (high CV1 scores) to a large, bulging beak end with a receding tip (low CV1 scores) (Figure 7d). The images with the lowest CV1 score are ID 70 (1980, cartoon; Figure 7a) and ID 87 (2001, cartoon; Figure 7h), as was also captured by their high PC1 score (see above). The highest CV1 score is represented by ID 5 (1605, Clusius' original sketch; Figure 1a), in which the tip of the beak is narrowest and smallest of all.

CV2 (27% of the total variance) mainly describes the curvature of the dorsal border of the beak and the degree of receding of the tip of the beak (Figure 8). Images with a high CV2 score have a horizontal and straight dorsal border and lack a receding tip. Their beak is proportionally longer with a more posteriorly placed nostril. The maximum score is represented by ID 118 (2009, cartoon (Figure 7e), which is also captured by the lowest PC3 score (see above). The lowest scores are represented by ID 14 (1634, sketch) (Figure 1c) and ID 179 (c. 1601, copper engraving), which both have a convex or bulging dorsal profile of their beak. An average score within the category fantasy is represented by, e.g., ID 151 (2012, animation; Figure 7g). The total shape variation among naturalistic images is less (with one outlier, ID 5; see above) than that among non-naturalistic images.

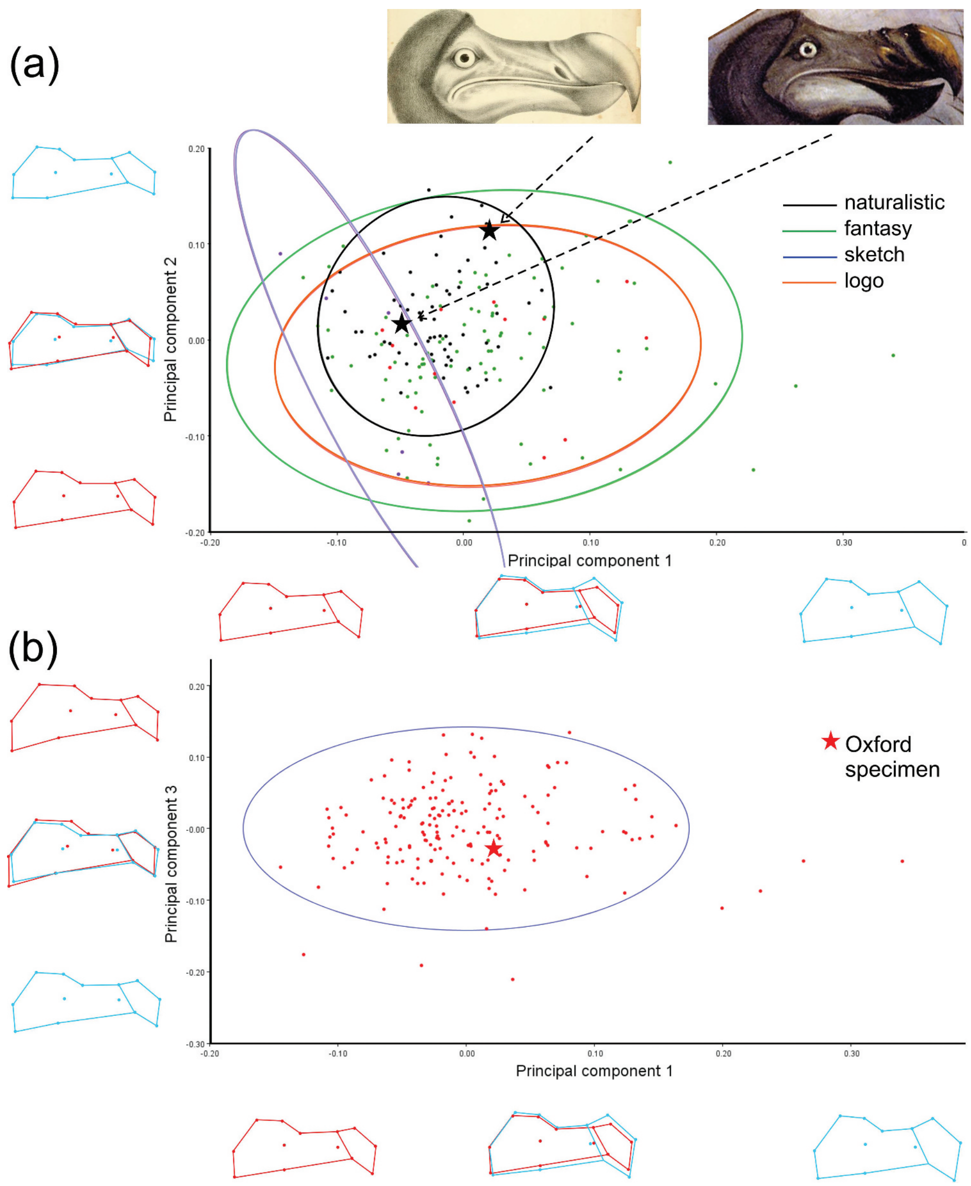

Figure 6. Principal Component Analyses plots. The wireframes of the first three Principal Components (PC1, PC2, PC3) represent minimal (red) and maximal (light blue) scores. (a) Principal Component Analyses plot showing PC 1 versus PC2. The images of the Oxford and Edward's dodo are starred. Purposes are categorised as naturalistic (a), fantasy (b), sketch (c) or logo (d). (b) Principal Component Analyses plot showing PC 1 versus PC3. The images of the Oxford dodo are starred. Scatter plots showing the results of Principal Component Analysis of the shape of the dodo's head in illustrations along with wireframes. High PC1 values coincide with extreme bulging beaks and higher and shorter skulls. High PC2 values coincide with straighter beaks. High PC3 values coincide with larger, rounder skulls and short beaks with a conspicuous hooked tip.

Regression of shape through time

The increase in morphological variation starts during the mid-19th century and increases further from the mid-20th century onwards (Figure 9) (see Table 2 for statistics). There is also a notorious gap in the record between the mid-17th century and the mid-18th century. Modern images have scored highest in regressions between the year of creation on the shape variation; they are all cartoon or animation images with a short, extremely bulging beak, such as ID's 70 (Figure 9c), 87 (Figure 7h), 160 (Figure 7b) and 110. The increase in number and variation of non-naturalistic images coincides with the publication of Carroll's *Alice's Adventures in Wonderland*. Before that, such images were extremely rare (e.g. ID's 24 and 26).

Naturalistic images are more constant in shape than are non-naturalistic images. The single exception (ID 5; Figure 1a) among naturalistic images is the one found in Carolus Clusius' (Latin for Charles de l'Écluse) on exotic animals (*Exoticorum*), book 10 (1605). The tip of the beak is here dark coloured and lacks the bulging dorsal profile. Feathers on top of its head are missing. Clusius probably copied the image from Admiral Van Neck's travel account, or Het Tweede Boek (1601). In the 1626 edition (published after his death), the image was replaced with Adriaen van de Venne's drawing (ID 12; Figure 1e). This latter image neatly falls within the variation of naturalistic images only.

Discussion

The lack of images of the dodo for about a hundred years after the mid-17th century is striking. This likely reflects a waning popular interest in the species: not only had the dodo gone extinct, but also it had practically disappeared from the scientific community due to

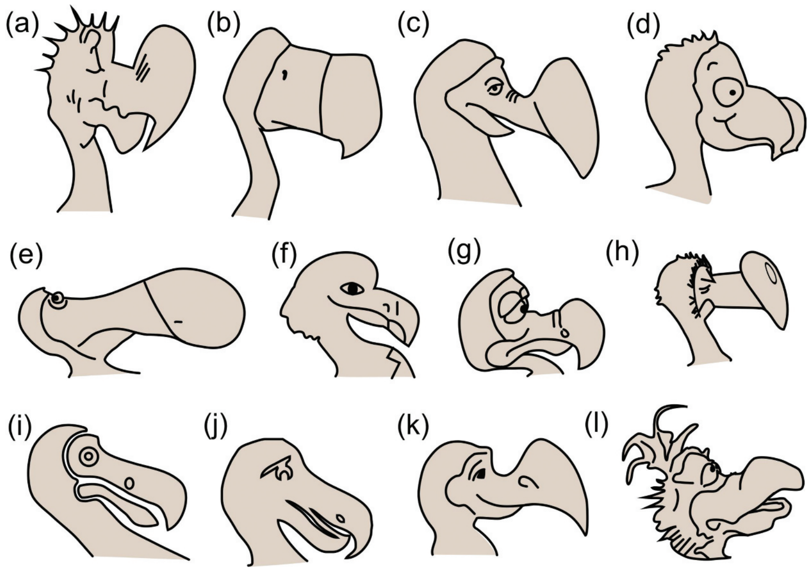

Figure 7. Dodo depictions in 20th and 21st century art and design. Redrawn after: (a) '*De weg naar west*' (1980) by Piet Wijn, comics series *De avonturen van Douwe Dabbert*; (b) *'The Lonely Dodo'* (2013) by Alistair McGowan, animation by Aardman commissioned by Durrell Wildlife Conservation Trust; (c) *'Ice Age'* (2002), animation by Blue Sky Studios; (d) Plantu Cartoon (2010) for the Reunionese edition of Le Monde; (e) Daniel Picouly's '*Lulu et le dernier des dodos*' (2009), book cover by Frédéric Pillot; (f) Coat of arms of Mauritius (1906) by Johann Van Der Puf; (g) *'The Pirates!'* (2012) animation by Aardman Productions; (h) *'Dodo de génie'* (2001) by Turk (Philippe Liégeois), Bob de Groot's *Léonard* comics series; (i) Logo of the Société Nationale des Parcs Zoologiques; (j) Logo of the musical band *'The Dodo'*; (k) Logo of a nightclub in Zhytomyr, Ukraine (2000); (l) Episode 415 with Anne Murray of *'The Muppet Show'* (1980), Michael Frith for Jim Henson Productions. Twelve images of the dodo from cartoons, animations and logos, showing cartoonesque reconstructions of its head with examples of exaggerated bulgy beaks, very large and/or long beaks and pointed, receding tips.

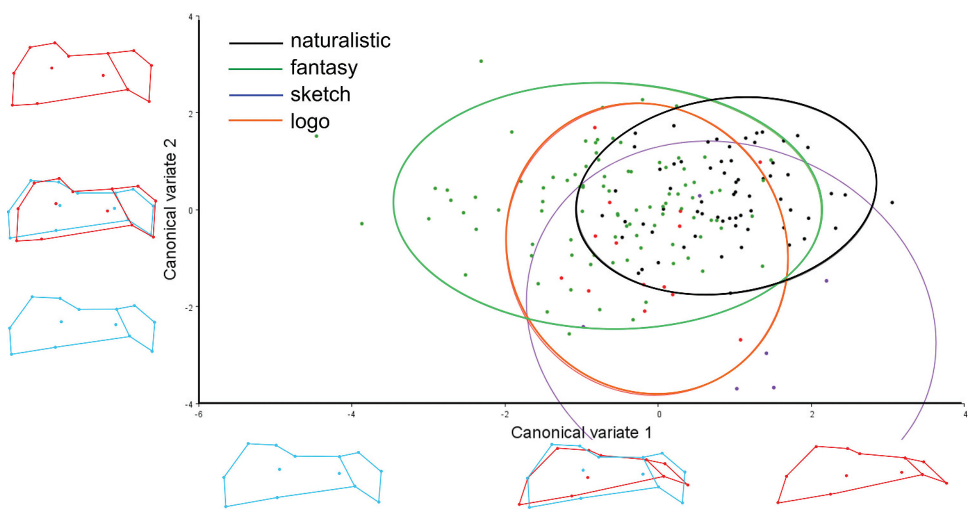

Figure 8. Canonical Variate Analysis on purpose, with CV 1 against CV2. The wire frames represent minimal (red) and maximal (light blue) scores. Purposes are categorised as naturalistic (a), fantasy (b), sketch (c) or logo (d). The variation amongst fantastic images and logos exceeds that amongst naturalistic images. The larger variation noted in sketches is the result of an outlier. Scatter plot of the results of Canonical Variate Analysis on purpose (naturalistic, fantasy, sketch or logo). The variation among fantastic images and logos is larger than that among naturalistic images.

the scarcity of its remains. Dodo remains were limited to natural history collections in Oxford, London and Copenhagen (e.g., Nowak-Kemp and Hume 2017a), and these few natural cabinets were typically accessible to the elite only. International and broad scientific interests in the dodo followed Acland's dissection of the Oxford dodo in 1847 and the resulting anatomical and taxonomic analysis by Strickland. Strickland presented his observations at the meeting of the British Association for the Advancement of Science at Oxford on an evening entirely devoted to the dodo (Baker and Bayliss 2002). The meeting stimulated the establishment of Natural Sciences teaching at the university, culminating in the building of a new, modern University Museum for research and teaching on the basis of its collections (Fox 1997). At its opening in 1867, the dodo's remains were exhibited on a separate table along with a painting in the aisle with birds, now visible to a large public. A newer display (1868) included a reconstructed skeleton, likely based on the one by Richard Owen (Owen and Broderip 1866), and incorporating recently exhumed subfossil dodo bones from the Mare aux Songes in Mauritius (Hume et al. 2009). Popularity increased, and in 1892, the dodo remains were considered to be among the chief treasures of the museum (Lankester 1892). Accordingly, they were placed prominently in an aisle facing the entrance in a case shared with their closest

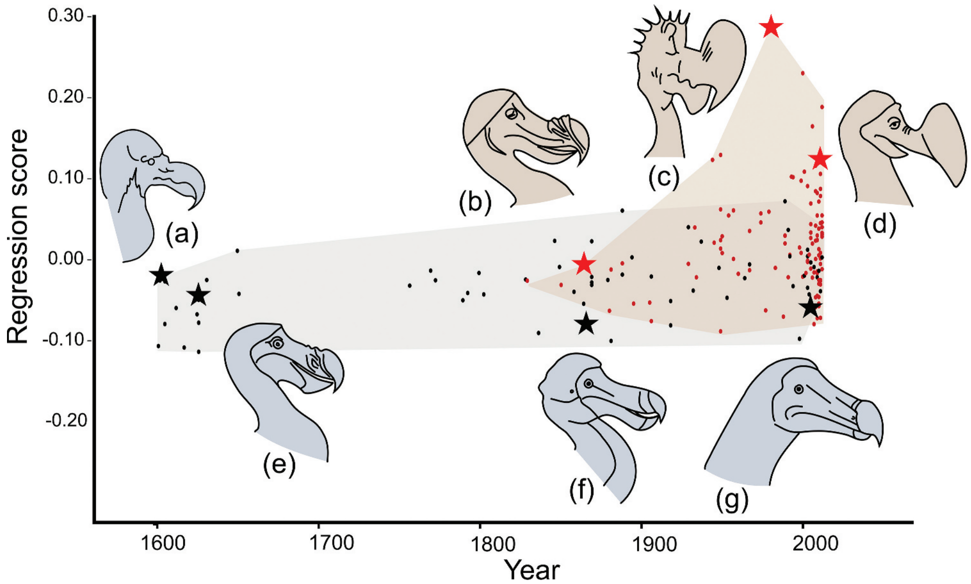

Figure 9. Regression of shape of dodo images over year of attribution. The variation in shape increases after the publication of *Alice's Adventures in Wonderland*, and again after c. 1950. Naturalistic depictions (in black) remain relatively constant in shape variation, compared to non-naturalistic depictions (in red). Sketched outlines of starred images are after (a) Joris Joostensz Laerle's sketches from the voyage of the VOC Gelderland (1601), (b), John Tenniel's dodo in Lewis Carroll's *Alice's Adventures in Wonderland* (1865), (c) dodo by Piet Wijn for the Dutch comics *De avonturen van Douwe Dabbert* (1980), (d) Animation *Ice Age* by Blue Sky Studios (2002), (e) Edwards' dodo by Roelant Savery (1626, (f) James Erxleben's dodo for Richard Owen's *Memoir of the Dodo* (1866), and (g) Julian Hume's reconstruction after skeletal measurements (2005). Visualisation of the multivariate regression of shape of dodo images over years of attribution. The variation in shape increases after the publication of *Alice's Adventures in Wonderland*, and again after circa 1950. Naturalistic depictions, indicated by black dots remain relatively constant in shape variation, compared to non-naturalistic depictions, indicated by red dots.

relative, the solitaire, and their living allies, the tooth-billed pigeon of Samoa (*Didunculus strigirostris*) and crowned pigeons of New Guinea (*Goura*).

One of the regular visitors to the dodo displays, before as well as after the transfer of the dodo remains to the new University Museum in the 1860s, was Reverend Charles Dodgson, a mathematics tutor at Christ Church and storyteller to the Dean's three daughters Lorina, Alice and Edith. After the publication of his *Alice's Adventures in Wonderland* (1865), under the pen name Lewis Carroll, a sudden increase in the number of popular images of the dodo took place, along with the dodo's fame and recognition as an icon of extinction, often with a romantic notion. The dodo in Carroll's novel by John Tenniel was directly copied from Savery's Edwards' dodo at the exhibition. Savery's paintings and drawings show only three postures of the dodo, which have since become archetypal.

The morphological variation of dodo images apparently increased since 1865. Its characteristic shape of the beak, settled by Strickland and Melville's (1848) high-quality lithography and specimen-based reconstruction, was often transformed into an extremely bulgy beak, often ending in a sharp, receding tip, and a naked, featherless face. Nonetheless, throughout these four centuries, all dodo representations that were intended to serve naturalists' audience, including museum exhibits for the public remained relatively uniform. Our regression of total shape over the year of depiction (Figure 9) shows that later naturalistic images have the same overall shape as the earlier images. Likely, paintings, drawings and descriptions of transported or taxidermy dodos from 1600 to 1639 have been informing the naturalistic iconography of the dodo ever since, with all major studies on the details of the head (Strickland and Melville 1848; Owen and Broderip 1866; Owen 1879; Figure 9f) reaching back to information reported in published travel reports (*Voyages*) and Roelant Savery's paintings (Figure 9e) and sketches of the early 17th century, despite the obvious differences in quality of rendering and direct purpose.

Before the publication of *Alice's Adventures in Wonderland* (1865), the main dodo imagery followed Savery and its intended purpose was naturalistic, to depict the dodo as accurately as possible. The substantial increase in morphospace after 1865 can likely be attributed to Tenniel's image that seems to have set the basis, aided and inspired by a continuation of the influence of Savery's paintings. Owen's models in his 1866 monograph (Figure 9f) still follow Savery in appearance, and only later (Owen 1871) he produced a more biologically correct and scientifically informed skeletal reconstruction. The majority, however, of the non-naturalistic dodos since *Alice's Adventures in Wonderland* still share the same overall shape with the naturalistic images. This is likely due to the restricted access to and unfamiliarity with more realistic images, drawn from life. For example, the sketches of Joris Joostenszoon Laerle are perhaps the most accurate drawings of the dodo (Hume 2003). They were drawn on Mauritius after living or recently killed specimens as part of the journal for the 1601–1603 voyage of the flagship Gelderland. The journal remained unpublished and unknown to a wider audience for most of its existence (Hume 2003). Similarly, the Indian miniature painting of a living dodo from the menagerie of Jahangir by Ustad Mansur (c. 1625), arguably the most anatomically accurate depiction (Hengst 2003), was only discovered in the late 1950s (Ivanov 1958). Thus, for centuries, all that most artists had at their disposal were Savery's works.

Logos with dodos appear to have increased in popularity only since the mid-20th century, when the famous icon was not only used by zoos and wildlife organisations (e.g., Figure 7i) but also for nightclubs, rock bands and pizzerias (e.g., Figure 7j, k). Earlier logos seem restricted to Mauritius itself, such as in the coat of arms of Mauritius (Figure 7f) and stamps. The graphic element of logos invariably portrays a dodo with an exaggerated bulgy beak tip even though the relative size and shape of the beak varies.

What seems to transform a bird into a dodo in the eye of the public, in logos as well as fantasy imagery, is the presence of this conspicuous bulgy beak: the rounder and higher the better, especially with the tip pointing downwards and backwards, well extending beyond the level of the occiput (see, for example, Figure 9c, after a cartoon from 1980). Logos work as visual shortcuts and apparently such a bulgy beak makes the dodo recognisable from a distance to the viewer. A few exceptions among the non-naturalistic images exist with, on the contrary, an elongated and very gently curved beak, without a bulgy part, more in the style of Van den Broecke (1634; Figure 1d) (likely coincidentally), among which the dodo of the Jim Henson's Muppet show (Figure 7l).

The increase in shape variation after 1865 is for the major part due to an exaggeration of the bulging tip of the beak. Such beaks are often, but not always, short, and are combined with a sharp, reclining tip (Figure 9c). The majority of fantasy images refrain, however, from exaggerations, and remain relatively close to naturalistic images (e.g. Figure 7g).

There are two main reasons why the dodo image was so sensible to cartoonist and humoristic displays. Firstly, its appearance in Carroll's book *Alice's Adventures in Wonderland* (1865) among a set of absurdist characters iconised its humoristic appearance. Secondly, in the chapter by Buffon (1770) and the monograph by Owen and Broderip (1866), aspects of stupidity and laziness have been recorded, and the dodo explicitly described as a tragic, degenerate failure of nature that was not fit to survive. This scientific notion of a failed, witless creature permeated society and led to the bird's further ridiculing through cartoons. Recent research has pointed, however, to quite the opposite – the dodo was a survivor, which as a species persisted on a volcanically active island for millions of years and survived extreme climatic bottlenecks (Rijsdijk et al. 2011). Moreover, body mass estimates indicate that representations of the dodo as an extremely fat bird are rather incorrect (Angst et al. 2011a). The anatomical features, as reconstructed based on 3D surface scans of the only complete dodo skeleton of a single individual in existence, suggest a muscular, sturdy, flightless bird, contradicting the popular, cartoonesque, over-weight build (Claessens et al. 2015). The downy plumage in some early descriptions was not a sign of degeneration or imperfection, but rather simply a stage of seasonal moult as revealed by bone histology (Angst et al. 2017). Furthermore, as brain endocasts reveal, the dodo was probably just as intelligent as other species of pigeons (Gold et al. 2016). As we have shown here, not only its body build but also its head and beak were, and still are, often exaggerated to the level of ridicule to comply with the long-held but incorrect popular belief that the dodo was a clumsy, tragic bird destined for extinction.

Conclusion

A waning public interest in the dodo likely lies behind the lack of dodo images between roughly 1650 and 1750. This was partly due to the bird's invisibility as dodo remains were limited to Oxford, London and Copenhagen, and accessible to the elite only. In the early 1800s, natural scientists including Cuvier and Owen, were much more interested in the dodo. The dissection of the Oxford dodo in 1847 and Strickland's subsequent anatomical and taxonomic analysis, culminating in his monograph with Melville in 1848 finally prompted broad international and national interests among scientists and the public alike. A regular visitor to the displayed dodo remains was Charles Dodgson, alias Lewis Carroll. After the publication of his *Alice's Adventures in Wonderland* (1865), the number of popular dodo images increased suddenly, along with its fame and recognition as an icon of extinction. Simultaneously, the morphological variation between these images increased as well.

Before 1865, the main imagery followed Roelant Savery's dodo paintings. Since *Alice's Adventures in Wonderland*, many non-naturalistic images continue to share the same overall shape with the naturalistic images. This is likely due to the lack of access to and unfamiliarity with more realistic images, drawn from life, of e.g., by Joris Laerle (1601) and Ustad Mansur (c. 1625), which did not enter the public realm until relatively recently. The later increase in variation is for the major part due to dodo images in fantasy settings. Logos with dodos appear to have increased in popularity only since the mid-20th century, and are used for a broad variety of purposes. In a few cases, such as in Jim Henson's Muppet show, the dodo's beak is elongated and minimally curved, lacking a bulgy part, more in the style of Van den Broecke (1634). The majority of the dodo images in logos as well as fantasy imagery shows a conspicuous bulgy beak: the rounder and higher the better, especially with a sharp, receding tip, well extending beyond the level of the occiput. Nonetheless, throughout the four centuries of depiction, all dodo representations that were intended to serve naturalists' audience, including museum exhibits for the public, remained relatively uniform.

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The authors declare there are no competing interests.

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Data Availability

The specimen data and associated sources are available in Table S1. The raw coordinates of the landmark configuration of the 211 specimens are available in Table S2.

Author contributions

AG and GL conceived the original idea; AG assembled the data; AG and GL led the analysis; GL made the figures; AG, GL, KR, LC discussed the results and wrote the manuscript.

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