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SHORT COMMUNICATION

The end of the fat dodo? A new mass estimate for *Raphus cucullatus*

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Abstract A new mass estimate for the dodo (*Raphus cucullatus*), based on the lengths of the femur, tibiotarsus and tarsometatarsus, is attempted. The obtained mean mass is 10.2 kg, which is less than previous estimates based on other methods, which ranged from 10.6 to 21.1 kg, and much lower than the 50 lbs reported by a seventeenth-century eyewitness. The new estimated mass, which is similar to that of a large wild turkey, seems more realistic than previous ones and supports the hypothesis that contemporary illustrations of extremely fat dodos were either exaggerations, or based on overfed specimens. Pictures of "fat" dodos may also have been based on individuals exhibiting a display behaviour with puffed out feathers.

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Introduction

Although it coexisted with humans for nearly a century on its native island of Mauritius, before its extinction sometime close to the end of the seventeenth century, many important features of the dodo (*Raphus cucullatus*) remain very poorly known (Hume 2006), which is hardly surprising since no naturalist had the opportunity to study it during that period. Even such a basic characteristic as the mass of an adult dodo is still a matter of discussion. This question is closely linked to the rather "bloated" appearance of the dodo on many contemporary (and later) illustrations, which has led to the common assumption that it was a very fat and heavy bird. In fact, there is no reliable record of the actual mass of a dodo. Contemporary tales of a ship's crew gorging itself on the flesh of only a few dodos have contributed to the idea of very bulky birds. Herbert (1634) noted that "few weigh less than fifty pound". This considerable weight has been accepted by many subsequent authors, notably Strickland and Melville (1848), who thought that "the bulk of the Dodo must have been prodigious", but it is unclear how it was obtained. Moreover, as noted by Hume (2006, p. 69), Herbert's writings "have a tendency towards exaggeration". Fifty pounds, or about 22 kg, is the average weight of *Rhea americana*, the greater rhea (Folch 1992), a significantly larger bird than *R. cucullatus*.

It is now widely accepted that the dodo was not necessarily as fat as depicted on the paintings by Roelandt Savery and his many followers (Ziswiler 1996), partly because other contemporary depictions of the dodo

(notably the seventeenth-century miniature by the Indian artist Mansur; Iwanow 1958), showing a slimmer bird, are now considered more realistic (Lüttschwager 1961). However, the actual mass of a "normal" dodo remains uncertain. Here, we present a new mass estimate for the dodo, which is lower than previous ones and in agreement with the idea that this bird was not as fat as frequently assumed.

Mass estimates for *R. cucullatus*

The idea of the fat, almost obese, dodo was challenged by Kitchener (1993), who envisaged a less bulky bird, on the basis of several independent approaches, including scale models, estimates of skeleton mass and scaling of leg bone measurements. The obtained mass range was 10.6 to 17.5 kg. To account for discrepancies in dodo depictions, Kitchener assumed that the dodo showed a seasonal fat cycle, as previously suggested by Oudemans (1917). Livezey (1993), who also assumed seasonal fatness changes, based his mass estimates on a regression line showing femur length versus mass in various flying birds, which yielded an estimated mass range of 6 to 10 kg. This was then corrected for flightlessness by adding 50% to 100% to the estimated mass (for the lean and fat phases, respectively). The result was a mass ranging from 15.9 to 21.1 kg (the upper figure being close to Herbert's 50 lbs).

To estimate the mass of an adult dodo independently of previous assumptions, we have first used the regression lines published by Zeffer et al. (2003), showing hindlimb bones and leg lengths vs. body mass in 323 species of birds from 74 families, including flightless forms. The bones considered are the femur, tibiotarsus and tarsometatarsus, which are well represented in collections of dodo bones. Leg length is obtained by adding the lengths of the three above-mentioned bones. Measurements of dodo bones were taken on specimens from various institutions (see Electronic supplementary material), consisting of 25 femora, 27 tibiotarsi and 30 tarsometatarsi. This includes measurements taken on what appears to be the only dodo skeleton corresponding to a single individual, in the Mauritius Institute in Port-Louis (Cheke and Hume 2008), whose proportions do not seem to differ significantly from those of composite skeletons. When the mean lengths of the femur, tibiotarsus, tarsometatarsus and leg of the dodo are simply plotted on the regression lines of Zeffer et al. (2003), a consistent mass of about 10 kg is obtained for the dodo (Fig. 1). However, partly because of the log scale used in the diagrams, the results obtained using this simple method are approximations. To refine this initial result, we have reversed the equations provided by Zeffer et al. (2003) to calculate the mass of the dodo on

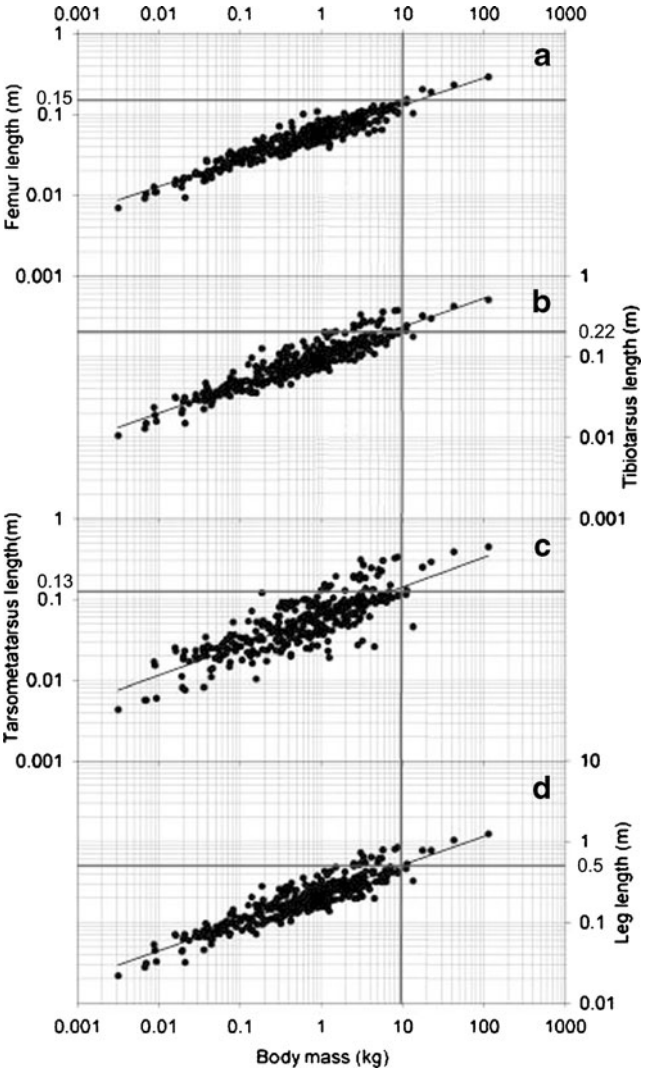

Fig. 1 Mass estimates for *Raphus cucullatus* based on leg bone measurements. Graphs illustrating relationships between body mass and limb dimensions, after Zeffer et al. (2003). **a** femur, **b** tibiotarsus, **c** tarsometatarsus, **d** total leg (femur+tibiotarsus+tarsometatarsus) in extant birds. *Horizontal* and *vertical lines* indicate the position of the dodo relative to extant birds. Dodo measurements represent means (see Electronic supplementary material for detailed lists of measurements). These data suggest an estimated body mass around of 10 kg for the dodo. Note the log scales

the basis of the lengths of the femora, tibiotarsi, tarsometatarsi and leg. The equation used is:

$$M = (\text{bone}/a)\text{^}(1/b).$$

Parameters for the various bones are: femur, a=0.0597, b=0.34; tibiotarsus, a=0.102, b=0.36; tarsometatarsus, a=0.0618, b=0.36 and whole leg, a=0.227, b=0.35. See Electronic supplementary material for detailed mass estimates. As shown by the resulting graph (Fig. 2), the results based on the femora alone, with a mean mass of 15.4 kg, are higher than those for the tibiotarsi (8.7 kg) and

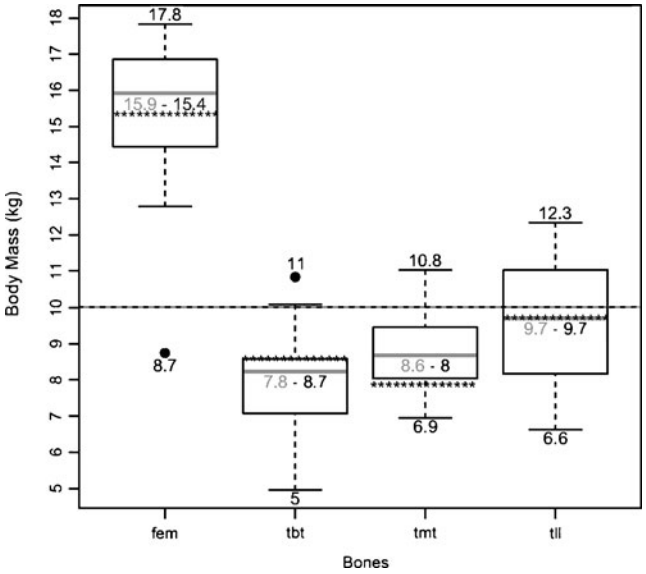

Fig. 2 Boxplot diagram showing mass estimates for *Raphus cucullatus* calculated from the lengths of femora (*fem*), tibiotarsi (*tbt*) and tarsometatarsi (*tmt*), as well as total leg lengths (*tll*), of various dodo specimens. A detailed list of specimens, with their measurements and the resulting mass estimates, is provided in Electronic supplementary material. For each group of bones, the greatest and smallest lengths are mentioned, as well as the median (in *grey*) and mean (in *black*). The *grey horizontal lines* show the median, the *lines of asterisks* the mean. The *continuous horizontal black line* corresponds to the 10 kg mass estimate obtained by plotting bone lengths on the regression lines of Zeffer et al. (see Fig. 1). The equation used to estimate the mass of the dodo on the basis of limb measurements is obtained by reversing that of Zeffer et al. (2003): $M=(\text{bone}/a)^{(1/b)}$. Femur, $a=0.0597$, $b=0.34$; Tibiotarsus, $a=0.102$, $b=0.36$; Tarsometatarsus, $a=0.0618$, $b=0.36$; Whole leg, $a=0.227$, $b=0.35$

tarsometatarsi (8 kg). The result for the whole leg is 9.7 kg, very close to the rough estimates obtained by plotting mean lengths on the regression lines. The mean of all these estimates is 10.2 kg, again in good agreement with the initial result. This is significantly lower than Herbert's 50 lbs, and very slightly under the lower end of the weight range estimated by Kitchener (1993). It is also close to Livezey's results prior to correction for flightlessness. As the regression line of Zeffer et al. includes both flying and flightless birds, including large, heavy forms such as ratites, there does not seem to be any need for correcting our results to account for flightlessness in the dodo. It should also be noted that the obtained result is an average mass: some dodos certainly could exceed 10 kg, while others were less heavy; this may have been accentuated by sexual dimorphism (Livezey, 1993). Nevertheless, our results seem to show that previous estimates, including those favouring a relatively "lean" dodo, were too high. With a mass of about 10 kg, which, for instance, is that of a large male wild turkey (*Meleagris gallopavo*; Porter 1994), the dodo still appears as a heavy bird, as shown by its position on the regression lines: few of the living birds recorded by Zeffer et al. (2003) are heavier than the dodo (they are mainly ratites such as the rhea, emu, cassowary and ostrich). However, this estimate seems more realistic than many of the previous ones and more in accordance with the overall size of the bird as indicated by both eyewitness accounts and skeletal remains, which do indicate a bird about the size of a large turkey, albeit with different proportions.

Conclusions

The new mass estimate presented above supports the idea that the few contemporary illustrations of the dodo which show it as a relatively lean bird (Fig. 3a), mostly produced at an early date and based on living dodos, are more realistic than those showing it as an extraordinarily fat bird (Fig. 3b), which are of a later date (post-1625) and

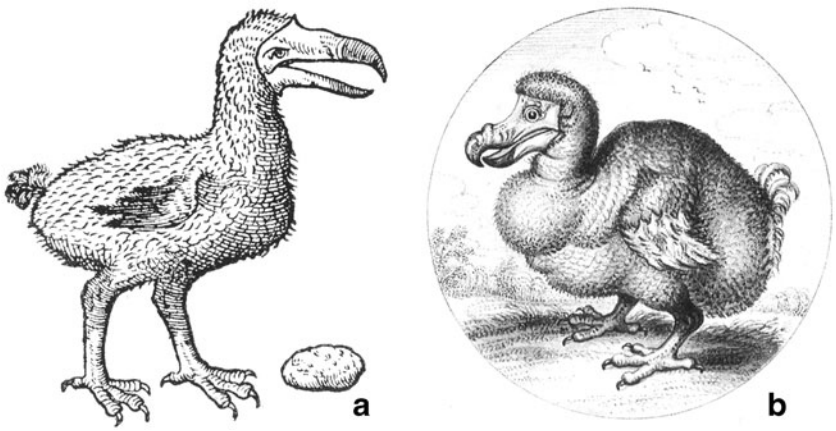

Fig. 3 Two seventeenth century depictions of *Raphus cucullatus*. **a** A lean dodo after C. Clusius (1605), copied from a drawing in Van Neck's lost journal. **b** A fat dodo by the artist A. Van de Venne (1626). The mass estimates in the present paper are in better agreement with **a** than with **b**, supporting the idea that pictures of extremely fat dodos are exaggerations, not necessarily based on living dodos and often copied from other artists. Both drawings are from Hume (2006), in which details about them can be found

generally of lesser documentary value (Hume 2006). Whether the dodo was subject to significant cyclical weight changes is a moot point, but our results do suggest that representations of the dodo as an extremely fat bird are either exaggerations (which were subsequently copied by other artists; Ziswiler 1996) or based on overfed captive specimens, as has already been suggested (Kitchener 1993). Illustrations of "fat" dodos may also have been based on male specimens exhibiting a sexual display behaviour, in which they may have puffed out their feathers and inflated their crop, as done by various birds, including Columbiformes (the group that includes *R. cucullatus*). The posture of the bird on some of the "fat dodo" illustrations (Fig. 3b), with "inflated" body and head thrown back, is in agreement with such an interpretation. However, it should be remembered that very few reliable descriptions of dodo behaviour are available (Hume 2006), and they do not specifically mention display.

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References

Cheke A, Hume JP (2008) Lost land of the dodo. T & AD Poyser, London

Folch A (1992) Rheidae (rheas). In: del Hoyo J, Elliott A, Saragatal J (eds) Handbook of the birds of the world, vol 1. Lynx Edicions, Barcelona, pp 84–89

Herbert T (1634) A relation of some yeares' travaile, begunne Anno 1626, into Afrique and the greater Asia, especially the territories of the Persian Monarchie, and some parts of the Oriental Indies and Isles adiacent. W Stansby & J Bloome, London.

Hume JP (2006) The history of the Dodo *Raphus cucullatus* and the penguin of Mauritius. Hist Biol 18:65–89

Iwanow I (1958) An Indian picture of the dodo. J Ornithol 99:438–440

Kitchener A (1993) On the external appearance of the dodo, *Raphus cucullatus* (L., 1758). Arch Nat Hist 20:279–301

Livezey B (1993) An ecomorphological review of the dodo (*Raphus cucullatus*) and solitaire (*Pezophaps solitaria*), flightless columbiformes of the Mascarene Islands. J Zool 230:247–292

Lüttschwager J (1961) Die Drontevögel. Die Neue Brehm-Bücherei, A. ZiemsenVerlag, Wittenberg Lutherstadt

Oudemans AC (1917) Dodo-studien. Verhand Koninkl Akad Wetensch Amsterdam 19:1–140

Porter WF (1994) Meleagrididae (turkeys). In: del Hoyo J, Elliott A, Saragatal J (eds) Handbook of the birds of the world, vol 2. Lynx Edicions, Barcelona, pp 364–375

Strickland HE, Melville AG (1848) The dodo and its kindred. Reeve, Benham & Reeve, London

Zeffer A, Johansson LC, Marmebro Å (2003) Functional correlation between habitat use and leg morphology in birds (*Aves*). Biol J Linn Soc 79:461–484

Ziswiler V (1996) Der Dodo. Fantasien und Fakten zu einem verschwundenen Vogel. Zoologisches Museum der Universität Zürich, Zürich