

Bringing the extinct dodo back to life

The dodo may long since have been extinct, but one zoologist has reconstructed the creature in sufficient detail for there to be evolutionary puzzles to be solved.

THAT the dodo deserves a better press is hardly anywhere disputed. While still extant, this flightless bird was both mocked and tormented by the sailors who found it marooned on Mauritius, in the Indian Ocean. Illustrations of an evidently ungainly animal were then taken as figures of fun by a cruel seventeenth century. A few specimens were captured on behalf of zoos, but did not long survive. And then the species (*Raphus cucullatus*) became extinct (around the year of Charles II's restoration to the British throne), except as a figure of speech (as in "As dead as a...") and in storybooks.

To set the record straight, one Bradley C. Livezy from the University of Kansas has now done his best to put the dodo on the sober basis any species deserves to be with a study labelled "An ecomorphological review of the dodo (*R. cucullatus*) and the solitaire (*Pezophaps solitaria*), flightless Columbiformes of the Mascarene Islands" (*J. Zool., Lond.* **230**, 247–292; 1993). The enterprise has been a mammoth undertaking, involving the use of data from more than 400 skeletal relics of the dodo, mostly at the Mauritius Institute. But that is only part of the puzzle of the dodo, a magnificently overweight pigeon.

Several questions arise. What, for a bird, are the benefits of not being able to fly? How did the dodo and the solitaire, distinct though they are, arise apparently independently on two islands that must be counted close neighbours by the yardstick of the Indian Ocean, but which are nevertheless nearly 600 km apart and thus too far for a flightless bird to make the passage? And why was the dodo such an ungainly creature?

In passing, Livezy inevitably provides his readers with a compelling comparison of the literary styles of the old and modern zoologists. Here, for example, is the description of the dodo due to H. E. Strickland and A. G. Melville in 1848:

These birds were of large size and grotesque proportions, the wings too short and feeble for flight, the plumage loose and decomposed, and the general aspect suggestive of gigantic immaturity.... So rapid and complete was their extinction that the vague descriptions given of them by early navigators were long regarded as fabulous or exaggerated, and these birds, almost contemporary of our great-grandfathers, became associated in the minds of many persons with the Griffin and Phoenix of mythological antiquity. The aim of the present work is to vindicate the honesty of the rude travellers of the 17th century....

Livezy first compares the two flightless birds with each other and with other

Columbidae. Of the two, the solitaire was the heavier bird — the average weight of males is estimated at between 20.9 and 27.8 kg, compared with 15.9 and 21.2 kg for the dodo. One striking feature of both species is the exaggerated sexual dimorphism; females were only two-thirds as heavy as males, and had much shorter bills.

It is clear from the comparisons of dodo and solitaire with other species that both are at the end of a spectrum. Altogether, representatives of 38 genera of Columbidae are used to show, for example, that while the wing-loading (in flight) of the other birds increased with overall mass, that based on the assumption that either the dodo or the solitaire could lift itself off the ground by flapping its undersized wings would be entirely off the regression line that accommodates the others. Dodos and solitaires were, perforce, perpetually grounded. They were too heavy to fly.

Interestingly, though, it seems that the adaptation of the bones of the legs and the pelvic girdle to a life on land is not nearly as great as that found in other flightless birds. To be sure, the femur is strong enough to support the whole weight of the bird, but it appears not to have been shortened in adaptation to the extent found elsewhere. The most marked differences are in the upper limbs, which are both lighter and shorter than in related birds, which is consonant with the absence of flight.

Livezy guesses at the lifestyle of the dodo on general physiological grounds. The physiology is simple allometry — the greater an animal's mass, the less will be its metabolic rate, and so on. But in the tropics, the dodo would have had to depend on seasonal fruits and other herbage accessible from the ground. So, the argument goes, each bird would have had to grow fat when food was plentiful to survive the privations of the thin season. That accords with accounts from the seventeenth century of the cycles of fattening and slimming in the dodo.

There are also contemporary accounts of the territorial behaviour of the bird. (Allometry has it that the bigger the bird, the bigger its territory and the more fiercely it is defended.) One early visitor to Mauritius described how dodos would defend their nests (made of a pyramid of palm leaves 18 inches high) to a range of 200 yards or so. Reproduction involved the laying of a single egg in the nest, which was incubated by each parent in turn. The young were slow to mature. The lifespan may have been as much as 30 years.

So how did two such similar species arrive at two islands in the same corner of a huge ocean? Livezy rejects the obvious notion that they belong to the same branch of a cladogram for the pigeon family that has not yet been constructed. It is not simply that there is no reasonable way of supposing that a pair of flightless birds would have made the 600 km crossing between the two islands, but also that the anatomical differences between them are no more impressive than their similarities with the Columbidae. And why not, anyway, allow that, if some small ancestral population of a species of the pigeon family can colonize an island and then abandon the capacity to fly for the evolutionary benefits of flightlessness, it might have happened a second time, or several times?

That is the fashionable way of thinking, but is not for that reason incorrect. In an island free from predators (as pristine Mauritius would have been), members of a primitive flighted population may have been able to survive even the disadvantage of being less strong flyers than their fellows, and may over the generations have followed the path of adaptation leading to the dodo in one case and the solitaire in the other. It may be too late to search the other islands of the Indian Ocean for surviving analogues of the dodo, but flightless birds are by no means uncommon — there are flightless rails in the Western Indian Ocean, for example.

Livezy's more intriguing evolutionary speculation picks up the phrase "gigantic immaturity" used by Strickland and Melville in their unavoidably second-hand account of the dodo. What did they mean by that? The untidy layout of a dodo's feathers, and its outer covering of down, for one thing. Elsewhere there is a description of a dodo as a "young duck or gosling enlarged to the dimensions of a swan", suggesting juvenility.

So was the dodo a consequence of paedomorphosis, the supposed phenomenon in which the development schedule of an organism is reorganized in such a way that it becomes sexually mature, and further development is halted, when some parts of its body have reached only an intermediate stage? That is all the more likely to happen when, from one generation to the next, the size of the individual members of a species is increasing. Livezy says of this as of many other questions about the dodo that perhaps we shall never know, but that may be too despondent; it is remarkable how much he has wrung from a few hundred bones.

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