

Research



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Palaeontology

Eggs of extinct dwarf island emu retained large size

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Islands off southern Australia once harboured three subspecies of the mainland emu (*Dromaius novaehollandiae*), the smaller Tasmanian emu (*D. n. diemenensis*) and two dwarf emus, King Island emu (*D. n. minor*) and Kangaroo Island emu (*D. n. baudinianus*), which all became extinct rapidly after discovery by European settlers. Little was recorded about their life histories and only a few historical museum specimens exist, including a number of complete eggs from Tasmania and a unique egg from Kangaroo Island. Here, we present a detailed analysis of eggs of dwarf emu, including the first record of an almost complete specimen from King Island. Our results show that despite the reduction in size of all island emus, especially the King Island emu that averaged 44% smaller than mainland birds, the egg remained similar sized in linear measurements, but less in volume and mass, and seemingly had a slightly thinner eggshell. We provide possible reasons why these phenomena occurred.

1. Introduction

Two dwarf and a smaller subspecies of the mainland emu (*Dromaius novaehollandiae*) once occurred on islands off southern Australia (figure 1). Relative to the mainland form, with nomenclature following [4], the King Island emu (*D. n. minor*), extinct by 1822, was around 44–45% smaller in size (physical height and body mass). The Kangaroo Island emu (*D. n. baudinianus*), extinct ca 1830, was approximately 25% smaller than mainland emu and Tasmanian emu (*D. n. diemenensis*), extinct ca 1850, was approximately 10% smaller [5–9] (table 1). All were victims of over-hunting by European colonists [9]. Island emus became isolated from the mainland in comparatively recent times after the separation of Tasmania around 14 kya, King Island at 11 kya and Kangaroo Island at 10 kya [12], but the Kangaroo Island emu, or a related population on nearby parts of the mainland, may have been isolated for much longer [1]. Dwarfism appears to have evolved rapidly [2,7], with a direct correlation between the extent of dwarfing and island size [7]: King Island, with an area of 1100 km², had the smallest species, followed by Kangaroo Island (4400 km²) and Tasmania (62 400 km²), respectively. Such was the rapidity of their extinction that the life histories of dwarf emus are virtually unknown; however, François Péron in 1804 provided details of the King Island emu, based on his questioning of a resident sealer, Daniel Cowper [3,13]. Cowper was evidently a careful observer, but not a trained naturalist, so interpretation of these details must be approached with caution. Cowper stated among other things that males were slightly larger than females, weighing 45–50 lb (20.4–22.6 kg), both shared incubation, and the clutch size ranged from 7 to 9. The life history of Kangaroo Island emu is unknown, whereas Tasmanian emu had a clutch size of 8–9 and shared incubation [9,14]. The eggs when fresh of both Tasmanian and Kangaroo Island emu were also finer grained and darker green in colour than those of mainland birds [10,14]. Mainland emu clutch size averages 6.7 per female, but one nest can contain the eggs of several females [15,16].

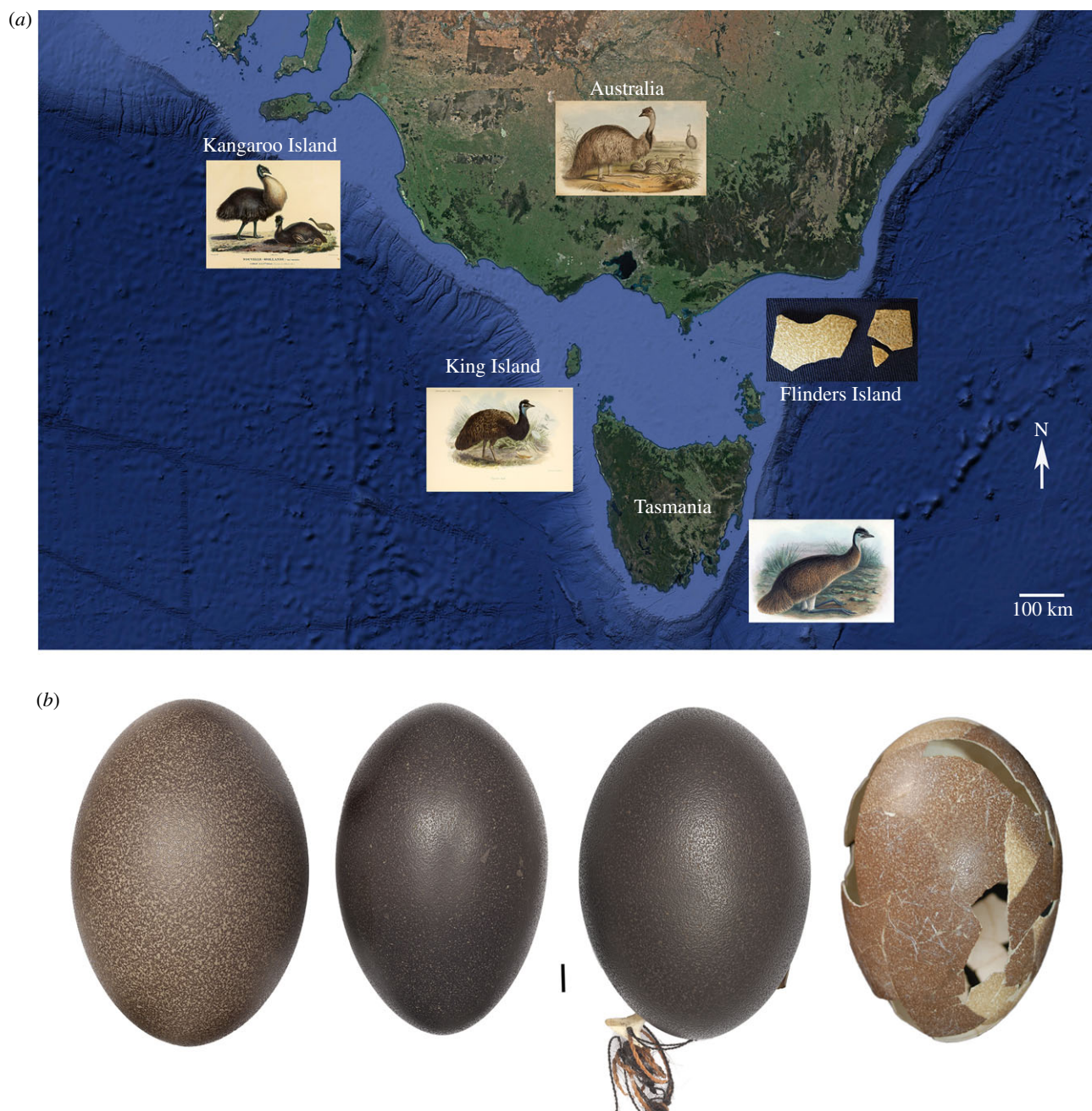


Figure 1. (a) The distribution of emus discussed in the text. Mainland emu (*Dromaius novaehollandiae novaehollandiae*); Tasmanian emu (*D. n. diemenensis*); King Island emu (*Dromaius n. minor*); Kangaroo Island emu (*Dromaius n. baudinianus*). Mainland emu illustration from [1], the remainder [2]. Flinders Island emu eggshell is referable to a Late Pleistocene deposit of mainland emu [3]; (b) comparison of eggs of the mainland and dwarf emus. From left to right: mainland emu (NHMUK 1941.9.4.2724); Tasmanian emu (NHMUK 1960.6.13); Kangaroo Island emu (NHMUK 1938.6.1.1); King Island emu (Christian Robertson/King Island Museum). Scale bar, 10 mm, taken at the base of egg.

Eggshell fragments collected in 1917 on Flinders Island, and thought to represent a new taxon [17], are referable to a Late Pleistocene deposit of mainland emu [18].

To test body size reduction in relation to egg size in each of the island emu taxa, in particular the extreme dwarfism in *D. n. minor*, we obtained measurements of femora to calculate body mass. We used measurements of museum and subfossil intact eggs and subfossil eggshell to ascertain egg size and volume and compared them with eggs of mainland emu.

2. Material and methods

(a) Samples

We used 38 eggs of mainland emu in our analysis, six intact eggs of *D. n. diemenensis*, a unique egg of *D. n. baudinianus* collected

ca 1834 [14], plus a unique egg of *D. n. minor* discovered by one of us [CR] in a sand dune deposit. Modern and dune deposit subfossil eggshell of *D. n. novaehollandiae*, dune subfossil eggshell deposits collected on King Island, and Kangaroo Island subfossil eggshell were also analysed, with all specimens listed in the electronic supplementary material, tables S1 and S2.

(b) Measurements

For estimated body masses of extinct taxa, we used the account of Cowper and dimensions of mainland emu, femora measurements of all dwarf emus from our data and from [7], and calculations following [11,19,20] (see electronic supplementary material, table S3). For intact eggs, all measurements were taken using dial calipers and rounded to the nearest 0.1 mm, with measurements using a micrometer rounded to the nearest 0.1 mm for eggshell thickness. The total length of complete

Table 1. Summary statistics for measurements of intact emu eggs. Data for adult body mass of extinct taxa are from electronic supplementary material, table S3, with means derived from mass estimates based on femur length and shaft width. Abbreviations: *n*—number; *L*—length; *W*—width; *V*—volume; *R*—range; *AV*—average; *s.d.*—standard deviation.

species	location	<i>n</i>	intact egg <i>L</i> mean (mm)		intact egg <i>W</i> mean (mm) ± s.d. [<i>R</i>]		<i>n</i>	intact egg <i>V</i> mean (ml) ± s.d. [<i>R</i>]		mean taxon <i>L, W, V</i> as a % of <i>D. n. novaehollandiae</i>		adult body mass (kg)	egg mass (g)
			± s.d. [<i>R</i>]	± s.d. [<i>R</i>]	± s.d. [<i>R</i>]	± s.d. [<i>R</i>]		<i>L, W, V</i> as a % of <i>D. n. novaehollandiae</i>	<i>D. n. novaehollandiae</i>				
<i>D. n. novaehollandiae</i>	Mainland	36	127.9 ± 5.22 [119.7–137.2]	88.8 ± 3.16 [80.8–95.1]	8	539 ± 0.45 [487–634]	100, 100, 100	♂ 32, ♀ 37 (from [10])	AV 595 (from [11])	approximately 568 (this paper)			
<i>D. n. diemenensis</i>	Tasmania	6	126.8 ± 5.07 [120.3–133.2]	85.0 ± 3.40 [81.7–90.5]	6	475 ± 0.56 [415–565]	99.1, 95.7, 88.1	30.3–34.2 (electronic supplementary material, table S3)	approximately 547 (from [11]; supplementary material, table S3)				
<i>D. n. baudinianus</i>	Kangaroo Island	1	126.9	88.8	1	506	99.2, 100, 93.8	23.8–27.4 (electronic supplementary material, table S3)	approximately 597 (this paper)				
<i>D. n. minor</i>	King Island	1	125.0	80.0	1	465	97.7, 90.0, 86.2	♂ 21.5 ♀ 22.6 ^a (Cowper in [12]) 20.2–23.3 (electronic supplementary material, table S3)	approximately 547 (from [11]; this paper)				

^aThis is in opposition to Cowper's statement that males were larger than females (this paper).

eggs was taken along the long axis and the width was measured along the short axis at the widest medial point. Calculation of emu egg volume from museum eggs, including extinct taxa, used the methodology described in [21], and egg mass data were presented as a percentage of mean body mass. Eggshell thickness was measured in the blowhole region of intact eggs, as described in [22], and recent museum and subfossil eggshell fragments were measured away from eroded or broken edges.

3. Results and discussion

Male mainland emus are smaller than females, with body masses averaging 32 kg and 37 kg for each sex, respectively [11]. Cowper's weight for King Island emu (20.4–22.6 kg) is within or slightly less than our data (20.2–23.3 kg) (table 1); therefore, body masses of mainland (32–37 kg) and King Island emu (20.2–23.3 kg) show a difference of 44.2% or 45.4% (table 1). Tasmanian and Kangaroo Island emus' body masses lie between these two measurements, with Kangaroo Island emu estimated at 23.8–27.4 kg and Tasmanian emu at 30.3–34.2 kg (table 1). Observations of living birds and other skeletal element measurements confirm this decreasing size trend from mainland emu, the largest, through to King Island emu [5,7], the smallest of all emu taxa.

We refute Cowper's statement that King Island emu males were reputedly slightly larger than females and suggest that the heaviest birds weighing 50 pounds (22.6 kg) [13] were female. Cowper most likely mistook brooding birds to be female, as in all other ratites except ostrich, males incubate the eggs and females are larger [11,15]. Mainland emus have an average recorded egg mass of 595 g [11,15,23], which accounts for 1.6% of its body mass. With a body mass of 23.3 kg for females, and the egg mass around 8% less than mainland emu eggs (table 1), a King Island emu egg of approximately 547 g would represent 2.3% of the body mass, yet the bird was around 44% lighter than the female mainland emu. Relative to length, width and volume percentages of mainland birds, eggs of dwarf emus are slightly shorter in greatest length in each taxon (97.7–99.2%), are narrower in greatest width in King Island and Tasmanian emus (90.0–95.7%) and have a more reduced volume in each taxon (86.2–93.8%) (table 1). However, the mean values for the egg measurements of each island emu fall within the size ranges of mainland emu, excepting only that the egg of the King Island bird is slightly narrower (80.0 mm) and has a smaller volume (465 ml) than the smallest mainland emu egg (80.8; 487) at 4.6% difference (table 1). *T*-test analysis showed a significant difference in volume only between mainland and Tasmanian emu egg size, with a *p*-value below 0.05 (electronic supplementary material, tables S4, S5 and S6), which supports our results. The eggshell thickness of the historically collected Kangaroo Island and Tasmanian museum eggs is thinner (6.8%/4.8%) than mainland emu, with subfossil eggshell of King and Kangaroo Island birds thinner still (table 2).

Our data thus demonstrate that the eggs of the island emus, despite the smaller dimensions of adults, were within or close to the linear size, and smallest volume and mass ranges of mainland birds (figure 2), and the eggshell was seemingly slightly thinner (table 2), but see below. What is less clear are the reasons why these phenomena occurred.

Emus, along with other ratites, have precocial young (juveniles that are relatively mature and mobile at the point

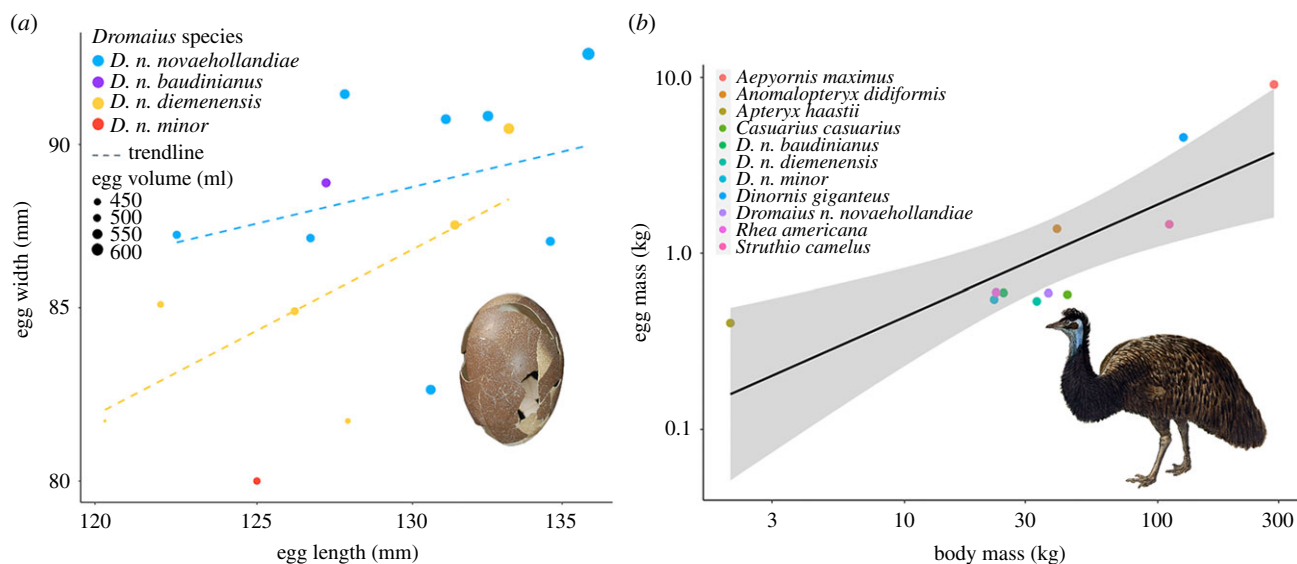


Figure 2. (a) Multiple linear regression analysis of dwarf emu egg size compared with mainland emu. Note that the egg of Kangaroo Island emu nestles within the mainland emu egg size, whereas Tasmanian emu averages smaller, and King Island emu is the smallest of all, both in length, width and volume. However, in egg length and width in the two different groups, neither was significant, with p -values higher than 0.05. These findings support our hypothesis that dwarf emu eggs did not differ significantly in linear size from mainland birds. (b) Correlation between body mass and egg mass among selected extinct and extant Palaeognathae. The regression line (Adj $R^2 = 0.60403$, intercept = 1.5456, slope = 1.0082 $p = 0.0029655$) is based on \log_{10} -transformed data. Grey zone represents s.d. Interestingly, dwarf emus cluster with South American Rhea (*Rhea americana*), whereas mainland and Tasmanian emu are closer to Cassowary (*Casuarus casuarus*). Kiwi (*Apteryx haastii*) is an outlier, which is reflected in adaptations to its extreme k -selected life history, whereas King and Kangaroo island emus are close to South American Rhea, which have a similar mass in both adult bird and egg.

Table 2. Summary statistics for thickness measurements of fragmentary emu eggs. Abbreviations: n —number; T —thickness; R —range; s.d.—standard deviation.

species	n	subfossil eggshell		non-fossil eggshell	
		T mean (mm) \pm s.d. [R]	n	T mean (mm) \pm s.d. [R]	
<i>D. n. novaehollandiae</i>	4	1.02 \pm 0.05 [1.0–1.1]	20	1.06 \pm 0.04 [1.0–1.1]	
<i>D. n. diemenensis</i>			2	1.01 \pm 0.007 [1.0–1.01]	
<i>D. n. baudinianus</i>	18	0.85 \pm 0.05 [0.80–0.96]	1	0.99	
<i>D. n. minor</i>	95	0.85 \pm 0.04 [0.80–0.99]	1	0.98 \pm 0.01 [0.97–0.99] ^a	
Flinders Island <i>D. n. novaehollandiae</i>	3	1.07 \pm 0.04 [1.07–1.11]	—	—	

^aBecause this egg was found *in situ* and unweathered, for clarity, it is included under non-fossil egg.

of hatching) [11]. Péron was informed by Cowper that all King Island emus synchronized laying to 2 days of the year, on July 25th–26th, clutch size was large, and that chicks left the nest within 3 days of hatching [13]. Although Cowper's egg-laying observation appears to be an exaggeration, mainland emu egg clutches, although laid sequentially, tend to hatch within two days of each other [23], which probably accounts for the confusion. Mainland emus also lay during the coolest time of the year, generally in July, and chicks leave the nest after 2–3 days of hatching [23–25]. Furthermore, in mainland emus, where body size is large relative to egg size, a single adult can incubate up to 15 eggs [15]. Thus, multiple laying by a number of females into one nest allows accumulation of a large clutch in a short period, as a single female emu can only lay one egg every 2 days [26]. This synchronized laying prevents embryo death from over-heating and exposure, and simultaneous hatching increases survival by dilution effects against predators [24].

Mainland emu eggs hatch after 56 days [10,15], so if the same duration applied to King Island emus, particular environmental conditions or food resources abundant at the

time of hatching may have caused synchronized breeding. July has the coolest annual temperature and highest rainfall on King Island [27], but the 56-day period of incubation would see chicks hatch at the start of spring in September. Because dwarfing of island emus occurred within at least the last 14 000 YBP [12], it appears that the evolutionary advantage for retaining a large egg size and precocial chick was primarily driven by limited food resources on their respective island homes. The chicks had to be sufficiently large after hatching to be able to consume the food that was seasonally available independently, and perhaps to develop adequate thermoregulation to enable them to cope with cool external temperatures, as in kiwi *Apteryx* sp. and mainland emu (see [28]). Although some aspects of ratite life history are r -selected, e.g. large clutch size, retention of large-sized eggs in dwarf emus appears to have been an evolutionary step towards an extreme k -selected life history, e.g. smaller clutch size, large egg, appearing to mirror that of the kiwi. However, the correlation between body mass and egg mass shows kiwi as a distant outlier (see also [29]) (figure 2b); therefore, kiwi egg size is a result of its atypical

life history and environmental pressures [11]. Emu hatchlings also have heavier and more residual yolk than many other avian species [30,31], and in studies of other precocial species, an increase in residual yolk correlated with increased egg size, resulting in increased hatchling survival under limited food resource conditions (see [24] and references therein). In Greater Rhea (*Rhea americana*), reduction in egg size may negatively affect embryo development and post-fledgling survival [24].

If predation was also a driving force for precocial adaptation on the southern islands, Tasmania had two large predators, Thylacine (*Thylacinus cyanocephalus*) and Tasmanian Devil (*Sarcophilus harrisii*), while thylacine formerly occurred on Kangaroo Island [7]. King Island reputedly lacked a large, terrestrial carnivore [7,32], but an extremely robust, but now extirpated Tiger Quoll (*Dasyurus m. maculatus*) was once resident, and formerly considered specifically distinct due to its large size [33]. It was certainly capable of taking emu chicks, as they prey on vertebrates many times larger than themselves [34].

Our data indicate that island emus had thinner eggshells than mainland birds, but this can occur intra-specifically due to a number of factors, including environmental conditions and calcium availability for eggshell development [35–37]. In addition, smaller eggs have thinner eggshells [38], so a 14% decrease in egg volume (table 1) is likely to result in a similar level of decrease in shell thickness. *T*-test analysis also showed no significant differences (electronic supplementary material, tables S7).

As small island size is clearly selecting for smaller dwarf emu adults, thus egg, and consequently chick size, presumably decline proportionately much less. However, this depends on dwarf emus producing a similar clutch size, as there is no certainty of how many eggs individuals of the different taxa actually laid themselves. If the clutch size remained large and was not the product of more than one female, this suggests that dwarf emus, relative to body weight, must have devoted a proportionately higher amount of energy to reproduction than mainland birds.

Compared with extant ratites, King island emu is morphometrically similar to rhea *Rhea* sp. (figure 2*b*), with an analogous breeding strategy. Rhea females lay an average of 20–30 eggs in one nest, incubated solely by a male, and piping stimuli from other eggs results in synchronized hatching [39]. In response to high predation, hatching of the entire clutch can occur in 24–28 h and chicks leave the nest within 2 days [40,41]. Female greater rhea have a body mass of

25 kg (King Island emu 23.3 kg) and an egg mass of approximately 618 g (approx. 547 g in King Island emu) [42], which equates to 2.4% of body mass (2.3% in King Island emu); thus, proportionally, the rhea averages a larger egg. However, egg size variation can be related to clutch size, seasonality and female body mass, and age at the time of laying [42,43]. Tasmanian emu is more similar to Cassowary (*Casuarus casuarius*) in morphometrics (figure 2*b*), but cassowary breeding strategy is not comparable [15].

Our study has shown that dwarf emus had a comparable breeding strategy to mainland emu that included a large clutch size, synchronized hatching of young to counter predator effects and thermos-regulation in hatchlings to provide warmth [10,21,23]. It was only on the southern Australian islands that limited resources resulted in rapid dwarfing and retention of a large egg. This scenario provides an interesting evolutionary response to island size, insular population and morphological plasticity in dwarf emus and warrants further study. However, due to their complete and rapid extinction, the true extent of these adaptations to a rapidly changing environment brought on by fluctuating sea levels is now impossible to determine.

Ethics. All research material was either fossil or from museum collections.

Data accessibility. Specimens used in this study are available at the palaeontological collections of TMAG, QVMAG and SAM, Australia and NHMUK, UK. The datasets supporting this article have been uploaded as part of the electronic supplementary material [44].

Authors' contributions. Conceptualization of the paper was by J.P.H. and C.R.; data curation and formal analysis were equally completed by J.P.H. and C.R.; funding acquisition was by J.P.H.; investigation and methodology by J.P.H. and C.R.; project administration by J.P.H.; resources by J.P.H. and C.R.; software by J.P.H.; supervision, where necessary, by J.P.H.; validation and visualization by J.P.H. and C.R.; writing—original draft by J.P.H.; writing—review and editing by J.P.H. and C.R. In addition, both authors gave final approval for publication and agree to be held accountable for the content therein.

Competing interests. The authors have no competing interests.

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