Repeated evolution of flightlessness in *Dryolimnas* rails (Aves: Rallidae) after extinction and recolonization on Aldabra

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The Aldabra Rail *Dryolimnas cuvieri aldabranus* (Günther, 1879), endemic to Aldabra Atoll, Seychelles, is the last surviving flightless bird in the Indian Ocean. Aldabra has undergone at least one major, total inundation event during an Upper Pleistocene (Tarantian age) sea level high-stand, resulting in the loss of all terrestrial fauna. A flightless *Dryolimnas* has been identified from two temporally-separated Aldabran fossil localities, deposited before and after the inundation event, providing irrefutable evidence that a member of Rallidae colonised the atoll, most likely from Madagascar, and became flightless independently on each occasion. Fossil evidence presented here is unique for Rallidae, and epitomises the ability of birds from this clade to successfully colonise isolated islands and evolve flightlessness on multiple occasions.

ADDITIONAL KEYWORDS: Aldabra Atoll – fossil – flightless – extinction – sea level rise – recolonisation

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INTRODUCTION

The White-throated Rail *Dryolimnas cuvieri* (Pucheran, 1845) is indigenous to islands in the southwestern Indian Ocean and occurs widely throughout the region (Fig. 1) where it is known from three subspecies. Volant *D. c. cuvieri* is found today on Madagascar and Mayotte, Comoros (Safford & Hawkins, 2013), with a totally flightless derivative on Aldabra, *D. c. aldabranus*, the last surviving flightless rail in the Indian Ocean (Stoddart & Wright, 1967), and a poorly-volant/flightless subspecies, *D. c. abbotti* (Ridgway, 1894) formerly on Assumption (Nicoll 1908), which became extinct between 1907 and 1937 (Safford & Hawkins, 2013; Hume, 2017). Possibly distinct, but now extinct, rail populations reputedly occurred on Ile aux Cèdres (Aldabra), Cosmoledo Atoll and Astove Island (Collar, 1993) (Figs. 1, 2), but no specimens were collected to confirm their status. A distinct *Dryolimnas* population on the tiny islet of Ile aux Cèdres within the Aldabra lagoon appears unlikely however. In addition, two *Dryolimnas* species once inhabited the Mascarenes; the large, flightless Réunion Rail *D. augusti* Mourer-Chauviré *et al*., 1999, which survived until at least the end of the 17th century (Mourer-Chauviré *et al*., 1999), and a probably flightless, undescribed *Dryolimnas* from Mauritius that was last recorded in 1638 (Hume, 2017).

The discovery of fossil remains of a flightless *Dryolimnas* (two humeri) at Bassin Cabri on Ile Picard confirms the bird's presence on Aldabra during the Middle Pleistocene (Chibanian age) to Upper Pleistocene (Tarantian age) (Hume *et al*., 2018) (Fig. 2). The absolute maximum age of Aldabra Atoll is unknown, but inferences made from sea level high stands dating back 400,000 years before present (YBP) show that the Aldabra platform was subject to at least one total inundation event around 340,000 YBP, with possibly two others at 240,000 and 200,000 YBP respectively (Braithwaite, 1984; Braithwaite *et al*., 1973) (Fig. 3). An undated limestone depositional sequence (Picard Calcarenites) exposed on present-day Ile Picard must be in excess of 136,000 years before present (YBP), as the younger, overlying and island-wide Aldabra Limestone has been dated from Ile Picard deposits between 136,000 (Middle Pleistocene) and 118,000 (Upper Pleistocene) YBP ± 9,000 (~127,000+) (Braithwaite *et al*., 1973; Thomson & Walton, 1972) (Fig. 3), which represents the most recent complete inundation event. The Bassin Cabri cavity-fill fossil material accumulated during this period (see Braithwaite *et al*., 1973 for a detailed depositional history). After the deposition of the Aldabra Limestone, and with falling sea levels, terrestrial soils were created, and a reptile-rich fossil deposit formed at Point Hodoul (inferred date ~100,000 YBP (Taylor

et al., 1979)), which included a distal tarsometatarsus of a *Dryolimnas* rail (Harrison & Walker, 1978).

MATERIALS AND METHODS

SPECIMENS

Two humeri held at the Smithsonian Institution National Museum of Natural History (USNM) and a distal tarsometatarsus held at the Natural History Museum, London (NHMUK) of Pleistocene *Dryolimnas cuvieri* were compared with modern specimens held at the Natural History Museum, Tring (NHMUK) of *D. c. cuvieri*, *D. c. aldabranus* and a unique skeleton of the extinct, *D. c. abbotti* (Supporting Information, Tables S1-S2).

MORPHOMETRIC ANALYSIS

Measurements were taken using a dial caliper and rounded to the nearest 0.1mm. Only humeri and distal tarsometatarsi were available, so measurements of total length, proximal width, proximal depth, shaft width, shaft depth, distal width and distal depth of humerus (Table 1; Supporting Information, Table S1), and distal width, distal depth and greatest depths taken proximal to trochlea. metatarsi II were used for tarsometatarsus (Table 2; Supporting Information, Table S2). Anatomical terminology follows Baumal & Witmer (1993).

RESULTS

MORPHOLOGY

The rail humeri from Bassin Cabri are almost undifferentiated from modern *D. c. aldabranus*, other than being more robust proximally, with the *crista bicipitalis* more expanded, the shaft more robust and straighter, and the *epicondylus dorsalis* less pronounced; like *D. c. aldabranus*, it also differs considerably in size from *D. c. cuvieri* and *D. c. abbotti* (Fig. 4; Table 1). In the few morphometrics available from the tarsometatarsus, the Point Hodoul specimen shows a very similar morphology to *D. c. aldabranus* and *D. c. abbotti* compared with nominate, with the *foramen vasculare distale* more deeply excavated and situated further distad, the *incisura intertrochlearis* more open, and *trochlea. metatarsi II* larger and directed further mediad (Fig. 5; Table 2); characters indicative of flightlessness (Olson, 1977). The more robust distal end of the tarsometatarsus in the Pleistocene specimen, together with the depth of the shaft proximal to the trochlea also greater than in nominate, suggests that *Dryolimnas* had become more terrestrial and flightless.

DISCUSSION

The complete inundation of Aldabra Atoll during deposition of the Aldabra Limestone resulted in the extinction of the endemic Aldabra Petrel *Pterodroma kurodai* Harrison & Walker, 1978, Aldabra Duck *Aldabranus cabri* Harrison & Walker, 1978 and loss of other bird taxa, as well as the flightless *Dryolimnas* rail (Taylor *et al*., 1979; Harrison & Walker, 1978). A number of reptiles also disappeared, including an endemic horned crocodile *Aldabrachampsus dilophus* Brochu, 2006, the giant tortoise *Aldabrachelys* cf. *gigantea* Loveridge & Williams, 1957, an *Oplurus* iguana and terrestrial skinks (Arnold, 1979). At the younger Point Hodoul fossil deposit, the occurrence of giant tortoise, iguana, skinks and *Dryolimnas* show that the atoll was seemingly rapidly recolonised on re-emergence, at least from 100,000 YBP (Taylor *et al*., 1979).

The presence of *Dryolimnas* at both deposits requires explanation. The Bassin Cabri humeri indicate the rail was already flightless at ~127,000+ YBP during the Middle Pleistocene; therefore it must have disappeared along with the other terrestrial fauna when the atoll was completely submerged (Thomson & Walton, 1972; Taylor *et al*., 1979). Furthermore, characters of the tarsometatarsus in the Pleistocene specimen suggest that it had evolved a degree of flightlessness at least comparable with *D. c. abbotti* (Harrison & Walker, 1978), being shorter and more robust than nominate and *D. c. aldabranus* (Fig. 5). This, and its presence on Aldabra today, provides irrefutable evidence that *Dryolimnas* subsequently recolonised Aldabra after inundation and became flightless for a second time. This scenario may seem surprising, but rails are known to be persistent colonisers of isolated islands and can evolve towards flightlessness rapidly if suitable conditions exist (Olson, 1977). Therefore, it is likely that the dispersal of nominate *Dryolimnas* from Madagascar to remote Aldabra occurred on multiple occasions, as did giant tortoises (Taylor *et al*., 1979). The Point Hodoul fossil record shows that giant tortoise, iguana and a number of lizard taxa, as well as *Dryolimnas*, successfully recolonised the atoll (Hume *et al*. 2018); however, the iguana and most other lizards subsequently perished. Based on the geological record (Braithwaite *et al*., 1973), this extinction event appears to be unrelated to inundation, and may have been the result of introduced black rats *Rattus rattus* (Linneaus, 1758), which were present on Aldabra in 1890 (Cheke 2010) but no doubt arrived much earlier.

Only relatively few taxa from the Middle to Upper Pleistocene fossil deposits on Aldabra survived into the Holocene, and of those the most notable, apart from breeding sea birds, are adept open-water travellers, including giant tortoise (by floating) (Gerlach *et al*., 2006), and

Dryolimnas rails (periodic, long-distance flight dispersal) (Wanless & Hockey, 2008). Evidence of multiple avian colonisation events with recurring flightlessness are extremely rare in the fossil record (e.g. Olson & James, 1991; Fulton *et al*., 2012), especially on smaller oceanic islands where long-term preservation of fossiliferous material is generally poor. We know of no other example in Rallidae, or of birds in general, that demonstrates this phenomenon so evidently. Only on Aldabra, which has the oldest palaeontological record of any oceanic island within the Indian Ocean region (Thomson & Walton, 1972), is fossil evidence available that demonstrates the effects of changing sea levels on extinction and recolonisation events. Conditions were such on Aldabra, the most important being the absence of terrestrial predators and competing mammals, that a *Dryolimnas* rail was able to evolve flightlessness independently on each occasion.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article at the publisher's web-site:

Table S1. Summary statistics for measurements (mm) of the humerus of *Dryolimnas*.

Table S2. Summary statistics for measurements (mm) of the tarsometatarsus of *Dryolimnas*.

Table S3. Raw measurements (mm) of the humerus of *Dryolimnas*.

Table S4. Raw measurements (mm) of the tarsometatarsus of *Dryolimnas*.

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REFERENCES

Arnold EN. 1979. Fossil reptiles from Aldabra Atoll, Indian Ocean. *Bulletin of the British Museum (Natural History), Zoology* **29**: 85–116.

Baumel JJ, Witmer LM. 1993. Osteologia. In: Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC, eds. *Handbook of avian anatomy: nomina anatomica avium*, 2nd ed. Cambridge, Massachusetts, USA: Publications of the Nuttall Ornithological Club, 45–132.

Braithwaite CJR. 1984. Geology of the Seychelles. In: Stoddart DR, ed. *Biogeography and ecology of the Seychelles Islands.* The Hague, Netherlands: Dr W. Junk Publishers, 17–38.

Braithwaite CJR, Taylor JD, Kennedy WJ. 1973. The evolution of an atoll: the depositional and erosional history of Aldabra. *Philosophical Transactions of the Royal Society of London B.* **266**: 307–340.

Brochu CA. 2006. A new miniature horned crocodile from the Quaternary of Aldabra Atoll, western Indian Ocean. *Copeia* 2: 149–158.

Cheke A. 2010. The timing of arrival of humans and their commensal animals on Western Indian Ocean oceanic islands. *Phelsuma* **18**: 38–69.

Collar NJ. 1993. The conservation status in 1982 of the Aldabran White-throated Rail *Dryolimnas cuvieri aldabranus*. *Bird Conservation International* **3**: 299–305.

Fulton TL, Letts B, Shapiro B. 2012. Multiple losses of flight and recent speciation in steamer ducks. *Proceedings of the Royal Society B, Biological Sciences* **279**: 2339–2346.

Gerlach J, Muir C, Richmond MD. 2006. The first substantiated case of trans-oceanic tortoise dispersal. *Journal of Natural History* **40**: 2403–2408.

Günther A. 1879. On the occurrence of a land-rail (*Rallus*) in the Island of Aldabra. *Annals and Magazine of Natural History* **3**: 164–168.

Harrison CJO, Walker CA. 1978. Pleistocene bird remains from Aldabra Atoll, Indian Ocean. *Journal of Natural History* **12**: 7–14.

Hume JP. 2013. A synopsis of the pre-human avifauna of the Mascarene Islands. In: Göhlich UB, Kroh A, eds. *Proceedings of the 8th International Evolution.* Vienna: Natural History Museum, 195–237.

Hume JP. 2017. *Extinct birds*, 2nd ed. London, UK: Christopher Helm.

Hume JP, Martill D, Hing R. 2018. A palaeontological review of Aldabra Atoll, Aldabra Group, Seychelles. *PlosOne* https://doi.org/10.1371/journal.pone.0192675

Perry CA, Hsu KJ. 2000. Geophysical, archaeological, and historical evidence support a solar-output model for climate change. *PNAS* **97**: 12433–12438.

Loveridge A, Williams EE. 1957. Revision of the African tortoises and turtles of the Suborder Cryptodira. *Bulletin of the Museum of Comparative Zoology, Harvard* 115: 161–557.

Mourer-Chauviré C, Bour R, Ribes S, Moutou F. 1999. The avifauna of Réunion Island (Mascarene Islands) at the time of the arrival of the first Europeans. *Smithsonian Contributions to Paleobiology* **89**: 1–38.

Nicoll MJ. 1908. *Three voyages of a naturalist.* London: Witherby and Co.

Olson SL. 1977. A synopsis of the fossil Rallidae. In: Ripley SD, ed. *Rails of the world A monograph of the Family Rallidae* Boston, Massachusetts: David R. Godine, 338–378.

Olson SL, James HF. 1991. Descriptions of 32 new species of birds from the Hawaiian Islands: Part 1, non-Passeriformes. *Ornithological Monographs* **45**: 1–88.

Pucheran MLD. 1845. Notes sur quelques espèces Madécasses de l'ordre des Échassiers. *Revue Zoologique par La Société Cuvierienne* (1845): 277-280.

Ridgway R. 1894. Descriptions of some new birds from Aldabra, Assumption, and Gloriosa Islands, collected by Dr. W. L. Abbott. *Proceedings of the United States National Museum* **17**: 371–373.

Safford R, Hawkins F. 2013. *Birds of Africa, vol. VIII: the Malagasy region*. London, UK: Christopher Helm.

Stoddart DR, Wright CA. 1967. Geography and ecology of Aldabra Atoll. *Atoll Research Bulletin* **118**: 11–52.

Taylor JD, Braithwaite CJR, Peake JF, Arnold EN. 1979. Terrestrial faunas and habitats of Aldabra during the late Pleistocene. *Philosophical Transactions of the Royal Society of London B.* **286**: 47–66.

Thomson J, Walton A. 1972. Redetermination of Chronology of Aldabra Atoll by $^{230}Th/^{234}U$ Dating. *Nature* **240**: 145–146.

Wanless RM, Hockey PAR. 2008. Natural behaviour of the Aldabra Rail (*Dryolimnas* [*cuvieri*] *aldabranus*). *Wilson Journal of Ornithology* **120**: 50–61.

Supplementary data

Supplementary Table S1 – xlsx file. Details of specimens used in this study, with location data and collector where known.