



Fight club: a unique weapon in the wing of the solitaire, *Pezophaps solitaria* (Aves: Columbidae), an extinct flightless bird from Rodrigues, Mascarene Islands

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The solitaire (Columbidae; *Pezophaps solitaria*) of Rodrigues was an extinct giant flightless pigeon and the sister taxon to the dodo (Columbidae; *Raphus cucullatus*) from neighbouring Mauritius. The appearance and behaviour of the solitaire was recorded in detail by two observers before it became extinct in the mid 1700s. They described a prominent wing structure termed the ‘musket ball’ (carpal knob), which was used as a weapon and to produce an audible signal by either sex in territorial combat. Our study of subfossil solitaire bones from cave localities shows that the carpal knob formed after skeletal maturity, and reached its greatest size in adult males. We describe the morphology of the carpal knob, including its histology in thin section. It is an outgrowth of the processus extensorius of the carpometacarpus, but differs morphologically from homologous structures in other bird taxa, and thus is unique in Aves. We also compare the pectoral and wing osteology of the solitaire with that of the dodo, which had a similar morphology, but lacked any bony outgrowths on the wing. Furthermore, we suggest some biological and environmental factors leading to the evolution of this remarkable and unique carpal weapon. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, 110, 32–44.

ADDITIONAL KEYWORDS: bird behaviour – intraspecific combat – *Pezophaps solitaria* – *Raphus cucullatus* – sexual dimorphism – territory.

INTRODUCTION

Pigeons and doves (Columbidae) are a diverse, widespread family of small to medium-sized birds that occur in a wide variety of environments, and that have successfully colonized remote islands and island groups (Gibbs, Barnes & Cox, 2001). Flightlessness and gigantism has evolved in only a few extinct pigeon genera, most notably the dodo, *Raphus cucullatus* (Linnaeus, 1758), and the solitaire, *Pezophaps solitaria* (Gmelin, 1789), of the Mascarene Islands, south-western Indian Ocean,

and the Viti Levu giant pigeon, *Natunaornis gigoura* Worthy, 2001, from Viti Levu, Fiji, South Pacific (Worthy, 2001).

The solitaire (Fig. 1) was endemic to Rodrigues, the easternmost, smallest, and probably the oldest of the Mascarene Islands (Cheke & Hume, 2008) and was the sister taxon to the dodo of neighbouring Mauritius (Shapiro *et al.*, 2002), which lies 538 km to the west. Both species became extinct in the 17th and 18th centuries soon after the arrival of humans and their commensal animals (Cheke & Hume, 2008). The solitaire’s behaviour was described in some detail by an exiled Huguenot, Francois Leguat, in 1691–93 (Leguat, 1708), and further by a marooned mariner, Julien Tafforet, in 1725–26 (Tafforet, c.1726; see

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Figure 1. The only known image of the solitaire *P. solitaria* drawn from life (from Leguat, 1708).

Cheke & Hume, 2008). Both observers described the aggressive behaviour of the solitaire (see below), particularly when incubating and rearing young. Leguat (1708) noted that the birds were sexually dichromatic and subfossil remains confirm strong sexual dimorphism in size, with females estimated to have averaged 60% of the weight of a mature male (Livezey, 1993), which is the greatest sexual dimorphism reported for any neognathous bird (Fig. 2). In Columbidae, sexual dimorphism is generally limited, but when present, the male is usually larger (Goodwin, 1983; Gibbs *et al.*, 2001). However, there is no direct evidence to confirm which of the sexes in the solitaire or dodo was greater in size; the assumption that it was the male is based on inference from earlier work (e.g. Newton & Newton, 1869; Owen, 1878, 1879; Newton & Clark, 1879). It is likely that the male was the larger bird, but until further confirming evidence is obtained, e.g. molecular sexing tech-



Figure 2. A mounted pair of solitaires *P. solitaria* [female (RCSHM/Aves 707) left, male (RCSHM/Aves 706) right] exhibited at the Hunterian Museum of the Royal College of Surgeons (RCSHM), London. Note the extreme size sexual dimorphism. By kind permission of RCSHM.

niques, sex determination using skeletal material alone must remain problematic.

Leguat and Tafforet both described the presence of a bony growth on the wing of the solitaire that they termed a 'musket ball' or 'bullet' (carpal knob herein), which they both stated was used in defence. So extraordinary was Leguat's account that it was initially considered fictitious by some authorities (e.g. Atkinson, 1922). However, the discovery of solitaire bones in calcarenite caves in 1786, 1867, 1871 and 1874 (Newton & Newton, 1869; Günther & Newton, 1879), and the rediscovery of Tafforet's account in the 1870s, verified Leguat's observations (North-Coombes, 1991). Several 19th century authors described the osteology of the solitaire (Strickland, 1844; Strickland & Melville, 1848; Newton & Newton, 1869; Owen, 1878), and noted that the carpal knob was used as a weapon. A brief description of the histology of the carpal knob was made in the late 1860s (Gedge, in Newton & Newton, 1869: 343), in which the tissue was said to have a fibrous texture and stellate [osteocyte] lacunae, resembling old bone callus.

Carpal weapons such as the solitaire's carpal knob are not unknown elsewhere in Aves (see below). A few

Table 1. List of subfossil skeletal specimens, with registration number for each

Species	Skeletal element	Registration number(s)
<i>Pezophaps solitaria</i> (male)	Coracoid	FLMR 93 (R); FLMR 40 (R); FLMR 180 (R); FLMR 165 (R)
	Sternum	NHMUK PVA1373; NHMUK PVA3606
	Humerus	NHMUK PVA1441.2 (R); NHMUK PVA9041
	Radius	FLMR 165.1 (R); NHMUK PVA1382 (R); NHMUK PVA1382 (L); NHMUK PVA1441 (L); UMZC 640 (R)
	Ulna	NHMUK PVA1382 (R); NHMUK PVA9043 (R); NHMUK PVAu/r (Ld); NHMUK PVAu/r (R); NHMUK PVAu/r (L)
	Carpometacarpus	MNHN MADu/r (L); MNHN MADu/r (L); MNHN MADu/r (R); MNHN MADu/r (L); MNHN MADu/r (R); MNHN MADu/r (R); FLMR 180 (L); NHMUK PVA1387 (R); NHMUK PVA3505 (L); NHMUK PVA9044 (L); NHMUK PVA1388 (R); NHMUK PVA1388 (L); NHMUK PVA9047 (R); UMZC 636 (L);
<i>Pezophaps solitaria</i> (female)	Coracoid	NHMUK PVA1441.2 (L); NHMUK PVA9042 (L); UMZC 639 (R)
	Sternum	NHMUK PVA1377; NHMUK PVA3506; UMZC 635
	Humerus	NHMUK PVA1441 (R)
	Radius	NHMUK PVAu/r (R); NHMUK PVAu/r (R); NHMUK PVAu/r (L)
	Ulna	NHMUK PVA1441 (R); NHMUK PVA1441 (R); NHMUK PVA1441 (R); NHMUK PVA1441 (L); NHMUK PVA1441 (L); NHMUK PVAu/r (R); NHMUK PVAu/r (L); NHMUK PVAu/r (L); UMZC 638 (R)
	Carpometacarpus	MNHN MADu/r (L); FLMR 224.19 (L); FLMR 165 (L); NHMUK PVA1389 (L); NHMUK PVA1441 (L); NHMUK PVA1389 (R); NHMUK PVA9045 (L); NHMUK PVA9046 (L); NHMUK PVA3507 (L); NHMUKu/r (R); UMZC 635 (L); UMZC 635 (R)
<i>Raphus cucullatus</i>	Scapulo-coracoid	AMNH u/r (L)
	Sternum	NHMUK PVA3622; NHMUK PVA726; NHMUK PVA729; NHMUK PVA1340; AMNH 8258
	Humerus	NHMUK PVAu/r (R)
	Radius	NHMUK PVAu/r (R)
	Ulna	NHMUK PVAu/r (R)
	Carpometacarpus	NHMUK PVAu/r (R); NHMUK PVAu/r (R); NHMUK PVAu/r (R); NHMUK PVAu/r (Ld)

Listing of skeletal material: 'u/r' unregistered, left (L) or right (R) prefixed by 'd' distal. The following institutional abbreviations have been used: AMNH (American Museum of Natural History); FLMR (Francois Leguat Museum, Rodrigues); MNHN (Muséum National d'Histoire Naturelle), Paris, with the prefix MAD for Madagascar; NHMUK (Natural History Museum, UK); UMZC (University Museum of Zoology, Cambridge), UK.

other bird species, including other columbids, also have a carpal spur or knob (Jefferies, 1881; Sclater, 1886; Rand, 1954; Livezey & Humphrey, 1985; Worthy, 2001). When present, these carpal spurs or knobs are restricted almost exclusively to the processus extensorius of the carpometacarpus, and are always used as weapons. Healed fractures are comparatively numerous among samples of solitaire bones (see Ottow, 1950). These have been widely considered to be the result of injuries sustained during the territorial combats such as witnessed by the writers of the early accounts, and possibly inflicted by the carpal knob.

In this paper, we re-examine the wing osteology of the solitaire (Table 1), with particular reference to the

development, histology, and function of the carpal knob, and we compare it with homologous structures in the wing skeleton of other birds (Table 2). We also compare the pectoral and wing skeletons of the solitaire and the dodo, and comment upon the role of the solitaire carpal knob in territorial behaviour.

THIN SECTION METHODS

Thin sections were taken by a standard method whereby the bone was embedded in epoxy resin before being cut, bonded to a glass slide, ground to a thickness of 30–50 µm, and coverslipped (see Chinsamy & Raath, 1992; Wilson, 1994). Sections were examined and photographed using a trinocular microscope. A

Table 2. List of skin (in parentheses) and skeleton specimens, with registration number and sex (if known) provided for each

Species	Registration number(s)
<i>Crax globulosa</i> (Cracidae)	NHMUK 1988.21.27 (♂) (skin)
<i>Chauna chavaria</i> (Anhimidae)	NHMUK 1891.7.20.95 (♂); NHMUK S/1954.3.3 (♂); NHMUK 1863.12.28.9 u/s
<i>Chauna torquata</i> (Anhimidae)	NHMUK S/1958.15.2 (♀); NHMUK 1896.2.16.46 u/s; NHMUK S/1966.52.19 u/s; NHMUK S/1954.5.3 (♀)
<i>Anhima cornuta</i> (Anhimidae)	NHMUK S/2009.2.1 u/s; NHMUK 2009.2.2 u/s; NHMUK S/1952.1.116 u/s
<i>Plectropterus gambensis</i> (Anatidae)	NHMUK 1898.5.9.5 (♀)
<i>Tachyeres patachonicus</i> (Anatidae)	NHMUK 1932.12.20.6 (♂)
<i>Tachyeres brachydactyla</i> (Anatidae)	NHMUK S/2002.1.34 u/s; NHMUK S/2004.7.1 u/s
<i>Merganetta armata colombiana</i> (Anatidae)	NHMUK 1892.2.1.410 (♂)
<i>Chionis alba</i> (Chionidae)	NHMUK 1949.78.82 (♂)
<i>Vanellus spinosus</i> (Charadriidae)	NHMUK 1859.3.23.1 u/s (skin)
<i>Vanellus senegallus lateralis</i> (Charadriidae)	NHMUK 1899.3.1.9 (♀) (skin)
<i>Vanellus armatus</i> (Charadriidae)	NHMUK S/1955.4.11 (♂) (skin)
<i>Vanellus novaehollandiae</i> (Charadriidae)	NHMUK S/1966.50.8 (♂) (skin); NHMUK S/1966.50.8 (♂)
<i>Vanellus chilensis cayennensis</i> (Charadriidae)	NHMUK 1896.1.3.4 (♂) (skin)
<i>Vanellus albiceps</i> (Charadriidae)	NHMUK S/1959.6.1 u/s (skin)
<i>Actophilornis africanus</i> (Jacanidae)	NHMUK 1923.8.7.842 (♂) (skin); NHMUK S/1963.9.1 (♀)
<i>Irediparra gallinacea novaehollandiae</i> (Jacanidae)	NHMUK 1900.6.11.200 (♂) (skin)
<i>Hydrophasianus chirurgus</i> (Jacanidae)	NHMUK 1922.3.5.4670 (♀) (skin)
<i>Microparra capensis</i> (Jacanidae)	NHMUK 1932.5.5.18 (♂) (skin)
<i>Jacana spinosa gymnostoma</i> (Jacanidae)	NHMUK 1914.12.1.306 (♂) (skin)
<i>Burhinus magnirostris ramsayi</i> (Burhinidae)	NHMUK 1922.7.25.15 (♂) (skin)
<i>Goura cristata</i> (Columbidae)	NHMUK 1889.2.10.492 (♂) (skin); NHMUK S/1966.52.60 u/s

All of these bird species have wing weapons, which are associated with combative territorial behaviour.

male carpometacarpus (NHMUK PVA1387) was sectioned transversely through the carpal knob and the underlying diaphysis. A male radius (FLMR 165.1) was sectioned transversely through the accessory exostosis and the underlying diaphysis.

ACCOUNTS OF SOLITAIRE BEHAVIOUR

The solitaire skeleton is known from thousands of subfossil bones collected from the caverns of Rodrigues. However, unlike the dodo, there is no record of any live specimens or skins leaving the Mascarenes (Cheke & Hume, 2008). It is very fortunate that two astute observers made detailed records of the solitaire's appearance (Fig. 1) and behaviour. The first was Leguat (1708):

‘... They never fly, their Wings are too little to support the Weight of the bodies; they serve only to beat themselves, and flutter when they call each other. They will whirl about for twenty or thirty times together on the same side, during the space of four or five minutes. The motion of their Wings makes then a noise very like that of a Rattle; and one may hear it two hundred Paces off. The Bone of their Wing grows greater

towards the Extremity, and forms a little round Mass under the Feathers, as big as a Musket Ball. That and its Beak are the chief Defence of this Bird.

... They never lay but one Egg, which is much bigger than that of a Goose. The Male and Female both cover it in their turns, and the young is not hatch'd till at seven Weeks' end: All the while they are sitting upon it, or are bringing up their young one, which is not able to provide itself in several Months, they will not suffer any other Bird of their Species to come within two hundred Yards round of the Place; But what is very singular, is, the Males will never drive away the Females, only when he perceives one he makes a noise with his Wings to call to the Female, and she drives the unwelcome Stranger away, not leaving it till 'tis without her Bounds. The Female do's the same as to the Males, whom she leaves to the Male, and he drives them away.

Leguat's account was later verified by Tafforet (c.1726), who made similar first-hand observations (although it must be noted that Tafforet had a copy of Leguat's publication during his visit!):

‘... They have a small stump of a wing, which has a sort of bullet at its extremity, and serves as a defence. They do not

fly at all, having no feathers to their wings, but they flap them, and make a great noise with their wings when angry, and the noise is something like thunder in the distance' (in Cheke & Hume, 2008).

Armstrong (1953) was unaware of Tafforet's account, but recognized Leguat (1708) as the earliest description of territorial behaviour in birds.

DESCRIPTION OF THE SOLITAIRE CARPAL KNOB

The distal wing elements (radius, ulna, carpometacarpus, and phalanges) of the solitaire sometimes have distinct callus-like exostoses. The largest of these is the carpal knob (musket ball), found on the proximal end of the carpometacarpus. The carpal knob is a single, double or rarely triple-lobed cauliflower-like growth that develops from the processus extensorius of the carpometacarpus (Fig. 3). In 58% ($N = 14$) of the 24 adult male and female solitaire carpometacarpi examined in this study (Table 3), the carpal knob was absent (Fig. 4A, C). However, in the remaining 42% ($N = 10$) of specimens that exhibited the growth, the total length of male carpometacarpi with a carpal knob ($N = 6$, mean 48.2 mm, SD 1.45) compared with males without ($N = 7$, mean 42.7 mm, SD 1.88) was statistically significant (Table 3; Fig. 4A, B). This is in contrast to differences in the female carpometacarpi with a carpal knob ($N = 4$, mean 39.0 mm, SD 1.18) and without ($N = 7$, mean 38.3 mm, SD 1.11), which showed that the size differences were less striking (Table 3; Fig. 4C, D). The largest carpal knobs seen in this study belong to the largest-sized male carpometacarpi, and the largest specimen measures 32.9 mm in diameter at its widest point, but is attached to the carpometacarpus by a base just 14 mm wide (Table 4). Furthermore, in an associated skeleton (NHMUK PVA3505) of a male with large carpal knobs, the distal ends of the radius and ulna also bear exostoses. The wing phalanx (phalanx I of *digiti majoris*) may be affected too (Fig. 5A).

The surfaces of the largest carpal knob specimens have a porous, spongy appearance. Smaller ones, which occur in females and some males, are smoother, and are not divided into multiple lobes. In thin section, the carpal knob resembles a cut cauliflower (Fig. 6A), although the exostosis on the distal end of the radius is unlobed (Fig. 6B). Both types of exostosis are composed of highly cancellous woven bone, containing numerous osteocyte lacunae. The tissue strongly resembles fracture callus, and we suggest that it might have formed in response to impacts sustained in combat. No growth marks are visible, which indicates that growth did not pause or follow any kind of cycle, but was continuous. We

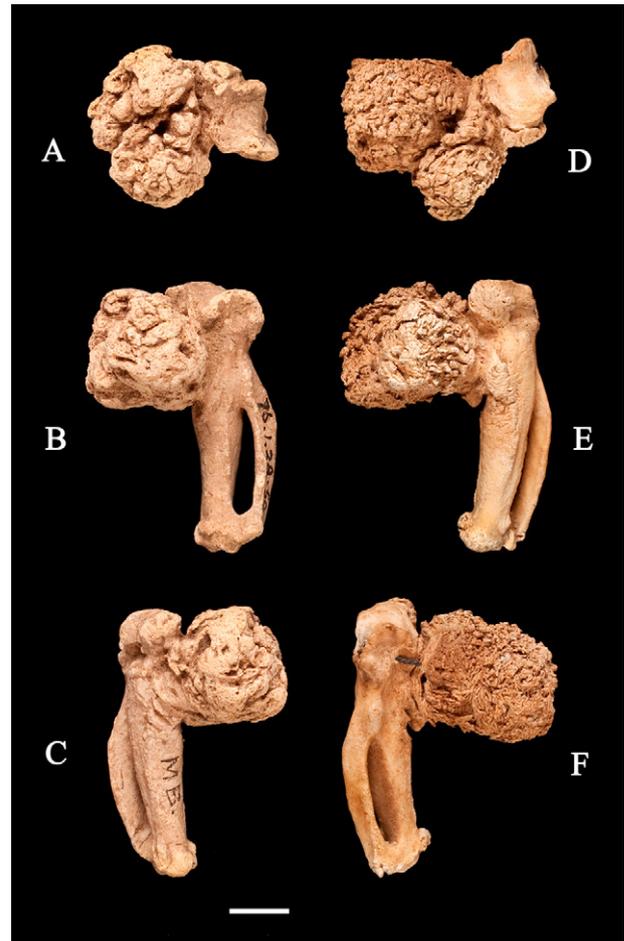


Figure 3. Two examples of the carpal knob on the carpometacarpus of male *P. solitaria*. Right carpometacarpus (NHMUK PVA9047): A, proximal surface; B, ventral aspect; C, dorsal aspect. Left carpometacarpus NHMUK PVA3505: D, proximal surface; E, ventral aspect; F, dorsal aspect. Scale bar = 10 mm.

cannot determine how rapidly it grew, but highly cancellous and disorganized tissue typically forms when bone growth is rapid. It is very likely that the carpal knob of the solitaire was covered in a thickened, cartilaginous integument (Newton & Newton, 1869) or keratinous horn (Jefferies, 1881), which would have made the structure even larger.

HEALED FRACTURES IN SOLITAIRE BONES

A significant number of solitaire pectoral girdle and wing bones appear to have been fractured and healed during life (see Fig. 7). Newton & Newton (1869) illustrated just two examples (a coracoid and an ulna) but an unpublished draft manuscript of their paper (General Library Collection MSS. ROY Manuscript) held in the Natural History Museum, London, includes many other examples that were not used in

Table 3. Measurements (mm) of the carpometacarpus of *Pezophaps solitaria* and *Raphus cucullatus*

Species	TL (n) range	TL (m) SD	PW (n) range	PW (m) SD	PD (n) range	PD (m) SD	SW (n) range	SW (m) SD	SD (n) range	SD (m) SD	DW (n) range	DW (m) SD	DD (n) range	DD (m) SD
<i>Pezophaps solitaria</i> (male with carpal knob)	(7) 41.0–46.6	(42.7) 1.88	(6) 13.5–14.5	(13.9) 0.37	(7) 7.5–10.8	(9.1) 1.18	(7) 4.4–9.3	(5.5) 1.68	(7) 5.5–10.1	(6.9) 1.50	(7) 7.9–10.7	(9.2) 0.87	(7) 5.1–7.7	(6.0) 0.81
<i>Pezophaps solitaria</i> (male without carpal knob)	(4) 37.6–40.5	(39.0) 1.18	(4) 12.8–15.7	(13.9) 1.30	(4) 8.7–11.8	(9.7) 1.41	(4) 4.8–5.6	(5.1) 0.32	(4) 6.1–6.4	(6.3) 0.12	(4) 8.0–10.5	(8.9) 1.09	(4) 5.7–5.8	(5.7) 0.06
<i>Pezophaps solitaria</i> (female with carpal knob)	(7) 37.0–39.9	(38.3) 1.11	(6) 13.1–15.3	(14.1) 0.93	(7) 8.1–9.9	(8.9) 0.62	(7) 4.5–5.0	(4.7) 0.20	(7) 5.4–6.7	(6.0) 0.54	(7) 7.5–9.5	(8.4) 0.81	(7) 4.8–7.1	(5.8) 0.92
<i>Raphus cucullatus</i> (female without carpal knob)	(3) 41.5–47.0	(43.5) 3.04	(3) 13.5–14.7	(13.9) 0.64	(3) 8.6–10.4	(9.3) 0.21	(4) 4.3–4.8	(4.5) 0.21	(4) 5.6–6.2	(5.9) 0.25	(4) 8.6–9.7	(9.0) 0.49	(4) 5.3–5.9	(5.5) 0.32

All measurements were made using digital calipers and rounded to the nearest 0.1 mm. TL, total length, from trochlea carpalis to facies articularis digitalis major in ventral aspect; PW, proximal width, proximal end from processus extensorius to facies articularis ulnecarpalis; PD, proximal depth, processus piciformis to dorsal surface of trochlea carpalis; SW, shaft width, in dorsoventral plane; DD, distal depth, in lateromedial plane. Statistical terminology is as follows: n, number of specimens; m, mean; SD, standard deviation. Anatomical nomenclature follows Baumel & Witmer (1993).

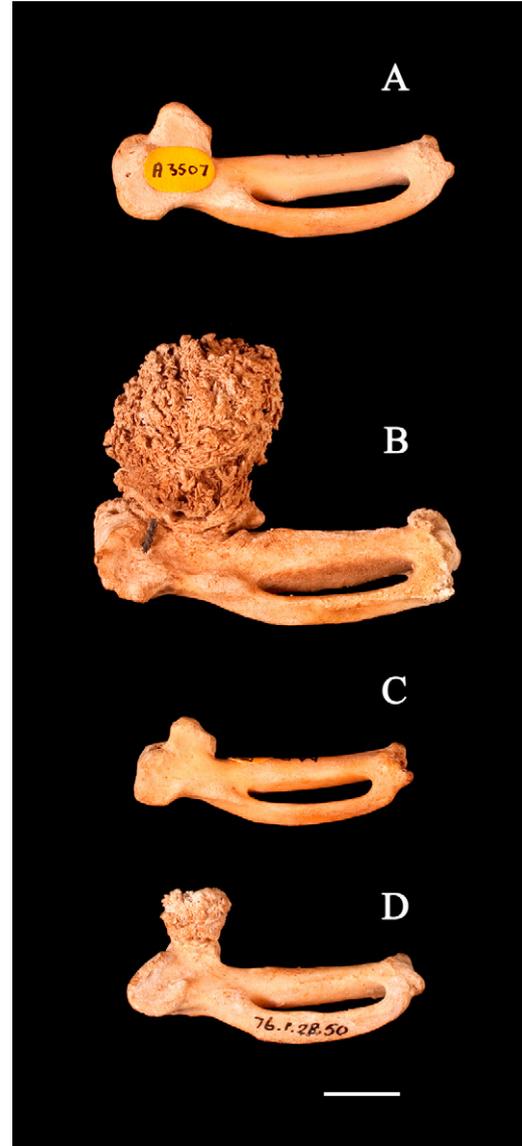


Figure 4. Comparison of adult male and female carpometacarpi of *P. solitaria*, showing specimens with and without carpal knob. Left side, ventral aspect: A, male without carpal knob (NHMUK PVA9044); B, male with carpal knob (NHMUK PVA3505); C, female without carpal knob (NHMUK PVA9046); D, female with carpal knob (NHMUK PVA9045). Scale bar = 10 mm.

the final publication. A few illustrations of healed fractures and other pathologies also appeared in Abel (1912) and Ottow (1950, 1951, 1952). Healed fractures occur in both sexes, and most of the healed fractures in our dataset are in ulnae. For example, of 101 ulnae examined, 15 (14%) exhibited healed fractures, but fractures are also seen in the humerus, radius, coracoid, and ribs (see Abel, 1912; Ottow, 1950, 1951, 1952). These pathologies are widely considered to be

Table 4. Measurements (mm) of the carpal knob of *Pezophaps solitaria*

Species	MBW (n)		MBD (n)		MBH (n)	
	Range	Mean (SD)	Range	Mean (SD)	Range	Mean (SD)
<i>Pezophaps solitaria</i> (male)	(6) 10.8–22.7	(18.8) 4.15	(6) 11.5–32.9	(22.7) 7.45	(6) 8.3–25.3	(16.7) 5.44
<i>Pezophaps solitaria</i> (female)	(4) 4.3–7.5	(6.04) 1.33	(4) 4.6–7.6	(6.17) 1.43	(4) 6.4–7.5	(6.91) 0.47
<i>Raphus cucullatus</i>	n/a	n/a	n/a	n/a	n/a	n/a

MBW, musket ball width, in dorsoventral plane; MBD, musket ball depth, in lateromedial plane; MBH, musket ball height, in ventral aspect. Note the extremely wide range of probable age-related sizes in the width and height of the structure in the male.

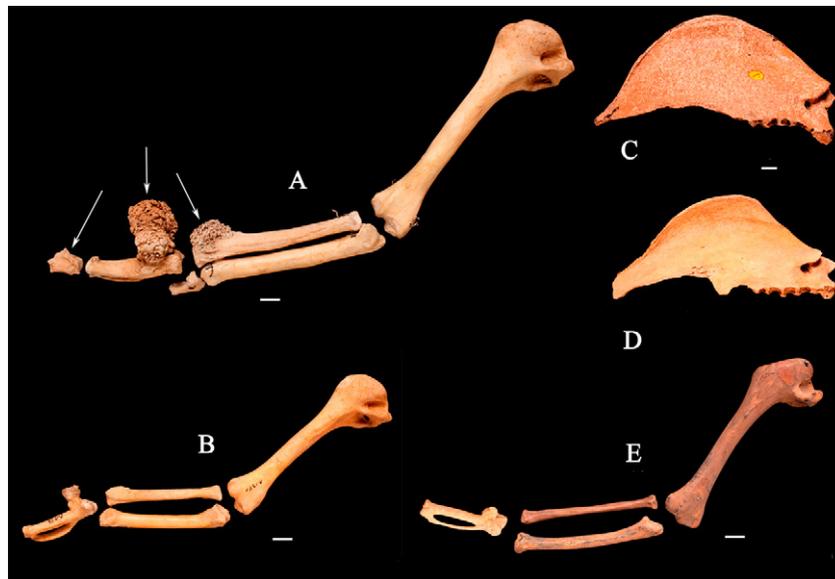


Figure 5. Comparison of the left wing skeleton, caudal view, of *P. solitaria* and *R. cucullatus*: A, *P. solitaria* male; B, *P. solitaria* female; E, *R. cucullatus*. Sterna in lateral aspect of: C, unsexed *R. cucullatus* (NHMUK PVA3622); D, female *P. solitaria* (NHMUK PVA1377). Note the more pronounced carina sterni in *P. solitaria*. Arrows indicate the full extent of carpal weapon growth in the male solitaire. This area was also covered with a thick integument, which would have made the carpal weapon even larger. Scale bar = 10 mm.

injuries sustained in combative behaviour (e.g. Newton & Newton, 1869; Abel, 1912; Armstrong, 1953; Livezey, 1993), which substantiates the credibility of the early accounts. However, Ottow (1950: 33) believed that the deformities were due to a pathological mutation, rather than the result of combat injuries.

DISCUSSION

CARPAL WEAPONS IN AVES

Carpal spurs or knobs are known to occur in several extant bird orders (Jefferies, 1881; Sclater, 1886; Rand, 1954; Livezey & Humphrey, 1985), but the morphology and position of these structures varies (Fig. 8). Well-known examples of genera with carpal

knobs include the steamer ducks *Tachyeres* spp. (Fig. 8D), the torrent duck *Merganetta armata* Gould, 1842, and other Anatidae, stone curlews *Burhinus* spp., sheathbills *Chionis* spp., pigeons (Columbidae), and some guans (Cracidae). All *Vanellus* plovers (Charadriidae) (Fig. 8C) and three out of the six jacana genera (Jacanidae) have a carpal spur to varying degrees, whereas in the other three, the radius is expanded into a triangular blade instead (Beddard, 1898: 125) (Fig. 8A). In screamers (Anhimidae) there is a carpal spur on the processus extensorius of the carpometacarpus, with an occasional second growth on the facies articularis digitalis major (Fig. 8E). In the spur-winged goose *Plectropterus gambensis* Linnaeus, 1766 (Anatidae) the spur is an extension of the os carpi radiale (Fig. 8F). The extinct

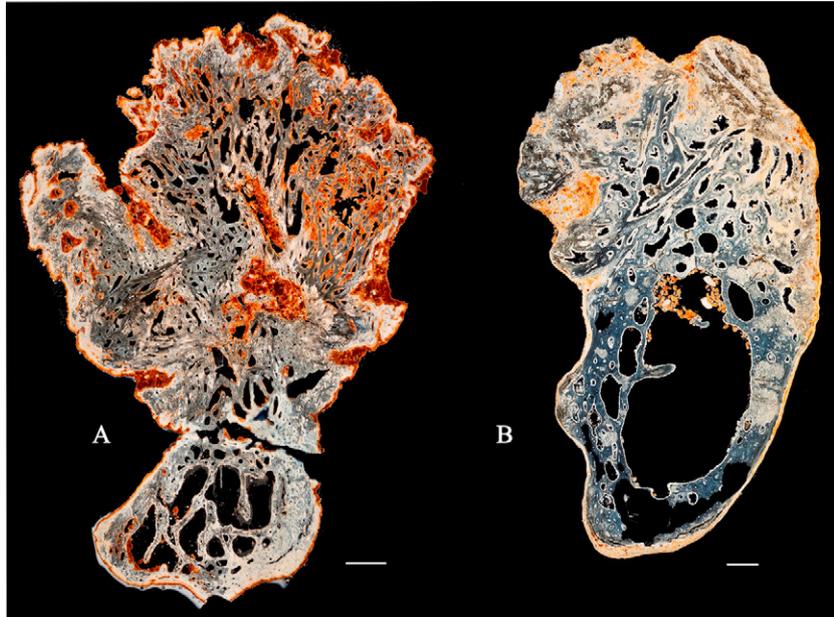


Figure 6. Transverse thin sections of male *P. solitaria* exostosis-bearing wing bones: A, carpometacarpus with carpal knob (NHMUK PVA1387); B, distal radius (FLMR 165.1). In both images, the exostotic tissue is towards the top, and the diaphysis of the bone is towards the bottom. Scale bar = 2 mm (A); 1 mm (B).



Figure 7. Selected pectoral elements of male and female *P. solitaria* comparing normal specimens with pathological specimens showing healed fractures: A, male right humerus (NHMUK PVA9041); B, (NHMUK PVA1441.1) in caudal view; C, female left coracoid (NHMUK PVA1441.2); D, (NHMUK PVA9042) in ventral aspect; E, male right ulna (NHMUK PVA1382); F, (NHMUK PVA9043) in ventral aspect. Arrows denote the areas of healed fractures. Scale bar = 10 mm.

Jamaican flightless ibis *Xenicibis xympithecus* Olson & Steadman, 1977 (Threskiornithidae) is unique in having a thick-walled elongate, inflated metacarpus (Longrich & Olson, 2011).

Within Columbidae (pigeons and doves), the extinct flightless *Natunaornis gigoura* and the extant *Goura*

ground pigeons both have a small bony outgrowth on the processus extensorius of the carpometacarpus (Goodwin, 1983; Worthy, 2001) (Fig. 8B), which closely resembles that of a female solitary. In our examination of carpal spurs and knobs, we note that the literature does not accurately reflect the number of

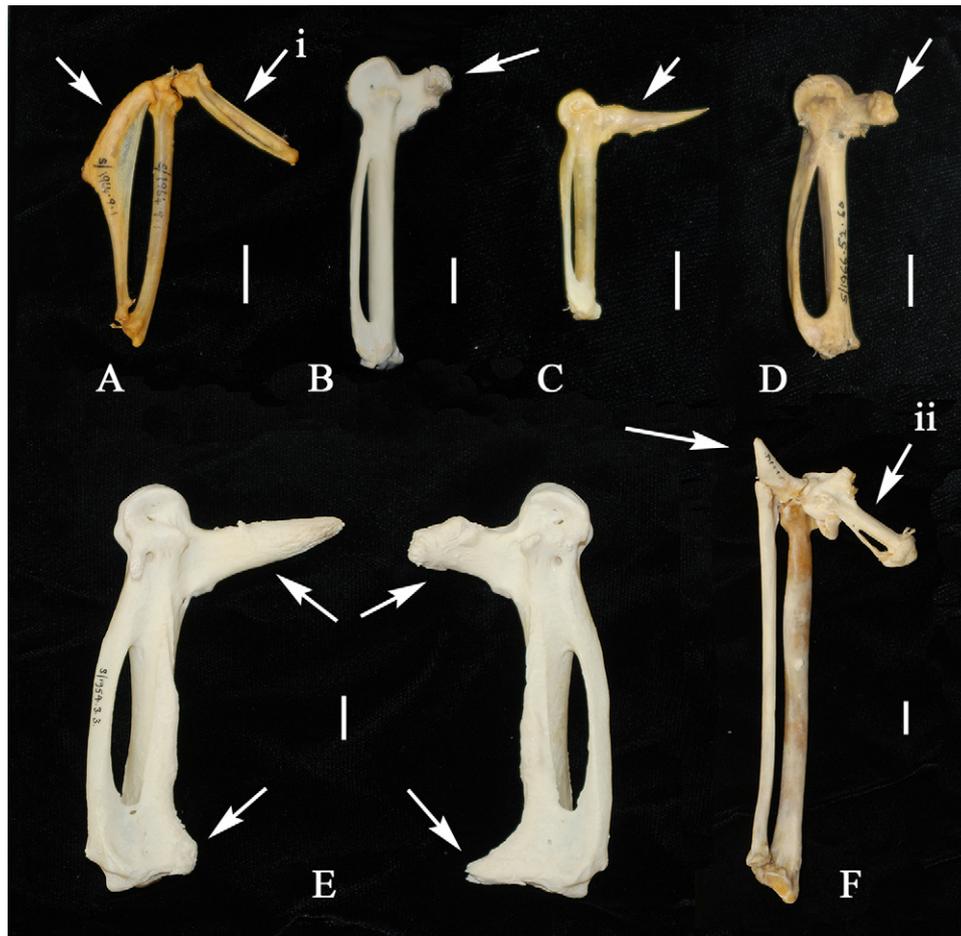


Figure 8. Selected examples of carpal weapons in other Aves, all in ventral aspect: A, *Actophilornis africana* NHMUK S/1964.91 has a blade-like extension of the radius (arrowed); B, *Goura cristata* NHMUK S/1966.52.60 has a carpal knob (arrowed), C, *Vanellus novaehollandiae* NHMUK S/1966.50.8 has a carpal spike (arrowed); D, *Tachyeres brachypterus* NHMUK S/2004.7.1 has a carpal knob (arrowed); E, *Chauna chavaria* NHMUK S/1954.3.3 has carpal spikes or knobs on either end of the carpometacarpus (arrowed); F, *Plectropterus gambensis* (NHMUK 1898.5.9.5) has a carpal spike (arrowed). Note that in A and F, the carpometacarpus (indicated by i and ii) does not form a carpal weapon. Scale bar = 10 mm.

taxa that exhibit some form of carpal growth, but without exception all of these structures are or were used as weapons (Jefferies, 1881; Sclater, 1886; Rand, 1954; Goodwin, 1983; Livezey & Humphrey, 1985; Worthy, 2001; Longrich & Olson, 2011). Our study confirms that the solitaire's carpal knob was also a weapon.

WHAT IS THE ORIGIN OF THE SOLITAIRE'S CARPAL KNOB?

In a series of detailed publications, Ottow (1950, 1951, 1952) argued that the solitaire's carpal knob and other wing bone exostoses formed as a result of a hereditary bone disease that he termed 'osteogenesis dysplastico-exostotica'. He believed that the soli-

taire had a pathological mutation that had spread through the population due to inbreeding and isolation on a remote island. Ottow was incorrect in his interpretation of the carpal knob and other exostoses as a manifestation of a genetic mutation, because such diseases typically do not produce lesions in such a specific region of the skeleton, but cause them to appear in any actively growing bony tissue. Besides, if Ottow's theory was correct, then surely similar diseases would have appeared in the dodo and other insular birds, but there is no evidence of this; Ottow's work remains unsupported (e.g. Amadon, 1951).

We believe that the carpal knob is not caused by a pathological mutation, but that the site of its formation (processus extensorius) contains metaplastic

bony tissue (Haines & Mohuiddin, 1968) that has the ability to form a spur or other type of protruding structure (as seen in most avian carpal weapons). We suggest that there are two alternative ways in which this might develop.

1. The structure grows in response to impacts sustained when combative behaviour begins in adult breeding life, in order to protect the wing bone at the site of impact. It would also create a more effective weapon, which would be favoured by natural selection.
2. The structure develops under the influence of hormones or other signals, when the individual pairs up with a mate and acquires a territory.

The available evidence is not sufficient to allow us to determine which of these mechanisms is the most likely in the solitaire, or in any of the other species that develop similar structures in the wing. Further studies of living species may help us to understand how these structures form, and their role in reproductive behaviour.

TERRITORIAL BEHAVIOUR IN THE SOLITAIRE

Our results show that the carpal knob develops after skeletal maturity, as our dataset includes fully ossified bones without a ‘musket ball’. We suggest that the development of this feature also corresponds with sexual maturity and the acquisition of a breeding territory. Livezey (1993: 273) estimated that the solitaire lived for approximately 28 years, based on weight estimates. A mature male that had successfully held a territory for many years would exhibit pronounced development of a carpal knob and callus growth on the radius and phalanges (Fig. 5A). A female paired with one of these males might also exhibit development of a carpal knob, but those of the females never develop to the same degree as the males (Table 4; Fig. 5B), and we have not seen a female radius or wing phalanges with the exostoses that are sometimes present in males. Livezey (1993: 275) considered the solitaire to be polygynous based on studies of other birds (e.g. Livezey & Humphrey, 1985), but we find no support for this notion in the descriptions left by Leguat and Tafforet.

The combined evidence of subfossil remains and contemporary accounts shows that paired male and female solitaires both participated in aggressive displays and combats, in which the wings were used as weapons. Furthermore, the wings were also used to create low-frequency sounds to communicate with the other member of the pair, and as a warning to rivals or intruders. We are unable to ascertain if the carpal knobs were knocked together or beaten on the bird’s

own body, as neither account is clear on this detail. According to Leguat (1708) the sound was audible from 200 yards (182 metres) away, which we believe (and Leguat implies) corresponds to the size of the territory. Armstrong (1953) also considered this to be the case.

Other birds use sounds made by the wings to establish a territory or to attract mates. Well-known examples include the ruffed grouse *Bonasa umbellus* (Linnaeus, 1766), which uses rapid wing beats (Atwater & Schnell, 1989), the club-winged manikin *Machaeropterus deliciosus* (Sclater, 1860) (Pipridae), which uses specialized wing bones (Bostwick, Riccio & Humphries, 2012) and wing feathers (Bostwick *et al.*, 2012), and the Eurasian woodcock *Scolopax rusticola* Linnaeus, 1758 (Scolopacidae) (Slabbekoorn, 2004) that combines wing-flapping with a complex variety of calls. Therefore, the mechanism employed by the solitaire to produce a wing-generated sound was unique.

DODO AND SOLITAIRE PECTORAL GIRDLE AND WING OSTEOLOGY

The solitaire’s closest relative, the dodo, is known from thousands of bones in numerous museums (Hume, 2005). Its skeleton has been repeatedly studied and described since the mid-19th century (Strickland & Melville, 1848; Owen, 1866, 1869, 1872, 1878). We have only seen one dodo bone with a healed fracture, a fused scapulo-coracoid (AMNH u/r), but Newton & Newton (1869: 355) mention a coracoid in UMZC (unseen by us). In contrast, there are numerous examples of healed fractures in solitaire bones (Fig. 7). This implies that of the two species, the solitaire was by far the more physically aggressive and combative.

We can be certain that the solitaire used its wings for combat, but there is no clear evidence that the dodo had a similar defensive behaviour. In fact, and as noted by Strickland (1844), Strickland & Melville (1848), and Newton & Newton (1869), the carina sterni in the dodo is shallower than that of the solitaire (Fig. 5C, D), indicating that it had relatively less pectoral (flight) muscle mass (musculus pectoralis major and musculus supracoracoideus). Although both species were flightless, the solitaire presumably required stronger pectoral muscles to move its wings with enough force to make an effective weapon. It appears that the dodo had insufficient pectoral musculature to do the same. The wing of the dodo (humerus, radius, ulna, carpometacarpus) also differed from that of the solitaire in its relative proportions and overall reduction in size (Fig. 5E). Our data (Table 3) show that the dodo

carpometacarpus was intermediate in total length between those of the male and female solitaire, but was less robust, especially in shaft width and depth. However, the dodo had a much larger, hooked bill than the solitaire, and early accounts of the dodo state that the bill was a formidable weapon (Cheke & Hume, 2008 and references therein); therefore, we speculate that the bill was used in territorial disputes in this species.

Pigeons and doves are noted for aggressive behaviour in which they often use their wings as weapons (Armstrong, 1953; Goodwin, 1983; Gibbs *et al.*, 2001). For example, in Madagascar turtle dove *Nesoenas picturata* (Temminck, 1813), disputing males raise one wing to signal a warning, before attacking with blows from the wings (J.P.H. pers. observ.). The mourning dove *Zenaida macroura* (Linnaeus, 1758) aggressively attacks its congeners and other competitive bird species with its wings and beak (Mirarchi & Baskett, 1994), and in the Eurasian wood pigeon *Columba palumbus* Linnaeus, 1758, combats between males are initiated with an audible wing flick followed by violent buffeting with the wings (Cramp, 1985). This behavioural trait was presumably present in the ancestral volant pigeon that colonized the Mascarene Islands. Livezey & Humphrey (1985) and Livezey (1993) noted that in steamer ducks (*Tachyeres* spp.) the combination of large body size, great sexual dimorphism and sedentary habit (i.e. flightlessness) was associated with intense territoriality that served to defend various resources such as feeding, nesting and brood-rearing sites. All of these criteria (large body size, great sexual dimorphism and flightlessness) apply to the solitaire, but sexual dimorphism in the dodo is less clearly defined (Livezey, 1993).

We should also consider environmental factors intrinsic to the two islands inhabited by these birds. Rodrigues receives approximately half of the rainfall of Mauritius (Mauritius Meteorological Services, 2012), and is subject to greater seasonal variation (Cheke & Hume, 2008), which must have influenced resource availability. Although speculative, this would have been an important factor in driving the evolution of combative territorial behaviour in the solitaire.

CONCLUSIONS

Our study has shown that the carpal knob of the solitaire differs morphologically from homologous structures in other bird taxa, and thus is unique in Aves. The method in which the solitaire used its wings as an audible signal is also unique. Furthermore, the sternum of the solitaire retained a comparatively large carina sterni compared with that of

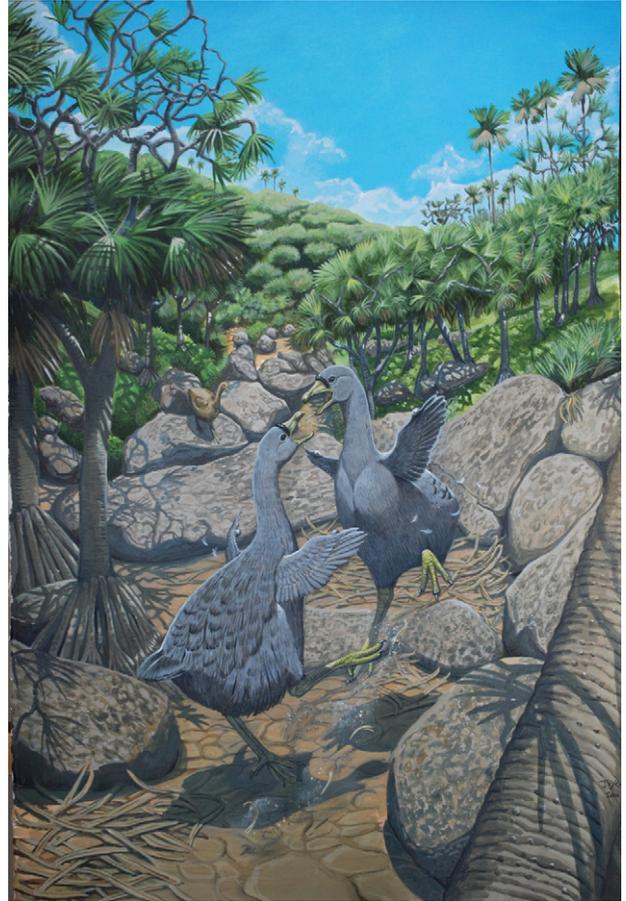


Figure 9. A pair of male solitaires *P. solitaria* fight over territory in the valley of Saint François, Rodrigues. An artistic reconstruction by Julian P. Hume. © Julian P. Hume.

the dodo, which provided the necessary musculature to swing the carpal appendages. The large numbers of solitaire bones with healed fractures are testament to the potency of this weapon, but also show that territorial disputes were not always fatal. The developmental mechanism of the solitaire's carpal knob is poorly understood; there are no living giant flightless Columbidae for comparative study. Nonetheless, numerous subfossil specimens and contemporary accounts provide unequivocal evidence that the solitaire used this unique weapon to great effect in intraspecific combat (Fig. 9).

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