



## A new species of extinct fossil scops owl (Aves: Strigiformes: Strigidae: *Otus*) from the Archipelago of Madeira (North Atlantic Ocean)

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### Abstract

The extinct Madeiran Scops Owl *Otus mauli* n. sp. is described from fossil bones found in Quaternary sites on Madeira Island (Madeira Archipelago, North Atlantic Ocean). It is the first extinct bird to be described from this archipelago and the first extinct species of Strigiformes known from anywhere in Macaronesia. The forelimb bones of the new taxon are similar in size to those of the Eurasian Scops Owl (*Otus scops* Linnaeus) but the hindlimb bones are longer, especially the tarsometatarsus, which is much longer and more slender than in *O. scops*. The estimated body weight and wing loading, together with the proportions of hindlimb bones (femur, tibiotarsus and tarsometatarsus) in relation to total length of leg bones (femur+tibiotarsus+tarsometatarsus), seem to indicate a ground-dwelling life-style. Human arrival and subsequent habitat alterations (introduction of alien taxa, burning, etc.) are the most probable causes of its extinction. The same species or a close relative is documented from dunes on the island of Porto Santo, but the quality of preservation of its bones precludes more certain identification.

**Key words:** Extinction, evolution of island biotas, Madeiran Scops Owl, *Otus mauli* n. sp., Macaronesia, Quaternary.

### Introduction

Existing vertebrate faunas of islands have usually been modified by two recent global events: (1) numerous extinctions and (2) introduction of alien taxa, both mainly caused by human arrival and subsequent alteration of insular ecosystems (Olson & James 1982a; Worthy & Holdaway 2002; Steadman 2006). Consequently, current autochthonous biotas are essentially human-influenced subsets of those originally present. Knowing the former diversity and species' distributions of pristine island faunas is critical for understanding the evolutionary history, biogeography, and conservation status of remaining species and ecosystems.

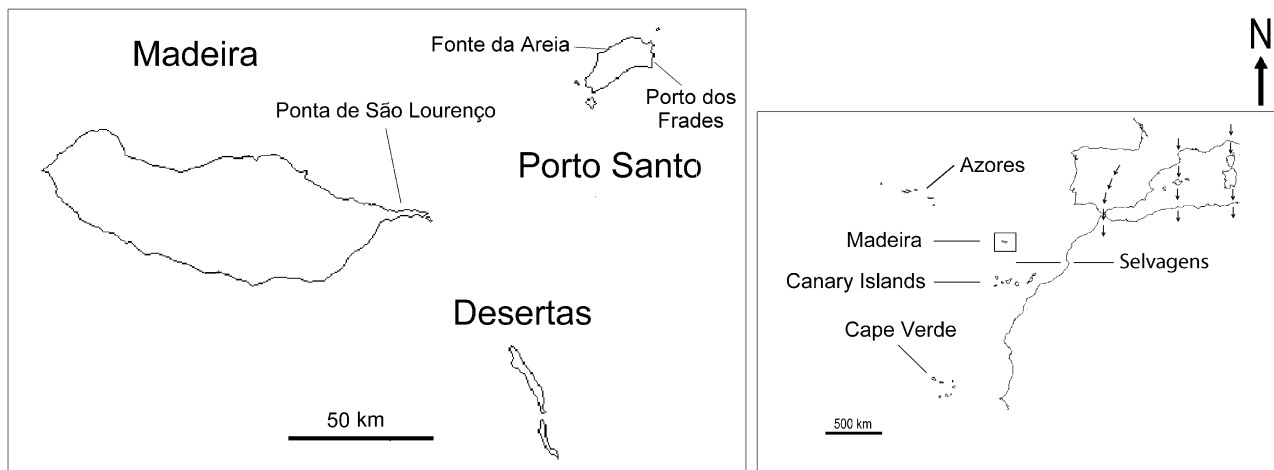
The oceanic Macaronesian archipelagos (Azores, Madeira, Selvagens, Canary Islands and Cape Verde) are located in the North Atlantic Ocean (15°N–39°N and 10°W–30°W), and between ~100 km (Canary Islands) and ~1350 km (Azores) from the Old World mainland (Fig. 1). The original Quaternary faunas of these islands have been poorly studied in the Azores, Madeira, Selvagens, and Cape Verde, whereas those from the Canary Islands are better known. The Canary Islands differ from other Macaronesian islands by: (i) the prehistoric presence of endemic non-flying land mammals (three extinct species of Rodentia and one of Soricomorpha), which are absent from the other archipelagos; and (ii) by their different history of human colonization. In the Canary Islands, two well differentiated waves of human arrival took place; the “aboriginal”, from north-west Africa, some time between 756 cal BC–313 cal AD (Alcover *et al.* 2009), and a second wave of colonization from Europe starting in the 14<sup>th</sup> century (Aznar *et al.* 2006). The other Macaronesian archipelagos were first populated from Portugal during the 15<sup>th</sup> century (Crosby 1988).

Six species of extinct endemic birds have been recorded so far from Quaternary sites in the Canary Islands: the Lava Shearwater *Puffinus olsoni* McMinn *et al.* 1990; the Dune Shearwater *P. holeae* Walker *et al.* 1990; the Canary Quail *Coturnix gomerae* Jaume *et al.* 1993; and three passerines, Trias's Greenfinch *Carduelis triasi* Alcover and Florit 1987; the Slender-billed Greenfinch *C. aurelioi* Rando *et al.* 2010; and the Long-legged Bunting *Emberiza alcoveri* Rando *et al.* 1999. In addition, the extinction of the Canary Islands Oystercatcher *Haematopus meadewaldoi* (Bannerman) took place during the 20<sup>th</sup> century (Martín & Lorenzo 2001), with a further five non-endemic birds being extirpated during Holocene and historical times (see Rando 2003 and references therein). All these extinctions seem to be directly correlated with aboriginal (Rando & Alcover 2010) or European colonization and subsequent environmental alterations (Alcover & Florit 1987; Jaume *et al.* 1993; Rando 2003; Rando & Alcover 2008). These data show that more than 50% of the endemic species of birds of the Canary Islands became extinct during the last two millennia.

In contrast to the well-known fauna of the Canary Islands, the original fauna of the Madeira Archipelago is poorly known. A preliminary paper on fossil bird remains from the Madeira Archipelago (Pieper 1985) reported the extinction of a high number of undescribed endemic (at least three flightless rails, quail, a scops owl, and several passerines) and nonendemic birds (Great Auk *Pinguinus impennis* (Linnaeus) and Hawfinch *Coccothraustes coccothraustes* (Linnaeus)), documenting an impressive change in the natural diversity of birds during the late Quaternary. The aim of this paper is to describe one of those birds, an endemic scops owl (genus *Otus*)—the first extinct bird to be described from this archipelago and the first extinct strigiform known from anywhere in Macaronesia. The morphology of the new taxon was compared with that of extant and extinct strigiforms and various morphological features and proportions of the limb bones are discussed in relationship to the most probable habitat, life style, and causes and chronology of extinction.

## Material and methods

Palaeontological investigations between 1979 and 1994 by H.P. produced a great number of bird bones (Pieper 1985) from Madeira Island (Ponta de São Lourenço) and Porto Santo Island (Fonte da Areia and Porto dos Frades) (Fig. 1), some of them belonging to a small owl (Strigiformes).



**FIGURE 1.** Geographic situation of Macaronesia showing the archipelago of Madeira. The bones described in this paper were collected at Madeira (Ponta de São Lourenço) and Porto Santo (Fonte da Areia and Porto dos Frades). The main migratory pathways of *Otus scops* between Europe and Africa in western Mediterranean are shown (arrows).

The fossil specimens are housed in the collections of the Museu Municipal do Funchal (MMF), Funchal, Madeira (24 specimens) and of the Departamento de Zoología de la Universidad de La Laguna (DZUL), Tenerife, Canary Islands (3 specimens). We compared the fossil material with recent skeletons of *Otus scops* housed in the Institut Mediterrani d'Estudis Avançats of the Balearic Islands (IMEDEA) all of which are from Mallorca and unsexed: IMEDEA 1258, 2199, 2205, 2210, 11952, 11954, 12093, 12459, 12526, 20298, 20646, 20647, 20648, 20670, 20777, 20909, 21810, 21865, 21866, 21868, 21897, 21901, 21902, 21906. Measurements from leg bones of

additional species of scops owls and related taxa are from specimens in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Anatomical terminology follows Baumel (1993) and Livezey and Zusi (2006). We took measurements with digital calipers to the nearest 0.01 mm, following the criteria of Campbell and Bocheński (2010). Nevertheless, all the measurements have been reported to 0.1 mm as this is all that is repeatable if necessary.

In order to estimate the weight of the new taxon we explored two approaches: (1) we used the expression  $Y = 0.56 X^{0.342}$ , where the femur length is the independent variable (X), and the estimated weight of the bird (Y) is the dependent variable (Olmos *et al.* 1996); (2) we used the expression  $Y = 2.414 X^{-0.069}$ , where Y = log body weight and X = log perimeter of the femur diaphysis (Campbell & Marcus 1992), estimating the diameter as the average of the depth and width of the shaft of the diaphysis. One of the approaches is based on a hindlimb bone, while the other one is based on a measurement of the section of a hindlimb bone.

The proportions of leg bones (femur, tibiotarsus and tarsometatarsus) in relation to total length of leg bones (femur+tibiotarsus+tarsometatarsus) in extinct and extant owl species are used in order to hypothesize the habitat use of the new taxon. We performed a Principal Component Analysis (PCA) to summarize the segregation and to explore morphological patterns in relation to leg bone proportions among scops owls, related species and extinct insular owls. All statistical analyses have been performed with SPSS 18.0 (PASW Statistic 18 2011).

## Results

### Systematic Paleontology

#### Order Strigiformes Wagler

#### Family Strigidae Leach

#### Genus *Otus* Pennant

Twenty seven nearly complete bones and fragments of a small strigiform species were collected. These bones are referred to the genus *Otus* on the basis of the following combination of characters: The coracoid is similar in size and shape to *Otus*, and it differs from the coracoid of the remaining small European strigiforms in that (1) the *processus procoracoideus* is characteristically narrow, with sides more or less parallel (not wide and triangular as in other species), and (2) the *processus acrocoracoideus* is elongated (cranio-caudally) and has a caudal lamellar process directed towards the *processus procoracoideus*. In *Athene*, *Asio*, *Strix*, *Bubo*, *Surnia*, *Aegolius* and *Glaucidium* this *processus* is absent. The scapula of *Otus* displays a characteristically very wide cranial region, with the scapular body narrow, and having a distinct extension in the cranial part of the *margo dorsalis scapularis*; this extension is also present in *Asio* and *Strix*, although it is less developed, and is absent in *Athene*. The cranial part of the scapula lacks a *foramen pneumaticum*, which is present in *Athene*, *Asio*, *Strix*, *Bubo*, *Surnia* and *Aegolius*. The humerus of *Otus* is highly characteristic. In addition to its small size, it has (1) a pointed *epicondylus dorsalis* more distant from the shaft of the bone (as in *Strix* and *Asio*, whereas it is closer to the shaft in *Athene*), and (2) the *fossa muscoli brachialis* longer and narrower than in *Athene*. The ulna has a pointed, narrow and markedly proximally elongated *olecranon* (in *Athene*, *Asio*, *Strix*, *Bubo* and *Aegolius* it is less prominent, with the general shape being more triangular); in relation to the length of the ulna, the exterior margin of the *labrum condyli* spreads more towards the shaft of the bone, and it slopes gradually to the cranial surface (in the other European genera there is a small indentation). The radius is relatively short in comparison to other strigids. The fragment from Porto Santo fits well in general shape and size with *Otus*. The carpometacarpus has the proximal end ventrally rotated in relation to the plane of the metacarpals II and III (as in *Strix*, *Asio* and *Bubo*, whereas in *Athene* and *Glaucidium* it is not rotated); the metacarpals are parallel, and less separated than in other genera (excepting *Glaucidium*). The femur has the *crista trochantericus* decidedly less developed proximally than in *Athene*, *Asio*, *Strix*, *Surnia*, or *Aegolius*. The tibiotarsus has the *sulcus extensorius* markedly shallower than in *Athene*; the *condylus medialis* is nearly continuous with the axis of the bone, whereas in *Athene*, *Asio*, *Strix*, *Bubo*, *Surnia* and *Aegolius* it is more medially inclined; *Surnia* and *Glaucidium* have the tibiotarsus distinctly flattened in the cranio-

caudal plane. The tarsometatarsus has the proximal articular surface well excavated; as in *Strix* and *Asio* the lateral margin of the shaft does not slope gradually towards the distal part but starts parallel with the medial side and ends more abruptly than in *Athene*; the shape and orientation of the three *trochleae* are the most diagnostic trait of the tarsometatarsus of *Otus*. The central *trochlea* (*trochlea metatarsi III*) has two articular surfaces separated by a groove. In *Otus* the medial articular surface of the central trochlea is more rounded, whereas in all the remaining European strigiform genera this articular surface is pointed and more projecting towards the posterior part of the bone.

***Otus mauli*, new species**

(Figs. 2 and 3)

**Holotype:** Complete right tarsometatarsus (MMF 41628; collected 11 April 1984; see Fig. 3C).

**Type locality:** Ponta de São Lourenço (Madeira Island).

**Horizon:** Late Quaternary.

**Status:** Extinct.

**Etymology:** The new fossil owl species is named after Dr. *honoris causa* (1995) Günther Edmund Maul (7 May 1909 Frankfurt/M.– 28 Sept 1997 Funchal), who came to Madeira in October 1930. He worked first as a taxidermist in the Museu Municipal do Funchal (História Natural) and was later (1940–1981) its director. He was the leading expert on the Madeiran fauna in general, and especially on marine fishes. The majority of his publications (beginning in 1945) were listed by Wilhelm (2009). Wilhelm (2002 a, b) and Bischoit (1997) have provided obituaries.



**FIGURE 2.** Comparison of wing bones of *Otus mauli* n. sp. (A–E) from Madeira island and *O. scops*, IMEDEA 2205 (A'–E'). (A, MMF 41633, A') humeri, caudal view; (B, MMF 41640, B') ulnae, ventral view; (C, MMF 41636, C') radii, lateral view; (D, MMF 41643, D') carpometacarpi, ventral view; (E, MMF 41632, E') coracoid, ventral view. Scale = 2 cm.



**FIGURE 3.** Comparison of leg bones of *Otus mauli* n. sp. (A–C) from Madeira main island and *O. scops*, IMEDEA 2205 (A'–C'). (A, MMF 41638, A') femora, caudal view; (B, MMF 41641, B') tibiotarsi, cranial view; and (C, MMF 41628, holotype, C') tarsometatarsi, dorsal view. Scale = 2 cm.

**Paratypes (locality and dates of collection are included):** Madeira (Ponta de São Lourenço): MMF 41629, distal half of a right humerus with damaged distal end (Sep 1986); MMF 41630, distal part of a right ulna with damaged distal end (Sep 1986); MMF 41631, distal half of a right tibiotarsus with damaged distal end (Sep 1986); MMF 41632, almost complete right coracoid with the *processus procoracoideus* slightly broken (11 Apr 1984; Fig. 2E); MMF 41633, distal half of a left humerus with a damaged end (11 Apr 1984; Fig. 2A); MMF 41634, complete left tarsometatarsus (11 Apr 1984); MMF 41635, distal two-thirds of a left tarsometatarsus with damaged trochleae (19 Apr 1984); MMF 41636, proximal half of a left radius with the *arcus origo musculi extensor longus digiti major* broken (8 Apr 1984; Fig. 2C); MMF 41637, distal half of a right femur (Sep 1988); MMF 41638, almost complete right femur, slightly eroded around the *impressio musculi obturatorius* (9 Sep 1985; Fig. 3A); MMF 41639, diaphysis of a right femur (Sep 1986); DZUL 3054, proximal two-thirds of a right femur, with some damage at the end (Sep 1988); MMF 41640, almost complete left ulna, with the olecranon slightly broken and the *condylus ventralis ulnae* broken (Sep 1990; Fig. 2B); MMF 41641, almost complete left tibiotarsus with the *condylus medialis* only slightly eroded (Sep 1990; Fig. 3B); MMF 41642, distal part of a right humerus with a damaged distal end (Sep 1990); DZUL 3055, right tarsometatarsus, without trochlea metatarsi II (May 1992); MMF 41643, proximal half of a left carpometacarpus (May 1992; Fig. 2D); MMF 41644, fragment of diaphysis of a left ulna (Sep 1994); MMF 41645, medial fragment of a right humerus (Sep 1994).

**TABLE 1.** Measurements of *Otus mauli* n. sp. and *O. scops*: sample size, mean length  $\pm$  standard error (mm), and range. Measurements as in Campbell and Bocheński (2010).

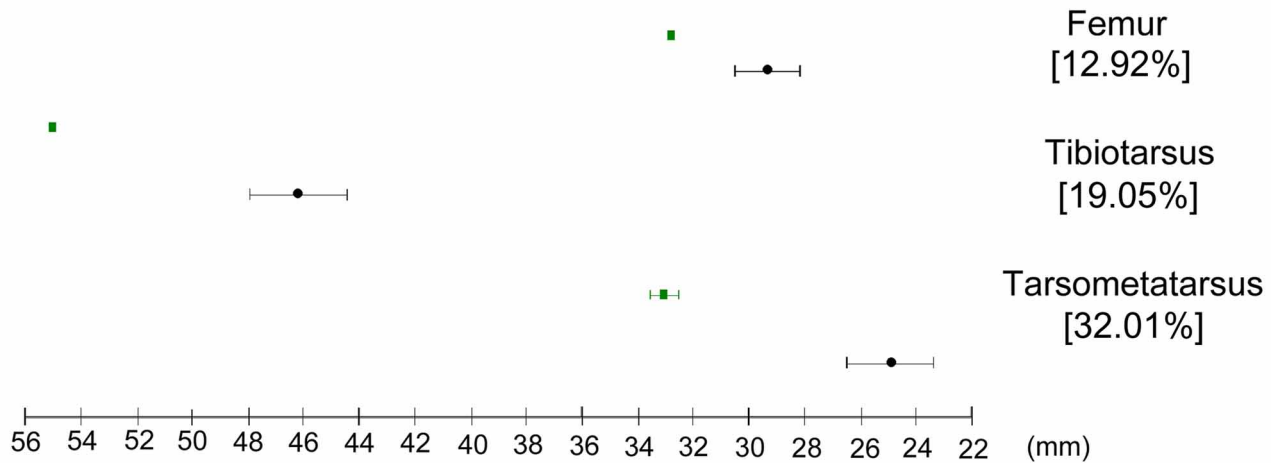
Measurements	<i>Otus mauli</i> n. sp.	<i>Otus scops</i>
Coracoid		
Length (A)	(1) 20.5	(25) 20.9 $\pm$ 0.6 [19.6–22]
Depth of acrocoracoid (B)	(1) 2.5	(25) 2.3 $\pm$ 0.2 [2–2.8]
Width of acrocoracoid (C)	(1) 3.3	(25) 3.5 $\pm$ 0.2 [3.3–4.1]
Width of shaft at procoracoid (D)	(1) 3.7	(25) 4.0 $\pm$ 0.2 [3.6–4.3]
Scapula		
Length fac. artic. humeralis (B)	(1) 2.5	(25) 2.8 $\pm$ 0.1 [2.5–3.0]
Width fac. artic. humeralis (C)	(1) 2.3	(25) 2.3 $\pm$ 0.2 [2.1–2.7]
Humerus		
Distal width (C)	(1) 7.4	(25) 7.5 $\pm$ 0.2 [7.0–7.9]
Ulna		
Proximal width (B)	(1) 4.8	(24) 4.8 $\pm$ 0.2 [4.5–5.1]
Proximal depth (C)	(1) 3.9	(25) 3.9 $\pm$ 0.2 [3.5–4.4]
Width of condylus dorsalis (D)	(1) 3.5	(25) 3.6 $\pm$ 0.2 [3.2–4.0]
Femur		
Length (A)	(1) 33.2	(25) 29.4 $\pm$ 1.0 [26.9–31.5]
Proximal width (B)	(1) 6.3	(25) 5.4 $\pm$ 0.2 [5.0–5.8]
Width at mid-shaft (C)	(2) 2.8 $\pm$ 0.1 [2.8–2.9]	(25) 2.4 $\pm$ 0.1 [2.2–2.7]
Depth at mid-shaft (D)	(2) 2.9 $\pm$ 0.1 [2.9–3.0]	(25) 2.4 $\pm$ 0.1 [2.0–2.7]
Distal width (E)	(2) 6.1 $\pm$ 0.05 [6.1–6.2]	(25) 5.5 $\pm$ 0.2 [5.2–5.9]
Distal depth (F)	(2) 5.3 $\pm$ 0.05 [5.3–5.3]	(25) 4.5 $\pm$ 0.2 [4.2–4.9]
Tibiotarsus		
Total length (A)	(1) 55.0	(24) 46.2 $\pm$ 1.6 [43.0–49.3]
Proximal width (B)	(1) 5.0	(25) 4.7 $\pm$ 0.3 [4.3–5.1]
Proximal depth (C)	(1) 6.0	(25) 5.3 $\pm$ 0.3 [4.5–5.8]
Width at mid-shaft (D)	(2) 2.4 $\pm$ 0.1 [2.3–2.5]	(25) 2.2 $\pm$ 0.2 [1.9–2.6]
Distal width (E)	(1) 5.4	(25) 5.2 $\pm$ 0.2 [4.9–5.6]
Condylus lateralis depth (F)	(1) 4.4	(25) 4.2 $\pm$ 0.2 [3.9–4.7]
Condylus medialis depth (G)	(1) 4.4	(25) 4.1 $\pm$ 0.2 [3.8–4.5]
Tarsometatarsus		
Total length (A)	(3) 33.4 $\pm$ 0.5 [33.8–32.8]	(25) 25.3 $\pm$ 1.6 [20.2–27.4]
Proximal width (B)	(3) 5.4 $\pm$ 0.2 [5.2–5.6]	(25) 5.1 $\pm$ 0.2 [4.7–5.3]
Hypotarsus length (C)	(1) 2.3	(25) 2.5 $\pm$ 0.3 [1.9–3.1]
Hypotarsus width (D)	(1) 1.3	(25) 1.4 $\pm$ 0.3 [1.2–1.7]
Minimum shaft width (E)	(4) 2.4 $\pm$ 0.1 [2.3–2.4]	(25) 2.4 $\pm$ 0.2 [2.1–2.7]
Distal width (F)	(2) 5.6 $\pm$ 0.1 [5.5–5.7]	(25) 5.5 $\pm$ 0.3 [5.1–5.9]

**Common name proposed:** Madeiran Scops Owl

**Diagnosis:** A species of *Otus* with forelimb elements about the same size as those of *O. scops*, but with relatively much longer and more slender hindlimb bones.

**Remarks:** This species appears to be closely related to *O. scops* because of the similar morphology of: *processus procoracoideus* and *processus acrocoracoideus* of the coracoid; acromial part of the scapula, including the *margo dorsalis scapularis*; both epiphyses of the ulna, femur, tibiotarsus and tarsometatarsus, with its characteristic central trochlea shape.

**Description.** Forelimb bones of *O. mauli* are very similar in size and morphology to those of *O. scops*, its closest living relative (Fig. 2 and Table 1). However, the hindlimb bones of both species are very different in size and proportions (Fig. 3). The total leg length (femur+tibiotarsus+tarsometatarsus) is 20.5% greater in the new species. The percentage of difference is not the same for each bone, being 12.92% (33.2 mm in *Otus mauli* vs. 29.4 mm in *O. scops* on average) for the femur; 19.05% (55.0 mm vs. 46.2 mm) for the tibiotarsus; and 32.01% (33.4 mm vs. 25.3 mm) for the tarsometatarsus (Fig. 4; Table 1). These percentages indicate that the relative proportions of leg bones in *O. scops* and *O. mauli* are different (Tables 2 and 3).



**FIGURE 4.** Leg bone lengths (mean  $\pm$  standard error in mm of femur, tibiotarsus and tarsometatarsus) of *O. mauli* n. sp. (squares) and *O. scops* (circles). The percentages of difference in mean length [%] between both species are also shown.

We estimated the weight of *O. mauli* to be c. 152 g (n = 1) through the Olmos *et al.* (1996) approach and c. 174 g (n = 2) through the Campbell and Marcus (1992) approach. The weight obtained from the femur length regression for *O. scops* is 107 $\pm$ 10 g (n = 25), the calculated range obtained with the same method (82–130 g) being close to the observed range for this species (64–135 g; Dunning 2008), while the weight obtained from the femur perimeter for *O. scops* ranges between 90 and 148 g (i.e., larger than the observed range). Although we should assume that they are overestimates of the weight of *O. mauli*, due to the similar size of the pectoral girdle of both species, our results seem to indicate that *O. mauli* probably had relatively weak powers of flight (Fig. 5).

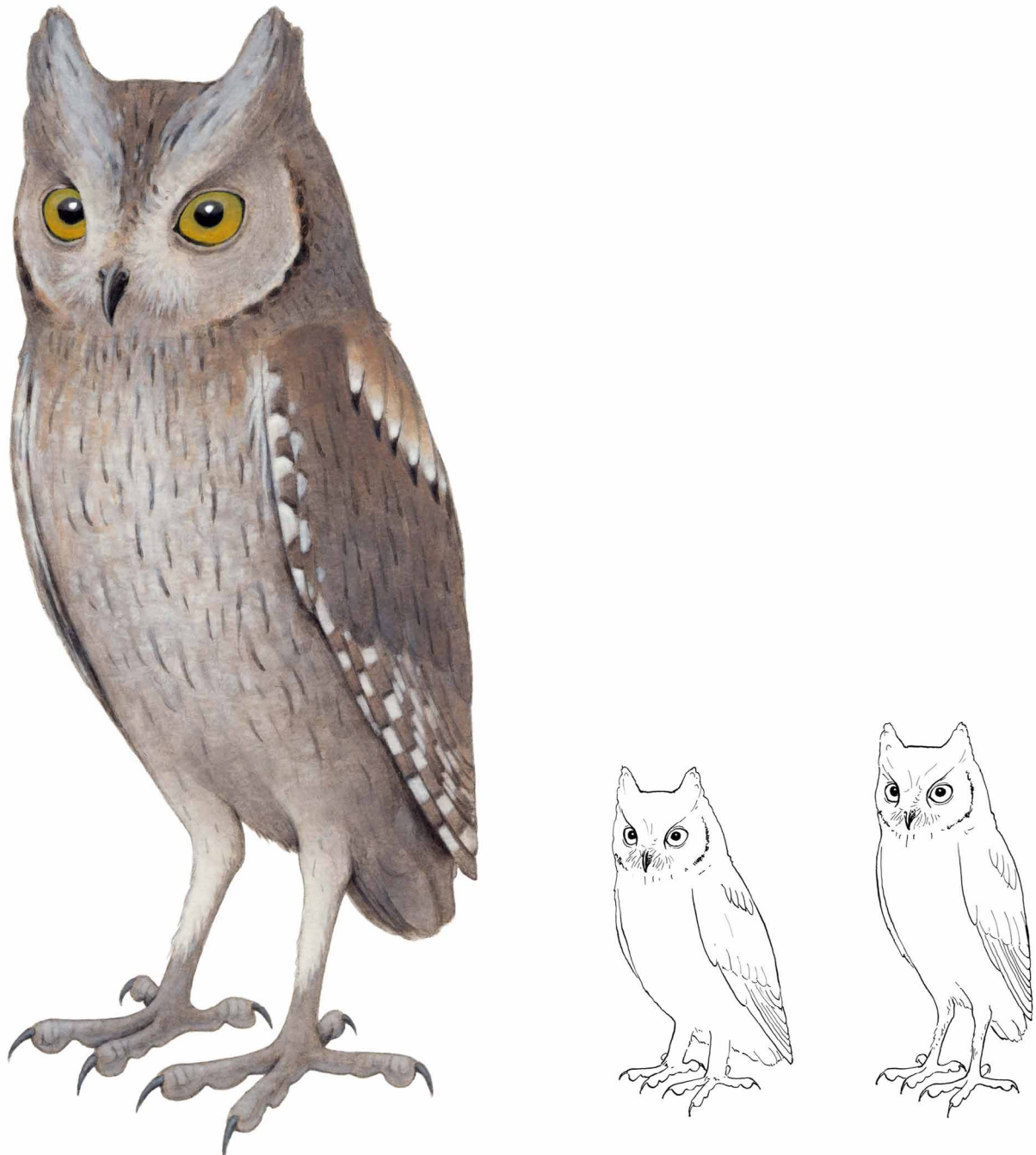
The PCA analysis performed with leg bone proportions (data from Tables 3 and 4) captured two principal components explaining 99.9% of total variance (Fig. 6). Of this total, 61.8% is explained by PC1 which shows a high positive weighting for tarsometatarsus length and a high negative weighting for femur length. The PC2 explained 38.1% of variance that measured tibiotarsus length.

**TABLE 2.** Mean length (in mm) and proportions (%) of leg bones (F: femur; Tbt: tibiotarsus; Tmt: tarsometatarsus) to total leg bone length (femur+tibiotarsus+tarsometatarsus) (Tot), and estimated weight (Em; in g) from mean femur length (using the approach of Olmos *et al.* 1996) for extinct insular owl species: *Otus mauli* from Madeira (this paper); *Athene trinacriae* from Sicily (Pavia & Mourer-Chauviré 2002); *A. cretensis* from Crete (Weesie 1982); *A. angelis* from Corsica (Mourer-Chauviré *et al.* 1997); *Mascarenotus sauzieri* and *M. murivorus* from Mauritius and Rodrigues (Mourer-Chauviré *et al.* 1994); *Grallistrix orion*, *G. geleches* and *G. erdmani* from Oahu, Molokai and Maui (Hawaii) (Olson & James 1991).

	Madeira <i>O. mauli</i>	Sicily <i>A. trinacriae</i>	Crete <i>A. cretensis</i>	Corse <i>A. angelis</i>	Mauritius <i>M. sauzieri</i>					
	%	%	%	%	%					
F	33.2	27.27	40.7	27.55	42.5	28.29	47.2	31.09	55.4	27.54
Tbt	55.0	45.24	66.1	44.75	65.4	43.54	65.2	42.95	85.2	42.29
Tmt	33.4	27.49	40.9	27.69	42.3	28.16	39.4	25.95	60.8	30.17
Tot	121.6		147.7		150.2		151.8		201.4	
Em	152		277		314		427		684	

continued.

	Rodrigues <i>M. murivorus</i>		Oahu <i>G. orion</i>		Molokai <i>G. geleches</i>		Maui <i>G. erdmani</i>	
		%		%		%		%
F	52.0	30.95	57.0	25.54	64.1	24.6	54.7	24.64
Tbt	72.5	43.15	100.5	45.03	116.0	44.51	98.0	44.14
Tmt	43.5	25.89	65.7	29.93	80.5	30.89	69.3	31.22
Tot	168.0		223.2		260.0		222.0	
Em	567		742		1045		687	



**FIGURE 5.** Left. Reconstruction of *Otus mauli* n. sp. (Madeiran Scops Owl). Right. Compared sketches of *Otus scops* and *Otus mauli* n.sp. Art by Pau Oliver.



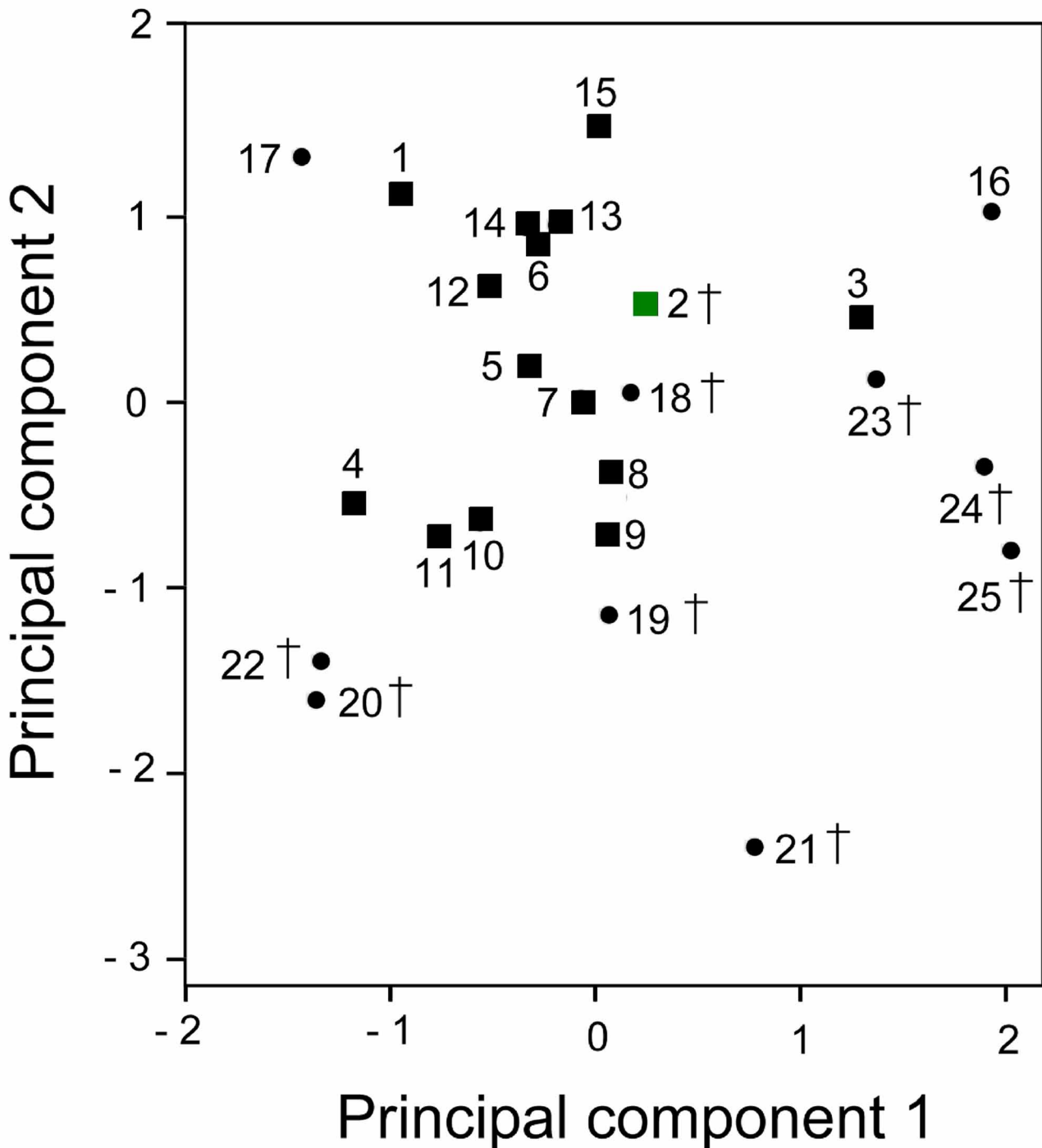
**TABLE 3.** Measurements and proportions (%) of extant scops owls and related taxa: sample size (n), mean length (mm) of leg bones (F: femur; Tbt: tibiotarsus; and Tmt: tarsometatarsus), and total leg bone length (femur+tibiotarsus+tarsometatarsus) (Tot).

<i>O. scops</i>		<i>O. elegans</i>		<i>O. nudipes</i>		<i>O. petersoni</i>		
(n)	24	%	4	%	5	%	1	%
F	29.4	29.13	32.6	27.21	34.3	25.36	32.9	30.3
Tbt	46.2	45.8	55.4	46.27	61.2	45.28	47.9	44.07
Tmt	25.3	25.05	31.8	26.52	39.7	29.36	27.8	25.62
Tot	100.9		119.8		135.2		108.6	
<i>O. watsonii</i>		<i>O. clarkii</i>		<i>O. choliba</i>		<i>O. atricapillus</i>		
(n)	3	%	1	%	5	%	1	%
F	35.6	28.36	37.7	28.14	33.9	28.04	34.2	27.98
Tbt	56.4	44.93	59.0	43.98	55.0	45.58	54.7	44.72
Tmt	33.5	26.7	37.4	27.88	31.8	26.38	33.4	27.29
Tot	125.5		234.1		120.7		122.3	
<i>O. trichopsis</i>		<i>O. magicus</i>		<i>O. kennicottii</i>		<i>O. asio</i>		
(n)	1	%	4	%	6	%	6	%
F	30.3	27.95	36.1	28.1	39.0	29.19	38.5	29.62
Tbt	48.0	44.31	58.7	45.66	58.8	44.02	57.0	43.91
Tmt	30.0	27.73	33.7	26.23	35.8	26.79	34.4	26.46
Tot	108.3		128.57		133.6		129.9	
<i>O. megalotis</i>		<i>O. bakkamoena</i>		<i>Ptilopsis leucotis</i>		<i>Gymnoglaux lawrencii</i>		
(n)	4	%	3	%	1	%	1	%
F	37.9	28.57	34.7	27.8	44.1	29.94	29.0	23.94
Tbt	60.5	45.18	57.1	45.69	67.7	45.98	77.7	45.91
Tmt	34.8	26.25	33.1	26.51	35.5	24.08	36.6	30.14
Tot	133.2		124.9		147.3		121.3	

### *Otus* cf. *O. mauli*

The Porto Santo Scops Owl  
(Fig. 7)

Due to fragmentation and poor preservation, it is impossible to refer the bones of *Otus* from Porto Santo to *O. mauli* with any degree of confidence. Nevertheless, as in the Madeiran *Otus mauli*, the wing bones are similar in size to *O. scops*, whereas the hindlimb bones are longer, roughly similar in size or slightly smaller than those of the Madeiran species. Thus, they clearly represent either *Otus mauli* or a close relative, and thus are listed here as *Otus* cf. *mauli*. The material from Porto Santo consists of (localities and collection dates indicated; Fig. 1): MMF 41646, damaged left ulna with the proximal end broken and the distal end slightly broken (Porto dos Frades, 21 Sep 1985); MMF 41647, left humerus with the proximal end broken and epicondylus dorsalis and condylus ventralis humeri slightly damaged (Fonte da Areia, 20 Sep 1985); DZUL 3056, fragment of diaphysis of a right tibiotarsus (Fonte da Areia, 20 Sep 1985); MMF 41648, left tarsometatarsus with distal articulation broken and *crista medialis hypotarsi* and *crista hypotarsi* broken (Porto dos Frades, 14 Apr 1984); MMF 41649, small proximal fragment of a left radius (Porto dos Frades, 21 Sep 1986); MMF 41650, right scapula with the acromion slightly eroded and the *extremitas caudalis* broken (Porto dos Frades, 22 Sep 1989); MMF 41651, fragment of diaphysis of a right humerus (Porto dos Frades, 18 May 1992).



**FIGURE 6.** PCA plot for the two principal components obtained from leg bones (femur, tibiotarsus and tarsometatarsus) proportions of existing scops owls (genus *Otus*, squares), related species and other insular extinct owls (†). Data from Tables 2 and 3. 1: *Otus scops*; 2: *O. maui* n. sp.; 3: *O. nudipes*; 4: *O. petersoni* Fitzpatrick and O'Neill; 5: *O. watsonii* (Cassin); 6: *O. choliba* (Vieillot); 7: *O. atricapillus*; 8: *O. trichopsis*; 9: *O. clarkii*; 10: *O. kennicottii* (Elliot); 11: *O. asio* (Linnaeus); 12: *O. megalotis* (Walden 1875); 13: *O. bakkamoena* Pennant; 14: *O. magicus* (Müller); 15: *O. elegans* (Cassin); 16: *Gymnoglaux lawrencii*; 17: *Ptilopsis leucotis* (Temminck); 18: *Athene trinacriae*; 19: *A. cretensis*; 20: *A. angelis* Mourer-Chauviré *et al.* 1997; 21: *Mascarenotus sauzieri*; 22: *M. murivorus* Mourer-Chauviré *et al.*; 23: *Grallistrix orion*; 24: *G. geleches*; 25: *G. erdmani*.



**FIGURE 7.** Comparison of bones of *Otus cf. mauli* (A–C) from Porto Santo and *O. scops*, IMEDEA 2205 (A'–C'). (A, MMF 41651, A') humeri, caudal view; (B, MMF 41646, B') ulnae, ventral view; and (C, MMF 41648, C') tarsometatarsi, dorsal view. Scale = 2 cm.

## Discussion

The location of Madeira more than 600 km from the mainland of Europe and Africa, and far from the main migratory pathways between those continents (Fig. 1), may have favored the ancient isolation of a population of *Otus* in the archipelago that subsequently gave rise to the endemic *O. mauli*. This situation differs from that of Mediterranean islands, where no endemic species of scops owl exists and *O. scops* is present in the fossil record in Pleistocene and Holocene levels on several islands (Alcover *et al.* 1992). The geographic situation of the Mediterranean islands, close to migratory pathways, probably precluded differentiation of the breeding insular populations of this migratory bird there.

The leg bone proportions of *O. mauli* probably reflect a different foraging behaviour and habitat from those of *O. scops*. Although having a long tarsometatarsus does not seem to be important for walking or hopping locomotion in birds (Zeffer & Norberg 2003), the long legs together with the high wing loading of *O. mauli* seem to indicate a more ground-dwelling life-style, as it has been also assumed for other insular strigiforms (e.g., Louchart 2005). This hypothesis is supported by the fact that the proportions of the leg bones of *O. mauli* are similar to those of *Athene trinacriae* Pavia and Mourer-Chauviré 2002 (Table 2), an extinct owl from the Pleistocene of Sicily, so both species are very close in the PCA analysis (Fig. 6). The size of the wings and legs of *Athene trinacriae*, especially the tarsometatarsus, were thought to indicate a terrestrial life-style (Pavia & Mourer-Chauviré 2002). The proportions of the leg bones of *O. mauli* and *A. trinacriae* are comparable with those of *A. cretensis* Weesie 1982 from the Pleistocene of Crete, with the femur and tarsometatarsus of approximately equal length (Table 2). Both extinct Mediterranean owls inhabited islands without terrestrial predators and fed mainly on small endemic rodents (Weesie 1982; Pavia & Mourer-Chauviré 2002).

The diets of the small scops owls are dominated by invertebrates (del Hoyo *et al.* 1999; Marchesi & Sergio 2005). *Otus mauli* may have inhabited the floor of laurel forests, an ecosystem with a great variety of species of invertebrates (Oromí 1995) and lacking other invertebrate-eating raptors. In addition, the dense and closed-canopy

ecosystem of the laurel forest may have offered protection from avian predators such as Eurasian Sparrowhawk *Accipiter nisus* (Linnaeus), Common Buzzard *Buteo buteo* (Linnaeus), and Common Kestrel *Falco tinnunculus* Linnaeus that inhabit the archipelago (Pieper 1985; Equipa Atlas 2008). This idea is supported by the PCA analyses, which place *O. mauli* and *A. trinacriae* close to *O. atricapillus* (Temminck), *O. trichopsis* (Wagler) and *O. clarkii* Kelso and Kelso 1935 (Fig. 6), three species that inhabit dense American forests and occasionally hunt on the ground (del Hoyo *et al.* 1999). These five species together with *A. cretensis* display a very close value in the PC1 axis. That is, they have similar proportions of femur and tarsometatarsus (Fig. 6). Because of the absence of rodents and the scarcity of predators in the archipelago, lizards (*Teira dugesii* (Milne-Edwards)) and small birds may also have been part of the diet of *O. mauli*.

Other extinct insular owls, especially those of larger size than *Otus* or *Athene*, have a proportionally longer tarsometatarsus (Table 2), i.e. *Mascarenotus sauzieri* Mourer-Chauviré *et al.* 1994 from Mauritius, and *Grallistrix orion* Olson and James 1991, *G. geleches* Olson and James 1991, and *G. erdmani* Olson and James 1991 from the Hawaiian Islands. These different proportions of the leg bones probably reflect different predatory behaviour from that of *O. mauli*, *A. trinacriae* or *A. cretensis*. In the case of *Gallistrix* the elongated legs and shortened wings are surely adaptations for bird-catching that parallel the bone proportions in the bird-eating hawks of the genus *Accipiter* (Olson & James 1991), which was confirmed by the discovery of fossil pellets showing that *Grallistrix* fed on birds (Olson & James 1982b).

The existing insular species *Gymnoglaux lawrencii* (Sclater & Salvin) from Cuba and Isle of Pines, and *O. nudipes* (Daudin) from Puerto Rico and the Virgin Islands, have very long tarsometatarsi comparable with those of the extinct Hawaiian owls (Table 3; Fig. 6).

Climatic and anthropogenic causes have been suggested to explain insular bird extinctions and in most cases a direct correlation with human arrival has been shown (Olson & James 1982a; Worthy & Holdaway 2002; Steadman 2006). The recent aspect of the bones of *O. mauli*, together with the Holocene <sup>14</sup>C ages obtained for some of the extinct birds from the Madeira archipelago (unpublished data), and the documented extinction of other vertebrates after human settlement elsewhere in Macaronesia (Rando & Alcover 2008; Rando *et al.* 2008; Rando & Alcover 2010) suggest that the extinction of *O. mauli* was related to human arrival. Forest habitat alterations due to human activities could have been the cause of extinctions, as has also been suggested for the extinctions of Hawaiian and New Zealand forest birds (James & Olson 1991; Olson & James 1991; Worthy & Holdaway 2002; James & Price 2008; Boyer 2008). Two main habitat alterations occurred in Madeira after human arrival—the burning of the forest and the introduction of alien rodents. Burning was the method used by the initial Portuguese settlers to clear the land for farming, and it has been suggested that, following the initial Portuguese firing, Madeira burned continuously for seven years afterward (Crosby 1988). Another dramatic habitat alteration probably occurred after the introduction of rodents. The chronology of the introduction of *M. musculus* Linnaeus 1758 is unknown, but it is very probably related to the first human presence (Gabriel *et al.* 2010). This event in Madeira has traditionally been linked to Portuguese people during the 15<sup>th</sup> century (Crosby 1988), but an earlier introduction cannot be ruled out (Förster *et al.* 2009). Very probably, after the Portuguese colonization, rats (*Rattus* spp.) were introduced also. Both kinds of rodents, especially rats, would have reached very high densities in the Madeiran laurel forest, paralleling the evidence available from the Canary Islands (Martín *et al.* 2000). Because *O. mauli* likely bred on or very close to the ground due to the absence of terrestrial predators, as has also been indicated for the extinct Hawaiian owls (Olson & James 1991), burning and rodent predation on eggs, nestlings, and prey of *O. mauli* probably had a significant negative effect on the species.

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