

## Long-term ecological change in a conservation hotspot: the fossil avifauna of Mé Auré Cave, New Caledonia

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**Abstract** Through the continuing accumulation of fossil evidence, it is clear that first human arrival on islands around the world was linked to a rise in the extinction rate for vertebrates. Bones in human-era fossil sites can also reveal changes in the composition and structure of ecological communities due to human environmental impacts. New Caledonia is a large and biogeographically distinct island in the southwest Pacific and is considered a critical priority for biodiversity conservation. We examined fossil birds from the Mé Auré Cave site (WMD007), located in lowland dry forest on the west coast of New Caledonia. Accumulation of bird skeletal material in the cave was primarily through deposition in barn owl (*Tyto alba*) pellets. The site recorded the island-wide extinction of two species and extirpation of at least two other species from the lowlands in the past 1200 years. Species richness of birds in the stratigraphic deposit was quite high, reflecting the catholic diet of barn owls on islands, and many species have continued to persist near the site despite loss and degradation of the dry forest. However, we found substantial turnover in relative abundance of species in the cave deposit, with edge and open country birds becoming more common through time. These changes may reflect the severe reduction of dry forest habitat during the colonial period. This work provides a temporal record of avifaunal and environmental change in the threatened dry forest habitat that should be particularly informative for ongoing conservation and restoration efforts.

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## Introduction

New Caledonia is a biodiversity hotspot, harboring extraordinary levels of species richness and endemism and is renowned for biotic assemblages found nowhere else in the world (Myers et al. 2000; Bouchet et al. 2002; Najit and Grandcolas 2002). Situated in the tropical southwest Pacific about 1200 km east of Australia and 1800 km northwest of New Zealand, the main island of New Caledonia is a large (18,575 km<sup>2</sup>) fragment of the ancient Gondwanan supercontinent with a complex geological history (Paris 1981; Heads 2008). It was separated from Australia around 80 million years ago (Neall and Trewick 2008), was subsequently submerged, and the current landmass was uplifted and emerged ca. 37 million years ago (Grandcolas et al. 2008). Such prolonged isolation, combined with the complex and varied landscape, has provided the evolutionary opportunity for multiple adaptive radiations (Smith et al. 2007) and the persistence of relictual fauna and flora. Nearly 90% of the native flora is endemic to the island (Jaffré et al. 2004), and there is exceptional endemism in lizards (Pascal et al. 2008) and invertebrates (Solem 1964; Chazeau 1993). New Caledonia has about 64 native terrestrial bird species, of which 20 are endemic (Ekstrom et al. 2002), and is among the Pacific region's top areas for the number of endemic restricted-range species of birds (Birdlife Intl. 2010). The IUCN Red List of Threatened Species (2009) lists 10 species of New Caledonian landbirds, including the nearly-flightless Kagu (*Rhynochetos jubatus*), the only surviving representative of the family Rhynochetidae.

The combination of high conservation value and a range of ongoing threats has led New Caledonia to be listed as a critical priority for biodiversity conservation (Olson and Dinerstein 1998). Prior to human impacts, the central mountains and mesic eastern slope supported evergreen rain forests, ultrabasic soils on the southern part of the island supported a highly endemic maquis shrubland, and the dry, western coast was characterized by sclerophyllous forest (Jaffré et al. 1998). These dry forests are considered among the world's most endangered based on the current extent of the forest, degree of endemism of the flora, lack of protected areas, and number of threatened species (Gillespie and Jaffré 2003). Over half of the vascular plants found in the sclerophyll forest (230 of 379 spp.) are endemic to New Caledonia and 59 species are restricted to that habitat alone (Bouchet et al. 1995; Jaffré et al. 1998). Extensive land clearance, cattle ranching, intentional and unintentional fires, and invasive ungulates have reduced dry forest cover to less than 2% of its original extent (Bouchet et al. 1995).

New Caledonia was first colonized by proto-Polynesian people around 3000 years ago (Sand 1996), and is still inhabited by their descendants, the Kanak people. Populous communities were supported by intensive agricultural systems, including cultivation of taro on hillside terraces and extensive dryland field systems (Sand and Ouetcho 1993; Kirch 2000), evidence of which is still visible on the landscape today (Sand 1996). Stratigraphic evidence indicates that ancient societies had a profound effect on the vegetation, in some areas converting lowland forest to a more open and species-poor landscape through repeated episodes of fire and erosion (Stevenson and Dodson 1995; Stevenson et al. 2001).

Since contact with European sailing ships in 1774 (Cook 1784), human ecological impacts on the island have intensified. French settlement began in earnest in 1864 with the

establishment of penal colonies along the west coast, and much of the early colonial agricultural settlement was carried out by convict labor (Compton 1917). Initial efforts were directed at establishing a sugar industry on the west coast (Thompson 1984). Large tracts of land were also granted to free settlers for cattle ranching, which expanded rapidly; by 1877 there were >75,000 head of cattle on the island (Parsons 1945). Introduction of rusa deer (*Cervus timorensis russa*) from Java in the 1870s was particularly damaging to the dry forest. The population reached an estimated 220,000 animals before World War II and is currently thought to number over 110,000 (de Garine-Wichatitsky et al. 2009). Today, browsing by deer is a serious threat to the dry forest understory and prevents regeneration of trees (de Garine-Wichatitsky et al. 2005; Spaggiari and de Garine-Wichatitsky 2006). It appears that in the first 50 years of European presence, frequent fires, clearing of forest, increasing aridity, and browsing by introduced ungulates resulted in the loss of a substantial portion of the remaining lowland dry forest, and the overall landscape of the west coast was considerably altered from its pre-European state.

Paleontological studies on other Pacific islands have revealed extensive extinctions of vertebrates, particularly of birds, that took place after first human arrival and were caused by ecological changes associated with the initial human settlement of the islands (Steadman 2006). Historical archives and museum specimens document that ecological deterioration has continued throughout historical time on many Pacific islands (Blackburn et al. 2004; Pimm et al. 2006). Vertebrate fossil records from the late Pleistocene and Holocene of these islands often reveal pre-human ecological communities that were very different in composition and structure from that occurring on the islands at present. Although interesting fossils have been described, the fossil record of New Caledonia is not as well known as that of Hawaii and New Zealand for example. A number of small collections of vertebrate fossils from New Caledonia were studied in the 1970s, and the work of Balouet (1984) and later Balouet and Olson (1989) added several important fossil localities. Balouet and Olson (1989) estimated that 40% of non-passerine birds became extinct in the late Quaternary. More recently, excavations on the Pindai peninsula provided additional support for substantial turnover in the fauna of large vertebrates during the Holocene (Anderson et al. 2010). At least 18 extinct species of birds are known from fossil remains, including a large snipe, large flightless rails, diverse guilds of pigeons and megapodes (Balouet and Olson 1989), and a giant flightless relative of megapodes, *Sylviornis neo-caledoniae* (Poplin and Mourer-Chauviré 1985). However, to date, only limited stratigraphic and chronological overlap has been documented between fossil vertebrates and humans (i.e. Anderson et al. 2010). Fossils of passerine birds have not been examined in detail, and important questions remain regarding the timing of extinction and extirpation in relation to both pre-contact Kanak and colonial-era ecological impacts.

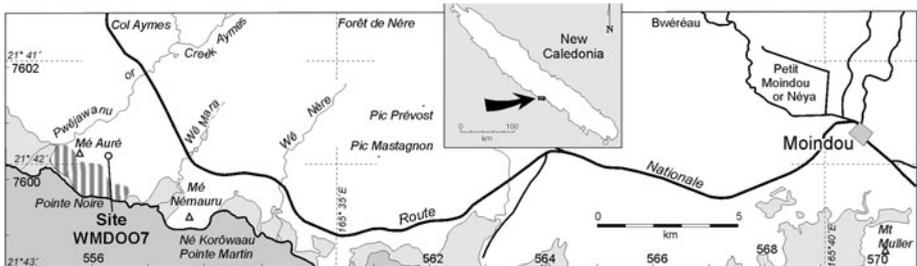
Considering the unique biogeography and critical conservation priority of New Caledonia, further exploration of the biotic history of the island is needed. In this study we analyzed a bone assemblage of primarily small-bodied birds from a cave deposit in a dry forest fragment in New Caledonia. This deposit, containing the only New Caledonian bird bone assemblage firmly dated to the human era, provided a continuous record of local avifaunal change over the past ~1200 years. In order to understand the effects of long-term changes in the dry forest habitat, we examined avifaunal turnover in the cave deposit in conjunction with a modern bird survey of the local area. Our primary goal was to understand the effects of long-term habitat degradation by examining the records of extinction, extirpation, and turnover of birds through time at the site.

## Previous work at Mé Auré Cave

### Excavations and collections

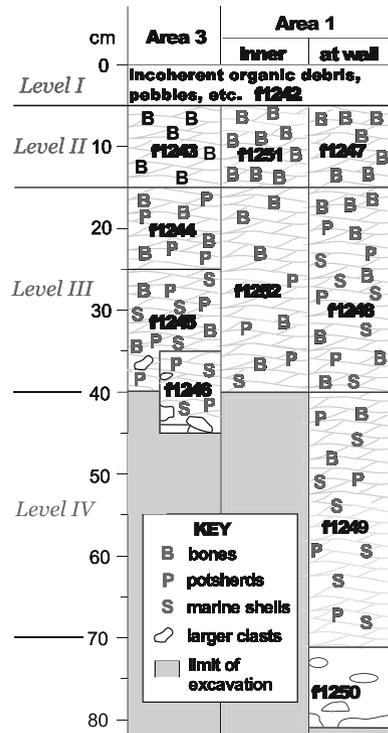
Mé Auré Cave, located approx. 13 km west of Moindou on the central southwest coast of New Caledonia (Fig. 1), was excavated in 1995 (Grant-Mackie et al. 2003). The site is designated WMD007 in the catalog of the Département Archéologie, Service des Musées et du Patrimoine de Nouvelle-Calédonie. The cave was formed in Eocene limestone about 750 m north of the coast and 50 m above sea level on the northeast face of a low hill. This hill and the neighboring Mé Auré hill are covered by remnant sclerophyllus forest and surrounded on the north and east by cattle pastures. The cave entrance is roughly triangular, about 2.5 m high, and opens to a sediment floor of about  $3 \times 3$  m. The far wall, about 3 m from the entrance, has a smaller opening about 2 m high  $\times$  0.6 m wide leading to a passage that is partially filled with limestone rubble and sediment and extends for  $\sim 6$  m until becoming completely closed by rubble. At the time of the 1995 excavation, the floor of the cave had a scattering of fallen roof slabs, and abundant small bones, plant debris, snail shells, and owl pellets; there was no visible sign of human activity.

Excavations of about  $1.5 \text{ m}^2$  of the cave floor in 1995 (details in Grant-Mackie et al. 2003) yielded three stratigraphic columns (in areas 1 and 3; Fig. 2) composed of dry, powdery wood ash and small charcoal fragments in thin lenses of dark and light gray and red-brown colored sediment (Horrocks et al. 2008). Interfingering with these were concentrations of small bones along with human bone, pottery sherds, landsnails, marine molluscs, and crab claws. In area 3, excavation was discontinued within this deposit at 45 cm depth, but in area 1 it extended to 80 cm where limestone slabs impeded further excavation. The potsherd/ash deposit began above 70 cm depth and from 80 to 70 cm depth the deposit consisted of limestone clasts and native land snail (*Placostylus duplex*) shells in a dark red-brown friable sandy deposit. All excavated material was passed through a 3 mm sieve then handpicked to remove debris. Stratigraphic control was rather coarse because of the limestone clasts encountered (see Fig. 2), and the excavation was divided into four broad stratigraphic levels: level I (surface, 0–5 cm depth), level II (5–15 cm), level III (15–40 cm), and level IV (40–70 cm). Bulk collections from each stratigraphic level were allotted a running number prefixed by NC/f, as in NC/f1242; here, however, the initial part of the catalog number is omitted and collections cited only as, e.g., f1242. Collections are held in the School of Geography and Environment, University of Auckland, and cataloged in the New Caledonian Fossil Record File (for collections of New Caledonian fossils held in New Zealand institutions).



**Fig. 1** Location map of Mé Auré Cave (site WMD007) and the “Deux Frères” dry forest (area indicated by hatched shading) on the southwestern coast of New Caledonia

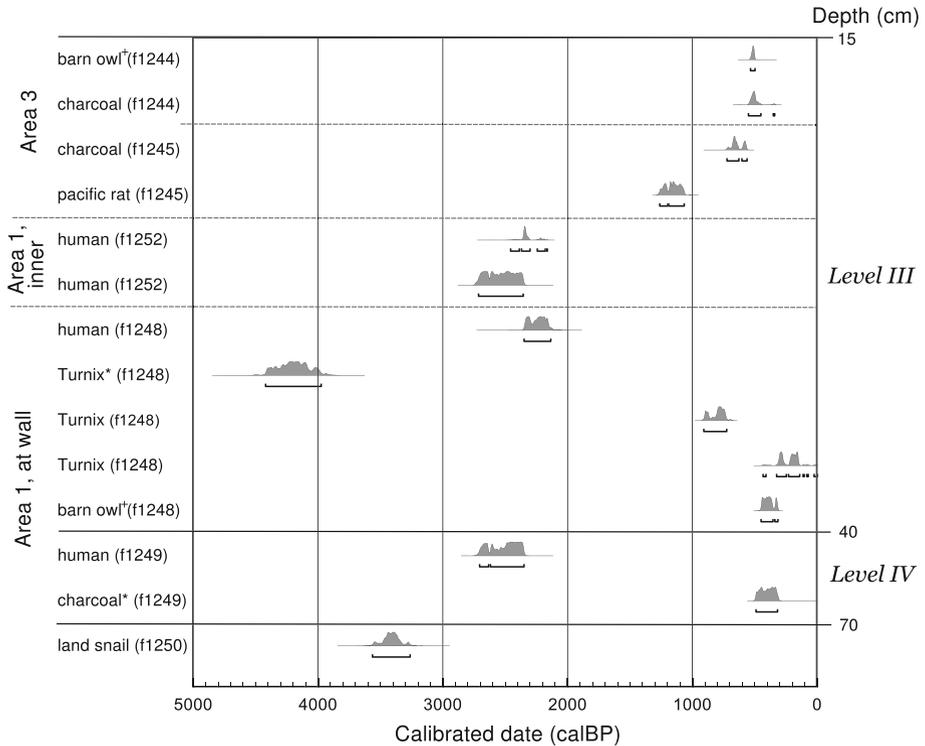
**Fig. 2** Stratigraphic diagram of Mé Auré Cave excavations showing locations of bone, potsherds, and shells. Modified from Horrocks et al. (2008)



**Chronology and faunal trends**

The deposits in Mé Auré Cave have been analyzed for their herpetofauna (Grant-Mackie et al. 2003), land snail content (Cowie and Grant-Mackie 2004), and plant microfossils (Horrocks et al. 2008). These studies provided a preliminary chronology of the deposits, which we summarize here. A radiocarbon age determination from a *Placostylus* land snail shell from the lowermost layer in area 1 (75 cm depth) returned a date of  $3240 \pm 60$  <sup>14</sup>C years BP (Fig. 3). Human use of the cave may correspond to ca. 2500–2300 years BP, the age of disassociated human bones found in levels III and IV in area 1. Abundant wood ash, charcoal, potsherds, marine shells and crab claws, and starch granules from taro and yams suggest that the cave was used as a cooking site (Horrocks et al. 2008). Because the style of the recovered potsherds is Podtanean (paddle-impressed) rather than Lapita (dentate-stamped), it is thought that the cave was not used by people until several centuries after New Caledonia had first been colonized (Horrocks et al. 2008).

At approximately 40 cm depth (level III) abundant bones of the Pacific rat (*Rattus exulans*) and frog (*Litoria aurea*) bones appeared. Both species are prey of owls and their appearance likely marked the arrival of the predator, not necessarily the prey (Grant-Mackie et al. 2003). The modern owl occupant is the barn owl (*Tyto alba*), part of a cosmopolitan species complex (Bruce 1999), and it could have colonized New Caledonia as recently as in prehistoric human times (Anderson et al. 2010). The Pacific rat was almost certainly introduced to New Caledonia as part of the canoe fauna transported by Polynesian people (Matisoo-Smith and Robins 2004; but see Anderson et al. 2010), and this is supported by the occasional occurrence of its bones in level IV. European-introduced rodent



**Fig. 3** Calibrated radiocarbon dates from the Mé Auré Cave excavations. + Dates obtained in this study. \* Regarded as anomalous by Horrocks et al. (2008)

species occur above 15 cm depth (level II), assumed to approximate early European contacts with New Caledonia over 200 years ago.

Land snails from the Mé Auré Cave deposits were examined by Cowie and Grant-Mackie (2004), who recorded 20 species with all but two being considered native. *Allopeas gracile*, widely introduced around the western Pacific by humans in pre-European times, was found in both pre- and post-European horizons, and *Achatina fulica*, a twentieth-century introduction, was found only on the surface (level I). With regard to the herpetofauna, bones of a native gecko with a wide distribution throughout New Caledonia (*Bavayia cyclura*) were identified from above 40 cm depth (levels I–III) and a single bone of the rough-snouted giant gecko (*Rhacodactylus trachyrhynchus*) was found in level IV (Grant-Mackie et al. 2003). This is the second-largest gecko in New Caledonia, a species previously considered restricted to the humid forests, and its occurrence in Mé Auré Cave suggests that the species once may have been more widely distributed in west coastal dry forests (Grant-Mackie et al. 2003).

## Methods

We examined all recovered bird bones from the 1995 excavation of Mé Auré Cave. Bones were identified by reference to the avian skeletal collections at the National Museum of Natural History (NMNH), Washington, DC, supplemented with selected skeletons from the

Florida Museum of Natural History (FLMNH), Gainesville, FL. Comparative material examined, listed in [Appendix 1](#), included skeletons of resident and migrant land bird and breeding seabird species from New Caledonia (following Doughty et al. 1999). We attempted to identify all bones to species. Juveniles were identified as such based on the porosity and texture of the surfaces of long bones. Anatomical inventory of the stratigraphic collection allowed the number of identified specimens (NISP) and minimum number of individuals (MNI) to be calculated. MNI was based on the most common element (right or left side) of each species in each broad stratigraphic level. We classified species into four general habitat categories (open country, secondary or disturbed scrub or forest, primary or closed-canopy forest, and wetlands) based on primary habitat affinity listed in Desmoulins and Barré (2005) and Doughty et al. (1999). Average body mass (in grams) of each species was obtained from USNM skeletal specimens collected in New Caledonia, where available (~50% of species), or was taken from literature sources (Dunning 2008; del Hoyo et al. 2009).

We obtained radiocarbon dates from two different individual barn owls from level III, the lowest level of owl bone occurrence in the cave (two right coracoids in units f1244 and f1248). Prior to dating, collagen was extracted from the bones, purified by passing through an XAD resin filter, and prepared to graphite using a protocol modified from Stafford (1991) in the Ostrom Stable Isotope Laboratory at Michigan State University. Dating was performed by the W. M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at the University of California, Irvine. Reporting of ages follow the conventions of Stuiver and Polach (1977). Sample preparation backgrounds were subtracted, based on measurements of  $^{14}\text{C}$ -free whalebone. All results were corrected for isotopic fractionation, with  $\delta^{13}\text{C}$  values measured on prepared graphite using accelerator mass spectrometry. Calendar year calibrations were performed for all dates based on the southern hemisphere atmospheric curve (McCormac et al. 2004) as implemented in OxCal v4.1.5 (Bronk Ramsey 2009). Previous studies of Mé Auré Cave provided a chronology of its deposits, and these dates along with the two dates obtained in this study are summarized in [Fig. 3](#). For convenience, we divide the chronology of Mé Auré Cave into two distinct periods; we refer to the period following human colonization, recognized by the occurrence of bones of the Pacific rat (*R. exulans*), as ‘prehistoric’, and the time after European contact with New Caledonia and introduction of the black rat (*R. rattus*), as ‘historic’.

We compared the faunal lists and abundances of species among the excavated strata with data from a recent bird survey of the adjacent “Deux Frères” dry forest fragment (area 73 ha; [Fig. 1](#)). The bird survey was conducted in September 2004 by Frédéric Desmoulins as part of the New Caledonian dry forest conservation initiative (Le Programme de Conservation des Forêts Sèches; <http://www.foretseche.nc>), with identifications being made by audio and visual survey at 17 survey points throughout the forest.

## Results

We identified 1338 bird bones from the Mé Auré Cave deposits to the species level. These represented at least 36 species in 20 families and nine orders ([Table 1](#)). 786 additional bones of small passerines were identified to genus and ca. 1500 bones consisting mainly of fragments (~21%), very immature birds (~12%), or postcranials of small passerines (~67%), were not determined to genus or species. The Mé Auré Cave avifauna is notable in its diversity; 56% of the living, native species of New Caledonian landbirds (36 of 64 spp.) and 76% of birds recorded in the area in 2004 (26 of 34 spp.) are represented.

**Table 1** Birds identified from Mé Auré Cave deposits

Order	Taxon	Modern survey			
		I	II	III	IV
Tumiciformes	<i>Turnix varius novaecaledoniae</i> <sup>a</sup>	22 (5)	57 (8)	77 (10)	1
Gruiformes	<i>Gallinulus philippensis</i>	8 (4)	19 (3)	7 (3)	-
	<i>Porzana tabuensis</i>	4 (1)	4 (2)	2 (2)	1
	<i>Porphyrio porphyrio</i>	-	-	2 (1)	-
Columbiformes	<i>Columba vitiensis</i>	-	-	-	-
	<i>Streptopelia chinensis</i> <sup>b</sup>	-	-	-	-
	<i>Chalcophaps indica</i>	6 (1)	10 (3)	2 (1)	-
	<i>Ptilinopus greyii</i>	16 (3)	9 (2)	-	-
Psittaciformes	<i>Cyanorhamphus novaeseelandiae</i>	1	-	-	-
	<i>Trichoglossus haematodus</i>	1	1	-	-
Cuculiformes	<i>Cacomantis flabelliformis</i>	1	-	1	-
	<i>Chrysococcyx lucidus</i>	4 (2)	-	-	-
	<i>Eudynamis</i> cf. <i>taitensis</i> <sup>c</sup>	-	-	2 (1)	-
Strigiformes	<i>Tyto alba lulu</i>	113 (10)	71 (8)	30 (4)	-
Apodiformes	<i>Collocalia</i> sp.	2 (1)	9 (3)	1	-
Coraciiformes	<i>Todiramphus sanctus</i>	49 (7)	40 (7)	1	1
Passeriformes	<i>Lichmera incana</i>	17 (5)	8 (3)	1	-
	<i>Philemon diemenensis</i> <sup>d</sup>	26 (9)	18 (5)	1	1
	<i>Myzomela caledonica</i>	1	5 (3)	-	-
	<i>Phylidonyris undulata</i> <sup>d</sup>	-	13 (4)	-	-
	<i>Gerygone flavolateralis</i>	14 (4)	2 (1)	-	-
	<i>Eopsaltria flaviventris</i> <sup>d</sup>	1	2 (1)	-	-
	<i>Pachycephala caledonica</i> <sup>d</sup>	-	-	-	-
	<i>Pachycephala rufiventris</i>	-	-	-	-
	<i>Pachycephala</i> sp.	n/a	10 (3)	2 (1)	-

**Table 1** continued

Order	Taxon	Modern survey				Level			
		I	II	III	IV				
	<i>Rhipidura fuliginosa</i>	*	-	-	-	-	-	-	-
	<i>Rhipidura spilodera</i>	*	-	-	-	-	-	-	-
	<i>Rhipidura</i> sp.	n/a	19 (2)	-	-	-	-	-	-
	<i>Myiagra caledonica</i>	*	-	-	-	-	-	-	-
	cf. <i>Clytorhynchus pachycephaloides</i>	-	1	1	1	1	1	1	1
	<i>Corvus moneduloides</i> <sup>d</sup>	*	-	5 (1)	-	-	-	-	1
	<i>Lalage leucopyga</i>	*	8 (3)	2 (1)	2 (1)	2 (1)	2 (1)	2 (1)	-
	<i>Ariamnes leucorhynchus</i>	*	4 (2)	4 (1)	2 (1)	2 (1)	2 (1)	2 (1)	-
	<i>Coracina analis</i> <sup>d</sup>	*	-	-	-	-	-	-	-
	<i>Coracina caledonica</i>	*	-	-	-	-	-	-	-
	<i>Coracina</i> sp.	n/a	5 (3)	-	-	-	-	-	-
	<i>Turdus poliocephalus</i> <sup>b</sup>	-	10 (5)	23 (8)	2 (1)	2 (1)	2 (1)	2 (1)	2 (1)
	<i>Aplonis striata</i> <sup>d</sup>	*	144 (28)	157 (16)	37 (9)	37 (9)	37 (9)	37 (9)	3 (1)
	<i>Acridotheres tristis</i> <sup>b</sup>	*	-	-	-	-	-	-	-
	<i>Hirundo tahitica</i>	-	1	-	1	1	1	1	-
	<i>Zosterops cf. lateralis</i>	*	26 (15)	34 (12)	2 (1)	2 (1)	2 (1)	2 (1)	1
	<i>Zosterops cf. xanchochroa</i> <sup>d</sup>	*	51 (25)	37 (13)	-	-	-	-	-
	<i>Zosterops</i> sp.	n/a	342 (52)	311 (85)	24 (9)	24 (9)	24 (9)	24 (9)	2 (1)
	cf. <i>Megalurulus mariel</i> <sup>d</sup>	-	-	3 (2)	1	1	1	1	-
	cf. <i>Erythrura psittacea</i> <sup>d</sup>	*	10 (8)	3 (1)	1	1	1	1	-
	<i>Esrrilda astrild</i> <sup>b</sup>	*	39 (8)	29 (6)	1	1	1	1	-
	Total elements identified	-	1022	886	203	203	203	203	13

Number of identified specimens (and minimum number of individuals) are organized by coarse stratigraphic level. Modern survey column reflects presence (\*) or absence (-) in standardized bird surveys conducted at the site in 2004

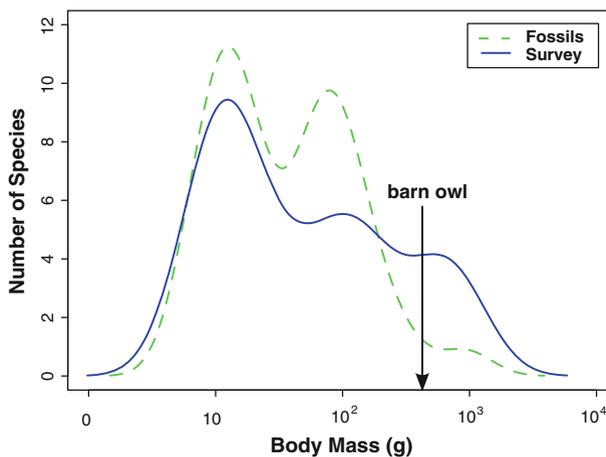
<sup>a</sup> Extirpated in New Caledonia, <sup>b</sup> introduced species, <sup>c</sup> non-breeding migrant, <sup>d</sup> endemic species

The most abundant species in the deposit were the white-eyes (*Zosterops lateralis* and *Z. xanthochroa*), followed by the striated starling (*Aplonis striata*), and the New Caledonian painted buttonquail (*Turnix varius novaecaledoniae*). Bones of the barn owl (*Tyto alba*), including many juveniles (47% of barn owl specimens), were also very common. One introduced species, the common waxbill (*Estrilda astrild*), was found in abundance in levels I and II, with one cranium in level III (f1248) that likely resulted from displacement during excavation. The species was introduced in the twentieth century and is now common throughout the west coast (Desmoulins and Barré 2005).

The two radiocarbon dates obtained from barn owl bones from level III (Table 2) are in accordance with the previously-published chronology of Mé Auré Cave (Fig. 3). Although not directly dated, levels I and II contain bones of introduced European rodents and therefore represent the two centuries following European contact (beginning in 1774 AD). Dates on barn owl, charcoal, Pacific rat, and *Turnix* from level III range from about 1200 to 300 cal BP, predating European colonization (Fig. 3). One *Turnix* bone from level III was dated at over 4000 cal BP, but Horrocks et al. (2008) regarded this date as anomalous. The four human bones dated from levels III and IV likely represent a single individual, and indicate human activity in the cave around 2500 years ago (Fig. 3). Occasional Pacific rats in level IV might have come into the cave as commensals with human habitation. The stratigraphy and dating suggest that barn owl usage of Mé Auré Cave postdated both

**Table 2** Radiocarbon determinations from barn owl (*Tyto alba*) bones from Mé Auré Cave, New Caledonia

Lab. no.	Provenance	% Modern $^{14}\text{C}$	$\delta^{13}\text{C}$	C/N	$^{14}\text{C}$ years BP	Cal BP (95.4%)
58802	Level III, f1244	93.78	-62.2	1.8	515 ± 20	534–498
58803	Level III, f1248	95.67	-43.3	1.8	355 ± 15	450–315



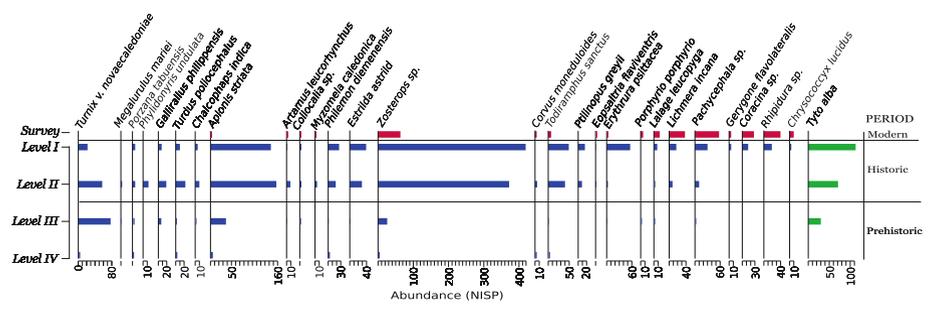
**Fig. 4** Distribution of body sizes of bird species recovered from the Mé Auré Cave bone assemblage (fossils: dashed line). Body size distribution of species observed in the modern ornithological survey of “Deux Frères” dry forest (survey: solid line) and the body mass of the local barn owl subspecies (arrow) shown for comparison

human occupancy and Pacific rats at the site. The vast majority of avian bones (99%) were found above level IV, at the same level as remains of the barn owl. Examination of species body sizes revealed that the majority of species found in the cave deposit were much smaller than the ~400 g barn owl, consistent with the site being an owl pellet deposit (Fig. 4). Barn owls would have been unlikely to roost in the cave while it was being occupied by humans. Consequently, we believe that owl pellet deposition in levels I–III reflects at most the past ca. 1200 years and does not provide a pre-human record of the local avifauna.

Although potsherds and other archaeological evidence were common, we found no positive evidence of human transport or use of birds and no domestic animals in the cave. However, we found two bones of the purple swamphen (*Porphyrio porphyrio*) in level III (f1248 and f1252), and the presence of this large (~850 g) species may not be attributable to barn owl predation. Only eight species were recorded from pre-owl level IV (Table 1), including New Caledonian crow (*Corvus moneduloides*), a species unlikely to be taken by owls, a single bone of the spotless crane (*Porzana tabuensis*), and several other species common in the deposit. Previously-described extinct species (i.e. Balouet and Olson 1989) were not found, however, and those species reached larger body sizes than the great majority of barn owl prey in the deposit. Thus we cannot conclude from this record that those species were absent locally at the time of deposition. No bird bones were obtained from f1246 in area 3 or from below 70 cm depth in area 1 (f1250).

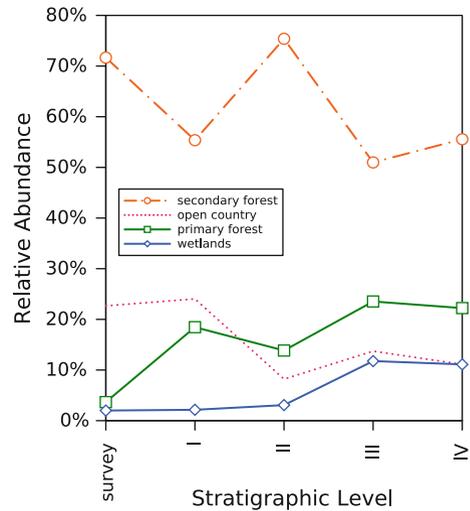
There was substantial change in species composition between stratigraphic units and also between the cave deposits and the existing avifauna at the site (Fig. 5). Although no undescribed extinct species were discovered, two species found in Mé Auré Cave apparently no longer exist on New Caledonia: the painted button quail, *Turnix varius novaecaledoniae*, and the Island thrush, *Turdus poliocephalus*. Other species, including the buff-banded rail, *Gallirallus philippensis*, and the emerald dove, *Chalcophaps indica*, also showed declines in abundance in the cave deposits, while abundance of other species increased, including: the red-throated parrot finch (*Erythrura psittacea*), long-tailed triller (*Lalage leucopyga*), dark-brown honeyeater (*Lichmera incana*), and whistlers (*Pachycephala* sp.) (Fig. 5).

Comparison with the local 2004 bird survey adds an additional level of temporal resolution. Of the 36–39 species recorded as fossils, 13 were not observed in the 2004 survey, mostly species that were already in decline in the deposit (Fig. 5) and that may no longer be present in the Deux Frères forest patch. Nevertheless, in December 2009 we personally observed *Gallirallus philippensis*, *Hirundo tahitica*, *Philemon diemenensis*, *Phylidonyris*



**Fig. 5** Stratigraphic distribution of selected bird species identified from Mé Auré Cave, with modern survey data for comparison. Bars show number of identified specimens (NISP) of each species at each stratigraphic level

**Fig. 6** Change in the relative abundance of birds in four habitat affinity categories by stratigraphic level. Relative abundance is based on the total minimum number of individuals (MNI) of species in each habitat category



*undulata*, and *Tyto alba* in west coastal lowlands within 20 km of the cave site, so we know that they survive nearby. Of the 34 species surveyed in the Deux Frères dry forest fragment, most were also recovered as fossils; only eight species (three large birds of prey, two introduced species, a large pigeon, a heron, and the New Caledonian flycatcher, *Myiagra caledonica*) were not found. Examination of species' body size showed that, with the exception of the flycatcher, these species have larger body sizes than most of the barn owl prey represented in the cave deposit (Fig. 4).

Classifying species by habitat affinity, we found that relative abundance of species associated with primary forests and wetlands declined through the deposit as the relative abundance of open-country birds increased; secondary forest species composed the majority of the assemblage in all stratigraphic units (Fig. 6). These trends continued through to the survey data. However, the marked decrease in primary forest species relative to open-country birds could be partially attributable to higher detectability of open-country birds in the survey (Ralph and Scott 1981).

## Discussion

The fossil avifauna of Mé Auré Cave provides roughly a millennium of temporal perspective on the history of human-era ecological change in New Caledonia's dry forest habitats. The bone assemblage appears to be more recent than the majority of avian bones from other fossil localities in New Caledonia (Balouet 1984; Anderson et al. 2010), and provides a record of small birds from the last 10 centuries of the prehistoric human period through the historic period (approximately the past 1200 years). A potential shortcoming of our data is that local habitats were likely to have been affected by almost 2000 years of human presence in New Caledonia prior to the accumulation of barn owl pellets in the cave (Sand 1996). However, the deposit does capture ecological changes associated with what may have been the most severe periods of habitat loss and degradation of dry forests, the periods of most extensive prehistoric agriculture, and the onset of historical ranching up to the present.

The taphonomy of deposition, body-size spectrum, and species composition of faunal remains in Mé Auré Cave are consistent with owl predation as the main form of deposition of vertebrate bones (Andrews 1990). Mé Auré Cave was an active barn owl (*Tyto alba*) roost at the time of excavation, fresh owl pellets were observed on the cave floor, and the back passage of the cave provides an ideal ‘twilight zone’ preferred by roosting barn owls. There are currently two tytonid owl species in New Caledonia, *Tyto alba* and *T. longimembris* (Doughty et al. 1999), and one extinct form, *Tyto letocarti* (Balouet and Olson 1989), although the validity of *T. letocarti* has recently been called into question (Anderson et al. 2010). One other species, the Boobok owl (*Ninox novaeseelandiae*), has been recorded in fossil deposits on the island (Balouet and Olson 1989; Anderson et al. 2010). Faunal remains at Pindai Cave, also in western coastal dry forest, included pre-human owl pellet accumulations, apparently from *T. letocarti*, and more recent accumulations from *T. alba* (Anderson et al. 2010). However, *T. alba* was the only species of owl occurring in Mé Auré Cave.

The stratigraphy and dating suggest that barn owl usage of Mé Auré Cave postdated occupation of the cave by prehistoric people as well as the first appearance of Pacific rats in the deposit. The temporal occurrence of Pacific rat bones before barn owl bones was also observed at Pindai caves (Anderson et al. 2010). It is likely that the barn owl was unable to establish a population in New Caledonia until after the introduction of suitable rodent prey in the form of the Pacific rat. Bones of rodents, frogs, and lizards are common in the Mé Auré deposit in addition to birds. In the surface layer, rodent bones were four to five times more abundant than those of birds, whereas frogs were found at roughly the same rate as birds. Lizards and bats made up a small fraction of the fauna. Overall, 89% of all resident and migratory New Caledonian birds suitable for owl prey (species <200 g, non-predatory) were recovered from the cave deposit. The richness of bird species in the deposit may be somewhat surprising given that rodents are the favored prey of barn owls (Taylor 1994). Barn owls are thought to adopt partially diurnal hunting, and consume a larger proportion of birds, on islands without diurnal predators (Bruce 1999), although, New Caledonia has diurnal predators in the form of three species of *Accipiter*. Perhaps the diversity of birds in these barn owl diets is not so anomalous in the context of island populations of barn owls elsewhere (e.g. Debrot et al. 2001).

In this rich owl-pellet deposit, we found substantial turnover in species composition and abundance, including two island-wide extinctions. New Caledonia was home to an endemic subspecies of painted button quail, *Turnix varius novaecaledoniae*, that may be distinctive enough to warrant specific rank (Debus 1996). In the cave deposits, the button quail was the most abundant species in level III but showed a sustained decline in abundance through time. Balouet and Olson (1989) and Anderson et al. (2010) also found it to be common in pre-European owl pellet deposits, and its presence in surface layers, both here (level I) and at the Pindai caves (Anderson et al. 2010), suggests it may have survived until quite recently. The taxon was described based upon a single museum study skin collected in 1889 (Ogilvie-Grant 1889) and the subspecies is now thought to be extinct. The reasons for its decline remain unclear, but the anthropogenic increase in fire frequency, loss of habitat, or introduced predators may all have been factors (Ekstrom et al. 2002). Whatever the causes, we know that it was present in substantial numbers through the prehistoric human period and into the historic period.

The cave deposits also provide a record of decline through the historic period in the island thrush. The subspecies *Turdus poliocephalus xanthopus* was endemic to New Caledonia, but recent surveys have failed to find the species anywhere on the main island (Spaggiari et al. 2007) and it is now restricted to an islet to the north of the main island

(Ekstrom et al. 2002). Its decline may be linked to the European introduction of the black rat, *Rattus rattus*, which has been implicated in the extinction of other subspecies of *T. poliocephalus* on Norfolk and Lord Howe islands (Garnett and Crowley 2000).

At least two other species from the cave deposit are now extirpated from the western lowlands. We tentatively identified two bones, from level I and III, as the southern shrikebill, *Clytorhynchus pachycephaloides*, a species that remains common in undisturbed, interior forest (Spaggiari et al. 2007), but is not found today in dry forest habitat (Desmoulins and Barré 2005). The endemic and secretive New Caledonian grassbird, *Megalurulus mariei*, was found in low numbers in levels II and III, but was absent from the record in level I. The species now occurs sporadically throughout New Caledonia in patches of thick undergrowth and dense scrub (Ekstrom et al. 2002; Spaggiari et al. 2007). Anthropogenic fires could be a threat to this species, but perhaps the most important factor affecting it is the complete destruction of understory in the dry forest by invasive ungulates.

Other species of interest not observed in the survey of Deux Frères dry forest include the endemic barred honeyeater, *Phylidonyris undulata*, and the red-bellied fruit-dove, *Ptilinopus greyii*. In recent island-wide ornithological surveys the barred honeyeater was listed as common to occasional in dry forest (observed in 9% of 420 survey points) and its distribution likely depends on the timing of flowering plants (Desmoulins and Barré 2005). Continued degradation of dry forest habitat could potentially threaten this species. The red-bellied fruit-dove was observed in only 8.7% of 420 dry forest survey points, but it is common in some (far northern and Nouméa area) coastal lowland forest fragments (Desmoulins and Barré 2005). Some authors have suggested that it is in a colonization phase of the main island (Desmoulins and Barré 2005). However, the presence of this species in considerable numbers in levels I and II suggests that it has been at Mé Auré Cave for several hundred years. The species was also found in a level dated at over 2000 years cal BP (85 cm depth) at Pindai Cave (Anderson et al. 2010).

Turnover in species composition over time was related to habitat affinity and may reflect substantial turnover in the available habitats at the site (Fig. 6). From level II to level I, several species associated with secondary scrub and forest edges increased their relative abundance, including the red-throated parrot finch (*Erythrura psittacea*), dark-brown honeyeater (*Lichmera incana*), and rufous whistler (*Pachycephala rufiventris*). These species were also common in the 2004 survey (Fig. 5). The long-tailed triller (*Lalage leucopyga*), an open-country bird, also increased in abundance. All of these species are common in disturbed habitats (Desmoulins and Barré 2005). Declines in forest and wetland species, and a substantial increase in the relative abundance of open-country birds from levels III to II appear to reflect habitat changes during the historic period. The British botanist R. H. Compton, who visited the island in 1914, described the landscape of the west coast at that time: “The natural vegetation over great areas of hill and plain appears poor and unprofitable. Vast areas are covered by a kind of savannah in which the only tree is the niaouli, *Melaleuca viridiflora*. The undergrowth consists almost entirely at the present day of alien grasses. Some of these afford fair pasture for cattle...” (Compton 1917). It appears that colonial agricultural practices during the first few decades after settlement resulted in a rapid and severe reduction of the remaining dry forest.

The owl-pellet deposit at Mé Auré Cave captures a critical period in the history of ecological change in the New Caledonian dry forest. Dry forest is one of the most endangered habitats across the Pacific islands, and entire dry forest bird communities on other islands have been lost. In Hawaii, for example, the surviving endemic forest birds are now largely restricted to relatively high elevation, mesic habitats, yet fossils from coastal

areas record the former presence of diverse communities including both extinct and extant species (Olson and James 1982). In contrast, the dry forest avifauna of New Caledonia, at least in the case of small-bodied birds, appears to have survived relatively intact through the late prehistoric and historic periods. Some species have disappeared while others have become rare and localized, but even small fragments like Deux Frères have retained the majority of the passerine species that were present before European colonization. This is in contrast to the larger bodied, non-passerine avifauna which suffered a high degree of extinction, apparently during the prehistoric human period (Balouet and Olson 1989; Anderson et al. 2010). Because large-bodied birds are extremely rare in the Mé Auré Cave assemblage, we cannot comment on whether the extinct birds described from other fossil sites were still extant when the Mé Auré bone assemblage was accumulating. We also do not yet know to what extent small-bodied birds were affected by ecological change earlier in the prehistoric human era on the island.

New Caledonia harbors the highest degree of endemism of any global landmass (Kier et al. 2009) and the dry forests are a particularly threatened component of the island's biodiversity (Gillespie and Jaffré 2003). Recent evaluations have concluded that existing reserves are inadequate to protect the numerous species of conservation concern in the sclerophyll forests (Jaffré et al. 1998), and efforts are now underway to expand the system of protected areas and eradicate invasive ungulates from priority sites. If the dry forest avifauna is relatively intact in the remaining fragments, then we have all the more reason to increase conservation of dry forest in order to secure the survival of these remaining populations.

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## Appendix 1: Comparative material examined

The primary reference collection used for fossil identification was composed of the following USNM skeletal specimens collected in New Caledonia: *Gallirallus philippensis* (USNM 561546), *Porphyrio porphyrio poliocephalus* (USNM 561549), *Chalcophaps indica* (USNM 561556), *Columba vitiensis hypoenochroa* (USNM 561555), *Drepanoptila holosericea* (USNM 562454), *Ducula goliath* (USNM 561561), *Eunymphicus cornutus uvaeensis* (USNM 561563), *Cacomantis flabelliformis pyrrhophanus* (USNM 561571), *Tyto alba lulu* (USNM 561574), *Collocalia spodiopygia* (USNM 561589), *Todiramphus sanctus* (USNM 561607), *Lichmera incana* (USNM 561807), *Myzomela sanguinolenta caledonica* (USNM 561808), *Philemon diemenensis* (USNM 561824), *Phylidonyris undulata* (USNM 561812), *Gerygone flavolateralis* (USNM 561669), *Eopsaltria flaviventris* (USNM 561676), *Pachycephala caledonica* (USNM 561710), *Pachycephala rufiventris* (USNM 561733), *Rhipidura fuliginosa* (USNM 561693), *Rhipidura spilodera* (USNM 561707), *Myiagra caledonica* (USNM 561681), *Clytorhynchus pachycephaloides* (USNM 561680), *Corvus moneduloides* (USNM 561641), *Lalage leucopyga* (USNM 561831), *Artamus leucorhynchus* (USNM 561620), *Coracina analis* (USNM 561665), *Coracina caledonica* (USNM 561660), *Aplonis striata* (USNM 561614), *Acridotheres tristis* (USNM

561835), *Zosterops lateralis* (USNM 561795), *Zosterops xanthochrous* (USNM 561754), *Megalurulus mariei* (USNM 400088), *Erythrura psittacea* (USNM 561844), *Estrilda astrild* (561845). We also made reference to over 50 additional skeletons from the southwest Pacific in the USNM and Florida Museum of Natural History (UF) collections, including: *Turnix varius* (USNM 500632), *Gallirallus philippensis* (USNM 560651, UF 42933, UF 43177), *Porzana tabuensis* (USNM 345124), *Poliolimnas cinereus* (USNM 560913), *Columba vitiensis* (UF 28543), *Ducula pacifica* (USNM 559586), *Ptilinopus superbus* (USNM 489040), *Ptilinopus rivoli* (USNM 489043), *Ptilinopus greyii* (UF 43162, UF 39593), *Ptilinopus tannenensis* (UF 42921), *Gallicolumba stairii* (USNM 576854), *Gallicolumba beccarii* (USNM 615012), *Gallicolumba criniger* (USNM 346463, UF 45053), *Gallicolumba luzonica* (USNM 346847, UF 19438), *Gallicolumba rubescens* (USNM 290145), *Gallicolumba rufigula* (UF 41434), *Chalcophaps indica* (UF 42904), *Chalcophaps stephani* (USNM 615011), *Streptopelia chinensis* (USNM 501286, UF 27711), *Macropygia amboinensis* (USNM 489045, UF 41528), *Macropygia phasianella* (USNM 612672), *Eunymphicus cornutus* (UF 44707), *Charmosyna papou* (USNM 613778, UF 39659), *Charmosyna placentis* (USNM 558317), *Cyanorhamphus novaezelandiae* (USNM 344438, UF 25958), *Trichoglossus haematodus* (USNM 612678, UF 43165), *Chrysococcyx lucidus* (USNM 620222, UF 39514), *Eudynamys scolopacea* (UF 41473), *Tyto alba* (USNM 559804), *Hirundo tahitica* (USNM 620241), *Turdus poliocephalus* (USNM 613705), *Poliolimnas cinereus* (USNM 560913).

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