The Late Glacial and Holocene avifauna of the island of St Helena, South Atlantic Ocean

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Bird bones from unconsolidated sediments provide a record of the changing avifauna of St Helena from the Late Glacial, at ~14 000 BP, until the present. Changes in avifauna apparently reflect climatic and associated ecological conditions, as well as the effects of human occupation since the island was discovered in 1502. Introduced mammals decimated birds in the seventeenth century and seven endemic species are now extinct, while seven other species are locally extinct. At least nine species that now breed on St Helena have been introduced anthropogenically to the island since it was discovered. The failure to find evidence of native songbirds in the former woodlands of the interior of the island deserves explanation.

Key words: St Helena, Atlantic Ocean, ornithology, avifauna, seabirds, extinction, endemic species, Late Glacial, Holocene.

INTRODUCTION

The purpose of this paper is to indicate, with reference to environmental conditions, which birds lived on St Helena during the past. This has been done by collection, identification and radiocarbon dating of bird bones from different stratigraphic layers at a variety of sites on the island (Table 1). Table 2 presents a list of birds present on St Helena at various times from ~14 000 BP (during the Late Glacial) until the present. This table is based on the work of Ashmole (1963a), Olson (1975) and other scientists, and on radiocarbon dating of bones that I collected on St Helena in 2004, 2005 and 2007. The species composition over time reflects changing environmental conditions on the island, including the effects of mammalian introductions subsequent to discovery of St Helena in 1502 (Gosse, 1990). No evidence, apart possibly from that of bones of *Dysmoropelia dekarchiskos* (St Helena pigeon/dove) linked with that of snail shells, has been discovered to indicate the avifauna of St Helena prior to the Late Glacial.

LOCATION, GEOLOGY AND GEOMORPHOLOGY OF ST HELENA

St Helena is an island of volcanic origin located at 15°56′S, 5°42′W, in the South Atlantic Ocean (Figure 1). Volcanic activity, associated with a hotspot (O'Connor *et al.,* 1999; Adam *et al.,* 2007; Weaver, 1990), formed two basaltic shield volcanoes (Baker, 1968), the older of which was active from before 14.6 million years ago (Myr) until ~11.4 Myr, while the younger was active from ~11.3 Myr until ~7.3 Myr (Baker *et al.,* 1967). Fluvial erosion and associated slope processes, since volcanic activity ended, has cut deeply incised and precipitous valleys into the volcanic rocks, the largest of which (on the southern and windward side of the island) is Sandy Bay valley (Figure 2).

The island is located within the Sub-Atlantic anticyclonic gyre of the southern Atlantic Ocean, where winds blow anticlockwise around the high-pressure cell located south west of Cape Town. Surface ocean currents within this gyre (Figure 1), influenced by winds, also flow in an anticlockwise direction (Edwards, 1990). They have facilitated the movement of flora and fauna from southern Africa and, *via* the Agulhas Current and its predecessors, from the Indian Ocean (especially Mascarene) region towards St Helena (Cronk, 1986, 1990) and, via the West Wind Drift, even from South America (Carlquist, 2001).

St Helena is ~17 km long from east to west, ~10 km wide from north to south and covers an area of 121.7 km^2 (Ashmole & Ashmole, 2000). This isolated land mass lies ~1800 km west of the coast of Angola (the nearest land in Africa), and 3260 km east of the nearest land in South America. The closest island, Ascension, lies 1300 km to the northwest.

St Helena is surrounded by a submerged wave-cut platform that, at depths of down to 120 m, is over seven km wide southwest of the island, but is less than two km wide to the northwest. There is then a steep descent to the abyssal depths, over 4000 m below the surface. Sands and shells cover much of the submerged platform, although it is rocky in places, (especially southwest of the island along Speery Ledge), and there are occasional patches of mud (Admiralty Chart, 1994; Figure 2).

Subsequent to the formation of the major valleys, shell-rich calcareous sands were blown onshore from the wave-cut platform "by strong Pleistocene winds" (Muir & Baker, 1968, 265) when sea level was low and it was exposed. These sands were deposited up to altitudes of ~275 m, as in the northeast of St Helena, on the landward side of Sugar Loaf Ridge. They also exist at numerous locations along the south coast, as at Potato Bay, Sandy Bay and in the vicinity of Lot's Wife's Ponds (Figure 2). The sands are partially consolidated and display dune bedding, which indicates their aeolian origin (Muir & Baker, 1968).

A submarine faunal assemblage within the aeolian sands (particles of the foraminiferans: *Eponides* sp., *Rotalia* sp., *Asterigerina* sp., *Heterostegina* sp., *Amphistegina* sp., *Quinqueloculina* sp., the echinoderm *Cidaris* sp.spines (abraded), Gastropoda 10 sp., *Polyzoa* 5 sp., and fragments of lamellibranches, schleractinian corals, ophiuroid schlerites and serpulid worm tubes) is indicative of their warm, shallow water, subtropical to tropical origin on the wave-cut platform surrounding St Helena. They may be of Miocene to Recent age (Baker, 1968). The remains of what appears to be guano, succeeded upwards by the remains of Brown Earth soil and then by a surface clitter of angular clasts derived from bedrock outcrops higher upslope, overlies the sands at some sites on Sugar Loaf.

Colluvial and other slope deposits occur on the floors and

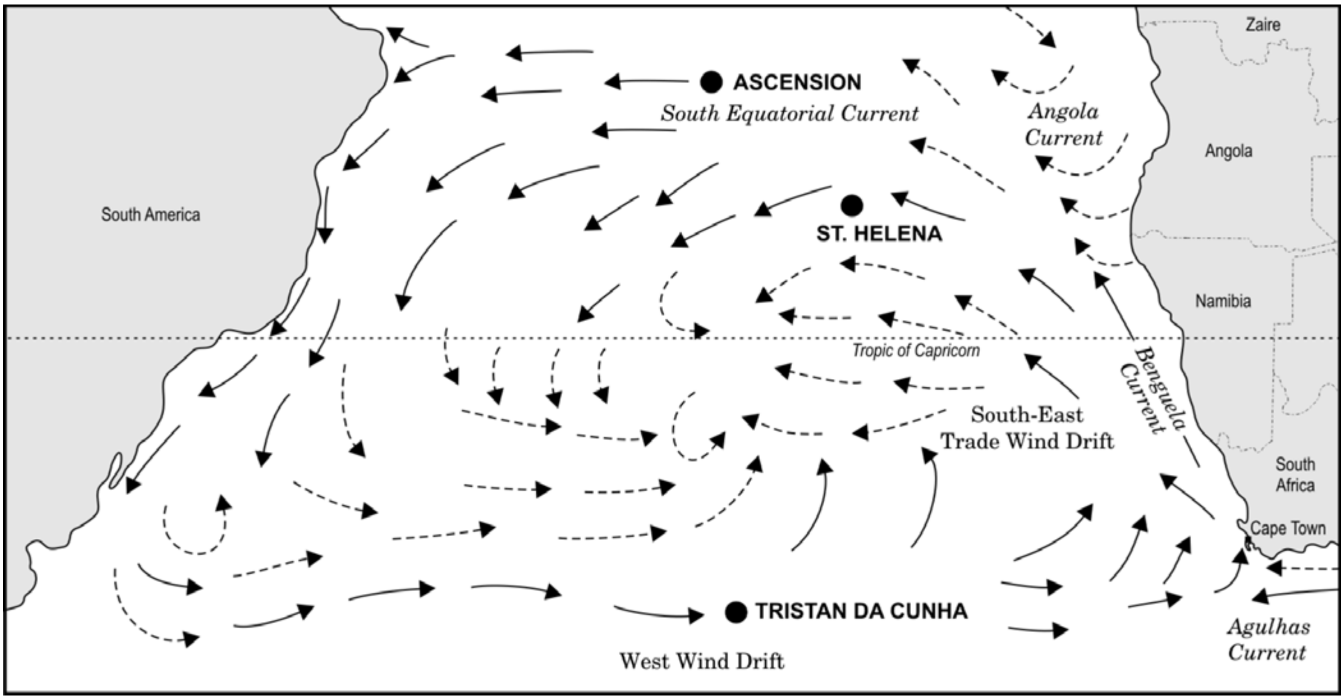

Figure 1. The location of St Helena in relation to other islands, and to Africa and South America, and to existing January surface currents in the South Atlantic Ocean. Solid arrows indicate currents of 51–74% constancy. Dashed arrows indicate currents of 25–50% constancy. (Based on Edwards, 1990.)

sides of various valleys in St Helena, especially in the lower part of the valley leading into Prosperous Bay and on the flanks of the lower part of Sandy Bay valley. These unconsolidated sediments have been incised by stream erosion in both valleys and are at least 9.5 m deep in parts of the Prosperous Bay valley.

COLLECTION AND IDENTIFICATION OF BIRD BONES

Bird bones exist in sediments overlying the aeolian sands at altitudes up to ~200 m, and in other unconsolidated deposits near the coastal margins of St Helena (Figure 2). Ashmole (1963a) and Olson (1975), in particular, have collected from these deposits, identified bones to species, and thereby produced information on the avifauna of the island, much of which is now extinct. The most important sites at which bone collection has taken place are west of Sugar Loaf Ridge, at Dry Gut, in the lower part of the valley leading into Prosperous Bay and in the lower part of Sandy Bay valley.

Sugar Loaf

Darwin (1844) inspected the Sugar Loaf deposits in 1836, concluding (correctly) that the Sugar Loaf calcareous sands (which were at that time referred to as "limestone") were of aeolian origin, derived from a shelving coast and transported to their present position by wind. Barnes (1817, 64) had already reported the existence of bird bones in "dark, friable earth, two or three feet in depth" overlying calcareous sands ("limestone") on Sugar Loaf Hill, and Darwin noted their presence in the "softer, finer-grained and less pure" upper beds of the "limestone". He stated, apparently on the authority of Captain Wilkes, R.N. (who may also have collected in the Prosperous Bay valley; Hutchinson, 1950; Walker, 1977), that they contained eggs: "as many as 10 eggs were found by one person". (Ashmole & Ashmole (2000, 97) suggest that the eggs Wilkes referred to might have come from the Prosperous Bay valley, and not from the Sugar Loaf deposits). Darwin did not state that he saw any eggs himself, but he mentioned (footnote 12 of his 1844 publication) that "earthy detritus" existed on slopes adjoining the limestone (calcareous sand) quarry (Figure 2, site 1) on Sugar Loaf (where sand had been mined for the production of lime in the lime kiln in adjacent Banks Valley after 1797 and before 1835; Lewis *et al.*, 2008). Consequently, the bones Darwin saw were probably, as he named it, in this "earthy selenite" rather than in the aeolian sands themselves.

Seale (1834) and Daly (1927) noted the existence of bird bones in a col, apparently on Sugar Loaf Ridge above Flagstaff Bay (Figure 2, probably site 3 on Sugar Loaf). Professor Arthur Loveridge collected bird bones from a hollow at an altitude of ~200 m on the seaward side of Sugar Loaf Ridge above the Dockyard, which is on the shore of Flagstaff Bay. This was probably the same site as that noted by Seale (1834) and Daly (1927). Loveridge submitted these bones to the Museum of Comparative Zoology at Harvard University (Olson, 1975, 11), and described the site in a letter dated: 14.8.1972. Although Olson did not locate that site, he reported Loveridge's finds (Olson, 1975, 36), as listed on Table 2.

Norman Kerr and, in 1959, Philip Ashmole, collected bird bones in the vicinity of the former Sugar Loaf quarry that Darwin had visited. In 1971 Olson (1975, 7) collected in the same area: "In most instances bones were lying exposed on weathered deposits of sediment and needed only to be picked up. My procedure ... was to recover every bone or fragment of bone that appeared to be identifiable". Olson noted that, at the Sugar Loaf quarry site (Figure 2, site 1 on Sugar Loaf), the bones "did not occur in the pure deposits of hard-packed sand, but rather where the sand was mixed with soil", which apparently agrees with the findings of Barnes (1817), Darwin (1844) and probably Blofeld (1852), who had collected "bird bones perfect and fragmentary" in greyish brown friable earth, apparently on Sugar Loaf (Walker, 1977). Olson (1975) also collected in a small valley on the flank of Sugar Loaf Hill (Figure 2, site 2 on Sugar Loaf). Subsequent to collection, Olson (1975) identified many of the bones to species and was therefore able to list the birds represented by bone remains at Sugar Loaf.

In 2005 I collected bird bones from the same area as Olson's

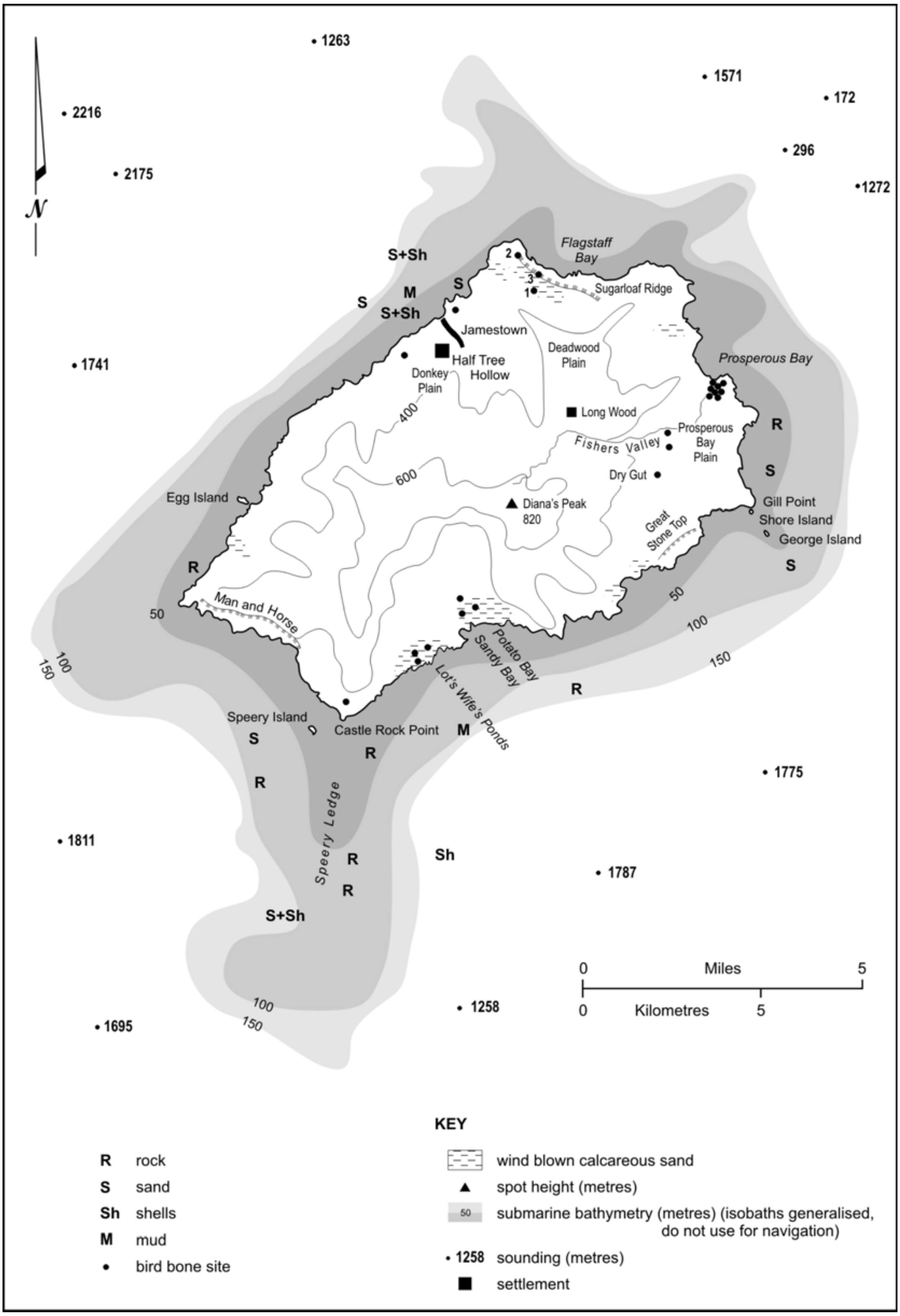

Figure 2. The topography and hydrography of St Helena and surrounding waters. The location is shown of bird bone sites, based on Ashmole & Ashmole (2000), and aeolian sand deposits on land, and of sediments on the submerged platform surrounding St Helena. Heights and depths in metres. Submarine information from Admiralty Chart 11230.

site 1, from a Brown Earth soil 0.3 m thick that underlay 0.2 m of surface clitter/stony wash deposits, and overlay shelly aeolian sand, the base of which was not exposed. In some cases the soil was exposed at the surface and bones protruded from it. Ashmole identified the bones as being of the St Helena gadfly petrel (*Pterodroma rupinarum*: 4 bones) and Audubon's shearwater (*Puffinus lherminieri*: 4 bones; e-mail of 21 Aug. 2005, personal communication). Samples of these bones were then radiocarbon dated (GrA-32452) to 11 900 ± 50 BP and calibrated to give a most probable Late Glacial age of 14 086 BP. (BP stands for Before the Present, which is AD 1950.)

I also collected from what I believed to be the same site as Olson's site 2, where I discovered seven bird bones and a rabbit skull in a natural exposure in the side of the small valley, in Brown Earth at a depth of 0.2 to 0.4 m below the surface, beneath a surface stony clitter of angular clasts and finer debris, and above an unknown depth of shelly sand. Ashmole identified the bird bones as those of the St Helena gadfly petrel. The bird bones appeared to me to be identical, in terms of weathering, to those I collected at site 1, and since they were of one of the same two species that I collected at Sugar Loaf site 1, I did not send them for radiocarbon dating.

In a hollow above the Dockyard (site 3), which was probably the same site as that at which Loveridge collected, in 2005 I found three bones, identified by Ashmole as of the St Helena gadfly petrel, in 19 cm of soil underlying 11 cm of clitter, and in the uppermost parts of what appeared to be 8 cm of guano overlying sand but underlying the soil horizon. The bones appeared similar, in terms of weathering, to those I collected at the other sites on Sugar Loaf and, since they were also of one of the two species that I had dated from Site 1, I did not submit them for radiocarbon dating.

Dry Gut

In 1958 Stonehouse discovered bird bones on the floor of Dry Gut at an altitude of ~300 m, where a major tributary from the western side of Bencoolen joins the main valley (Figure 2). Alluvium, partly overlain by slope deposits, rather than wind-blown sand (such as exists on Sugar Loaf and at various sites on the windward side of St Helena), occurs on the floor of that valley (Ashmole, 1963a, 393). The alluvium now exists as low, fluvially dissected, mounds (Olson, 1975, figure 4 on p. 9) between what Ashmole hyperbolically described as ravines. Ashmole, Loveridge and Olson subsequently collected at that site. Ashmole (1963a, 393) reported that he found "Bone fragments ... thinly distributed through the soil forming the banks of the ravines".

When I visited Dry Gut in 2005 I found bird bone fragments on the surface of the alluvial mounds, where vegetation cover was absent, and mixed in the angular clitter that overlay the alluvium in places. The clitter appears to have been derived from the valley sides by slope processes subsequent to the deposition of the alluvium. I failed to find any bones *in situ* in sections exposed in the alluvium. The bones that I found seemed, to me, to be similarly or less weathered than those I saw at Sites 1–3 on Sugar Loaf. I did not collect any bones at Dry Gut since I was unable to record them in stratigraphic position, no bones being seen in geological sections. Consequently, I did not submit any bones from Dry Gut for radiocarbon dating.

Unlike the sandy deposits on Sugar Loaf, which were derived from the now-submerged coastal platform and deposited under windy and essentially dry conditions (sand is unlikely to have been wind-blown when it was wet, when individual sand grains would have adhered to each other), the sediments at Dry Gut probably testify to the following sequence of events:

i) The transport of alluvium to, and its deposition at the site, under conditions that were sufficiently moist for stream flow to occur off the adjacent uplands, depositing alluvium where slope gradient reduced at the study site.
ii) Reduction of stream flow, with slope processes, possibly due to occasional heavy rainfall, temporarily becoming dominant at the site, resulting in the deposition of surface clitter.
iii) Renewed/increased stream flow, causing stream incision into the slope deposits and alluvium at the site.

The above sequence of events is suggestive of wetter and less windy conditions than those prevailing on Sugar Loaf during the Late Glacial immediately before, and possibly during, the deposition of the bird bones that have been discovered there. (The Late Glacial extended, in the Eastern Cape of South Africa, from ~18/17 000 BP to ~12/10 000 BP, Lewis, 2008). The deposits at Dry Gut may therefore date to the Holocene, when the climate was less windy in the southeast Atlantic, within the South Atlantic gyre that largely governs the climate of St Helena (Lewis *et al.,* 2008), than in the Late Glacial (Stuut *et al.,* 2002; Dupont *et al.,* 2004). Temperatures were also warmer during the Holocene in southern Africa than in the Late Glacial (Partridge *et al.,* 1999), and were associated with vegetation changes (Lewis, 2008): there is no reason to believe that the same did not apply in St Helena.

Prosperous Bay

Much attention has been paid, since the first half of the nineteenth century, to unconsolidated deposits, rich in bird bones, existing beside the stream that drains from Fishers Valley into the sea at Prosperous Bay (Figure 2). Ashmole (1963a), Olson (1975) and other investigators have collected and identified bones from these unconsolidated and essentially colluvial valley floor sediments (Figure 3), but mainly from the overlying mixed guano and fine silt unit, and the stratigraphically higher Brown Earth (soil) deposits. The valley floor sediments are well developed in the final 800 m of the valley before the sea is reached. Unfortunately the collectors failed to give exact stratigraphic details of where bones were collected, contenting themselves with such general descriptions as "The bones seem to be most numerous in the upper layers of the soil, and many are actually exposed.... we collected in the surface layers of the soil" (Ashmole, 1963a, 392) and, in relation to the collection of bones of *Pterodroma rupinarum,* "Collected in recent sediment deposits at Prosperous Bay" (Olson, 1975, 14). Ashmole (1963a) and Olson (1973, 1975) identified the bones to species.

I collected bird bones in the Prosperous Bay valley in 2005 from brown coloured soil ~10 mm deep, that underlay a surface clitter of angular clasts derived from the valley sides, and from what appeared to be a mixture of guano and fine silt, up to ~50 mm thick, that underlay the brown soil. These appear to be the same stratigraphic horizons as those from which most of the bones collected by earlier workers had been obtained, so that they should be of the same or comparable age.

Philip Ashmole (e-mail of 21 Aug. 2005, personal communication) subsequently identified to species the bones I had collected at depths of not more than 60 mm below the surface clitter. Samples of bone from this collection, which came from two identified land birds (St Helena hoopoe, *Upupa antaios* (one bone); and St Helena rail, *Aphanocrex (ex Atlantisia) podarces* (Bourne *et al.,* 2003); one bone) and three identified sea birds (Audubon's shearwater, (10 bones); white-faced storm-petrel, *Pelagodroma marina* (one bone); frigatebird sp., *Fregata sp.*; one bone), as well as from five bird bones not identified to species, were then submitted for radiocarbon dating and produced a most probable calibrated date of ~AD 1640 (Pta-9589), as discussed under radiocarbon dating.

In 2004 I collected bones from colluvium at a depth of ~7 m, although they were too crushed to be identified to species. They were radiocarbon dated to 4770 ± 50 BP (GrA-27134). Although this might be a minimum age, (*vide* the section on radiocarbon dating), it proves that accumulation of colluvium, and occupation of the area by birds, was taking place by at least that date. In 2007 I collected bird bones, which could not be identified to species, in fluvial/slope wash deposits, 9.4 m below the surface of the unconsolidated sediments (Figure 4). They were radiocarbon dated to 2398 ± 25 BP (UBA-7896), which calibrates to between 2458 BP and 2370 BP. This date is thought to be a minimum age, for reasons given in the radiocarbon section of this paper.

Figure 3. Prosperous Bay valley. The colluvial/alluvial deposits, into which the streams are incised, contain bird bones. The bones are particularly plentiful in the guano/silt/Brown Earth sediments that rest on top of the colluvium/alluvium and beneath a surface clitter of angular clasts and other debris.

Sandy Bay

Olson collected at two sites on the eastern side of the Sandy Bay valley (Figure 2). Site A was "a low embankment of soil about 400 m north of the beach at Sandy Bay proper. At its base is the footpath leading to Sandy Bay" (Olson, 1975, 11). When I inspected the area in 2004 I saw bird bones, some of which protruded from the surface of the deposit and some of which were lying on the surface.

Further up the valley, in a road cutting on the east side of the valley less than 200 m upstream of the most seaward bridge across the Sandy Bay stream, I noted more bird bones in slope sediments. They existed in a road cutting in angular colluvium/scree that was at least 2.1 m deep and derived from bedrock outcrops higher up slope. The surface slope of the valley side at that location was 22°. At this site I collected, at a depth of 1.6 m below the surface, the bones of a bovid (goat *Capra*

Figure 4. Water-laid colluvial/alluvial fan-like sediments in Prosperous Bay valley, from which bird bones were collected in 2007 at a depth of 9.4 m below the ground surface. Notice the palaeosol, sloping from left to right, from approximately the level of Micko Paajanen's head. This palaeosol is particularly obvious on the right of the section and its presence evidences the elapse of an appreciable (but unknown) time period between the deposition of the sediments that under- and overlie it.

Table 1. Radiocarbon ages and calibrations.

Sample	Site and depth	Radiocarbon age	Most probable age	Calibrated age to 1-sigma
UBA-7850	Sugar Loaf 1, surface	48 340 ± 769 BP	Unknown	Invalid age for calibration[1]
UBA-7851	Sugar Loaf 1, from face of section	44 269 ± 527 BP	Unknown	Invalid age for calibration[2]
GrA-32452	Sugar Loaf 1, between 0.2–0.5 m	11 900 ± 50 BP	(14 086) BP	14 152 to 14 020 BP[3]
GrA-27134	Prosperous Bay, ~7 m	4770 ± 50 BP	A minimum age*	Not determined[4]
UBA-7896	Prosperous Bay, ~9.4 m	2398 ± 25 BP	2458 to 2388 BP**	0.788 probability #[5]
Pta-9589	Prosperous Bay, <60 mm	320 ± 60 BP	AD (1643)	AD 1516–1590, 1622, 1661[6]
GrA-27638	Sandy Bay, 1.6 m	650 ± 35 BP	AD (1316, 1352, 1390)	AD 1303 to 1401***[7]

Key: *"As we did not do the C/N ratio of this bone it is not possible to determine if the collagen was adequately preserved. My suspicion is that it was not and that this is a minimum age" (comment by Stephan Woodborne in his *Report of Radiocarbon Analysis* of GrA-27134, dated 24 Feb. 2005, personal communication).

**This is the calibrated age range within a 1-sigma range with # the relative area under probability distribution of 0.788. See comment in final paragraph under the heading 'Radiocarbon dating'.

***When calibrated using the Southern Hemisphere Marine 98 file, the most probable age was AD 1664 and the 1-sigma range AD 1664–1680 (M. Pienaar, personal communication). Material dated: [1]Snail shell (*Chilonopsis helena*). [2]Snail shell (*Succinea sanctaehelenae*). [3]Bird bone. [4]Bird bone. [5]Bird bone. [6]Bird bone. [7]Bovid bone (goat or sheep).

hircus or sheep *Ovis aries,* see Appendix I). A sample of bovid bone was subsequently radiocarbon dated (GrA-27638) to 650 ±35 BP, producing a most probable age, using the atmospheric calibration curve, of AD (1316, 1352, 1390), as discussed in the section on radiocarbon dating. When dated using the Marine 98 file, the sample calibrates to AD 1664.

The calibrated date, using the atmospheric curve, is probably misleading, since St Helena was supposedly only discovered in 1502 (Gosse, 1990), and no terrestrial mammals were present on the island when it was discovered. The calibrated age is therefore probably more than a century older than the true age of the remains. Nevertheless, the bovid bone indicates that the bird bones at that site are unlikely to be more than 500 or 600 years old. The age of the bovid bone also indicates the enormous amount of erosion and deposition that has taken place on the eastern side of the Sandy Bay valley since the area was discovered.

The bones that Olson collected at Sandy Bay site A, judged by the similarity in appearance of the bones I saw at that site in 2004 and at the goat-bone site described above, are likely to be similar in age to those at the latter site. They are likely to be no more than ~600 years old and probably post-date discovery of St Helena in 1502. Olson (1975, 36) collected and identified to species 95 bones from this site, as shown in Table 2.

The second site at which Olson collected bird bones in the Sandy Bay valley was in gullies above an aeolian sand deposit at the head of the last eastern tributary valley to join the main valley before reaching the sea. The calcareous shelly sand at this site has been mined for lime production and pathways lead upslope to the last remnants of the un-mined sands. Olson found bones of the St Helena gadfly petrel (10 bones) and of Audubon's shearwater (two bones) at this site, but since their stratigraphic position was not recorded this discovery is of limited value.

RADIOCARBON DATING

Samples of bird and bovid bones were submitted to the Quaternary Dating Research Unit (QUADRU) in Pretoria, South Africa, and snail shells and bird bones to the Chrono Centre at Queen's University Belfast, Northern Ireland, for radiocarbon dating. Three samples sent to QUADRU were forwarded to the dating laboratory in Groningen, The Netherlands, for analysis.

Dates obtained by the QUADRU laboratory in Pretoria (Pta-) and the Groningen laboratory (GrA-) were subsequently calibrated using the Southern Hemisphere Atmospheric Calibration Curve of the Pretoria Programme (Talma & Vogel, 1993) to give the most probable date and the 1-sigma range (Table 1). Calibration using the Southern Hemisphere Marine 98 file was applied to GrA-27638 although, since the sample dated was from a terrestrial mammal, the calibrated age may be too young. The same Marine 98 file could not be applied to Pta-9589, since the radiocarbon age of that sample was younger than the Marine 98 file could calibrate. Only the most probable dates are given elsewhere in this paper. Where more than one date is most probable (because the data transects the curve at more than one point), the most probable dates are given in brackets in this paper.

Calibration of dates obtained by the Chrono Centre (UBA-), where possible, was done using Radiocarbon Calibration Program (used in conjunction with Stuiver & Reimer, 1993) CALIB REV5.0.2 and the calibration data sets Intcal04 Marine04 and Sohem04 curves, using 50% southern hemisphere terrestrial and 50% marine calibration curves on the basis that the bones were from birds of mixed feeding (e-mail of 28 Jan. 2008 from R. Reimer, personal communication). Calibrated ages were given as 1-sigma ages within a probability distribution of 0.283 except as shown on Table 1 (Reimer *et al.,* 2004). Calibrated dates were not given for samples UBA-7850 and UBA-7851, which were from snail shells, since their radiocarbon ages were invalid for the Intcal04.14c calibration curves.

Rando *et al.* (2008) consider that radiocarbon dates for snail shells may be misleading due to the possibility that fossil carbonate may have been incorporated in them due to the diet of the snails (Goodfriend & Hood, 1983; Goodfriend & Ellis, 2000; Romaniello *et al.,* 2008).This may result in over-estimation of the age of the shells (Lang *et al.,* 2003).

R. Reimer (e-mail of 22 Oct. 2007, personal communication) considers that "the date ... reported [for sample UBA-7896; 2398 ± 25 BP, calibrating to between 2458 and 2370 BP within a 1-sigma range under a probability distribution of 0.788: (http://calib.qub.ac.uk/radiocarbon/certificate/certificate.php?UBNo=7896)] should be considered a young limit". That was because the sample was not pre-treated "according to our usual procedure for bone. It went through a less rigorous removal of humic acids in order to leave more collagen behind".

BIRDS, TIME AND PLACE

Table 2 lists the birds present on St Helena at various times from the Late Glacial, at ~14 000 BP, until ~AD 1640, as evidenced by bones collected and identified from various sites on the island. The table is based on Olson (1975, 36) and on Ashmole & Ashmole (2000, 283), and on calibrated radiocarbon dates derived from bird and bovid bones that I collected in

Table 2. Avian species present on St Helena, prior to human introductions, as evidenced by bones collected and identified from various sites (Olson, 1975, 36; *Ashmole & Ashmole, 2000, 283).

Species	SL1	SL2	SL3	Dry G	P Bay	SBA	P	PS
Seabirds								
Pelagodroma marina	313	187	1	83	163	26	no	AV
Bulweria bifax	240	nil	1	12	nil	9	no	EE
Pterodroma rupinarum	182	7	38	790	93	25	no	EE
Puffinus pacificoides	73	nil	nil	nil	nil	nil	no	EE
Puffinus lherminieri	68	86	nil	19	848	10	no	AV
Oceanodroma castro	3	27	1	5	13	nil	yes	RB
Puffinus griseus	2	nil	nil	nil	nil	nil	no	AV/PM
Sterna fuscata	1	nil	1	nil	201	4	yes	RB
Fregata ariel trinitatis	nil	2	nil	nil	899	6	no	FB
Fregata minor	nil	1	nil	nil	48	nil	no	FB
Sula dactylatra	nil	nil	nil	2	17	nil	yes	RB
Gygis alba	nil	nil	nil	1	2	1	yes	RB
*Larus dominicanus**	nil	nil	nil	2	nil	nil	no	E
Phaethon aethereus	nil	nil	nil	nil	3	nil	yes	RB
Sula sula	nil	nil	nil	nil	9	nil	no	AV/FB
Landbirds								
Dysmoropelia dekarchiskos	11	nil	nil	nil	nil	nil	no	EE
Aphanocrex podarces	3	nil	nil	11	20	8	no	EE
Charadrius sanctaehelenae	nil	nil	1	1	2	nil	yes	RB
Porzana astrictocarpus	nil	nil	nil	22	21	10	no	EE
Upupa antaios	nil	nil	nil	9	4	nil	no	EE
Nannococcyx psix	nil	nil	nil	nil	1	nil	no	EE
Date	~14 000 BP	LG?	LG?	Holocene?	~AD1640	~AD1500+	Present	

Key: SL 1 = Sugar Loaf site 1. SL 2 = Sugar Loaf site 2. SL 3 = Sugar Loaf site 3. P Bay = Prosperous Bay valley. SBA = Sandy Bay site A. P = Present. PS = present status of the species. Numbers in the columns are the number of bones of each species collected and identified for each site. no = not a resident breeder on St Helena at present (AD 2004). yes = resident breeder on St Helena at present (AD 2004). AV = accidental visitor to St Helena; EE = extinct endemic; PM = passage migrant; E = extinct; RB = resident breeder at present; FB = former breeder; (McCulloch, 2004). The dates for SL 1, P. Bay and S. Bay A are calibrated radiocarbon dates, as discussed in the section on radiocarbon dating. Note that if the marine calibration curve was applied, Sandy Bay A would date to ~AD 1664. LG? = assumed as Late Glacial, as discussed in the section on collection and identification of bird bones. Holocene? = assumed as Holocene, as discussed in the section on collection and identification of bird bones.

Present = AD 2004.

2004, 2005 and 2007, as listed on Table 1. The present status of each species, in relation to St Helena, is also indicated on Table 2.

DISCUSSION: THE AVIFAUNA OF ST HELENA PRIOR TO ANTHROPOGENIC INTRODUCTIONS

The Late Glacial avifauna at ~14 000 BP: Sugar Loaf sites 1–3

The oldest absolutely dated bird remains on St Helena are those of Sugar Loaf site 1, dating to the Late Glacial at ~14 000 BP. They consist of eight seabird species: *Pelagodroma marina, Bulweria bifax, Pterodroma rupinarum, Puffinus pacificoides, Puffinus lherminieri, Oceanodroma castro, Puffinus griseus* and *Sterna fuscata,* three of which are now extinct (*B. bifax, P. rupinarum* and *P. pacificoides*) and two landbirds, the St Helena rail (*Aphanocrex podarces*) and the St Helena dove/pigeon (*Dysmoropelia dekarchiskos*), both of which are also extinct.

Landbirds

The two landbirds: St Helena rail (Wetmore, 1963) and St Helena dove/pigeon were apparently flightless by the time their bones were deposited (Olson, 1973; 1975, 30). Worthy (1980) has shown that, in New Zealand, the wing length of Finsch's duck (*Euryanas finschi*) "declined 10% between the Late Glacial 10–12 kyr ago and the Late Holocene" (Worthy & Holdaway, 2002, 239), proving that substantial wing reduction can occur in "just a few thousand years". Olson (1973, 34) suggests that, in rails, wing reduction and the evolution of flightlessness "can probably be measured in generations rather than in millennia".

The St Helena rail is believed to have fed on pelagic fish, squid and crustacea dropped by sea birds while feeding their young; on the eggs of seabirds; and probably on snails (Olson, 1973, 11, 22). The seabird colonies evidenced by bone remains on Sugar Loaf "would have provided a veritable cornucopia" of dropped food for *Aphanocrex podarces* (Olson, 1973, 22).

The remains of the St Helena dove/pigeon have not been recorded from any site other than Sugar Loaf site 1. Ashmole & Ashmole (2000, 101) suggest that "The extinction of this pigeon could have been caused by ancient climatic or volcanic events or have been linked to consequent changes in the vegetation". Since the last known volcanic event on St Helena occurred ~7.3 Myr ago, it is most unlikely that extermination of this bird occurred then or previously, especially since the bones found are not fossilised in the geological sense of that word.

Terrestrial snail shells that I collected on Sugar Loaf in 2007 were identified by F. Naggs (e-mail of 13 Jun. 2007, personal communication) as *Chilonopsis helena* and *Succinea sanctaehelenae. Chilonopsis helena* is now believed to be extinct (Smith, 1892), although Ashmole & Ashmole (2000, 298) suggest that *Chilonopsis* "were typical of the areas with dry gumwood forest in the north of the island". A *Chilonopsis* shell collected on the surface in the area near Sugar Loaf site 1 was radiocarbon dated (uncalibrated) to 48 340 ± 769 BP (UBA-7850). A shell of *Succinea sanctaehelenae,* which still lives on St Helena (Ashmole & Ashmole, 2000, 299), was collected near Sugar Loaf site 1 and radiocarbon dated (uncalibrated) to 44 269 ± 527 BP (UBA-7851).

The above dates, which may be questionable (as stated in the section on radiocarbon dating), coincide with an interstadial within the Last Glacial Stage, that is known to have existed in the Eastern Cape of South Africa from before ~45 000 BP until ~24 000 BP (the Birnam Interstadial; Lewis, 2008). The snail shells in the vicinity of Sugar Loaf site 1 may be the remains of snails that lived during that interstadial. The colder conditions of the succeeding Last Glacial Maximum (LGM; ~24 000 until ~18/17 000 BP; Lewis, 2008) may have been unsuited to the continued existence of these snails on Sugar Loaf. Further investigation is needed to ascertain whether the shells were buried by deposition of aeolian sand or other sediments during the LGM and, if so, to determine when they were subsequently exposed by erosion.

I did not collect any bones of the St Helena dove/pigeon during my visits in 2004/5 and 2007, and I have not obtained access to bones collected previously, so it has not been possible to date that bird by radiocarbon analyses of bone remains. The probability exists, since its bones have only been found at Sugar Loaf site 1, and the shells of extinct snails apparently dating to the interstadial prior to the LGM exist in the same vicinity, that the St Helena dove/pigeon lived during and possibly before the same interstadial, and also became extinct due to environmental changes during the LGM.

The presence of one bone assigned to *Charadrius sanctaehelenae* (wirebird) at site 3 on Sugar Loaf may indicate that this species existed on St Helena in the Late Glacial, although it is unwise to place too much reliance on so little evidence, especially since no absolute date has been obtained for this site.

Seabirds

Seabird remains on Sugar Loaf reflect the nature of the terrain, the soft soil overlying the aeolian sands and, particularly, the climatic conditions of the Late Glacial. Increases in global temperatures after the extreme cold of the LGM caused a rapid rise of global sea level between 14 600 and 14 300 BP, to ~80 m below that of the present (Hanebuth *et al.,* 2000) after its LGM low of ~–120 to 135 m (Clark & Mix, 2002). This would have submerged much of the wave-cut platform surrounding St Helena (Figure 2). Nutrients from remains of the drowned vegetation, soil, and fauna that could not escape the rising sea, would have increased the productivity of the sea in the vicinity of St Helena, to the benefit of plankton, fish, and the remainder of the food chain upon which seabirds depended. Mixing of seawater as the South East Trade Wind Drift Current (Figure 1; Edwards, 1990), [driven by a stronger South East Trade Wind than that of the present (Dupont *et al.,* 2004)], impinged on the newly drowned land, probably also increased the nutrient productivity of the sea surrounding the island.

Sea surface temperatures at ~14 000 BP, as evidenced by sediments from a borehole off the coast of Namibia, were probably ~2°C below those of the warmest phase of the Holocene that succeeded the Late Glacial, and may have fallen further during the Antarctic Cold Reversal and the Younger Dryas that post-dated ~14 000 BP but predated the beginning of the present (Holocene) interglacial (Dupont *et al.,* 2004). Consequently, petrels and shearwaters that fed on planktonic crustaceans, squid and small shoaling fish, and especially those used to cold offshore and pelagic waters and which flew close to the sea surface (Gould, 1974) and would thereby have avoided the strongest of the Late Glacial Trade Wind, were at an advantage at that time. Consequently it is not surprising that remains of *Pelagodroma marina* (white-faced storm-petrel; Carbonerus, 1992, 268), *Puffinus griseus* (sooty shearwater; Carbonerus, 1992, 254), and *Puffinus lherminieri* (Audubon's shearwater; Carbonerus, 1992, 256–7), occur at Sugar Loaf site 1, at ~14 000 BP.

Oceanodroma castro (Madeiran storm-petrel; Carbonerus, 1992, 269) presently occurs in warm waters, which may be why there are few of its remains at Late Glacial site 1 on Sugar Loaf. Whether Sugar Loaf site 2, where its remains are more abundant, is also Late Glacial, is uncertain. Three of the other seabirds evidenced at site 1: *Bulweria bifax, Pterodroma rupinarum,* and *Puffinus pacificoides* were endemics that are now extinct (McCulloch, 2004, 82–3; Rowlands *et al.,* 1998, 207). Little is known of their environmental preferences, except that they occupied some coastal areas of St Helena by ~14 000 BP and, in the case of the first species, continued to do so until within the last five or six hundred years, while the second species survived until ~AD 1640 (Table 2).

The single bone of *Sterna fuscata* (sooty tern) discovered at Sugar Loaf site 1 may be younger than the majority of bones there. *Sterna fuscata* is a tropical seabird, breeding on islands surrounded by seas with surface water temperatures of 23°C or higher (Ashmole & Ashmole, 2000, 284). Only two *Sterna fuscata* bones have been identified from the three "Late Glacial" sites on Sugar Loaf, compared with 201 from the Holocene Prosperous Bay deposits. *Sterna fuscata* was therefore probably a Holocene immigrant to St Helena.

Audubon's shearwater, which is widespread in the "warm parts of the Indian and Pacific oceans" (Ashmole & Ashmole, 2000, 273), is also much better represented by remains at Prosperous Bay than on Sugar Loaf, and may have been more common on St Helena in the Holocene than in the Late Glacial.

The bones of frigatebirds (*Fregata ariel trinitatis* and *Fregata minor*) at Sugar Loaf site 2 may be in secondary position, washed down from the cliffs above after the birds died. The cliffs above site 2 were probably attractive roosting, and possibly nesting, places for frigatebirds, the remains of which are particularly common in the deposits in the Prosperous Bay valley (Table 2) which date to ~AD 1640, but are absent at all earlier sites apart from Sugar Loaf 2. Consequently it is likely that frigatebirds utilised the rocks above Sugar Loaf site 2 at the same time as they utilised the Prosperous Bay valley, in the Holocene and not in the Late Glacial.

The Holocene avifauna prior to discovery of St Helena in AD 1502

Dry Gut

Although no absolute date has been obtained for bird bones discovered at Dry Gut, the geomorphological evidence already presented indicates that the bone remains at this site probably date from the Holocene. They consist of eight seabird species and four landbird species (Table 2). No human settlement remains exist in the Dry Gut area and the bird bones may predate discovery of the island.

Seabirds

The fairy tern (*Gygis alba*) appears for the first time in the bone record at Dry Gut, as does the masked booby (*Sula dactylatra*) and a gull (probably *Larus dominicanus*).

The masked booby feeds mainly on flying fish (McCulloch, 2004, 33), which are most numerous when sea surface temperatures reach and exceed 23°C (Ashmole, 1963b, 340; Bruun, 1935). Such high temperatures occurred during the Holocene

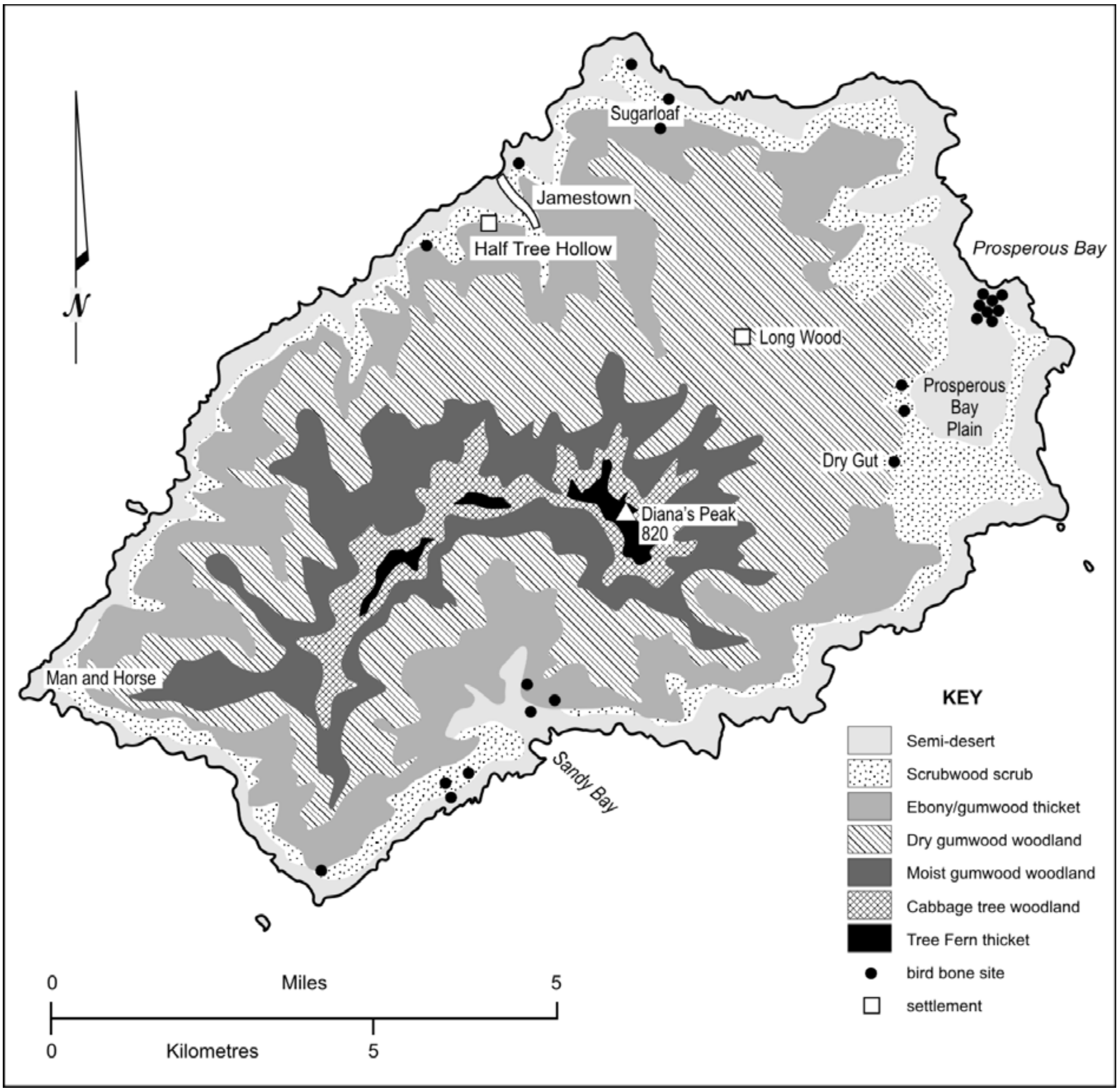

Figure 5. Vegetation zones believed to have existed on St Helena when the island was first discovered, in AD 1502. These zones essentially correlate with the modern orographic precipitation regions (Feistel *et al.*, 2003). Altitude in metres. (Based on Cronk, 1989 and redrawn after Ashmole & Ashmole, 2000, plate 5).

and not in the Late Glacial, if information from Namibian waters is applicable to St Helena (Dupont *et al.,* 2004). This supports the geomorphic evidence indicating that the Dry Gut remains date from the Holocene.

Sula dactylatra and *Gygis alba* may have colonised St Helena after the cold and windy environment of the Late Glacial had been replaced, judging by Namibian offshore sedimentary evidence, by warmer and less windy Holocene conditions (Dupont *et al.,* 2004). Gulls also existed on St Helena in the Holocene, as evidenced by two bones, that Ashmole & Ashmole (2000, 283) believed to be of *Larus dominicanus* (kelp gull), discovered at Dry Gut. Kelp gulls scavenge around seabird colonies, which must have been sizable at Dry Gut, judging especially by the number of bones there of *Pterodroma rupinarum* (Table 2). No gulls exist on St Helena at present and it is uncertain whether they ever bred on the island.

Landbirds

Two of the landbirds evidenced by bones at Dry Gut: the St Helena crake (*Porzana astrictocarpus*) and St Helena rail, are believed to have been scavengers in seabird colonies, consuming food dropped by sea birds as they prepared to feed their young, (Olson, 1973, 11, 22). The presence of their remains at Dry Gut, where there are plentiful seabird remains (Table 2), is only to be expected. Bones of *Porzana astrictocarpus* have not been found at the Sugar Loaf sites, and it may be that this species was a Holocene immigrant to St Helena.

The presence of bones of the St Helena hoopoe indicates the character of the Dry Gut area when avian remains were accumulating there. Hoopoes are grassland, glades and open woodland birds (Olson, 1975, 35) and environments of those sorts must have occurred at or near Dry Gut when St Helena hoopoes occupied that area.

Cronk (1989) believed that seven vegetation regions existed on St Helena in the immediate pre-discovery (1502) period (Figure 5 and Appendix II), although the antiquity of these regions is unknown. The endemic vegetation of St Helena differs remarkably from that of other parts of the World, with trees such as gumwood (of four different species; Eastwood *et al.*, 2004) having evolved from a very limited number of ancestors, some of which were on the island by the Early Pliocene (Muir & Baker, 1968). The vegetation regions may thus have existed for a long time, although they probably expanded and contracted in sympathy with climatic oscillations. The bones of *Upupa antaios* have been found "in shallow water-worn channels" on Prosperous Bay Plain (Ashmole & Ashmole, 2000, 117), and the fringes of that saline semi-desert and of the adjacent former Scrubwood scrub region, and the Dry Gumwood region (Figure 5), apparently provided suitable habitats for them.

Hoopoes eat terrestrial invertebrates, of which the world's largest earwig (*Labidura herculeana*), "which lives in burrows and under stones in dry soil" (Olson, 1975, 35), lived on Prosperous Bay Plain and in the open Gumwood Forest areas. Presumably this creature would have provided feasts for St Helena hoopoes! (*Labidura herculeana* may now be extinct, since no living specimens have been found since the 1960s; Ashmole & Ashmole, 2000, 335–6; 2004, 6, 24).

Dry Gut is immediately south of Prosperous Bay Plain and, according to Cronk (1989), lay within the scrubwood zone (Figure 5). The canopy height in that zone was only about 1 m and there would probably have been open space between the scrubwoods, providing suitable habitat for insect-feasting hoopoes to exist. The remains of St Helena hoopoe at Dry Gut are thus explicable, even though the bird seems to have had "restricted, if not entirely abrogated, powers of flight" (Olson, 1975, 34) and is thus unlikely to have moved far from its feeding areas.

The single bone discovered of the wirebird is also explicable. Wirebirds presently favour "open terrain at medium altitudes (*c.* 300–450 m), inhabiting pastureland ... arid waste ground and recently 'cleared' earth" (Rowlands *et al.*, 1998, 150). They occupy parts of the semi-desert area of Prosperous Bay Plain as well as grasslands around Longwood and on Deadwood Plain north of Longwood (Figure 2). They also occur on grasslands at Man and Horse, in the west of St Helena, and elsewhere. The Dry Gut site is at an altitude of ~300 m and is thought to have been located within the scrubwood and adjacent to the semi-desert region at the time of discovery of the island (Cronk, 1989; Figure 5). These are environments within which wirebirds still exist (McCulloch & Norris, 2001), so there is no reason why its remains should not have been discovered at Dry Gut.

The Holocene avifauna of St Helena at and soon after discovery of the island

Evidence of the avian population at, or soon after, the discovery of St Helena in 1502 (Gosse, 1990) comes from bird remains at Sandy Bay site A and from the Prosperous Bay deposits. The latter deposits, in particular, evidence widespread extermination of much of the avian population of St Helena less than one and a half centuries after the island was discovered.

Sandy Bay site A

The avian remains from this site, as already argued, are unlikely to be more than 500 to 600 years old and probably date to soon after the discovery of St Helena, possibly to ~AD 1664 (*vide* Radiocarbon Dating section). They consist of seven seabird and two landbird species (Table 2). The seabird remains, as befits the exposed windward coast of St Helena, comprise the bones of petrels of various kinds, frigatebirds and terns. The two landbirds whose bones have been collected and identified are the now extinct St Helena crake and St Helena rail, both of which were scavengers in seabird colonies. The absence of any other landbird remains is not unexpected, given the windy and inhospitable nature of the area, which Cronk (1989) believed lay within the arid semi-desert region prior to and at discovery of the island (Figure 5).

Judged by the number of bones seen in valley-side slope deposits in the lower portion of that valley when I examined it in 2004/5 and 2007, Sandy Bay valley must have been a great seabird roosting, and possibly nesting, area at the time of discovery of the island.

Prosperous Bay valley

Of the 16 bird species evidenced by bird bones in the Prosperous Bay deposits (Table 2), which date from ~AD 1640, only five were of land birds, the remainder, judged by the number of bones discovered and identified, comprised mainly frigatebirds, shearwaters and petrels.

Seabirds

The most common remains were of *Fregata ariel trinitatis* (lesser frigatebird). Although no longer present on St Helena, the related Ascension frigatebird (*Fregata aquila*) nests "among rocks on flat areas or broad cliff ledges" (McCulloch, 2004, 39). Predation by human introduced rats and feral cats *Felis sylvestris* has caused immense decline in frigatebird numbers on Ascension (McCulloch, 2004, 39), and the same fate presumably befell frigatebirds on St Helena. In 1682 John Fryer reported that "Wild Cats" were "a mischievous vermin" on St Helena (quoted from Gosse, 1990, 79).

Feral cats, which originated from introduced domestic cats (Beeckman, 1718), caused problems in the Longwood area, near Prosperous Bay, by the 1750s if not before. In 1753 it was reported that "Poultry (have been) killed in the Long Wood by Wild Cats, which daily increase" (St Helena Records, Book 35, 3/9/1753). The fact that bird bones from the Prosperous Bay deposits date to ~AD 1640, and that no more recent frigatebird bones have been dated on St Helena, suggests that cats and rats prevented them from breeding and rearing their young on the mainland from about that date. In 1666, and again in 1698, frigatebirds were noted on Speery Island (Figure 2; Rowlands *et al.*, 1998, 130) where they might have continued breeding after that had become impossible on the mainland. Frigatebirds no longer exist on St Helena or its' offshore islands.

The second most common bones were those of Audubon's shearwater, which nests on "sandy or otherwise soft soil" (Carbonerus, 1992: 256–7) and is sedentary when on land, rendering it "vulnerable to human exploitation and predation by introduced mammals" (Carbonerus, 1992, 257). Cats, rats, dogs *Canis domesticus* and other mammals (possibly including pigs *Sus scrofa,* which Gosse (1990, 18) reports that Captain Thomas Cavendish found abundant on St Helena as early as 1588) probably decimated this species by ~AD 1640. Audubon's shearwater is now a very occasional visitor to St Helena, although it breeds in the Caribbean and is well known on the east coast of the United States (Carbonerus, 1992, 257).

Other ground-nesting seabirds and/or their eggs and fledglings, including the sooty tern (*Sterna fuscata*), the white-faced storm-petrel (*Pelagodroma marina;* which is "An obligate burrower" (Rowlands *et al.*, 2004, 119)), the masked booby, the Madeiran storm-petrel (*Oceanodroma castro*) and the red-footed booby (*Sula sula*), must also have been easy prey for cats, rats and other mammals, including humans. *Sula dactylatra, Pelagodroma marina* and *Oceanodroma castro* continue to breed on St Helena's offshore islands, where feral cats and rats do not exist. Sooty terns still attempt to breed on the "Bird Ground", a flattish area on top of the cliffs at Gill Point, overlooking Shore and George Islands (Figure 2), where it is decimated by cats and possibly by rats. The remains of sooty terns were found in cat dens on Bird Ground in 1997 (Rowlands *et al.*, 1998, 161) and wings of *Bulweria bulwerii* were found there in 1995 (Ashmole *et al.,* 1999). I saw unidentified wing remnants there in 2007, as well as plentiful cat scats. I also saw rat footprints in 2007 beside the footpath to Bird Ground. The nests of sooty terns have also been seen in the area of Castle Rock, in the south west of St Helena, "within the last few years" (P. Ashmole, 2008, personal communication).

Eggshells, believed by Olson (1975, 16) to be of *Pterodroma rupinarum* (St Helena gadfly petrel), occur in the Prosperous Bay deposits and at sites 1 and 2 on Sugar Loaf. They indicate that this petrel was ground nesting, which must have made it vulnerable, like the species listed above, to destruction by cats and other mammals. *Pterodroma rupinarum,* which had existed on St Helena from at least the Late Glacial (Table 2), failed to withstand the mammal onslaught, and is now an extinct endemic (Rowlands *et al.,* 1998, 112).

The only other seabirds represented by bones at Prosperous Bay are two birds that still breed on the mainland of St Helena: *Phaethon aethereus* (red-billed tropicbird), and *Gygis alba* (fairy tern). Tropicbirds nest on precipitous cliffs inaccessible even to cats and, probably, rats, as at Great Stone Top (Figure 2), and on offshore islands (Rowlands *et al.,* 1998, 121). *Gygis alba* breed in trees, on inaccessible cliffs and on offshore islands (Rowlands *et al.,* 1998, 121). They, unlike most of the other seabirds whose remains exist at Prosperous Bay, escaped extinction caused by the unwitting actions of humans in introducing, particularly, cats and (unintentionally) rats to St Helena.

Landbirds

These included the endemics St Helena crake and St Helena rail, which were essentially scavengers of seabird colonies. They no longer exist and their demise is probably linked with that of the massive seabird colonies that formerly occupied at least coastal areas of St Helena. Additionally, being flightless (Olson, 1973), the rail and the crake must have been easy prey for cats, rats and some other mammals. They were probably extinct by ~AD 1640, or soon thereafter.

The three other land birds recorded in the Prosperous Bay deposits were the St Helena hoopoe, the wirebird and the St Helena cuckoo (*Nannococcyx psix*). Of these, the hoopoe and the cuckoo are now extinct. Since only four bones identifiable to *Upupa antaios* have been found in the deposits, two to *Charadrius sanctaehelenae* and one to *Nannococcyx psix,* it is probable that these species were present in the Prosperous Bay area in small numbers. The bones may even have been incorporated in the deposits after the bodies, or parts of the bodies, of the birds had been washed down from higher ground by floods. *Charadrius sanctaehelenae* presently lives on Prosperous Bay Plain, above the gorge that leads into Prosperous Bay but within the drainage area of the Fishers Valley stream that enters the sea at Prosperous Bay (Figure 2).

Hoopoes, as already stated, were suited to life in semi-desert and scrubland/dry Gumwood land. The existence of Gumwood as late as 1744, between the waterfalls in the gorge-like valley that leads to Prosperous Bay, is testified by the terms of a lease of "Gumwood Land" granted by the English East India Company to Joseph Whaley Jnr, who had to "keep up and Preserve the full Quantity and Proportion of Wood and other trees that are growing there" (St Helena Records, Book 29, 358). There is therefore no reason why *Upupa antaios* should not have frequented that area of the Prosperous Bay valley at that time or in the previous century, unless it had already been exterminated. Since the St Helena hoopoe had "much restricted, if not entirely abrogated, powers of flight" (Olson, 1975, 34), it must have been easy prey for cats and rats and it may well have been exterminated by ~AD 1640.

Nothing, apart from one bone, is known of the St Helena cuckoo. If it were a woodland/forest dweller, the deforestation of St Helena would have destroyed its habitat by the early eighteenth century, if not before. In 1720 it was stated that "the Island in twenty years time will be utterly ruined for want of wood ... no man ... can say there is one tree in the Great Wood [at Longwood], or other woods less than twenty years old, consequently it will dye with age" (St Helena Records, 7 Mar. 1710). The cuckoo, if not extinct by ~AD 1640, must have succumbed soon thereafter.

EXTINCTION AND INTRODUCTION

The early years of the seventeenth century, judged by bird remains at Prosperous Bay, witnessed the extermination of much of the avian population of St Helena, probably mainly by anthropogenically introduced cats and, directly and otherwise, by rats, as on many islands worldwide (*e.g.* Courchamp *et al.,* 2003; Flannery & Schouten, 2002; Quammen, 1996; Towns *et al.,* 2006). Thirty years after the introduction of a cat and her three kittens in the Kerguelen Archipelago, for example, "the population of 3500 cats destroyed 1.2 million birds per year" (Pascal, 1980).

The introduction of rabbits to St Helena may have led to increased cat predation on birds. Rabbits, *Oryctolagus cuniculus huxleyi* (the Mediterranean subspecies), were introduced by the Portuguese in the sixteenth century, with further introduction ~1770 (Ashmole & Ashmole, 2000, 264). On Macquarie Island, south of Australia, rabbits provided food for cats in winter, when seabirds were absent from the island. This enabled cat numbers to increase, resulting in hyper-predation of birds when they visited the island and, especially, "the decline of burrow-nesting petrels" (Brothers, 1984, quoted from Courchamp *et al.,* 2003, 360). A similar chain of events may have occurred on St Helena, where there were ~30 000 rabbits in 2008 (SHI, 2008).

Petrel chicks are preyed on by rats on New Zealand islands. On Little Barrier Island, north of Auckland, "small burrowing seabirds [are] now confined to offshore rocky islets" apparently devoid of rats (Towns *et al.,* 2006, 864). On Moutohora (Whale Island) in the Bay of Plenty, where rabbits were introduced about 1968 and, by the early 1970s competed for vegetable food with rats, "no petrels were fledged (in 1973) due to heavy rat predation" (Towns *et al.,* 2006, 878).On Lundy Island, in the Bristol Channel off the coast of the west of England, rats caused declines in the number of puffins and shearwaters (Appleton *et al.,* 2002). On islands off the west coast of Scotland "small-bodied burrow-nesting seabirds [e.g, …storm-petrels…] are particularly susceptible to predation by rats" (Stapp, 2002, 838). Particularly vulnerable to rats are: "small terrestrial birds, with weak flight [that] are surface or crevice nesters near ground level; small burrowing seabirds … and surface-nesting seabirds … such as petrels… " (Towns *et al.,* 2006, 886). The Laysan rail (*Porzana palmeri*), for example, was exterminated within two years of rats arriving on its last island refuge in the Hawaiian Islands in 1943 (Flannery & Schouten, 2002, 153).

There is little doubt but that rats, [which King (1985) believes "have been implicated in the greatest number of extinctions (of island birds globally) due to predators (54 per cent)"], as well as cats, caused devastation among the avian inhabitants of St Helena. That was particularly because the birds were predominantly small burrowing and surface-nesting seabirds, especially petrels and shearwaters, and terrestrial birds with weak (or no) flight.

In the eighteenth century Beeckman (1718) reported that there were "vast numbers of cats ... living among the rocks ...

Table 3. The breeding birds of St Helena at the opening of the Twenty first Century.

Species name	English name	Main/important food	First recorded/introduced
Seabirds			
Bulweria bulwerii	Bulwer's petrel	Small fish, squid	?1995?[1]
Oceanodroma castro	Madeiran storm-petrel	Planktonic crustaceans, small fish, squid	14/13 000 BP[2]
Phaethon aethereus	Red-billed tropicbird	Fish + squid	~1640 AD[3]
Sula dactylatra	Masked booby	Flying fish	~1640 AD[4]
Sula leucogaster	Brown booby	Fish + squid	1925[5]
Sterna fuscata	Sooty tern	Flying and other fish	14/13 000 BP[6]
Anous stolidus	Brown noddy	Small fish + squid	1950[7]
Anous minutus	Black noddy	Small fish + squid	1608?[8]
Gygis alba	Fairy tern	Small fish	Holocene
Landbirds			
Charadrius sanctaehelenae	Wirebird	Ground living insects and other invertebrates	? possibly Late Glacial[10]
Gallinula chloropus	Moorhen	Vegetable matter and small animals	1670[11]
Landbirds known to have been introduced			
Alectoris chukar	Chukar partridge	Seeds, plant shoots, insects	~1531[12]
Phasianus colchicus	Ring-necked pheasant	Seeds, seedlings, shoots, bulbs, tubers, insects and other invertebrates	~1531[13]
Columba livia	Feral pigeon	Seeds, shoots, seedlings	~1578[14]
Geopelia striata	Peaceful dove	Seeds, especially from trees	~1775[15]
Acridotheres tristis	Indian myna	Seeds, seedlings, fruit, insects, worms, small mice, geckoes, eggs, nestlings	1885[16]
Foudia madagascariensis	Madagascar fody	Seeds, nectar, insects	Possibly 1673[17]
Padda oryzivora	Java sparrow	Seeds	1775 or before[18]
Estrilda astrild	Common waxbill	Mainly grass seeds	Probably between 1764 and 1782[19]
Serinus flaviventris	Yellow canary	Small seeds	? 1776[20]

References, which relate to first record on St Helena, or date of introduction to the island from which the present birds descend: [1]McCulloch, 2004, 25. [2]Lewis, this paper. [3]*ibid.* [4]*ibid.*, see also Temple, 1919, 332: Peter Mundy's record of 1634.[5] Olson, 1975, 24. [6]Lewis, this paper. [7]Rowlands *et al.*, 1998, 165; previously not distinguished from black noddy, probably long resident. [8]Rowlands *et al.*, 1998, 168. [9]Bones recorded from Dry Gut (Olson, 1975) but not radiocarbon dated. [10]Bones recorded from Sugar Loaf (site 3) (Olson, 1975), but not radiocarbon dated. [11]McCulloch, 2004, 63. [12]Rowlands *et al.*, 1998, 133. [13]Rowlands *et al.*, 1998, 138. [14]*ibid.*, 175. [15]*ibid.*, 177. [16]*ibid.*, 186; Ashmole & Ashmole, 2000, 290, name this the Indian myna, Rowlands *et al.* name it the common myna. [17]McCulloch, 2004, 75. [18]Rowlands *et al.*, 1998, 194. [19]*ibid.*, 197. [20]*ibid.* 202.

Additional information on Table 3 is derived from McCulloch, 2004.

feeding on young partridges ... as great a plague as the rats" (quoted from Gosse, 1990, 140). By 1713 black rats (*Rattus rattus frugivorus,* Ashmole & Ashmole, 2000, 264), thought to be descendants of rats brought unintentionally to St Helena on ships in the sixteenth century, from which they escaped on-shore, were even barking the top branches of gumwood trees, thereby killing them (Gosse, 1990, 167). In 1755 it was reported that mice as well as rats were "barking the young trees in the Longwood" (Ashmole & Ashmole, 2000, 265). Mice (*Mus musculus brevirostris,* native to the Iberian Peninsula) were introduced, probably unintentionally, from Portuguese ships in the sixteenth century (Ashmole & Ashmole, 2000, 267). The activities of alien rodents thus contributed to the destruction of the natural vegetation of St Helena, probably to the detriment of the avian population, as on Hawai'i (Athens *et al.*, 2002), the islands of New Zealand, and islands of the Caribbean. As a result of rat eradication in 1995 on Great Bird Island in the Lesser Antilles in the Caribbean, for example, by 2003 "vegetation biomass and diversity increased…, red-billed tropic birds (*Phaeton aetherecus,* (*sic.*)) doubled in number" (Towns *et al.*, 2006, 879). Whether rodent-induced destruction of natural vegetation on St Helena predated the eighteenth century is uncertain, but by 1682 rats "ate potatoes while they were still in the ground" and islanders grew yams "because they were too bitter (until boiled) to be eaten by rats" (Ashmole & Ashmole, 2000, 40). Rat poison was imported in 1678 (Royle, 2007, 171).

Alien mammals may even have introduced infectious diseases to St Helena, as in the Hawaiian Islands, although it is unlikely that such introduced diseases caused avian extinctions (Smith *et al.*, 2006).

During the sixteenth century human colonists started to introduce birds to St Helena. The period between ~AD 1531, (when the first anthropogenic bird introduction apparently took place), and ~AD 1640, (when evidence from the Prosperous Bay deposits suggests that many bird species had been exterminated), was therefore one in which the pre-colonial avian population was being decimated by alien mammals and, to some extent, replaced by alien introductions, as discussed in the next section.

THE AVIFAUNA OF ST HELENA FROM 1531 TO THE PRESENT

Table 3 lists the breeding birds present on St Helena at the opening of the Twenty-first Century. They consist of nine species of seabirds and eleven species of landbirds. The table also indicates the main food of each species and the date at which each species was first recorded on, or anthropogenically introduced to, the island. Of the land birds, at least nine have been anthropogenically introduced to the island since about AD 1531. There is doubt about whether or not the moorhen (*Gallinula chloropus*) was introduced or whether it was a natural immigrant to the island (McCulloch, 2004: 63). All the sea birds are natural immigrants or migrants. In addition to the breeding population, St Helena is regularly visited by the cattle egret (*Bubulcus ibis*) (McCulloch, 2004: 55). At least thirty other species have occasionally been recorded on the island, and are regarded as accidental visitors (McCulloch, 2004: 84–5).

Landbirds

St Helena was discovered in 1502 by Portuguese seafarers (Gosse, 1990). The first settler was a disgraced Portuguese nobleman: Dom Fernando Lopez, who lived on the island from 1516 until 1546, apart from one visit to Europe (Rowlands *et al.*, 1998, 251–2). Two game birds that are still present: *Alectoris chukar* (Chukar partridge) and *Phasianus colchicus* (ring-necked pheasant), as well as *Numida meleagris* (guinea fowl), were introduced to St Helena by 1531, during Lopez' time there, presumably to provide food and (important to a nobleman, perhaps!), sport. The partridge may have been imported from the Persian Gulf area (Rowlands *et al.*, 1998, 134), while the pheasant probably came from China, with later importations from India (Rowlands *et al.*, 1998, 138). The guinea fowl were probably from West Africa, but became extinct, for reasons unknown, by 1936 (Rowlands *et al.*, 1998, 142). *Columba livia* (feral pigeon) was also introduced to St Helena during the Portuguese period, probably before 1578, from Europe and from India (Rowlands *et al.*, 1998, 175).

In 1659 the English East India Company sent settlers to St Helena and in 1673, after a brief period when the island was in Dutch hands, King Charles II granted a charter making the company Lords Proprietors with all the rights of sovereignty (Ashmole & Ashmole, 1990, 39). Importations of small and beautiful landbirds, (some of which are noted for their songs), followed as British settlers tried to make St Helena feel "like home". The following were successful: the Madagascar fody (*Foudia madagascariensis*), probably from Mauritius or Madagascar, by about 1673 (McCulloch, 2004, 75); the common waxbill (*Estrilda astrild*), probably from South Africa between 1764–82 (Rowlands *et al.*, 1998, 197); the peaceful dove (*Geopelia striata*), probably from Mauritius (where it had been introduced from Malaysia) by ~1775 (Ashmole & Ashmole, 2000, 289); the Java sparrow (*Padda oryzivora*) from Java, also by about 1775; and the yellow canary (*Serinus flaviventris*) from the Cape of Good Hope region by 1776 (Rowlands *et al.*, 1998, 202). Since at least some of the foods eaten by those birds (Table 3) were present on St Helena when the island was discovered, the apparent absence of native songbirds is puzzling. The isolation of the island may have made it impossible for songbirds to colonise it from Africa or from any other landmass, but were they really absent, or has their former presence not yet been detected?

The hill myna (*Gracula religiosa*) was introduced to St Helena in 1829. This proved unsuccessful, as was that of Indian mynas (*Acridotheres tristis*) imported earlier, in 1815, supposedly to control cattle ticks (Rowlands *et al.*, 1998, 186). Five more Indian mynas were imported and released in 1885, from which the present population descends (Ashmole & Ashmole, 2000, 289–90).

The only endemic landbird to survive the period of extinction in the seventeenth century, apparently caused by introduced mammals, is the wirebird. Mundy reported of St Helena in 1638, that of "land fowl ... only that one kind [*Charadrius sanctaehelenae*] here to be seen" (Temple, 1919). This suggests that all other landbirds, apart from those introduced by the Portuguese, were already extinct. The wirebird continues to occupy much the same territory as previously: the grasslands around Longwood, Prosperous Bay Plain and its surrounds, and, in the west of St Helena, the grasslands of Man and Horse (Rowlands *et al.*, 1998, 150).

Another landbird permanently resident on St Helena is the moorhen, which occupies damp valley bottoms where there are crops of yams (McCulloch, 2004, 63). This bird was first recorded on the island in 1670 and it is uncertain whether it was a natural arrival, or whether it was introduced. Rowlands *et al.* (1998, 148) surmise that *Gallinula chloropus* "reached St Helena of its own accord" and colonised the island because environmental changes brought about by humans, especially the introduction of yams as a food crop, provided a suitable environment for the survival of this immigrant.

In addition to permanent residents there is at least one regular landbird visitor, as already mentioned, the cattle egret, although this bird has not yet nested on St Helena (McCulloch, 2004, 55).

Porzana astrictocarpus, *Aphanocrex podarces*, *Upupa antaios* and *Nannococcyx psix*, which were present on St Helena in the seventeenth century, as evidenced by their remains in the Prosperous Bay deposits, are now extinct.

Seabirds

With the exception of *Bulweria bulwerii* (Bulwer's petrel) and *Anous stolidus* (brown noddy) the predecessors of the seabirds that breed on St Helena at present, as listed on Table 3, have lived on the island since at least ~AD 1640. Of the seabirds represented by bones in the Prosperous Bay deposits, *Fregata ariel trinitatis* and *Fregata minor* and *Sula sula* no longer breed on or even visit St Helena (McCulloch, 2004, 83); Audubon's shearwater and white-faced storm-petrel are very infrequent and probably accidental visitors (Rowlands *et al.*, 1998, 114, 119). St Helena gadfly petrel is now an extinct endemic (Rowlands *et al.*, 1998, 112). St Helena Bulweria petrel, whose bones were discovered at Sandy Bay site A and probably existed within the last 600 years, is also an extinct endemic (Rowlands *et al.*, 1998, 111).

CONCLUSION

With the possible exception of St Helena dove/pigeon, which may have lived before and/or during the interstadial that preceded the Last Glacial Maximum (LGM), no evidence has yet been found of the avifauna of St Helena before the Late Glacial. The Late Glacial and Holocene avifauna from the Late Glacial at ~14 000 BP until the present, is summarised on Table 4. *Dysmoropelia dekarchiskos* probably became extinct before or during the LGM. St Helena shearwater probably became extinct towards the end of the Late Glacial, or in the early part of the Holocene, as temperatures rose and climate ameliorated. The remains of the sooty shearwater, a sub-antarctic species (Ashmole & Ashmole, 2000, 273), have only been found in the Late Glacial deposits at Sugar Loaf site 1, and it probably abandoned St Helena as temperatures increased (Table 4).

White-faced storm-petrels, St Helena gadfly petrels, and Audubon's shearwater, were present on St Helena from at least the Late Glacial until ~AD 1640, when introduced mammals made life on the island untenable for them. The St Helena Bulweria petrel was present on St Helena from at least the Late Glacial and survived until ~500/600 years ago, (and possibly until ~AD 1660), as evidenced by its remains at Sandy Bay site A. The absence of this species from the Prosperous Bay

Table 4. The Late Glacial and Holocene avifauna of St Helena.

Time/radiocarbon date	Species present	Environmental conditions
Late Glacial, ~14 000 BP	*Pelagodroma marina, Bulweria bifax, Pterodroma rupinarum, Puffinus pacificoides, Puffinus lherminieri, Oceanodroma castro, Puffinus griseus, Aphanocrex podarces,* ?*Dysmoropelia dekarchiskos,* ?*Sterna fuscat*a.	Rapid sea level rise between ~14 600 and 14 300 BP from ~135 to ~80 m below present sea level, submerging much of wave-cut platform surrounding St Helena and increasing marine productivity. Sea surface temperature probably ~2°C below Holocene maximum, stronger SE Trade Wind than at present. Probably scrubwood scrub on Sugar Loaf.
Holocene to Sixteenth/ Seventeenth Century AD, before major extinctions	*Pelagodroma marina, Bulweria bifax, Pterodroma rupinarum, Puffinus lherminieri, Oceanodroma castro, Sterna fuscata, Fregata ariel trinitatis, Fregata minor, Sula dactylatra, Gygis alba,* ?*Larus dominicanus, Phaethon aethereus, Sula sula, Aphanocrex podarces, Porzana astrictocarpus, Charadrius sanctaehelenae, Upupa antaios, Nannococcyx psix*.	Warmer and less windy than in Late Glacial. Seven essentially altitudinal vegetation belts ranging from semi-desert at low altitude to Tree Fern thicket at high altitude, correlating with increases in orographic precipitation with increasing altitude. Sea level at and sometimes slightly above present. Temperatures possibly higher in earlier rather than in later Holocene.
Seventeenth Century AD, by ~AD 1640	Species existing in Holocene but apparently exterminated by ~AD 1640: *Pelagodroma marina, Bulweria bifax, Pterodroma rupinarum, Puffinus lherminieri, Larus dominicanus, Sula sula, Aphanocrex podarces, Porzana astrictocarpus, Upupa antaios, Nannococcyx psix.*	Anthropogenically introduced rats, cats, mice, dogs, and other mammals following discovery of St Helena in AD 1502, plus human activities, led to alteration of natural vegetation and extinction of much of the avifauna by ~AD 1640, as evidenced by radiocarbon-dated bones in sediments in the Prosperous Bay and Sandy Bay valleys.
Post ~AD 1640	Table 3 lists the breeding birds of St Helena at the start of the Twenty-first Century. Nine anthropogenically introduced species of landbirds have been established. Only one pre-existing landbird (*Charadrius sanctaehelenae*) survived post-discovery extinctions. Only nine seabird species are now known to breed on St Helena and its islands. *Sula leucogaster, Bulweria bulwerii, Anous stolidus* and *Anous minutus,* present on St Helena at the start of the Twenty-first Century, may also have been present earlier, but are not evidenced by identified bone remains. Frigatebirds, present on St Helena as late as AD 1698, may have left the area due to assumed sea surface temperature decline in the Little Ice Age, which may have caused flying fish, the mainstay of Frigatebirds to abandon the vicinity of St Helena.	Nine species of landbirds have been successfully introduced as a result of human colonisation of St Helena. Only minor remnants of the pre-discovery natural vegetation still exist. A possible decrease in sea surface temperatures during the Little Ice Age (~AD 1500–1930) may have adversely affected food supplies of some birds, especially those largely dependent on flying fish, which favour sea surface temperatures of 23°C and above (Bruun, 1935).

valley deposits may be due to local factors.

Frigatebirds (*Fregata ariel trinitatis* and *Fregata minor*) apparently established themselves during the Holocene, as temperatures rose and sea surface temperatures became high enough for the presence of the flying fish on which they depend. The sooty tern also seems to have been primarily a Holocene immigrant, as does the masked booby, fairy tern, red-billed tropicbird, red-footed booby and kelp gull.

There are no gulls, frigatebirds or red-footed boobies on St Helena at present and Ashmole & Ashmole (2000, 283) suggest that there may never have been a breeding population of gulls on the island. The reasons for the absence of frigatebirds and red-footed boobies are unclear, since they could have continued to breed, unmolested by cats and rats, on offshore islands. Perhaps there were sea surface temperature reductions during the Little Ice Age, between ~AD 1500 and ~AD 1930 (Andersen & Borns, 1994, 96), which affected their food supplies.

No evidence has been found in any of the bone deposits of *Sula leucogaster* (brown booby), *Bulweria bulwerii* (Bulwer's petrel), *Anous stolidus* (brown noddy) and *Anous minutus* (black noddy), all of which occur on St Helena at present. This may be because these birds are cliff nesters and does not necessarily imply that they are recent immigrants to the island.

St Helena crake, St Helena hoopoe, and wirebird, probably established breeding populations on the present area of St Helena in the Holocene, although they may have lived on the sandy shelf surrounding the island at an earlier date, moving inland as sea level rose in the Late Glacial. The St Helena rail may have established itself during, or possibly before, the Late Glacial. Of these landbirds, only the wirebird survived the mass extinction caused by human-introduced mammals in the seventeenth century. The single bone yet found and ascribed to the St Helena cuckoo is insufficient evidence to establish whether there was ever a breeding population of this species on St Helena. Ashmole & Ashmole (2000, 100) suggest that this cuckoo occupied "an insectivore niche" on the island, and "parasitized at least one other extinct forest bird, so far undetected in the fossil deposits".

NEED FOR FURTHER RESEARCH

Further research is needed, as Benson (1950) and den Hartog (1984) have already suggested, to determine whether woodland areas in the interior of the island, (as opposed to the dry woodland and semi-desert areas around the margins in which the St Helena hoopoe, wirebird and possibly St Helena cuckoo existed during part of the Holocene), had their own birdlife. Since those areas are moist to wet, favouring decay rather than preservation of organic matter, it may be that no bones or other evidence of former bird populations has survived and it may be impossible to determine whether birds existed in those areas.

Research is also needed to establish the avifauna of St Helena prior to the Late Glacial, in the earliest ~14.5 Myr of the island's existence. Hare's suggestion (in Olson, 1975, 13), that the bird bones identified and tabulated by Olson (1975) date from "well back in the Pleistocene" has not been substantiated by radiocarbon dating. Apart, possibly, from *Dysmoropelia dekarchiskos,* they record only the avifauna of St Helena during portions of the last ~14 000 years. The suggestion of Ashmole & Ashmole (2000, 101): that at least some of the bones date "within the last 2–3 million years", is correct, but misleading. The Miocene, Pliocene and most of the Pleistocene bird life of St Helena remains a mystery. The indiscriminate collection of bone remains on St Helena should be prohibited, so that those bones that are left can be studied scientifically in their correct stratigraphic position, as has been done in New Zealand and elsewhere (*e.g.* Worthy & Holdaway, 2002; Olson & Hearty, 2003), in order to provide the maximum possible information on the avifauna of the island and of St Helena's climatic and environmental history.

Finally, rat and cat-free areas should be created on the mainland of St Helena, where birds can breed unhindered by alien predators, as has been done in the Karori Wildlife Sanctuary near Wellington in New Zealand (Courchamp *et al.,* 2003, 363). The "Bird Ground" near Gill Point, as suggested by Ashmole & Ashmole (2000, 166), should be a suitable site for such an area unless deemed too near the proposed airport (SHC, 2006), being isolated from most of the remainder of the mainland by broken and largely barren terrain, and being in view of the seabird colonies on Shore and George Islands. The effects of such predator-free areas on the avifauna of St Helena would provide an excellent topic for future research and may have implications for the future management and, through ecotourism, economy of the island.

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Appendix I

Vertebrate remains from Sandy Bay Valley, St Helena Island, South Atlantic

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This report describes a small bone collection from Sandy Bay valley on the island of St Helena. The material consists mainly of the remains of domestic goat, *Capra hircus.* One specimen, a femur, may be that of a marine mammal.

Description

?OTARIIDAE ?Fur seal

A femur shaft fragment is tentatively identified as that of a marine mammal, because of its irregular cross-section and because the bone tapers distally. The specimen is quite robust, suggesting that it may belong to a fur seal rather than a true seal. (This bone was collected from unconsolidated normally bedded sediments beneath the surface of Broad Gut, about 300 m inland from the present high-tide mark).

ARTIODACTYLA, Bovidae indeterminate

A small–medium sized bovid is represented by two sternum pieces, a rib articulation, a shaft fragment of a humerus and a tibia shaft of a very young individual, possibly that of a fetus. These remains cannot be identified to genus or species, but is likely to represent the domestic goat, as described below.

Caprini, *Capra hircus* (domestic goat)

The domestic goat is represented by a left distal humerus and by a virtually complete distal phalanx.

The distal humerus is typical of goats, as opposed to sheep, being medio-laterally compressed. The distal phalanx has minor damage on its dorsal surface. It can be identified as goat, because of the poor development of the processus extensorius and because of its pronounced transverse compression.

Appendix II

Vegetation types and regions on St Helena immediately prior to discovery of the island in AD 1502 (after Cronk, 1989)

1. Tree fern thicket from ~700–820 m, with a canopy height of 3–4 m, growing on leached thick mor humus soils that tend to be damp or wet because precipitation is high and mist frequent.
2. Cabbage tree woodland from ~600–720 m, with a canopy height of 5–6 m, growing on richer (but nevertheless damp to wet) soils than those of the Tree fern zone. The Black cabbage tree (*Melanodendron integrifolium*), that gives its name to this zone, is drought intolerant (Eastwood *et al.,* 2004).
3. Moist Gumwood woodland from ~500–650 m, with a canopy height of 4–5 m, growing on Brown Earth soil that sometimes becomes so dry due to occasional lack of precipitation that the nominative species (*Commidendrum robustum*/ Gumwood) developed drought resistance (Eastwood *et al.,* 2004).
4. Dry Gumwood woodland from ~300–500 m, with a canopy height of 5–6 m, growing (like plants of the Moist Gumwood zone) on Brown Earth soil.
5. Ebony-Gumwood thicket from ~100–500 m, with a canopy height of 1–3 m, growing on Brown Earth soil in rocky places.
6. Scrubwood scrub from sea level to ~350 m, with a canopy height of ~1 m, growing on Brown Earth soil.
7. Saline semi-desert from sea level to ~250 m where conditions are very dry and the ground level, as at Prosperous Bay Plain in the extreme east of the island. The vegetation in this region was (and still is) dominated by halophytes and the soils are Solonetz, patchy and saline.

The above zones/regions are shown in Figure 5.