

The timing of arrival of humans and their commensal animals on Western Indian Ocean oceanic islands.

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Abstract: The principal island groups, Comoros, Mascarenes, and granitic Seychelles were first settled by humans at very disparate times: The Comoros during the 8th century CE, the Mascarenes from 1638, and the Seychelles not until 1770. As the settlers in the Comoros did not chronicle their lives, evidence of commensal arrival relies on archaeology, and there is no useful historical information on these animals until Europeans began visiting in the 1500s. By contrast in the Mascarenes, although ship rats preceded the first Dutch visit in 1598, Europeans documented their releases of livestock (various ungulates) on Mauritius and Réunion in the early 1600s, and the arrival (deliberate or not) of many other species thereafter. Releases were later, not until the 1730s, in Rodrigues (though rats were there by 1691). Cats arrived in the 1680s on the larger two islands, but Norway rats not until the 1730s. In the Seychelles ship rats were present in 1773, but their arrival date is uncertain; ungulates have been feral at various times, but are now longer so. Various other commensal or human food-related mammal, bird and reptile species are now present on many of the islands. In the Mascarenes particular waves of extinctions can be related to colonisation by specific introduced mammals. The low coral islands of the area have very disparate human and feral animal histories; details are given for the Aldabra group, the only low islands with significant endemism.

Introduction

The three principal groups of oceanic high islands in the western Indian Ocean have very different histories of human discovery and settlement. The Comoros, lying between mainland Africa and Madagascar, may have had temporary settlements from 1000BCE, but were settled permanently in the first millennium CE. The settlement history here is closely tied to that of the interactions of Austronesians (proto-Malagasy) and native East African groups in the 7th and 8th centuries CE (e.g. Dick-Read 2006, Allibert 2007). By contrast the Mascarenes and the granitic central Seychelles, far out beyond Madagascar, where not formally discovered until the 16th and 17th centuries, and not settled till the 17th and 18th; however there is some evidence of earlier non-European sightings and (in the Seychelles) visits.

To keep this review within bounds, I have confined my analysis to those islands with land vertebrates endemic at the specific level or higher. These comprise the 'high' (volcanic and granitic) islands, and the raised coralline islands of the Aldabra group. The numerous low islands, as follows, are thus excluded: Maldives, Chagos (BIOT, to UK), Amirantes, Providence/Farquhar (to Seychelles), Agalega¹ & St.Brandon/Cargados (to Mauritius), the French 'Isles Eparses' (Tromelin, Glorieuses & the Mozambique Channel low islands) and the low islands of the central Seychelles (Denis & Bird, and outliers Coëtivy & Platte). Denis and Bird now harbour some Seychelles endemic lizards (Cheke 1984, probably introduced), Bird also has the sunbird *Nectarinia dussumieri*

1. Agalega has an endemic race (*P. b. agalegae*) of the Réunion forest day-gecko *Phelsuma borbonica* (Cheke & Lawley 1984), the only low island apart from the Aldabra group with any vertebrate endemism.

(introduced in 2006, Gerlach 2007), and the Seychelles race *rostrata* of the ubiquitous *Nesoenas* (formerly *Streptopelia picturata*, and Denis the Seychelles Fody *Foudia sechellarum* (introduced 2004, Gerlach 2007²).

Humans inevitably brought both livestock deliberately and facultative commensals by accident to all these islands. In this paper I am taking ‘commensals’ to include domestic livestock, whether escaped or deliberately released (goats, cattle, pigs, chickens, guinea-fowl, bees), other animals kept or released primarily for food (deer, tenrecs, lemurs, tortoises, giant snails), anthropophilic species that arrived through this association (rats, mice, house shrews, house geckos), plus a few others (e.g. cats, civets, domestic pigeons) with other or additional functions in human society. Apart from cats, I have not considered biological control agents (nor most of the pests), animals intended purely as sporting targets (game-birds, ducks) or escaped cage-birds, although several of these have had important roles in altering or degrading ecosystems. In general I have related the animal imports to the settlement pattern, and so most of my discussion relates to the 18th century and earlier. The issue of commensal plants is also extremely important, and their invasion of islands often synergistic with introduced animals, but it is outside the scope of this paper.

As the introduction dates of commensals has been covered in less detail in the published literature, I have given more space to the Comoros and the Seychelles than the Mascarenes, which are covered in Cheke (1987) and treated more fully in Cheke & Hume (2008). However information here should not be considered definitive, as there is probably more to be gleaned from more obscure literature, and from unpublished sources, such as the English ship’s logs noted by Allibert (1984) in his list of early visitors (1557- 1819) to the Comoros. This paper is an extended version of a talk given at the conference on “Evolution and extinction of the terrestrial biota of the western Indian Ocean archipelagos” held at the Linnean Society in London on 1-2 October 2009.

Comoros

As the first unequivocal historical records of the Comoros are as recent as the 12th century CE (el-Edrisi’s *Description of the world*, 1154; e.g. Gevrey 1870, Allibert 1990, Liszkowski 2000), there is no accurate written dating of the first discovery or

Table 1. Discovery and settlement of the major Western Indian Ocean islands

Island/group	First sighted (documented)	First landing (documented)	First settled
Comoros	?	[? 1000 BCE]	7thC CE, Africans
Mauritius	1516, Portuguese (+ earlier Arabs)	1598, Dutch	1639, Dutch
Réunion	1510, Portuguese	<1528, Portuguese	1660, French
Rodrigues	1528, Portuguese	1601, Dutch	1735, French (from Mauritius)
Granitic Seychelles	1503, Portuguese	1609, English	1770, French (from Mauritius)
Aldabra	?, Arabs	1742, French (from Mauritius)	1880, Seychellois

2. The Seychelles Fody also thrives on D’Arros, an atoll where it was introduced in 1965 (Gerlach 2007).

settlements, although there is some archaeological evidence. The generally accepted oldest recorded sites are on Mohéli³ (Mdjini) and Mayotte (Koungou, Dembeni 1), both ceramic and carbon-dated to the 8th century CE, with 9th century sites confirmed on Grande Comore and Anjouan (Wright 1984, Allibert & Verin 1996, Allibert 2002, Louette *et al.* 2004). However there are suggestions from recent excavations of the presence of stone-age people of African origin on at least Grande Comore on the 5th century BCE or earlier, together with domestic animals (Walsh 2007⁴), potsherds under a layer of volcanic ash dated to the 7th century CE (Allibert & Verin 1996: 468, footnote), and there is a (possibly anomalous) charcoal date of 40CE on Anjouan (Wright 1984). Some orally transmitted accounts of the islands' settlement refer to the islands being originally uninhabited and also support a first colonisation on Grande Comore that failed, followed by permanent settlement later (Kana-Hazi 1997, Verin & Saleh 1982), although the legendary ethno-chronology is wholly unrealistic⁵. The early settlement remains to be confirmed, but the islands have certainly been inhabited continuously for the last 1300-1400 years, by first Africans, then (proto-)Malagasy, Arabians, & 'Shirazi' (Gulf) peoples; the dominant languages remain island-specific dialects related to Swahili (Walsh 2007). The first European (Portuguese) eye-witness description dates from 1529 (Grande Comore, no landing) and more fully in 1557 (Allibert 1984), but there very little on the fauna, domestic or otherwise, before 1599; there is a brief Portuguese second-hand account from 1506 (Liskowski 2000) which mentions cattle, goats and chickens on the islands as a whole.

The 8th century settlers at Koungou and Dembeni (site 1) on Mayotte had cattle, goats (2 breeds), chickens, cats *Felis (sylvestris/lybica)* 'catus', and ate giant snails *Achatina fulica*, lemurs (*Eulemur* spp.), tenrecs *Centetes ecaudatus*, land tortoises *Asterochelys yniphora* and terrapins *Erymnochelys madagascariensis* (Allibert 1989, Allibert & Verin 1996), the last four endemics imported from Madagascar⁶; rats *Rattus rattus* were also present. Allibert (1989) suggested the Malagasy animals were collected by hunting parties going to the Red Island, but all could have been kept and/or released for local hunting. A layer of *Achatina* shells marked the horizon above which archaeological remains were found, suggesting they may have been the first deliberate import, followed by a population explosion. By the 9th-10th centuries there were tenrecs and goats on Anjouan (Sima), and on Grande Comore (M'Bachile), in addition to goats, remains of mice *Mus musculus* and a single pig tooth were found, tentatively identified as *Sus scrofa* (Wright 1984). Rats first appear on Anjouan in the 11th century, and chickens there around the same time (Wright 1992). Sheep are not confirmed until

3 I use the familiar French island names here, but in Comorian they are known as Mwali (Mohéli), Maoré (Mayotte), Ndzuani (Anjouan) and Ngazidja (Grande Comore); Anjouan was known in English as 'Johanna' in the 19th and earlier centuries.

4 According to Comorian press reports, Tanzanian archaeologist Felix Chami has carbon-dated material from a site at Hawengwe to 1000BCE (e.g. Ahamada 2008), but there has as yet been no formal publication to support this.

5 The first inhabitants are dated to shortly after the death of the biblical King Solomon (which chimes with the 1000BCE early settlement date), but are also said to have been Portuguese with African slaves! See Allibert (1984) for some variants of these tales.

6 Wright (1984, 1992) refers to tenrecs and lemurs as native to the Comoros, a view categorically refuted by zoologists (e.g. Louette *et al.* 2004)

the 11-12th sites on Mayotte (Wright 1984). The first records of rats and mice are earlier than any on Madagascar (11thC; Duplantier *et al.* 2002, Goodman *et al.* 2003); rats are repeatedly found in archaeological sites, but there are no other early Comorian finds of mice. Both rodents probably spread around all the islands at an early date.

Feral pigs exist on Mayotte and were present until recently on Grande Comore (Louette *et al.* 2004), but no other ungulates still have feral populations. The pigs are feral *Sus scrofa* (Louette 1999, Louette *et al.* 2004), not African bush pigs *Potamochoerus larvatus* as has been widely claimed (from Benson 1960 onwards, e.g. Lever 1985 & numerous websites - see Walsh 2007:101). However Keller (1901), writing in the 1890s, stated that “there were formerly many swine in Mayotta that had run wild, but they are now extirpated”, suggesting there may have been an earlier population (of bush pigs?), subsequently replaced by a later release or escape of domestic pigs; however his remarks are unattributed and he didn’t go there himself. Introduced bush pigs (Paulian 1961, Goodman *et al.* 2003), are common and long-established (e.g. Sganzin 1840) in Madagascar, the likely source for Mayotte. However two days of trekking in the forests and abandoned clearances in 1838⁷ produced no pigs for Leigh (1849), though he mentioned several bird species, flying-foxes, guinea fowl, lemurs and feral cattle⁸, and there’s equally no hint in Gevrey’s (1870) extended commentary on Mayotte of wild pigs, though domestic ones are briefly mentioned. Zoological collector François Pollen mentioned no pigs (feral or otherwise) on Mayotte in 1863 (Schlegel & Pollen 1868), though he discussed bush pigs in Madagascar at length. Milne-Edwards & Oustalet (1888), claiming to compile a complete list of mammals and birds in the islands, are equally silent. Nicoll (1908), visiting Mayotte in 1906, referred to lemurs and tenrecs, but said nothing of pigs. The substantial negative evidence suggests that there were no feral pigs on Mayotte between 1840 and 1906⁹, and that the animals now present escaped or were released sometime between then and Benson’s visit in 1958. Alone of the Comoros, Mayotte has an ancient population of Malagasy origin, the Shi-Bushi (=Ki-Buki) who were not Islamised until the (mid?) 19th century (Hébert 1991), and thus, unlike the other islands, might have appreciated a population of wild pigs for hunting. In contrast, pigs were so abhorred by the Muslim inhabitants of Mohéli, that when Leguével (1840) was shipwrecked there in 1828, and two of the ship’s pigs came ashore, they were killed instantly, together with his pet dog. Seventeenth century English and Dutch visitors, reporting on supplies acquired or available in the islands, never mentioned pigs on Grande Comore, Moheli or Anjouan; they do not feature in a very full description of Anjouan in 1743 (Braad 1753), and are specifically stated as absent there in 1813 by Prior (1819) - this probably reflects their by then solidly Muslim populations. Mayotte, with treacherous reefs, was however rarely visited by

7 Leigh did not date his visit ‘a few years since’, but Allibert (in Liskowski 2002) gave it as September 1838; Leigh’s ‘king’ of Mayotte ‘Dansulu’ (=Adrian Souli of Gevrey 1870) is currently spelt Andriantsoly (Verin 1994, Harpet 2002).

8 At this date Mayotte had been depopulated by the slave trade and emigration due to endless wars (Gevrey 1870), and cattle had apparently been abandoned to go wild (Leigh 1849).

9 German naturalist Alfred Voeltzkow travelled the islands in 1903, but unfortunately kept only to the shore and reefs in Mayotte (Voeltzkow 1904).

Europeans (Allibert 1984, Liszkowski 2000), who left us only minimal details prior to the mid-19th century; goats, cattle and chickens feature (Allibert 1984: 123), but no pigs. The characterisation by the ruler of Anjouan in 1818 of the pre-Islamic inhabitants as savages who killed wild pigs and goats with sticks (Verin 1994: 62) must surely be considered apocryphally metaphorical.

The early (8th-10thC) sites all contain ungulate bones which, where identification is possible, have been confirmed as goats (Wright 1984, 1992, Allibert 1989), whereas sheep are mentioned for the 11th century on Mayotte (Wright 1984), but not at the same period in Anjouan (Wright 1992). The first Europeans recorded goats very generally: on the Comoros (island unspecified) in 1506 (Liszkowski 2000), and on all the islands individually during 1599-1614 (accounts in Purchas 1624-26, vols 2 & 4 and Grandidier *et al.* 1903-20, vols 1-2), after which they are regularly noted. By contrast 17th century European travellers mentioned sheep only four times that I can find: on Anjouan in 1614 (van den Broecke; Grandidier *et al.* 1903-20, 2:90; Newitt 1983), and on Moheli in 1602, 1607 and 1615 (Pyrard *in* Gray & Bell 1887; *Gelderland* visit as quoted by Saris in Purchas 1624-6, vol.2: 497; Roe, in Foster 1926). However by the mid-18th century Braad (1753) reported that “large flocks of sheep and goats abound” on Anjouan in 1751, though Prior (1819) specifically commented for Anjouan in 1813 that “sheep, swine, horses, mules, asses and dogs have not been introduced”. Sheep (and cattle) are mentioned as raised in large numbers in the islands as a whole in the late 19th century (anon. 1911). There are no feral goats today (Louette *et al.* 2004), and sheep were probably never feral. Domestic cattle and chickens are mentioned by nearly all 17th and 18th century visitors; apparently feral cattle were encountered on Mayotte in 1646 (Smart *in* Grandidier 1903-20, 5:496).

Feral cats may be under-reported, but were recorded from Anjouan in the 1880s (Milne-Edwards & Oustalet 1888) and 1950s (Benson 1960¹⁰), and have been observed recently (Louette *et al.* 2004) on Mayotte and Grande Comore. Ship rats are on all four islands, but there is no evidence of Norway rats *R. norvegicus* (*ibid.*, *contra* Benson 1960). Lemurs were reported by early European visitors (e.g. on Anjouan in 1655, Mundy 1608-67). They were still eaten a century ago (e.g. Schlegel & Pollen 1868, Nicoll 1908), but are largely nowadays instead both persecuted as fruit pests and sought after as pets (Walsh 2007), though old habits die hard - on Mayotte some are still eaten as a traditional ‘picnic’ in the field, despite CITES and official protection (Harpet 2002). *E. fulvus* is present on Mayotte, and *E. mongoz* on Anjouan and Moheli¹¹. Tenrecs, presumably long feral, escaped the notice of Europeans until the 19th century (e.g. Sclater 1864, Anjouan, Moheli; Peters 1869, Grande Comore); they are established

10 Benson’s (1960) hearsay report of a wild ‘lynx’ on Anjouan, attributed to *Felis lybica caffra*, appears to have been based on feral cats from Anjouan being identified as ‘*Felis cafra*’ by Milne-Edwards & Oustalet (1888).

11 Grant (1801), plagiarising an unacknowledged source, reported the presence on Anjouan of, in addition to the ‘mungoo’ (*Eulemur mongoz*), the ‘mauaulo’, clearly from the detailed description *Lemur catta*. It is thus possible this species was also feral at one time. Grant also briefly mentioned a ‘black mauaulo’, apparently *E. fulvus*. Prosseri (1957), presumably in error, claimed that both *E. fulvus* and *E. macaco* were wild on Mayotte.

on all four islands (Louette *et al.* 2004). Ploughshare tortoises, already found in 8th-14thC middens (above & Walsh 2007), were still being traded as food into the islands during the 17th to 19th centuries (Walsh 2007). Prior (1819) listing domestic animals stated that “bullocks, goats, poultry and the *land tortoise* are numerous” on Anjouan in 1813 [my italics], and indeed the first specimen known to science originated on Grande Comore, bought ca.1885 by Humblot from Arab sailors (Bour 2007). There is no evidence this species went feral, but Prior’s remarks suggest they may formerly have been kept domestically quite extensively, as Radiated tortoises *A. radiata* have been in Réunion since the early 19th century (Cheke & Hume 2008 & below).

We have no data on when guinea-fowl *Numida mitrata*, house geckos nor honey bees *Apis mellifera* arrived, although guinea-fowl and honey are mentioned among local products in the early 17th century - Sir Thomas Roe wrote of ‘hunny’ at ‘Molalia’ (=Mohéli) in 1615 (Foster 1926) and Peter Mundy reported ‘Guinny henns’, also on Mohéli, in 1628 (Mundy 1608-67). Feral guinea-fowl survive on Grande Comore and Anjouan (Louette 2004); on Mayotte, while common in the mid-1800s (e.g. Leigh 1849), and still present in 1958 (Benson 1960), they are now extinct (Louette 1999, Clément *et al.* 2008). Domestic pigeons *Columba livia* are kept in the Comoros, apparently increasingly, but do not appear to have established fully wild populations (Louette 1988, Louette *et al.* 2004); they were no doubt introduced originally by Europeans. Four species of *Hemidactylus* inhabit houses in the Comoros (Carretero *et al.* 2005), but nothing is known of their history, and 2 species may be native (see origins section below).

The Comoros share with Madagascar and the east African islands (Zanzibar etc.) the presence throughout of the Small Indian civet *Viverricula indica*, apparently brought long ago from India for its commercially important scent glands (Louette *et al.* 2004, Walsh 2007). Indian traders were active in the area by 11thC century, and probably well before (Dick-Read 2006, Beaujard 2007), but the earliest attested date for the civet I have found is from the mid-1820s on Anjouan where Leguével (1840) witnessed a civet hunt (for musk). Schlegel & Pollen (1868) added Mayotte, Milne-Edwards & Oustalet (1888), Grande Comore, and Voelzkow (1904), Mohéli. The house shrew was recorded from Grande Comore in the 19th century (Hutterer & Tranier 1990), and apparently also on Anjouan (Sclater 1864¹²), but there are no recent (or archaeological) records (Louette *et al.* 2004). The current distribution of introduced animals is discussed by Louette *et al.* (2004), who also include a survey of the vegetation and its alteration through human activity.

Mascarenes

Out on the other side of Madagascar, the Mascarenes appear on Arabian charts in the 14th century, but there is no evidence of landing until the Portuguese appeared in

12 “A Rat with a musky odour, is also a great annoyance in Joanna, tainting wine, sugar and anything it may pass over” - John Kirk’s description, quoted by Sclater, exactly matches the classic lore of the rat musqué in the Mascarenes (Cheke & Hume 2008:106, 310). It is a mystery why this successful animal, apparently established on two islands, should have died out; it is perhaps preyed on by Indian civets, absent in the Mascarenes.

the 1500s, and even then the only recorded landfall was on Réunion, sometime before 1528 (North-Coombes 1980). They apparently left goats, as ‘flocks’ were reported by the next recorded landing in 1612 (Cheke & Hume 2008, from which the rest of the Mascarene section is also drawn). The ship rats present on Mauritius prior to the first recorded landing in 1598, by Dutch mariners, probably came from shipwrecks - the Dutch found evidence of one. Rodrigues, with a nearly complete fringing reef, was very hard to land on, and after a brief reconnaissance in 1601, was rarely visited until Leguat’s party of intended colonists was deposited there in 1691; ship rats were by then already present. Current distributions of introduced species, and full details of their spread and, in some cases, extinctions, can be found in Cheke & Hume (2008), as can a detailed examination of human impact on the islands’ ecology.

Mauritius

It was the habit of the European East India companies to carry livestock both for fresh meat on board but also for release on island way-stations to provide a food source for future visits, even if there was no settlement or intention to settle. In Mauritius the Dutch documented the release of chickens (short-lived) on their first visit, and goats, cattle and pigs in 1606¹³. Monkeys *Macaca fascicularis*, first recorded in 1606, were probably unwanted pets released on the homeward journey of the 1598 ships in 1602. Mauritius was a popular stopping place for ships of several nations in the early 17th century, being blessed with two large safe natural harbours and abundant feral ungulates, in addition to endemic giant tortoises *Cylindraspis* spp., popular for curing sailors’ scurvy.

Mauritius was settled temporarily during 1638-1658, during which time a fourth ungulate, the deer *Cervus timorensis* was introduced in 1639 from Java, as were domestic pigeons. After a hiatus the Dutch returned in 1664 and remained until 1710, though human numbers stayed small. To judge from a sudden decline of ground-nesting birds in the late 1880s, cats *Felis catus* probably appeared around 1885, but their release

Table 2. Introduction of domestic meat animals 1: Herbivores (sheep & chickens which rarely go feral omitted). Ex = feral population extinct (and in subsequent tables)

Island/group	Cattle	Goats	Pigs	Deer	Rabbits
Comoros	9thC.Ex	?[<<1506].Ex	?? Ex + 20thC	19thC.Ex	-
Mauritius	1606.Ex	1606.Ex	1606	1639	18thC.Ex
Réunion	1649.Ex	<<1612.Ex	1629.Ex	1758.Ex + 19thC	-
Rodrigues	1862.Ex	c1730.Ex	<1795.Ex	1862.Ex	19thC.Ex
Granitic Seychelles	1771.Ex	1740s ? .Ex	<1773.Ex	19thC.Ex	-
Aldabra	-	<1878 [1867 Astove]	- [Astove only, 20thC]	-	- [Cosmoledo only, 20thC]

13 There is no evidence whatever for Hachisuka’s claim (1953:2) that the Portuguese introduced “hogs, goats and fowl” in 1512, nor for the long-standing claim that they introduced monkeys (see Cheke & Hume 2008:76).

was undocumented, the first report being in 1709. The departing Dutch in 1710 left some deserters and escaped slaves, although there is no record that any were still present when the French from Réunion re-established a permanent human presence in 1722 -pirate and other ships calling in the interval may have taken them off. The 18th century saw the release of various gamebirds, beginning with guinea-fowl *Numida melaegris* from Madagascar (which the French released as ‘game’ rather keeping them as livestock). Norway rats appeared around 1735, and house shrews *Suncus murinus* in the 1760s. Mice are first mentioned in 1753 (but may have been missed), and honey bees *Apis mellifera*, surprisingly, are only recorded for the first time in 1768 (Bernardin 1773, Mamet 1993), although they are likely to have been brought from Réunion by the first settlers, as claimed by Staub (1993; in 1721 according to Crane 1999, citing no source). Of the other animals under consideration, giant snails from Madagascar, initially *A. fulica*, were well-established by 1781, *A. immaculata* appearing in the 1840s; both were introduced deliberately. Tenrecs were released around 1785, rapidly became an important food source for African and Malagasy slaves. House geckos (initially *Hemidactylus frenatus*) are first noted in 1770; by the turn of the century *Gehyra mutilata* was also present; since then *H. brookii* and *Hemiphyllodactylus typus* have also appeared. Rabbits *Oryctolagus cuniculus*, imported early in the French occupation, never established on the mainland, but were feral on several offshore islets in the 19th century, surviving on Round Island until eradicated in 1986. After native tortoises ran out, large numbers were imported for food from first Rodrigues (*Cylindropsis* spp.), then the granitic Seychelles and finally Aldabra (forms of *Dipsoschelys dussumieri*), and small stocks of the last were (and are) maintained by captive breeding. The only feral population was on offshore Flat Island 1883-1950s, though there have been recent releases on island reserves as part of ecosystem restoration. The history of feral descendants of domestic pigeons is unclear – there is no evidence that the 17thC Dutch imports went wild, and only kept birds are mentioned in the 18th and early 19th centuries, but feral pigeons were common by 1859 (Cheke 1987, Cheke & Hume 2008: 322 [note 81]).

The northern offshore islets of Mauritius (up to 24 km distant) have a rather different history from the rest of the island which is worth mentioning briefly. Round Island acquired rabbits and goats in the 19th century, but no rats; other islets (Flat & Gabriel Is., Gunners Quoin) also acquired lagomorphs (rabbits & black-naped hares *Lepus nigricollis*), but also by the mid-19th century, rats - not to mention feral donkeys *Equus asinus* on Flat, which had also been used for grazing in the late 18th century. Introduced mammals have been exterminated on all these islets in recent decades.

Réunion

Pre-settlement Réunion was a less popular stopover than Mauritius, as it lacked natural harbours. As in Mauritius visitors left livestock long before the island was settled - English mariners releasing pigs and adding more goats in 1629, the French adding cattle in 1649. Occasional dissidents from the French outpost at Fort Dauphin in Madagascar were exiled there in the 1640s and 1650s, but there was no permanent settlement until 1665. Initially the island was still rat-free, but ship rats arrived in the mid-1670s, followed by cats ca. 1685 (again inferred from avian extinctions, confirmed

by retrospective reports in 1703 & 1705). Honey bees were introduced in 1666. The pattern in the 18th century echoed that in Mauritius: guinea-fowl and short-lived rabbits in ca.1715, Norway rats in 1735, house shrews around the same time (but died out), deer (short-lived) in the 1750s, giant snails in the 1780s and tenrecs in 1801-2. Mice were first reported in 1754, but may have been around for some time by then. Unlike in Mauritius, feral pigs (here probably of European origin) were killed out through hunting by c1800, though there was a resurgence in the 1860s and 1870s; deer were re-introduced from Mauritius around 1900. Guinea-fowl died out around 1790. Monkeys were kept out by legislation and vigilance, but lemurs *Varecia variegata* (escaped pets rather than food) established, probably in the 1820s, and persisted until the later 1870s. House geckos, probably present for decades, were first noted in 1801, and not identified to species before the 1860s, which is also when house shrews reappeared after a gap of 120+ years. The same four house gecko species found in Mauritius are present in Réunion. Domestic pigeons are mentioned in 1705, but apparently feral birds were first reported in 1801, being widespread by the 1860s (Cheke 1987). Giant snails *A. fulica* were introduced for bizarre medical reasons in the 1780s¹⁴; *A. immaculata*, introduced at an unknown date, is now more abundant. As in Mauritius, tortoises from the same sources were imported when the native ones became extinct, but here an especially large trade developed in Radiated tortoises from Madagascar (Bour 1981), which from the 1830s have been kept and bred in large numbers initially for food and in more recent years as domestic pets, though they have not become feral.

Rodrigues

Two-year stays by Leguat's party 1691-3 and English pirates in 1707-9, and a 9-month stranding by Tafforet and crew in 1725 added no commensals to the ship rats already present. Tafforet's mission was to take possession for France and establish a settlement, but his ship was blown off the island after only an advance party, but not the settlers, had landed, and the project aborted. However the early years of the 18th century saw increasing use of the island by trading ships to harvest tortoises, and eventually in 1735 the French in Mauritius set up a small settlement for that sole purpose. Meanwhile, sometime between 1725 and 1733, one of the passing ships had left goats. By 1755 the island had feral cats, and by 1761 domestic cattle, sheep, chickens and ducks; pigs brought in later had gone feral by 1795, which was also when mice were first reported. The tortoises ran out in the 1760s, and apart from a handful of people the island was deserted until permanently settled by new colonists from 1792. Guinea-fowl, common in 1833, were probably released around 1805; they were eliminated in the wild as agricultural pests in the 1960s, but free-ranging, possibly feral, birds were seen in 1999 (Showler 2002). Rabbits from about the same early 19thC date were apparently briefly feral on the mainland, and into the 1970s on the offshore islet île Frégate. While deer were introduced into Mauritius for food, their release on Rodrigues in 1862 was purely

14 Mead (1961) transferred this account to Mauritius based on an account from Bosc in 1803, but the 'Mauritius governor' in question was actually in charge of Réunion, two decades before the 1803 story (Cheke & Hume 2008).

for ‘sport’; they were shot out in the 1950s. House geckos *Gehyra mutilata* first noted in 1874 are likely to have been there a long time, likewise bees, not reported before 1914 (Bertuchi 1923); other house geckos (*Hemidactylus frenatus*, *H. brookii*, *Hemiphyllodactylus typus*) are now also present; the native *Lepidodactylus lugubris* also uses houses extensively. Domestic pigeons were late arrivals; absent in 1874, they were first reported, already feral, in 1914 (Showler 2002). Bones attributed to Norway rats were found in 1874, but the first mention of them alive dates from 1914; giant snails, apparently absent before 1917, were formally recorded only in the 1960s when *Euglandina rosea* was brought in to control them, so must have been by then a long-established pest. For a long time Rodrigues was relatively protected against commensal invaders by supply ships being unable to come alongside, but this was ended when a new pier was built in 1980, and self-introduced house shrews appeared in 1997.

Seychelles

Granitic Islands (*Central Seychelles, excluding Coëtivy, Platte, Dennis & Bird*)

Allegedly Arabic tombs in Silhouette (since mostly lost to the sea, Lionnet 1972), supposedly Arabic inscriptions on North Island, and “an arrow head of hard black wood” found embedded in a large felled *bois blanc* *Hernandia nymphaeifolia* (Pike 1872), are the only physical indications of apparently pre-European visitors to the granitic Seychelles (though the evidence is lost or of indeterminate origin¹⁷). A Portuguese ship saw people and a fire ashore in 1503, but did not stop to investigate (McAteer 2001). The first documented landing was by an English ship on North Island and Mahé in 1609 (Lionnet 1972 reprinted John Jourdain’s account). Although pirates

Table 3. Introduction of domestic meat animals 2: Miscellaneous + bees

Island/group	Tenrecs	Guinea-fowl	Tortoises	Giant snails	Honey bees
Comoros	9thC	? [<<1628]	[9thC, not feral. Ex]	10thC	? [<<1615]
Mauritius	1780s	1720s	- [tortoises imported, not feral ¹⁵]	1770s	? [<<1768]
Réunion	1801	1714.Ex	- [“]	1780s	1666
Rodrigues	-	c1805.Ex	-	?1920s [<1960]	? [<<1914]
Granitic Seychelles	c1880	1787.Ex	- [“ ¹⁶]	<1838	?
Aldabra	-	-	[native species survives]	-	-

15 Native Mascarene tortoises *Cylindraspis* spp. are long extinct on all three islands. There are currently conservation-related feral populations of *Dipsochelys dussumieri* and *Astrochelys radiata* on Mauritian offshore islets (Griffiths et al. 2010)

16 Native Seychelles tortoises *D. dussumieri* subsp. are extinct in the wild. Conservation-related feral populations of Aldabran *D. dussumieri* have been established on several islands (Gerlach 2007).

17 In addition Newton (1867) was told of Arabic inscriptions on the hill on Félicité, but failed to find them himself. In an unpublished study the Silhouette graves were carbon-dated to 200 years old (c.1800) (J. Gerlach in litt. 2010), and, though apparently Muslim (perhaps ship’s crew or slaves), thus post-date European colonisation. The ‘Arabic’ inscriptions on North Island consist of ‘geometrical engravings’ but no script (L. Davolls to J. Gerlach in litt. 2010).

are said to have used the islands in the interim (e.g. Bradley 1940, McAteer 2000, 2001¹⁸), and artefacts on Frigate have been ascribed to them (Gardiner 1907), it was not until 1742 that there was another documented visit; after that there were several expeditions from Mauritius, but the islands were not settled until 1770 (Mahé & islets) and 1785 (Praslin) (Fauvel 1909, Lionnet 1972, McAteer 2001). As late as 1821 settlement had only extended to La Digue and Silhouette (Moresby 1842). Further islands were settled gradually over the next few decades; the larger granitics were all peopled by 1867 (Newton 1867, Wright 1868). Mahé is by far the best documented island - the timing arrival of commensals (and even humans) is often unclear on the smaller islands of the group. Eighteenth century information is from Fauvel (1909) unless otherwise stated; Gerlach (1995) reviewed 18th century observations, but confined his material to the native fauna.

Some time after 1742 goats were released, and by 1768 they were common on Mahé, though a release in 1768 (Lionnet 1984a) on Praslin failed; the animals were thought to have been eaten by the then abundant crocodiles *Crocodilus porosus*¹⁹. Further introductions occurred soon after the first settlement - initially on Mahé pigs and cattle: pigs were already wild in 1773, and cattle by 1785; these feral populations were thriving in 1787 (Malavois in Fauvel 1909), but had disappeared by the mid-19th century (no mention in Newton 1867, Pike 1872). Escaped cattle established a feral group on Félicité in 1962 (Racey & Nicoll 1984), culled in the late 1980s (Hill *et al.* 2002; still present according to Gerlach 2007), and also on North (eliminated in 2002, Gerlach 2007).

By 1773 there were ship rats on Mahé, and by 1787 they were reportedly widespread on 'nearly all the islands of the archipelago' (Malavois, in Fauvel 1909), though a few of the smaller islands (e.g. Cousin, Cousine, Aride) have always remained rat free (Cheke 1984), as was Bird until 1967 (Racey & Nicoll 1984), and Frigate until 1995 (Thorsen 2000). Norway rats did not reach the islands until very recently. None were found during trapping on Mahé and Praslin in 1976-7 (Racey & Nicoll 1984), and although they probably arrived in the late 1970s (Gérard Rocamora *in litt.*) or the 1980s (Hill *et al.* 2003), they were not reported until 1994 when they were well established on Mahé (Meyer, cited in Hill *et al.* 2003). They are now present on Mahé (and offshore Anonyme) and Praslin, having invaded and been eliminated on Conception and Frigate (Thorsen 2000, Hill *et al.* 2003, Gerlach 2007, Rocamora *et al.* in prep.). Ship rats

18 There is only one reference to the Seychelles in Rogoziński's recent (2000) study of Indian Ocean piracy (1680s-1720s), in which it is emphasized that the Seychelles's prime pirate suspect Olivier La Buse never went there! The Comoros, Réunion, Mauritius and the Maldives feature frequently in addition to the pirate base on Ile Sainte-Marie, Madagascar. However McAteer (2000, 2001) and various websites tell of coffins found on Mahé and chests and tombs on Frigate with characteristics of pirate burial and activity, but there is a shortage of traceable references. However if pirates had frequented the islands they would surely have discovered the then extremely rare and valuable coco-de-mer nut (*Lodoicea maldivica*), and marketed it, but there is no evidence of this - until Frenchmen based in Mauritius did precisely that from 1769 onwards (Lionnet 1970).

19 The now extinct crocodiles have generally been referred in the literature as *C. niloticus* of African origin, but Gerlach & Canning (1994) examined skulls from the Seychelles and demonstrated they were in fact the Indo-Australasian *C. porosus*.

have been eliminated on North Is (Rocamora *et al.* in prep.), and also from the low islands of Bird and Denis (Gerlach 2007). Ship rats may never have been present on Conception (Rocamora *in litt.*), hence the abundant survival there of the endemic white-eye *Zosterops modesta*.

Feral cats were already a nuisance to domestic chickens and hatchling tortoises on Mahé and Praslin in 1787; by 1867 they (and rats) abounded on Mahé, Praslin, La Digue and Félicité, Newton (1867) commenting on the scarcity of birds on the last compared to (then) cat- and rat-free Marianne nearby. Cats are currently feral on Mahé, Thérèse, Silhouette, Praslin, and La Digue (Gerlach 2007); their establishment on Silhouette appears recent, as the wide-ranging cats there were said to be still domestic in the mid-1990s (Gerlach *et al.* 1997). Frigate was cat-free until the 1950s, when domestic animals went feral; this population was finally eliminated in 1981-2 to protect the endemic magpie-robins *Copsychus sechellarum* (Watson *et al.* 1992); they have also been eradicated from Aride and Cousine (Gerlach 2007). Newton (1867) reported feral dogs on Mahé; although neither Lionnet (1984b) nor Racey & Nicoll (1984) regarded the numerous stray dogs as truly feral, Gerlach (2007) reported dogs as feral on Mahé, Thérèse, Praslin and La Digue; domestic dogs have been present since the beginnings of settlement. In 1787 chickens, guinea fowl, goats and sheep were free-ranging on St. Anne Island off Mahé; in 1867 there were feral chickens on Félicité (Newton 1867). Unlike on other islands under discussion, there was no general establishment of feral guinea-fowl in the Seychelles. Tenrecs, apparently brought from Réunion around 1882 (Lionnet 1984b), are present only on Mahé (+ satellites Anonyme & Thérèse) and Praslin (Gerlach 2007). Deer brought from Mauritius were feral on Silhouette during the 19th century (dates unspecified; doubted by Gerlach 2007), and until the 1950s on Frigate (Lionnet 1984b). Giant snails, initially *A. fulica*, were first reported in 1838 (Dufó 1840, Mead 1961) presumably on Mahé, and were already a pest by 1859 (Clark 1859: cvi). Both species were present in the 1930s on Mahé, Praslin and Silhouette (Dupont 1935), and have since spread to most of the granitic islands (Gerlach 1987, 2006b). The dates mice, house geckos, and honey bees²⁰ arrived are apparently not known. Mice are present on surprisingly few of the islands (Mahé, Silhouette, Praslin, Aride, Frigate and Bird; Gerlach 2006a, 2007). Stump-toed Geckos *Gehyra mutilata* are known from the late 1880s (locality unknown), but found in 1905 on Mahé; now present on almost all islands (Gerlach 2007, Rocha *et al.* 2010b). *Hemidactylus mercatorius* dates from 1905 on Mahé, though not seen again until 1995; it had spread to Frigate by 2002. *H. frenatus* was first found only in 1992 in the granitics (Gerlach 2007; still only on Mahé, Rocha *et al.* 2010), but it is possibly native (Cheke 1984) by drift (or introduced off shipwrecks) on many of the low islands. Rabbits *Oryctolagus cuniculus* were probably brought in as domestic food animals early on, but information is lacking; they are currently feral only on the tiny islets of Mammelles, Chauves-Souris & Recif. After native animals were

20 Crane (1999) claimed that bees were recorded in 1768, citing Bernardin (1773) who was in fact writing about Mauritius. There were bees reported in 1768, but the abeilles reported and described by the Marion Dufresne expedition of that year were not honey bees but native solitary bees of the genus *Megachile* (Lionnet 1984a).

reduced to a handful (currently captive-bred, e.g. Gerlach 2007), Aldabra tortoises were imported for food during the 19th century (Moresby 1842, Mondini 1990), and in addition to penned animals, feral populations have existed at various times on Curieuse (Stoddart & Peake 1979, Hambler 1994), Frigate and Cousin (pers.obs. 1970s, Bour 1984). Feral Pigeons are a recent arrival; birds established on Frigate in the 1970s may have been the source of the current population on Mahé, Praslin, La Digue and Silhouette (Skerret *et al.* 2001). The current distribution of vertebrates across all the islands, including introductions, are tabulated in Gerlach (2006a) and more fully discussed by Gerlach (2007); the impact of human activities on the islands was summarised in Stoddart (1984b).

Aldabra group

One of the world's largest atolls, Aldabra first joins history as 'Al-Hadra' (and variants) on early 16th century Portuguese maps (e.g. Skerrett & Mole 1995); however as the name is clearly Arabic, the Portuguese were borrowing from previous Arabian knowledge, and a probably Islamic sherd has been found (Stoddart 1971). Apart from the sherd²¹, there is no evidence of any landing prior to 1742, when Lazare Picault made landfall there²² on a rather tortuous journey to the Seychelles from Mauritius (Fauvel 1909, Skerrett & Mole 1995). As an island without surface fresh water²³, Aldabra was unsuitable for settlement, and served human interests solely as a source of tortoises, turtle and fish on short term visits over the next 135 odd years until the Seychelles authorities granted a concession in 1888, since which time, with some breaks, small numbers (never more than 200) people have lived there, mostly on Ile Picard (Stoddart 1971, Skerrett & Mole 1995) - recently only a handful looking after what has been since 1982 a World Heritage nature reserve. There are four main island around the lagoon rim: Picard (=West Is.), Polymnie, Malabar (=Middle Is.) and Grande Terre (=South Is.).

As on other uninhabited islands, goats were released on Aldabra to provide a food supply for temporary visitors, though here this did not happen until the late 19th century,

Table 4. Introduction of 'camp followers'.

Island / group	Ship rat	Norway rat	House mouse	House shrew	House crow	House geckos
Comoros	<9thC	-	?	? [<19thC G.C. only. Ex]	- [pied crows native]	?
Mauritius	<1598	c1735	<1750	c1765	c1900	<1770
Réunion	c1674	c1735	<1754	1730s.Ex + 1860s	2004 ?Ex	?[<<1801]
Rodrigues	<1691	? [<1874]	<1795	1997	-	<<1860
Granitic Seychelles	<1773	1970s	?	-	1970 ?Ex	? [<<1885]
Aldabra	<1890	-	-	-	- [pied crows native]	1970s

21 Some undateable stone enclosures could be pre-European (Stoddart 1971).

22 Picault thought he was on 'Juan de Nove' (the then name for Farquhar) but from his description it is clear he was on Aldabra.

23 A fresh water well was eventually dug in the 19th century at Takamaka (first reported by F. Rivers in 1878, see Diamond 1981).

the animals being first reported in 1878, already on more than one of the atoll's islands (Stoddart 1981). Although long known on Picard and Grande Terre, the first record from Malabar was in 1953 (Prosperi 1957²⁴); goats were eradicated from Picard and Malabar islands in 1993-5 and much reduced on Grande Terre (Rainbolt & Coblenz 1999), where they have since increased (Wanless n.d.). A report in 1878 suggesting that pigs should not be introduced (Skerrett & Mole 1995) was too late, as Rivers, visiting that year, was told that several had been released on Grande Terre 'some years ago' and had 'destroyed many young tortoises' before dying out, being all males (Diamond 1981). Ship rats were abundant (at least on Picard) in 1890 (Spurs 1892), and were 'spread over the whole atoll' by 1908 (Fryer 1911); they are currently found throughout (Stoddart 1971); records of *R. norvegicus* are in error (*ibid.*). Cats were recorded in on Grande Terre in 1892 and 1908-9, apparently introduced c.1890 by James Spurs for rat control. By the 1960s they were also on Malabar, Picard (Stoddart 1971) and in 1977 on Polymnie (Racey & Nicoll 1984), but are now common only on Grande Terre (which has some freshwater pools), sporadic on Malabar, and gone from Picard and Polymnie (Wanless et al. 2002). A few feral dogs on Grande Terre in the late 1960s subsequently disappeared (Racey & Nicoll 1984). The facultative house gecko *Hemidactylus mercatorius* is native (as on the neighbouring atolls), but *Gehyra mutilata* appeared in the 1970s (Cheke 1984), presumably through the increased activity of biological researchers (!), but may not have become fully established until 2005 (Gerlach 2007). A plan in 1906 to release rabbits, hares and cattle to increase food for settlers (Beamish 1970) was fortunately not carried out.

The other islands of the group, with far less land area, held fewer native vertebrates. Like Aldabra, they are dry, lacking in surface fresh water and hostile to human habitation; drinking water can only come from rain-water catchment. Although still only visited sporadically by turtle fishermen as late as 1878 (Diamond 1981), Assumption (from 1908) and Astove (from before 1927²⁵) later supported massive guano extraction industries for many years, whose effects wiped out most of the native vertebrates through almost complete removal of the vegetation, especially on Assumption (Dupont 1935, Bradley 1940, Stoddart *et al.* 1970, Bayne *et al.* 1970b, Staub 1993).

First visited by Nicolas de Morphey in 1756 (Fauvel 1909), Assumption was not settled until 1908 (Stoddart *et al.* 1970); it is the only island in the group which still has a permanent settlement (Guébourg 1999). In 1878, goats, said to have been introduced in 1867, numbered 5-600 (Diamond 1981, Stoddart 1981); they thrived for decades (*ibid.*), but were thought by Roger Gaymer to be extinct in 1964, though some were said by locals to survive in 1967 (Stoddart *et al.* 1970), though they are now gone (Gerlach 2007). Rats, arrival date unknown, were abundant in 1906 (Nicoll 1908). As on Aldabra, Dupont wanted to add hares and rabbits in 1907 (Stoddart *et al.* 1970). Dogs, cats and chickens (apparently domestic) were seen in 1967 (*ibid.*); by 1986 only cats remained (Roberts 1986; not mentioned by Gerlach 2007). A pair of Feral Pigeons

24 Prior to subsequent confirmation, Stoddart & Wright (1967) doubted Prosperi's record, as well they might, as his book is full of egregious errors (see e.g. Benson 1960: 7-8).

released 1990-91 increased to 69, but were eliminated in 1996 (Skerrett 1994, Skerrett *et al.* 2001)

Astove is said to have hosted survivors from a Portuguese shipwreck in the eighteenth century for 30-40 years; evidence of later wrecks can still be seen (Bayne *et al.* 1970b, from which the rest of this section is taken). It was then scarcely visited until settled intermittently by a few labourers and fishermen from 1895. There was no major impact until phosphate mining began in the 1920s; the island was then continuously inhabited until abandoned in 1978 or a little after (Ron Gerlach *in litt.*²⁶). Rats, perhaps from the Portuguese ship, were abundant in 1895; pigs and chickens, brought in soon after settlement, were described as ‘semi-wild’ in 1960 (Piggott 1969); domestic cattle, ducks and turkeys were added in the 1960s. Pigs left when the settlement was abandoned have gone fully feral (Mortimer *et al.* 1996, Gerlach 2007). No goats or cats were released here.

Like the other atolls, Cosmoledo was irregularly visited for fish and turtle, but never permanently settled, although a small habitation based on Menai existed from the early 1890s (Bayne *et al.* 1970a) until abandoned in 1992 (Rocamora *et al.* 2003). There are 8 main and several smaller islands on the rim of this large atoll. Goats were present on Menai in 1878 (Diamond 1981, Stoddart 1981) - even then in poor condition due to drought; they thrived briefly in the 1890s, but had died out by the 1960s (Bayne *et al.* 1970a²⁷). Rats were reported abundant on Menai in 1901 (*ibid.*) as they still are (Rocamora *et al.* 2003), and also reached Wizard (=Grand Ile) and Grand Polyte (*ibid.*); they were eradicated from Grande Ile and both Polytes in 2005-7 (Rocamora *in litt.*). Rabbits released c1906 on South Is (=Sud-Ouest) (Bayne *et al.* 1970) are still present in small numbers (Rocamora *et al.* 2003). Cats, first reported in 1968 on Wizard, were still evident in 1999 (*ibid.*).

Table 5. Intentional introduction of other common commensals (miscellaneous).

Island /group	Cats	Civet	Lemurs <i>Eulemur</i> spp. [L] / Monkeys <i>Macaca fascicularis</i> [M]
Comoros	9thC	?[ancient]	9thC [L] [as food]
Mauritius	1680s	-	1602 [M] [?unwanted pets]
Réunion	1680s	-	?1820s [L] [?escaped pets].Ex
Rodrigues	1740s	-	-
Granitic Seychelles	<1787	-	-
Aldabra	c1890	-	-

25 Data for guano extraction at Astove appear to exist only from 1927 (e.g. Bayne *et al.* 1970, Stoddart 1984b), but probably began several years earlier.

26 There appears to be no published information on exactly when the Astove settlement was abandoned, the nearest being ‘in the 1980s’ on Wikipedia!

27 Bayne (*et al.* 1970) and Racey & Nicoll (1984) claimed that Piggott had reported goats on North Is. In 1961; I have not seen the original 1961 typescript report, but there is no mention of goats anywhere on Cosmoledo in the published version (Piggott 1969). The presence of feral pigs was claimed in relation to turtle conservation in 1995 (Mortimer *et al.* 1996), but presumably in error as there is no other reports of pigs (tame or wild) on the atoll.

Mice²⁸, honey bees and giant snails appear to be absent from the Aldabra islands.

Geographical origins of commensals

While on islands other than the Comoros we have fairly good records of the arrival times of commensals, history does not always indicate their places of origin.

Rodents & shrews

Mauritian ship rats *Rattus rattus* have 42 chromosomes, but this appears to be a local mutation derived from 38 chromosome 'Oceanian' stock (Baverstock *et al.* 1983, Thiele *et al.* 1997), possibly indicating a very small founding population, but whether from Madagascar or South Asia is not clear. On Madagascar the rats have standard Oceanian $2n=38$ karyotypes (Duplantier *et al.* 2003, Fuller & Boivin 2009); the Oceanian type is native to southern India and Ceylon. The question of whether they came direct across the ocean or via East Africa (Fuller & Boivin 2009), has been resolved by DNA studies (Tollenaere *et al.* 2009) which confirm that rats in Madagascar share haplotypes with Indian and Arabia, and they may have colonized once only, long ago, by animals originating in Oman, via East Africa. Grande Comore appears to have been colonized anciently from East Africa independently of Madagascar. The dates calculated by Tollenaere *et al.* (2009) from mutation rates for the rats reaching Madagascar and Grande Comore (c3000 yr BP) precede known times of human contact, so should probably, as they themselves suggest, be treated cautiously. The oldest attested dates for Madagascar are 11thC (Goodman *et al.* 2003), later (as with mice) than for any of the Comoros, which must reflect lack of suitable archaeological records, as the DNA clearly shows that Mayotte acquired its animals from Madagascar; rats there are grey-brown (photo in Louette 1999: 53), as they are in Madagascar (photo in Glaw & Vences 2007). Réunion animals (Tollenaere *et al.* 2009) have a different origin, probably Europe - their pelage is predominantly blackish (as it is in Mauritius, pers.obs.). Rats from Rodrigues and Seychelles have yet to be studied in detail, but in Rodrigues brown morphs predominate (Cheke & Hume 2008: 350, note 464), as they do in the Seychelles (Racey & Nicoll 1984, Hill *et al.* 2003, Gerlach 2007) - which in both cases is odd if the rats came, as presumed, from Mauritius; likewise Aldabran rats are mostly the white-bellied brown form *frugivorus*, grey-bellied *alexandrinus* also occur (Racey & Nicoll 1984). Both house mice *Mus musculus* and house shrews *Suncus murinus* in Madagascar have been related to arriving via Arabian trade routes (Hutterer & Tranier 1990, Duplantier *et al.* 2002). House mice in Yemen have been separated as *Mus (musculus) gentilulus*, and it appears the Malagasy population is descended from a single colonisation of the Yemeni line (Duplantier & Duchemin 2003, Fuller & Boivin 2009); Comorian mice are likely to be from the same source, possibly via Madagascar. Given that the first European colonists frequently visited Madagascar and were busy

28 Keller (1901), citing H. Schinz, included mice amongst introductions on Aldabra, but as no one else recorded them this is presumably an example of the common 'rats & mice' error, where the presence of one is thought to imply the other.

trading throughout South Asia and the Sunda islands ('East Indies'), both mice and shrews could have arrived in the Mascarenes from either Madagascar or Asia, or, in the case of mice, directly from Europe. In a now rather old DNA study (Yonekawa *et al.* 1981): Mauritian and Seychelles mice were placed phenotypically and genetically with the western European *M. m. domesticus*, with some evidence of Asian introgression. Rats and mice in the Seychelles probably arrived from Mauritius. Shrews in Mauritius were included in a study by Yamagata *et al.* (1995), who found they were very close to mainland Malaysian specimens, which in turn clustered with those from Indonesia, suggesting a source (given the arrival date) from European trade in the East Indies; however they did not include any Malagasy or African-Arabian animals in their samples.

Ungulates

Goats and sheep in the Comoros probably came from Africa, as they are not attested earlier in Madagascar, though the cattle could have been of Asian origin (carried by Austronesians). Since domestic pigs on Pemba were introduced by the Portuguese (Walsh 2007), no archaeological evidence exists of pre-European domestic pigs in East Africa (Blench 2000), and only bush pigs were introduced early to Madagascar (and even there archaeological evidence is lacking: Goodman *et al.* 2003), it suggests the pig remains found in the 9thC midden on Grande Comore, although tentatively identified as *Sus scrofa* by Wright (1984), probably came from a bush pig. It seems unlikely that there was a continuous presence of feral pigs of any kind, and that if there was a pre-19th century population on Mayotte, it came from a later introduction.

Goats in the Mascarenes are presumed to have come from Europe, transported later thence to the Seychelles from Mauritius and to Rodrigues from (probably) Réunion (all Mascarene data from Cheke & Hume 2008). However both the animals thought to have been released by the Portuguese, and the further ones from Thomas Herbert, in Réunion, as also Dutch release in Mauritius, could have originated in the East Indies. Cattle in Réunion are known to have originated in Madagascar, but the initial release in Mauritius was on an outward journey from Holland (Moree 1998), hence the animals may have been European; further animals, from Madagascar, were sent for, but (*contra* Cheke & Hume 2008) the *Concord* failed in that mission due to storms (Barnwell 1948:14-15). Madagascar was, however, a major source of domestic cattle for the Mascarenes in the 18th and 19th centuries. Pigs were released in Mauritius at the same time as cattle, so presumably also of European origin, while for Réunion it is likely that Thomas Herbert (1634) acquired pigs (and goats) in India²⁹ - Pring (Kerr 1824, vol.9) was able to get "twenty hogs" in Masulipatnam (=Machilipatnam = Bandar) on the east coast in 1619. For Mauritius at least, where feral pigs remain common, their origin should be easily found using DNA, given the markers known for different centres of domestication (Larson *et al.* 2005, Luetkemeier *et al.* 2010). The deer in Mauritius came

29 He mentioned unexpectedly eating pork with the British factor in Isfahan (while pointing out that pigs & other 'unclean' animals were banned in Persia), and as a product of Ceylon - but nothing about collecting such livestock en route.

from Java. All ungulates briefly feral in 18th century Seychelles were brought from Mauritius (Fauvel 1909), as were pigs and cattle in Rodrigues.

House geckos

House geckos in the Mascarenes first appeared in times of active trade with India and the East Indies; all are Asian species, *Gehyra mutilata* and *Hemidactylus* spp. with DNA identical or very close to Asian mainland or Sri Lankan populations (Rocha *et al.* 2009, Vences *et al.* 2004); however it appears that the Mauritian and Réunion populations of *H. frenatus* have different mainland origins (Vences *et al.* 2004, fig.1). From Mauritius they then reached Rodrigues and probably the granitic Seychelles, and Aldabra (*Gehyra* only) from the Seychelles. However two clearly differentiated DNA lineages of *Hemidactylus frenatus* occur in the Seychelles, one occurring on the low islands (+Mahé), the other only on Mahé (Rocha *et al.* 2010a), suggesting two invasions, possible long separated in time - the low island DNA shows affinities with Ceylon and Burma, the Mahé-only animals with Réunion (and, oddly, the Andamans³⁰). This would correspond to an early invasion (natural drift or via pre-European voyagers) to originally uninhabited low islands (Cheke 1984; Poivre, Desroches & Bird sampled for DNA), recently carried to Mahé, and a later very recent influx from the Mascarenes. *H. mercatorius*, native on the southern atolls occurs commensally on Mahé in low numbers, apparently a recent import (1995, Gerlach 2007³¹) from East Africa or Mayotte (Rocha *et al.* 2010a). The situation in the Comoros is even more complex (Rocha *et al.* 2005, 2010a; Vences *et al.* 2004): two species, *Hemidactylus platycephalus* and *H. mercatorius* probably colonised naturally from East Africa (Rocha *et al.* 2010), but both also show signs in their DNA of additional recent human-mediated transport³² - *mercatorius* from Madagascar, and *platycephalus* from Mozambique. *H. brookii* (Anjouan & Mohéli only), as in the Mascarenes, is an introduction, haplotypes being closest to an animal from Réunion (from which the islands were formerly administered), while *H. frenatus* individuals are close to those from Madagascar but not the Mascarenes. They are thus likely to have been introduced to the Comoros from Madagascar, but the origin of the Malagasy animals is unclear, as these animals have a third haplotype group intermediate between but unlike those in either the Seychelles low islands or the Mascarenes, and without (so far) clear links to continental lineages (Fig.5 in Rocha *et al.* 2010a, who did not interpret this pattern³³). Note that Louette *et al.* (2004) retained, with some reservations, an older classification that did not distinguish between *H. platycephalus*, *mercatorius* and (extralimital) *mabouia*.

30 Although Indian Ocean Islands (apart from the Maldives & Chagos) were well sampled, continental areas and Indonesia unfortunately were not, so source areas of the lineages are not closely identified.

31 There is also a record from 1905, but it appears to have died out in the interim (Gerlach 2007).

32 Both species are facultative commensals, and *mercatorius* is frequent on the Aldabra group (all four atolls) in the almost complete absence of human activity, having colonized naturally from Madagascar (Rocha *et al.* 2010a); see Gerlach (2007) for distribution on other low atolls.

33 One individual from Réunion groups with the Malagasy/Comoros examples, but its haplotype is nevertheless separated from them by 6 substitutions.

Miscellaneous commensals

Cats in the Comoros and Madagascar must have originated in Africa, as on both domestic and feral cats pre-date European contact (Wright 1984, Goodman *et al.* 2003). In the Mascarenes (and hence the Seychelles) feral cats descend from European imports intended to control rats. Comorian civets, as mentioned above, come from India, while Mauritian monkeys hail from Sumatra or Java. Lemurs and tenrecs are endemic to Madagascar, so must have originated there. Guinea fowl are African in origin, though feral populations in any or all the islands (except perhaps the Comoros) could have come, as in Mauritius, from introduced populations in Madagascar. In the Mascarenes and Seychelles, they survive wild only in Mauritius, possibly (like many game birds) subject to repeated introductions. Honey bees in the Mascarenes (and hence the Seychelles) were originally all *A. m. unicolor* from Madagascar (e.g. Smith 1879), though other breeds have been introduced since (e.g. Staub 1993). The giant snails *Achatina fulica* and *A. immaculata* (= *panthera*) are native to East Africa, but introduced to Madagascar (Paulian 1961) and thence to Réunion and Mauritius, then from Mauritius to Rodrigues and the Seychelles; in the Comoros they may have come directly from Africa. There seems to be no information on when they reached Madagascar (Paulian 1961, Mead 1961, Pearce 2003).

One commensal, a late arrival not discussed above, arrives by hitching rides on ships - unlike rats, mice and house-shrews that live on board, house crows *Corvus splendens* from India and Sri Lanka use ships facultatively for scavenging, and sometimes travel with them to their next port. They have spread round much of the Indian Ocean this way, appearing in Mauritius around 1900, though much more recently in the Seychelles [1970] and Réunion [2004] (Cheke 2008). The presence of native pied crows *C. alba* may have kept them out of the Comoros and Aldabra (and Madagascar), though they have successfully invaded East African coastal ports (Lever 2005).

Consequences

The significance of these introductions is of course their effects on the pre-human ecology. These are outside the scope of this paper, except that is appropriate to recall the major issues; the following summary is taken from Cheke & Hume's (2008) review (where further references can be found), unless otherwise mentioned.

Ungulates degrade unadapted vegetation, largely by eating seedlings. **Pigs** root around destroying undergrowth (including tree seedlings) and are serious predators on eggs, and sometimes young, of chelonians and ground-nesting birds. **Cats** eat vulnerable young animals (all groups), flightless birds and naïve adults of flighted birds up to the size of pigeons, and are known to attack and eat lemurs in Madagascar (Brockman *et al.* 2006). They are severe predators of hatchling turtles (e.g. Seabrook 1990 for Aldabra).

The **civet** in the Comoros has been there too long to know what effect it may have had, but it is likely to have altered the ecology in islands previously without native

34 The date mynahs arrived in the Seychelles is disputed, but I see no reason to question Dupont's statement (1930, Lionnet 1984b) that they were released around 1830; the suggestion, echoed by Skerrett *et al.* (2001), that they were introduced in the 1770s appears to be pure speculation. Newton (1867) was told they had been released on Silhouette some 20 years previously (i.e. c.1847), presumably from birds already on Mahé.

ground predators (apart from land crabs). **Ship rats**, adept climbers, attack birds' nests and any reptiles in a size range too large to hide and too small to eat the rat; **Norway rats** are ground predators on birds' nests and reptiles, and both species are important seed predators, and ship rats keep shrew numbers down. Issues with rats were amply summarised by Atkinson (1985). **Monkeys** impact on birds in the same way as ship rats, but also attack larger species; they also destroy many tree fruits before they can ripen. **House shrews** and **tenrecs** are major predators of native invertebrates and small reptiles. The generalist **cheechak** or common house gecko *Hemidactylus frenatus* is a major competitor to similar-sized native lizards, and eats their hatchlings. **Mice** are not generally seen as a problem in the Indian Ocean, but elsewhere have become serious predators of seabirds. **Giant snails**, when abundant as they often are, consume enormous amounts of vegetation, some endemic island plants being particularly vulnerable. Even such apparently benign animals as **honey bees** compete with day-geckos *Phelsuma* spp. for flower nectar. All this is of course additional to crop damage caused by several of these species.

This is just the commensals - the Indian Ocean islands have also been subjected to a whole gamut of species introduced for sport, biological control or as escaped pets. Of these probably the most insidious is the small Indian mongoose *Herpestes auropunctatus*, introduced in 1900 to Mauritius to control rats (Cheke & Hume 2008), and between 1958 and 1981 to Grande Comore for no known reason (Louette *et al.* 2004); it is devastating for ground nesting birds, though it also keeps shrew and tenrec numbers down. Most of the introduced birds in the Indian Ocean are anthrophilous and have little impact on native ecosystems, but there are exceptions: the Asian Red-whiskered bulbul *Pycnonotus jocosus*, now on Mauritius, Réunion, Assumption, and briefly on Mayotte, attacks nests of small native passerines, predated invertebrates, and, together with the Peking robin *Leiothrix lutea* (Réunion only) spreads seeds of invasive exotic plants through eating their fruits. The Indian Ring-necked parakeet *Psittacula (krameri) manillensis* (Mauritius only) and the common mynah *Acridotheres tristis* (most islands³⁴), also from India, competes with native species (Echo parakeets *P. eques*, tropic-birds *Phaethon lepturus*) for nest-holes. In the granitic Seychelles the barn owl *Tyto alba* was introduced in 1949 as a putative rat controller, but only succeeded in decimating endemic microbat *Coleura seychellensis* (e.g. Racey & Nicoll 1984, Paula Senior pers.comm. - but see Gerlach 2009³⁵) and fairy terns *Gygis alba* on the larger islands (Skerrett *et al.* 2001); the tern is also susceptible to cats and rats (*ibid.*). The full effects of the recently introduced but rapidly spreading escaped large pet Malagasy gecko *Phelsuma grandis* (Réunion, Mauritius) are yet to be evaluated, but it harasses smaller endemic congeners and probably eats their young. The soft-shelled turtle *Palea steindachneri* from Asia (Mauritius) eats fresh-water life in general including hatchling birds, and the effects of the American red-eared slider *Trachemys scripta* (Réunion,

35 This suggestion is disputed through lack of direct evidence, but the bat's decline coincides with the spread of barn owls (Carl Jones pers. comm.); also a Barn Owl has recently been seen targeting *Coleura* at a roost in Mahé (Paula Senior pers. comm.). However the influence of cats and overgrowing of roost entrances by invasive plants (Gerlach 2009) may also be significant.

birds, and the effects of the American red-eared slider *Trachemys scripta* (Réunion, Mauritius) have yet to be assessed. The Indian wolf snake *Lycodon aulicum* is credited with eliminating endemic skinks on Réunion and Mauritius, and the African guttural toad *Bufo* (sometimes *Amietophrynus*) *gutturalis* is blamed, together with shrews and tenrecs, for devastating native snail populations. In the Mascarenes the mammalian insectivores and toads had done most of the damage before the notorious rosy wolf snail *Euglandina rosea* was introduced to control giant snails, but they are known to annihilate endemic snails elsewhere, mostly where (unlike the Indian Ocean islands) there are no native carnivorous snails (Gerlach 2001). Finally there are a whole gamut of invasive arthropods, some vectors of diseases affecting both humans and wildlife, of which only a few can be mentioned here: the yellow crazy ant *Anoplolepis gracilipes* is a particularly insidious species, present on several of the central Seychelles and at high density on Bird Is., Seychelles (Hill *et al.* 2003b, Gerlach 2004); another highly impactful invasive ant *Pheidole megacephala* is almost everywhere (e.g. Ward 1990, Dorow 1995); the widespread tropical scale insect *Icerya seychellarum* has invaded Aldabra (e.g. Newberry & Hill 1985); and recently the Australian venomous Red-backed spider *Latrodectus hasseltii* spider has arrived on an offshore nature reserve, Gunner's Quoin, in Mauritius, probably off a yacht on a world cruise (Cole *et al.* 2009)

Game birds (several species), ducks (2 species), swampheens *Porphyrio porphyrio* and black-naped hares introduced into the Mascarenes purely for sport hunting have had little observed impact on the native ecology, and in Mauritius have been drastically reduced in species and numbers by the mongoose. Black-naped hares, brought from Mauritius in the 1920s or 1930s, also occur on Cousin Is., Seychelles (Racey & Nicoll 1984, Lionnet 1984b, Gerlach 2007).

A brief round-up of land vertebrate extinction events

The extinction histories of the different island groups could hardly be more different. In the Comoros, with no early documentation, and until now only one exploratory (and unsuccessful) search for subfossils (Julian Hume pers. comm.), there are no recorded vertebrate extinctions, though it seems likely that there will have been species formerly present that disappeared after humans and commensals arrived, as in Madagascar and elsewhere.

Likewise on Aldabra, but here because human impact has been minimal, there is only one recorded extinction (the warbler *Nesillas aldabrana*; Rocamora & Skerrett 2001), possibly unrelated to humans/commensal activity, though rats could be a factor. However on other islands in this group it is different: Astove and Assumption, which shared many bird species with Aldabra (e.g. Lionnet 1984c, Skerrett *et al.* 2001), have been heavily impacted by guano (phosphate) quarrying, and have lost most of their native wildlife (including seabirds) together with their vegetation cover. Cosmoledo is less damaged, but its land area is quite small, and had fewer species to lose. Aldabra is the only island where a pre-Holocene fauna has been found - in Pleistocene deposits from an inter-glacial period (refs. in Braithwaite 1984).

The granitic Seychelles have not lost many species overall since discovery, largely because there are several islands with different histories of human and commensal

impact; species lost on some islands have survived on others. The extinction rate on Mahé and Praslin is quite high, and Marianne, one of the most bird-rich islands in the mid-19th century, has since been completely deforested, invaded by rats, and lost almost all native species. The animals lost from the archipelago as a whole are the saltwater crocodile (Gerlach & Canning 1994) and three birds, one of which, the ‘poule bleu’ disappeared before being scientifically identified (Lionnet 1984c). Conservation work in the last four decades has ensured the continued survival of at least four bird species (e.g. Rocamora & Skerrett 2001, Skerrett *et al.* 2001). As in the Comoros only exploratory subfossil investigation has taken place, with so far no discoveries of new species (Hume 2004).

Finally the Mascarenes, which have become, through the Mauritian dodo *Raphus cucullatus*, iconic examples of island extinctions. Extinct subfossil species are still being discovered (Julian Hume pers. comm.), but as of 2008 Mauritius had lost 23 species, Réunion 26 and Rodrigues 25 (Cheke & Hume 2008). Mauritius has done best because of offshore islet refuges, and intensive conservation work since the mid-1970s has helped several species, notably the Mauritius Kestrel *Falco punctatus* whose numbers fell to 4 wild individuals (+ 2 captives) in 1974-5.

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Table 6. A selection of the worst invasive non-commensal vertebrates in the islands (biological control agents = BC)

Island / group	Mon- goose	Barn owl	Common Mynah	Red-whiskered bulbul	Great green day-gecko	Wolf Snake	Guttural Toad
reason	BC - rats	BC - rats	BC -locusts	Esc/freed birds	cage- Esc/freed pets	carried with cargo	BC – mosquitoes
Comoros	?1960s Grande Comore	[native]	?	1985/6.Ex Mayotte only	-	-	-
Mauritius	1900	-	1762	1892	1980s	1870s	1922
Réunion	-	-	1759	c1970	1994	<1839	1927
Rodrigues	-	-	1820s.Ex <1874	-	-	-	-
Granitic Seychelles	-	1949	c1835	-	-	-	-
Aldabra	-	Ex [native]	-	1985 Assumption only	-	-	-

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