Mammalian faunal collapse in Western Australia, 1875-1925: the hypothesised role of epizootic disease and a conceptual model of its origin, introduction, transmission, and spread

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ABSTRACT

Information relating to the early decline of native mammal species in the western third of Australia, before the establishment of rabbits and foxes, was sought from recollections of oldtimers, archival records, historical documents, and searches of museum collections. Based on the information discovered, the hypothesis is advanced that the early decline was caused by an exotic disease. The evidence available is suggestive of a first wave of mammal declines and extinctions in Western Australia (WA) commencing about 1875. From this single, contingent historical event, it is postulated that 33 species (about one third of the non-volant mammal fauna of WA) changed significantly in distribution and abundance.

The pattern of the decline both geographically and over time is consistent with epizootic disease as the primary factor, but probably interacting with drought and predation by feral cats as secondary factors. Much of the decline occurred before food shortages or habitat destruction caused by sheep grazing, habitat destruction caused by wheat farming, and changes in Aboriginal fire regimes.

Dated and localised records of disease affecting conspicuous (often pest) species, when integrated with other records of early declines, are suggestive of the epizootic spreading rapidly from the Shark Bay district in the 1880s. The lower south-west area was affected last, before 1920. Descriptions of clinical signs are imprecise but do refer to numerous dead or dying animals, mange, alopecia, eye disease, withered ears, and scabs on the nose. Plausible explanations of the source of the disease (south-east Asia), its transmission (mosquitoes), and the pattern and scale of its spread (exceptionally wet summers) are proposed. Other possible vectors are discussed but do not adequately explain the pattern and scale of the spread.

Many other early declines of mammal species in WA that are difficult to explain convincingly may have been influenced by this epizootic. Disease as a primary factor is considered to provide a more satisfactory explanation of early declines in WA than predation by feral cats. Impacts of these declines on ecosystem processes were likely to have been profound. The applicability of the conceptual model developed is discussed in relation to the early decline of some mammal species in eastern Australia, The need for ongoing, vigilant quarantine to minimise the risk of animal diseases being introduced is emphasised.

Key words: Disease, mammal, extinction, decline, Western Australia, historical ecology

'…the extraordinary disappearance of the small marsupials in many parts of the State' (Royal Commission 1901, p. 7).

'It is of great interest to learn that in 1854 the pig-footed bandicoot [Chaeropus ecaudatus]*, the nest-building rat* [Leporillus]*, the wurrung* [Lagorchestes hirsutus]*, and the hare wallaby* [Lagostrophus fasciatus] *were plentiful in districts where they are now extinct, and it is almost certain that their disappearance is not due to the action of the settlers but to one of those inexplicable calamities that now and again decimate wild animal communities.'* (Colebatch 1929, p. 158).

'At present, the hyperdisease hypothesis is an abstraction awaiting marriage with suitable empirical data.' (MacPhee and Marx 1997, p. 191).

Introduction

For nearly 70 years from its foundation in 1829, the settled parts of Western Australia (WA) swarmed with native mammals. Although some species contributed to the larder of settlers, many were fearless and themselves sought food from settlers. Animals foraged around campsites (Ducker 1988, p. 97; Leake 1962, p. 45) and in houses and storerooms (Gould 1863, pp. 76, 310, 312; Millett 1872, p. 201; Leake 1962, p. 51), browsed foliage of crops and vegetables (Gould 1863, p. 278; Anon. 1896; Hasluck 1929, p. 8; Flynn 2002, p. 55), consumed sown seed (Gell 1895), ate grain (Gould 1863, p. 30; Haddleton 1952, p. 97), defoliated fruit trees (Clairs 1895), and killed

sheep (Gould 1863, p. 404; Piesse 1895) and poultry (de Burgh and de Burgh 1981, p. 245; Carter 1987, pp. 71-2). Digging activities of *Bettongia lesueur* in ballasting threatened to destabilise a railway in 1908 (Bird 1986, p. 224) and impaired the function of the newly constructed rabbit proof fence (Crawford 1904, Wilson 1906), and those of *Macrotis lagotis* presented a hazard to horses (Abbott 2001a, p. 280).

Collectors for museums in the 1860s and 1870s (G. Masters and W. Webb) and 1890s (K. Dahl and J. Tunney) were able to obtain with apparent ease in parts of WA mammal species which subsequently became rare, or even extinct, on the mainland (Glauert 1950; Norrington 1995). However, until 1900, the rudimentary road network hampered collection effort. Local Aboriginal names of mammal species are often the only indication of late nineteenth century occurrences, which would otherwise have gone unchronicled (Abbott 2001b).

Explanations of subsequent declines and extinctions of native mammals in WA appear to have been based largely on the visibility to humans of the results of obvious factors and processes. Emphasis has thus been given to modification of habitat, in particular by the removal of vegetation for the development of farms and cities (Kitchener *et al.* 1980; How and Dell 2000), changed fire regimes (How *et al.* 1987; Calver and Dell 1998), and the logging of forests (Rhind 1996; Lindenmayer and Recher 1998; Calver and Dell 1998). Other historical and scientific research (Brooker 1977; Burbidge and McKenzie 1989; Morris *et al.* 2000, Abbott and Whitford 2002; Burrows and Abbott 2003; Abbott 2004; Short 2004) has so far not confirmed a primary role for any of these factors in explaining the chronology of declines at regional scales in WA. Instead, the significant contribution of a much less conspicuous process (nocturnal predation by introduced foxes and cats) has been highlighted by Christensen (1980a), Hayward *et al.* (2003), Kinnear *et al.* (2002), and Short *et al.* (2002), and by the Desert Dreaming, Western Shield and Project Eden programs of the former Department of Conservation and Land Management (Christensen and Burrows 1994; Morris *et al.* 1998; Algar and Smith 1998).

The influence of another, highly invisible factor – wildlife disease – in the decline of mammal species in WA may also have been underestimated. Before I commenced this project, reports by collectors and naturalists of the abrupt decline of various species in the period 1880-1940 attributable to disease were few, were based on anecdotal information, and offered no credible mechanism (Shortridge 1910; Glauert 1928a; White 1952; Perry 1973; G. Gardner in How *et al.* 1987). Consequently, disease has been acknowledged as a relevant factor but has not previously been analysed further for want of additional information (Main *et al.* 1959; Kitchener *et al.* 1978; Prince 1984; Burbidge and McKenzie 1989).

Nevertheless, the role of diseases in causing major, usually episodic, mortality in mammal populations is well known and amply documented, for example for dogs and foxes (Elton 1942), indigenous people (Davidson 1978; Green 1984; Campbell 2002), and European people (Zinsser 1935; Curson and McCracken n.d.; Ziegler 1998). The use of introduced diseases to control pest animals is also documented (Ratcliffe *et al.* 1952; Spennemann and Wiles 2002).

When gathering data for various papers relating to mammals (Abbott 2001a, b; 2002; 2004; submitted), I discovered a considerable body of information strongly suggestive of disease as largely responsible for the early decline of mammal species in much of WA. This led to a more systematic and thorough search for further information in official files and reports. Once these records were analysed and collated, a discernible temporal and spatial pattern in these declines began to emerge.

The objective of this paper is to synthesise into a coherent theory all available historical, ecological and anecdotal information relevant to the role of disease in accounting for declines of native mammal species in WA. This theory should be solidly based on reliable, locality-specific evidence of sudden declines or disappearance of particular mammal species. From this should flow logical inferences about the point of origin of the disease, how it may have been spread, which species may have been affected, and which ecosystem processes may have been impaired. Improved understanding of otherwise inexplicable events can also add to the credibility of the disease theory.

Methods

Anecdotal information on declines of species was obtained first by interviewing >200 oldtimers (people born in the period 1901-30, and who lived most of their early life on a farm). Next, WA local and regional histories were searched for relevant information, by reading them in their entirety because indexes of most of these books were non-existent, inadequate or unreliable. These books also provided the essential context with which to understand the extent of pastoral and agricultural activities before evaluating their possible impact on native fauna. Books and articles written by naturalists, colonists and visitors; museum records of specimens; biological journals published in London and Australia up to 1930; official government reports and parliamentary papers; and Departmental files (both current and archived) were also searched for information. The material discovered was then integrated with the results and interpretations of numerous modern, scientific studies.

Time did not permit systematic reading of the many newspapers in circulation in WA up to *c.* 1930. Occasionally I chanced upon clippings in archived files and then read (on microfiche) several issues published before and after the referenced issue. However, perusal of microfiched newspapers is tedious, inefficient and time consuming.

Not all of the anecdotal material discovered about declines has been included, particularly if the account appeared exaggerated or equivocal (e.g. Anon. 1895; 'Bengalee' 1887; Gaston n.d., pp. 27, 36, 81, 181) or was not precisely dated (Tuckey 1950). Some accounts could not be used because of vagueness (e.g. Forrest 1877).

In assessing retrospectively the degree of apparent resistance of species to the epizootic, I have used eyewitness records of impact and the extent to which the geographical range was reduced prior to the establishment of the fox and the

operation of other threatening processes (based on maps in Strahan 1995 and McKenzie *et al.* 2000), as well as on the absence of reports of disease. However, given the quality of the information available, this assessment cannot be rigorous and is offered as a framework for future studies of disease. Localities mentioned in the text are shown in Figure 1.

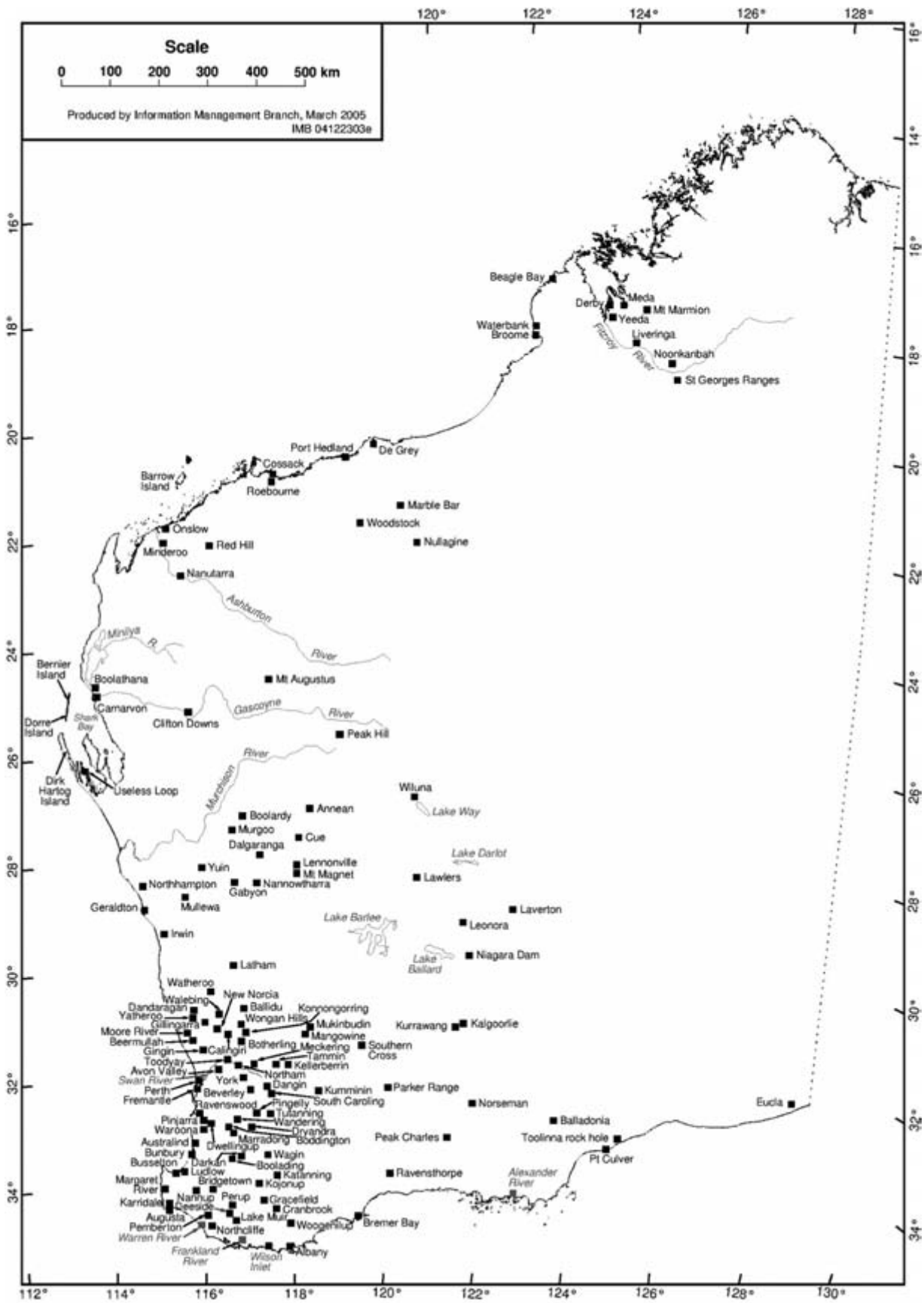

Figure 1. Localities mentioned in the text.

Results

Clinical signs of disease

Although disease is a normal occurrence in animal populations, few early endemic records in the period from *c*. 1839 to 1905 were found. All were stated to be mange, which is caused by large numbers of mites irritating the skin. In none of the sources cited in Table 1 were dead or dying animals reported. Mange is an indigenous disease (not introduced) to which native species had adapted. However, the irritated scabby skin observed may have resulted from stress, nutritional deficiencies, parasites or fungal or bacterial skin diseases.

In contrast, dead and dying animals were reported by Abjornssen (1913), Doust (1966), Grasby (1913), How *et al.* 1987, O'Connor (1913), Richards and Short (1996), Wansbrough (1919) and Weston (1921) during the period from the 1880s to 1921.

Descriptions of 'starving animals' (Anon. 1900b), 'fur falling off' (Abjornssen 1913), 'eye disease' (Tunney 1913a), 'weak and wasted' animals (Wansbrough 1919) and animals with 'withered ears and scabs on their noses' (Spencer 1966) are suggestive of degeneration of the nervous system, leading to ataxia (lack of co-ordination of movement), and marasmus (severe loss of weight). These symptoms are insufficiently characterized to link them unequivocally to any particular disease.

It is likely that most affected animals died in their tree hollows or burrows (Abjornssen 1913; Tunney 1913a; Wansbrough 1919). This would explain why no carcasses or diseased animals were seen by Brown (in Abjornseen 1913), Stevenson (1919), Cahill (1919), Hicks (1919), Clifford (1919), Shanhun (1919), Hardey (1919), Kemp (1919), McVicar (1919) and Ryan (1919). Tree hollows filled with possum bones were recorded by several observers (H. Hall, pers. comm.; Roe and Roe 1992; Tunney 1913a).

H. Wilson, the Secretary of the Rabbit Department, noted that inquiries 'did not at all show conclusively that the disappearance of these marsupials *[T. vulpecula]* was due to death from any disease; no evidence was forthcoming of any sick or dead opossums being seen, and no disease was found to be present in the animals submitted for scientific examination' (Wilson 1902, p. 93; see also Anon. 1900a, 1900b). However, no details of the localities or number of animals examined were provided. Later attempts to obtain diseased specimens for examination were also unsuccessful (Tunney 1913a; O'Connor 1913; Aldrich 1919).

Records of early decline of mammals explicitly stated to be linked with disease

The relevant evidence pertaining to reports of disease is presented in chronological sequence in Table 2 so as to facilitate the detection of any pattern in the diffusion of disease. The records (Figures 2 and 3) indicate that disease and local disappearance of native mammals were detected earlier in northern parts of WA than southern parts of WA.

South of the disease front, there are numerous records of possum *[T. vulpecula]* populations that do not mention occurrence of disease or local decline. This indicates that a large portion of the lower south-west remained free of disease until at least the period 1897-1914 (Figure 3).

Other records of early decline of mammals, not perceived to be linked with disease

Localities where declines occurred and the timing of these declines (as documented in Table 3) are included in Figures 2 and 3. Any record of decline that was linked in the original document to shooting or trapping has been excluded.

In December 1895 J.T. Tunney was appointed to the permanent staff of the Western Australian Museum as collector (Whittell 1938). Owing to funding difficulties, his position was terminated in December 1903, but his services were subsequently used on a casual basis until 1913. The information provided in the next paragraph on Tunney's mammal collections is based on a search of the specimen databases of the WA Museum, Perth; United States National Museum of Natural History, Washington DC; Australian Museum, Sydney; and Museum of

Table 1. Early records of mange in native mammals. Spellings in quotations follow the original exactly.

Year and locality	Record and comment	Reference
1839-40, ? Avon Valley	'the great difficulty of getting [*Bettongia lesueur*] with a perfect coat, in one burrow especially I shot at least 20 and they were all more or less bare of hair on the back, and several were so bad they had scarcely a hair on the whole of the back, whether it is a disease or not, that this particular species is subject to, I can scarcely venture to say of all, but several specimens certainly had the appearance of something very like the mange in dogs.'	Gilbert (n.d.). These remarks were later paraphrased and much abridged by Gould (1863, p. 278)
1841, Australind	a dingo 'half-starved…very little hair…with the mange'.	Russo (1995, p. 222)
1875, Marradong	When F. Cowcher settled in Williams district [in 1875 at Marradong, according to Chate 1952], the dingo was 'generally a mangy cur'.	Lindley-Cowen (1897, p. 110)
1896, Broome	Six *B. lesueur* were captured 'but they all had the mange so were no good' [to make into specimens].	Tunney (1896)
1905, Albany district	'so many of the specimens [*Setonix brachyurus*] obtained had mange or some kind of fur disease that only about one out of six are fit to skin'.	G. C. Shortridge, letter to O. Thomas 27 February 1905, in Short (2004, p. 608)

Table 2. Records of early decline of mammals explicitly stated to be linked with disease. Sequence is chronological. Spellings in quotations follow the original exactly.

Year and locality	Record and comment	Reference
c. 1880, between Port Hedland, Carnarvon and Peak Hill; between Laverton and Eucla	'Up to quite recently – within the last twenty-five or thirty years [before 1905 or 1906] – from abundant evidence many of the Western Australian mammals had a much wider range than at the present time, their disappearance, which is said to have been first noticed about 1880, being most sudden and accountable. Their former existence is still remembered both by natives [Aborigines] and old colonists around Port Hedland, Cossack, Carnarvon, Peak Hill, Laverton, Eucla, and many other widely separated localities…The entire disappearance of so many species, over such large tracts of country, is generally considered to be due to some epidemic or disease, which I have been told appeared to be a kind of marasmus…'.	Shortridge (1910, p. 818)
c. 1884, Minilya River	'It is a curious fact that many species of bush quadrupeds completely died out here some years ago; their unoccupied habitations [?boodie warrens] are seen all over the bush. The Kangaroos [?wallabies] in this district were almost totally exterminated some years [ago] when so many natives [Aborigines] succumbed to the "measles" [?1884]: they say the Kangaroos [?wallabies] and other species contracted this disease. It is, however, certain that some species have died out entirely; others are increasing again'.	Carter (1889, p. 268)
Before 1886, Geraldton district	"I cannot account for it, unless it is a disease…At Champion Bay there were numbers of animals 30 years ago [1871]; but for the last 15 years [i.e. since 1886] there has not been one'. Craig was temporarily headquartered at Geraldton in June 1885, October 1886 and in 1896 to control outbreaks of scab in sheep.	Craig (1901, p. 23)
c. 1888, between Konnongorring and Botherling	'About twenty-five years ago, according to Mr. Chitty, all the 'possums *[T. vulpecula]*, bandies [?boodies], snakes, and goannas died. Every hollow log had its dead or dying inhabitant and the inference is only natural that the same disease that occurred then will protect this State from a plague of rabbits'. The article provides the name of the homestead as Batbatting. C.H. Chitty took up a leasehold there in 1875.	Grasby (1913, p. 6)
?1880s, ? Roebourne district	'in the early days of this State there were in the North-West a number of animals which have now disappeared, and how did they disappear? It could not have been by sportsmen or natives [Aborigines], because there were not enough of them to bring that result. Neither could it have been by drought, because if there had been drought, sufficient [animals] would have been left for breeding. I take it some disease got among the [animals]…'. Hicks lived at Roebourne in the period 1891-8.	Hicks (1901, p. 535)
1880s, Carnarvon district	Residents of Carnarvon district informed G. Shortridge that as late as the 1880s 'wallabies were as plentiful around Carnarvon as on Bernier Island and the idea of everyone here seems that the most acceptable way of explaining the complete disappearance of mammals – which is that some epidemic probably to do with white settlement or the introduction of sheep – killed them all off.'	Letter to O. Thomas, 10 November 1906, quoted by Ride and Tyndale-Biscoe (1962, p. 86)
1880s/1890s, Balladonia	William Ponton, who helped establish Balladonia station in 1880, informed his niece of 'a strange virus which attacked all small marsupials, killing many species right out…I think… in the 1880s or 1890s'.	A. Crocker in Richards and Short (1996, p. 90)
Before 1891, between Southern Cross and Kalgoorlie	In 1891 'all the rodents, with the exception of kangaroos' had disappeared from east of Southern Cross to east of Coolgardie, evidently before they disappeared from the wheatbelt. Brush fences and pitfalls used by Aborigines had fallen into disuse. 'Possibly a virus, introduced by a European domestic animal killed off the smaller marsupials; but if this was the case it would be strange that those east of Southern Cross should be carried off first, as one would not expect the disease far beyond settlement.'	Leake (1962, p. 44)
c. 1893, Meckering	'no opossums *[T. vulpecula]* exist in Meckering Police Sub District. Old Settlers & Aboriginal natives here inform me that about 20 years ago opossums were Plentifull this District at which time some contagious Disease spread amongst them and they all died out of existence and have not existed since'.	Department of Aborigines and Fisheries (1913)

Late 1890s, Gingin	Before E. Horan (b. 1891) came to Gingin in 1901, possums *[T. vulpecula]* had been 'wiped out with some disease. The big red gums that were in the Police paddock were full of their skeletons'. F. Edwards, whose family had been resident at Millbank, Moore River since *c.* 1850, stated that possums 'died out about the same time [?1893, 1898] as the Aborigines had died of measles'. F. Wedge (b. 1900, and living at Whakea *c.* 5 km north of Gingin) noted that possums 'died in a plague'. Possums were once present at Strathalbyn, 3 km north of Gingin but 'they were killed by disease' (I. Edgar, b. 1901). de Burgh (1976, p. 99) refers to the shooting of possums near Nabaroo in 1894.	Roe and Roe (1992)
Late 1890s, ?Gingin	'I do not know the name of the disease but this I do know, that during the last few years the opossums and kangaroo-rats have nearly disappeared from some of the districts in this part of the colony. Moreover, from information I have been able to obtain, I have come to the conclusion that they have died from some contagious disease. Whilst the opossums have been dying, no domestic animal or bird has suffered.'	Brockman (1900, p. 3)
c. 1897-8, Toodyay to Beverley	'[15 or 16] years ago they *[T. vulpecula]* were to be found in large numbers in the eastern districts, but they contracted a disease there and in a few months the whole of the opossums were cleared out of that district'.	Mitchell (1913)
c. 1899, Moore River to Toodyay district	[Mr F. King of Gingin] 'told me that about 14 years ago [1899] some kind of disease killed the opossums *[T. vulpecula]* right out of the Moor[e] river and Toodyay Districts'.	Abjornssen (1913, p. 11)
c. 1899, Beverley district	A circular letter was issued by the Aborigines and Fisheries Department in 1919 to Police officers, Fisheries inspectors, and honorary inspectors and guardians of wildlife. C. P. Wansbrough of Beverley replied that in *c.* 1899 and 'for a few years afterwards…I used to find the oppossums *[T. vulpecula]* during clearing opperations suffering undoubtedly from some disease. I have found them in hollow limbs, so weak and wasted as to be unable to get away, also I have found them asleep at the foot of trees too weak to climb up & I have found them dead both in hollows & on the ground. The only noticable feature about them was that they were in most cases mangey and lousy… With regard to the Boodies *[B. lesueur]*…at about the time they dissapeared [after *c.* 1899] I remember them being also mangey & alive with lice but only remember finding two dead ones'.	Wansbrough (1919, pp. 37-8)
?1890s	'The epidemic which played such havoc with our fauna several decades ago exterminated the dalgyte *[Macrotis lagotis]* in many areas. The natural fertility of the species and the fact that man has done but little to interfere with its food supply have resulted in a great increase in numbers, and slowly but surely the animal is making its way back to its old haunts'.	Glauert (1928a, p. 11)
1900, Northam, York and Beverley	'reports were received some days ago by the Lands Department to the effect that a serious disease had broken out amongst opossums, and that in some districts the marsupials had in consequence become extinct. The Minister of Lands has requested the Chief Inspector of Stock to investigate the matter and report to him'. 'From inquiries instituted by the Stock Department of the police in the Eastern districts, it would appear that the marsupials had not succumbed from disease. Some of the settlers of the district have also communicated with the department, to the effect that the opossums appeared to have died from starvation'.	Anon. (1900a, p. 4; 1900b, p. 4)
c. 1900	'A mystery attaches to the disappearance and reduction of numbers of many small marsupials. No one can explain it, but it cannot be said to be due to the action of man. What appears to be an undisputed fact is that some twenty-five years ago a mysterious disease of some kind swept over the country and killed off the majority of the smaller marsupials'.	Grasby (1925, p. 207)
1900-1, Toodyay district	Possum *[T. vulpecula]* hunting continued as a worthwhile industry in Toodyay district until the turn of the century, when disease wiped out many colonies of possums and their habitat was destroyed as trees were cleared.	Erickson (1974, p. 255)
c. 1900-1	'The "epidemic" practically wiped out the animals *[B. lesueur* and *B. penicillata]* about the beginning of the century and although 30 years have elapsed, it is only here and there that they have been able to re-establish themselves. Many old boodie warrens are now occupied by rabbits, cats and dalgites *[Macrotis lagotis]*'.	Glauert (1930a, p. 9)

Before 1901, Toodyay to Beverley	'It is well known that a few years ago opossums *[T. vulpecula]* were a scourge in some parts of the Eastern districts, until a disease attacked and almost exterminated them'.	Harper (1901, p. 117)
1901	[A disease] 'has been amongst our opossums, and we have tried to get samples, but we have failed so far'.	Craig (1901, p. 23)
c. 1901	'It seems pretty certain that an epidemic of some kind swept through the country about the beginning of the present century. Whilst some forms were completely wiped out, others were merely decimated, and these remnants… are slowly but surely becoming re-established in some of their old haunts'.	Glauert (1928a, p. 6)
c. 1901, ?Bridgetown	'I also remember seeing them *[Trichosurus vulpecula]* dead in dozens in rocky outcrops, in particular, due to some disease. This would be at least 65 years ago. A few years later wallabies *[?Setonix brachyurus]* shared the same fate. You could [previously] shoot them in dozens in any of the gullies and suddenly dead bodies could be found everywhere'.	Doust (1966, p. 65)
1902	'whether the destruction of rabbits might not be brought about by the transmission to them of a disease which was supposed to be carrying off the opossums *[T. vulpecula]* in certain districts of the State?'	Wilson (1902, p. 93)
c. 1900-6	'When I was a boy [1870s-80s] Kangaroo rats *[B. penicillata]* & ringtailed oposums *[Pseudocheirus occidentalis]* were very numerous around Bridgetown. Of recent years I have seen none East of Nannup [i.e. between Nannup and Bridgetown] – They died out East of Nannup when the Bubonic plague visited W.A.'	Allnutt (1919, p. 31)
c. 1904	T. Smith noted that he had been 'shooting and trapping for nearly 40 years and I can assure you that diseases do get among the marsupials at times and kill them off in great numbers. Some 26 years ago an epidemic affected the 'possums *[T. vulpecula]* of the South-West and killed them by the thousand. It also attacked the kangaroo rat *[B. penicillata]* and this animal is practically extinct to-day. Strange to say, the kangaroo *[Macropus fuliginosus]* seemed immune'.	Glauert (1930b, p. 36)
1904, Beverley-Kumminin	'Although there has been no opossum *[T. vulpecula]* Kangaroo rats *[B. penicillata]*, or Boodies *[B. lesueur]* in this locality [Beverley] for the last fifteen years. Prior to then there were large numbers of each extending as far East as Kumminin. In my opinion it was undoubtedly a disease that exterminated them'.	Wansbrough (1919, p. 36)
1905, Ludlow pine plantation	'There was a disease among the opossoms *[T. vulpecula]* 14 years ago & a number of them died but do not hear of any other marsupials being affected'.	Banfield (1919, p. 64)
Before 1905	*'[Trichosurus vulpecula]* seems to be subject to some epidemic that at times almost clears them out of districts where they were plentiful previously'.	Shortridge (1910, p. 830)
1909, Ravenswood	'Opossums *[T. vulpecula]* are practically extinct in this locality. They used to very plenty-full about here some ten years ago, but they disappeared but nobody seem to know the cause. Others tells me that some years ago there was a disease amongst the Oppossums killing them out'.	Forsberg (1919, p. 62)
c. 1910-11, area approx. circumscribed by Pinjarra, Boddington, Darkan, Kojonup and Bridgetown	'In the first years of settlement there were kangaroos, dingoes, emus, dalgites *[Macrotis lagotis]*, opossums *[T. vulpecula]*, tamars *[Macropus eugenii]*, kangaroo rats *[B. penicillata]*, boodirats *[B. lesueur]* and nambats *[Myrmecobius fasciatus]*. About 1910/11…all the smaller creatures disappeared [i.e. not kangaroos, dingoes or emus]. According to…William Gibbs [who settled in the Darkan area in 1862], some kind of disease was the cause, and they all disappeared approximately from Pinjarra to Bridgetown to a line just west of the Albany Road [Albany Highway].'	Spencer (1966, pp. 75-6)
c. 1911, ?Darkan	W. Gibbs noticed that 'the last opossums caught [after a regional collapse of the mammal fauna] had withered ears and scabs on their noses'.	Spencer (1966, p. 76)
c. 1911, Kojonup district	'I do not consider that the disease now exist in the District, as I consider the disease has almost exterminated the opossum *[T. vulpecula]*…about 2 years since the disease was at its worst… One resident of Kojonup was ringbarking…close to town & he found as many as ten dead opossum in one day'.	O'Connor (1913, p. 22)

c. 1911-12, Kojonup district	'I have examined trees in the districts I have been through & judging by tracks I would certainly say the animals *[Trichosurus vulpecula]* are scarcer now than they were a year or so ago when the opossums were attacked with disease they remain in their holes & die, consequently it is only a chance if one gets a sick animal. The Rats *[B. penicillata]* & Boodies *[B. lesueuri]* have become extinct in the district and yet no one ever saw a dead or sick animal about, therefore the same thing applies to the opossoms'.	Tunney (1913a, p. 15)
1913 and before, Kojonup	Police reported that settlers and others had seen dead bodies of possums *[T. vulpecula]* in the bush before 1913. A Senior Inspector of Fisheries then visited this district, interviewing bush workers, and was told of one old possum seen 'with the fur falling off'.	O'Connor (1913, p. 5); Abjornssen (1913, p. 10)
Before 1913, Toodyay, Northam, York and Beverley district	'As no doubt you know opossoms *[T. vulpecula]* were numerous in the Newcastle & Eastern district at one time now there is scarcely one to be found there. In that district they died from some eye disease & there is every reason to suppose it is the same thing that killed out the Bettongia family & as a number of opossoms live in Boodie *[B. lesueur]* holes it is possible for them to contract the disease'.	Tunney (1913a, p. 16)
c. 1912, Tutanning district	Boodies *[B. lesueuri]* were extinct in the Tutanning district before *c.* 1915, as G. Gardner (b.1912) recalled in conversation with me that when a child his father showed him large wombat-like burrows without animals (boodies) in them. In his published memoirs he states that a viral disease rapidly swept through the district in 1912.	Gardner (2000, p. 61)
Before 1913, the south-west in general	'it is a known fact that the opossums *[T. vulpecula]* right through the South-West are dying through some disease, which has been killing them off for some considerable time'. [Ward lived at Kojonup].	Ward (1913, p. 6)
Before 1913, Kojonup district	'I have been informed that a few years back their were thousands of Boody & Kangaroo rats *[B. lesueuri and B. penicillata]* in this district & now it is almost impossible to get one. Just recently Mr J.T. Tunney "one time collector for the Museum" wanted to get some specimens for the museum & zoological gardens & had the greatest difficulty in finding them, it is quite evident that some disease has almost exterminated them'.	O'Connor (1913, pp. 5-6)
1913, *c.* 15 km north of Cranbrook	Aborigines had informed a resident of Kojonup district that 'the disease had passed through Kojonup and was now some 30 miles south where the opossums *[T. vulpecula]* are dying'.	Abjornssen (1913, p. 10)
1919, Busselton, Augusta, south of Pemberton, and Lake Muir	'Tom Carter who has been touring through the South Western portion of the State informs me that whilst in the extreme South West he was told that opossums *[T. vulpecula]* & other marsupials are being killed by some disease'. [Carter visited Lake Muir, the mouth of the Warren River, and Cape Leeuwin in March 1919 and the Vasse in April 1919].	Aldrich (1919, p. 24)
Before 1919, Dwellingup-Waroona district	'to all practical purposes the opossum *[T. vulpecula]* is extinct in the district between Dwellingup & Waroona…I have been unable to find any trace of them…but [some] people…state that a few still exist in some places but they are very scarce. The cause of their disappearance is always put down to the disease to which you refer & I believe the same disease also attacked other marsupials…there has been no recurrence of the disease'.	Sunderland (1919, p. 72)
1921, Pemberton district	'there appears to be some epidemic amongst the "quoggas" *[Setonix brachyurus]* down here, especially along the Warren River. Dead "quoggas" can be seen in the bush every day'.	Weston (1921)
Early 1920s, Northcliffe district	'swamps around Northcliffe were full of Quokka bodies'.	G. Gardner in How *et al.* (1987, p. 565)

Comparative Zoology, Boston (The Macleay Museum, Sydney; Academy of Natural Sciences, Philadelphia; and American Museum of Natural History, New York advised me that they have no mammal specimens collected by Tunney). The correspondence files of the Mammal Section and accession registers of the Zoology Department of the Natural History Museum, London also yielded numerous records (K. Taylor, pers. comm.).

In January 1896, Tunney collected between Gillingarra and Dongara, obtaining only the kangaroo *Macropus fuliginosus*. He then spent March-May 1896 in the Carnarvon district, but only obtained specimens of native mammals on Bernier Island. In August-October 1897 he collected in the upper Murchison district, but obtained only the kangaroos *Macropus rufus* and *M. robustus*. In February and March 1898 he collected in Shark Bay and Carnarvon districts, but only obtained mammals from Bernier Island. In March 1899 he collected mammals on Dorre Island, Shark Bay. From August to December 1899 he collected in the east

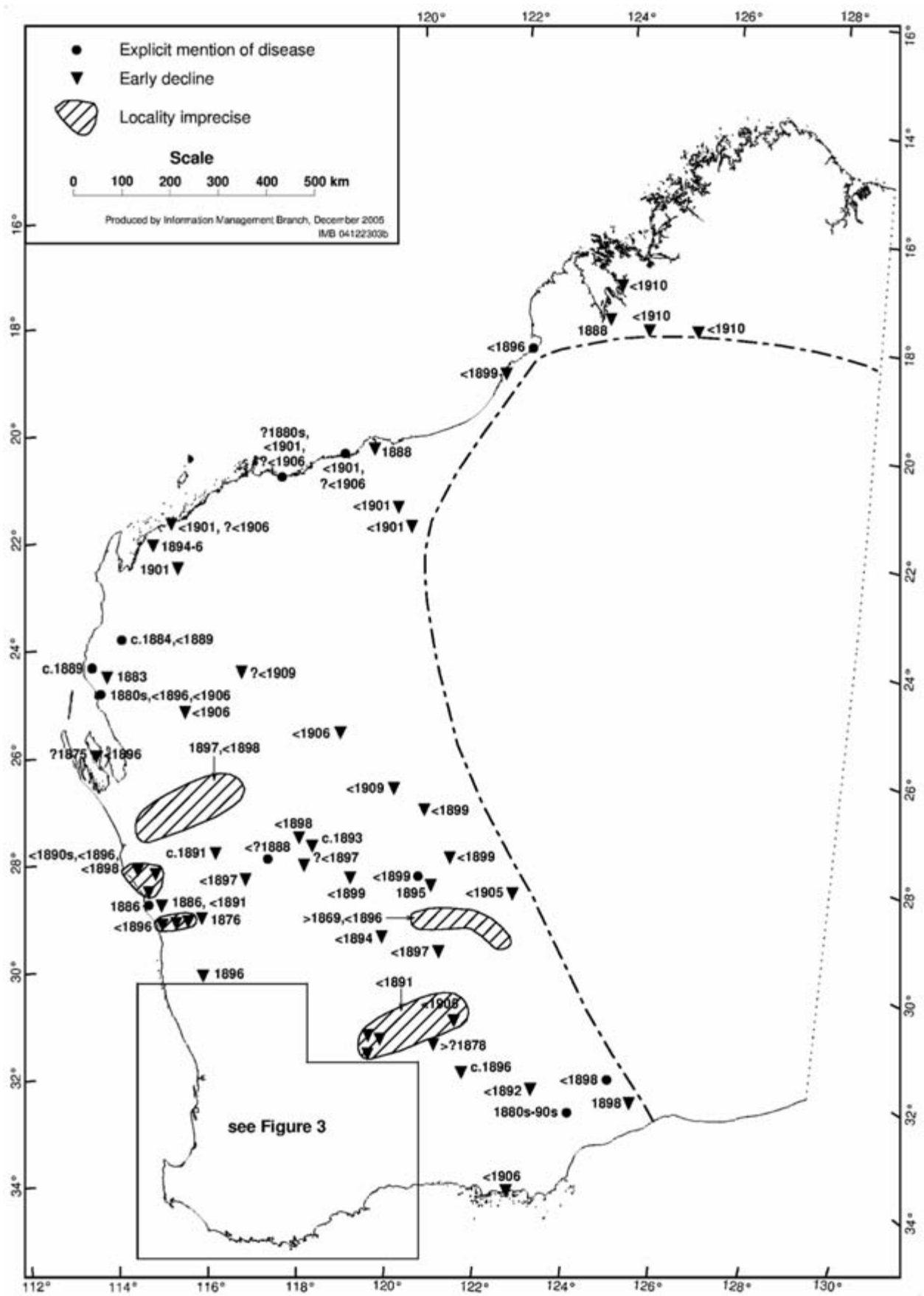

Figure 2. Location of records of reported early declines of native mammals in Western Australia, prior to the establishment of foxes. The dashed line indicates the eastern limit of records. Hatched areas refer to less precisely localised records.

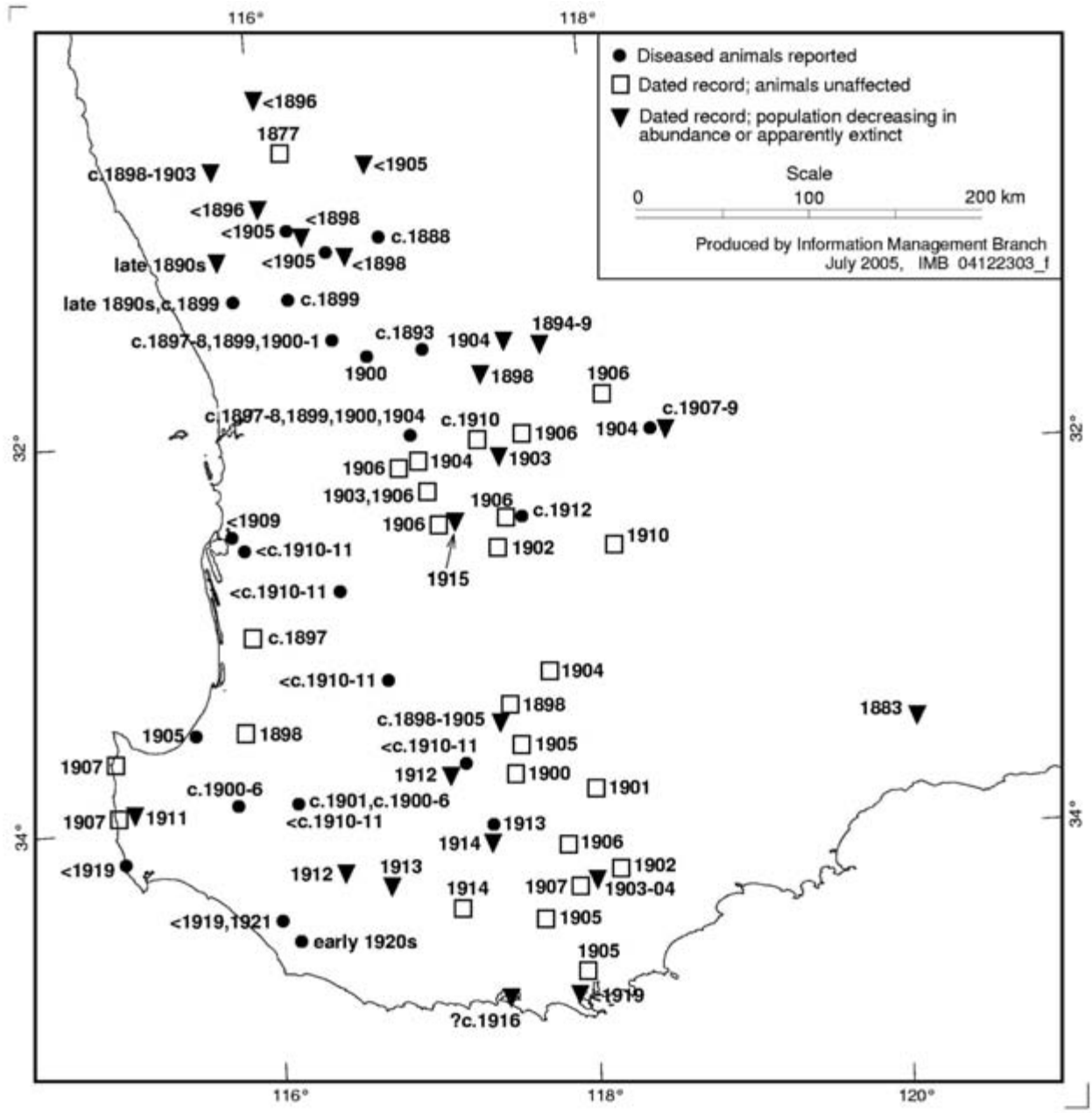

Figure 3. Location of records of early declines of native mammals in the lower south-west portion of Western Australia, prior to the establishment of foxes. The records of unaffected populations are of *Trichosurus vulpecula:* 1877, near Berkshire Valley (Broad and Broad 1992, p. 192); c. 1897, Harvey (Vivienne 1901, p. 104); 1898, Donnybrook (Frost 1976, p. 15); 1898, Cartmeticup (Bird 1986, p. 110); 1900, west of Broome Hill (Carter 1923, pp. 138-9); 1901, Gnowangerup (Marshall 1993, p. 155); 1902, Stirling Range (Anon. 1902b, p. 6); 1902, north of Wickepin (Facey 1981, p. 19); 1903, Brookton (Hill 1903, p. 107); 1904, Mt Kokeby (Clemens 2000, p. 97); 1904, Dumbleyung (Anon. 1999, p. 347); 1905, Mt Barker (Parnell 1982, p. 74; Shortridge 1910, p. 831); 1905, King River (Shortridge 1910, p. 831); 1905, Katanning (Bignell 1981, p. 200); 1906, Yetemerup (Bignell 1977, p. 167); 1906, Bruce Rock (Ewers 1959, p. 97); 1906, Brookton and Pingelly (Peacock 2003, p. 29); 1906, c. 30 km west of Beverley, c. 50 km east of Beverley and c. 30 km east of Pingelly (Shortridge 1910, p. 831); 1907, Yallingup and Margaret River (Shortridge 1910, p. 831); 1907, Woogenilup (Glover 1979, p. 232); 1910, Kulin (Greble 1979, p. 28); 1912, Kojonup (Bignell 1971, p. 205); and 1914, Perillup (Glover 1979, p. 61).

Murchison district as far inland as Mt Magnet, Lake Way, and Lake Darlot; he obtained only *M. rufus* and *M. robustus*. For much of the period October 1900 to August 1901 he collected between Onslow and Port Hedland, inland to Nanutarra, Woodstock and Nullagine and obtained only *M. rufus* and *M. robustus*. In contrast, on Barrow Island he collected during a residence of nearly 3 months a large series of a diverse mammal fauna, ranging in size from *M. robustus* (largest) to *Pseudomys nanus* (smallest). Tunney's collecting methods were evidently satisfactory, as he also secured specimens of native rodents and the smaller marsupials in his 1901-2 expedition to Arnhem Land, Northern Territory (Thomas 1904).

The following information extracted from letters written in the field by Tunney to the Curator of the WA Museum (B. H. Woodward) supports the above interpretation:

- 'We have not seen much game up this way yet' (3.1.1896, Gillingarra)
- 'I have had some natives out but they could not get anything, so I will not waste my time here…There are no rats opossoms or any small animals about here so the natives tell me' (10.1.1896, Watheroo)
- 'there are no animals up here but Kangaroos' (27.1.1896, Irwin)
- 'I don't think there is much to be got about there [Northampton]' (8.2.1896, Mullewa)
- 'there is nothing to be got near the coast here' (10.3.1896, Carnarvon)
- 'This is a very poor place for specimens…I am told there are no wood mice here now, only the common mice' (26.3.1896, Carnarvon)
- 'This is the worst place I ever was in for specimens, there are no birds or animals near here' (31.3.1896, Fresh Water Camp, Shark Bay)
- 'Game is very scarce in this part' (7.9.1897, Cue)
- 'mammals are scarce in this part, in fact Kangaroos are the only animals we have seen so far' (15.9.1897, Cue)
- 'I went down the coast 100 miles after the mice or rats but was not very successful. I am sending few specimens of same' (31.12.1898, Broome)
- 'I have not seen any animals about' (3.10.1899, Lawlers)
- 'only a few birds to be seen and no animals' (14.10.1899, Lake Way)
- 'There are very few animals in the district. I was only able to get one Kangaroo on the trip. I heard of a lot of game about 150 miles further east from where I was (3.11.1899, Lawlers)
- 'I have not seen any mice about this part' (20.11.1899, Nannowtharra)
- 'I have not been very successful so far, find that game is scarce in this part in fact there are no small animals' (24.2.1901, Red Hill [100 km south-east of Onslow])
- 'This country is not much for game, so far I have not been able to get anything fresh' (29.3.1901, Marble Bar)
- 'very little game to be had…There are no small animals to be had about here now…I have been out since yesterday with a party hunting with dogs through the plain country about 12 miles from here and we never saw any track of small animals so they cannot be numerous in this part (21.4.1901, Nullagine)
- 'The only small marsupial I have got here is a P. lagotis *[Macrotis lagotis]* and they are very scarce' (28.4.1901, Nullagine)
- 'practically no game' (?1906, Alexander River, east of Esperance)

In marked contrast to this lack of success in his collecting efforts on the mainland between Gillingarra and Port Hedland between 1896 and 1901, Tunney obtained many specimens of native mammal species from the southern part of WA in the period April-July 1897, January 1898, July 1899, January-September 1900, January 1904-September 1905, April-July 1906, and at various times in 1907, 1908 and 1909 (based on material held in WA Museum, Perth; United States National Museum of Natural History, Washington DC; Australian Museum, Sydney; and Museum of Comparative Zoology, Boston).

The only native mammals collected by G. Shortridge in inland parts of WA in 1905-6 were *Macropus robustus* (Clifton Downs), *Macropus rufus* (Clifton Downs, Laverton), *Cercatetus concinnus* (Parker Range), *Macrotis lagotis* (Parker Range), *Tachyglossus aculeatus* (Parker Range, Clifton Downs), and several species of bats (Parker Range, Kurrawang, Laverton) (Shortridge 1910, 1936).

After fieldwork in 1909 in a 20 km wide spinifex plain between Limestone and Bore Wells, *c.* 60 km west of Wiluna, Whitlock (1910, p. 204) noted that 'were it not for the bird-life on these spinifex plains silence would absolutely prevail. During a month's constant tramping I never saw a kangaroo or other marsupial.'

In 1909, on a cattle droving trip, Facey (1981, pp. 154-165) became lost for seven days at Lyons River near Mt Augustus. He recorded kangaroos, emus, brumbies and dingoes, but makes no mention of smaller animals. This is consistent with other accounts of small mammals having had already disappeared from the Murchison district.

The failure of the Swedish scientific expedition to record small and medium-sized mammal species near Fitzroy River in 1910-12 (Table 3) cannot be due to inadequate

Table 3. Records of early decline of mammals not stated to be linked with disease. Sequence is chronological. Spellings in quotations follow the original exactly.

Year and locality	Record and comment	Reference
1876, ?Strawberry	'It is 22 years since I saw them *[M. lagotis]* on the Upper Irwin.'	Watson (1898)
1883, Ravensthorpe district	'Ravensthorpe settlers report that prior to the year 1880 Opossums *[T. vulpecula]*, Tamar *[M. eugenii]*, Paddymelon *[?B. penicillata]* and Morning *[Lagostrophus fasciatus]* were very numerous but by 1883 the two latter had become practically extinct, the opossum and tamar are also on the decrease… no one is after them for the skins'.	Mitchell (1919, p. 70)
1883, *c.* 23 miles north of Carnarvon	'no 'possums *[T. vulpecula]* about there'.	Gribble (1905, p. 28)

c. 1884	'Settlers had all said that kangaroos [?wallabies] were very plentiful all over the Gascoyne district when it was first settled, but they disappeared, or died, at the same time as the natives [Aborigines] had a severe epidemic of measles (of which scores died). Kangaroos [?wallabies] must have been numerous on the Minilya River, as there were the remains of several large V-shaped fences (or wings) made of brushwood, leading to a deep pool at the end of the V, down which the natives used to drive them and then kill them for the meat'.	T. Carter 1889, in Carter (1987, p. 99)
1888, between Yeeda and De Grey	'no game to be got'.	Cammilleri (1986, p. 24)
c. 1889, Boolathanna	At Boolathanna station in 1887 a species of 'wallaby' was noted as abundant in a thicket. 'A couple of years afterwards, not one could be seen'. Carter suggested that sheep may have driven the wallabies away. He also mentions shooting wallabies in this thicket.	T. Carter 1889, in Carter (1987, p. 7)
Between 1880s and 1920, Dirk Hartog Island	'formerly small mammals were plentiful, but were now seldom seen' [attributed to predation by feral cats]	Whitlock (1921, pp. 129-130)
Before 1891, Geraldton district	At Geraldton in May 1891, a visitor was advised by Mr Brown that Geraldton district 'was practically a gameless one, with the exception of kangaroos, emus, wild ducks and wild turkeys'.	Mennell (1892, p. 76)
c. 1891, upper Murchison district	At Yuin animals 'were far more numerous in those days [?1875]…the small furred animals…mostly seem to be extinct [?at Murgoo]'. He implicated a drought in 1891.	F. Wittenoom in Lefroy (2003, pp. 38, 41)
Before 1892, Fraser Range	'The natives in these parts…have scarcely any game to catch. Game seems to have disappeared during the dry season'	Anon. (1892)
Before or *c.* 1893, Cue district	'For the past 30 years or more' *Bettongia lesueur* 'has rarely been seen. That it was plentiful at some earlier date seems evident by the large numbers of warrens to be found almost anywhere on limestone or opaline country. Bungarras and rabbits now occupy the homes of the "boody", who so mysteriously disappeared'.	Anon. (1923)
1894, near Lake Barlee	'We did not see a living thing with the exception of one turkey and a few birds. No [Aborigines]. They could not live here'.	Smith (1979, p. 206)
1895, Lawlers	'The absence of animal life…is remarkable'.	Gibson (1895)
Between 1895 and 1910, near Broome [Waterbank pastoral station], Derby, Fitzroy River, Meda and Beagle Bay, inland to Mt Marmion, Liveringa, Noonkanbah and St George Ranges	The Swedish Expedition of 1910-12 did not record or collect *Bettongia lesueur*, possums or bandicoots (Lönnberg 1913). This contrasts with bandicoots *(Isoodon auratus)* in 1887 being 'very plentiful in all this country…hopping round the campfire at night' (Froggatt 1934, p. 73). In 1896, some 12 miles north of Broome, *Trichosurus vulpecula* were 'occasionally met with', 'the ground was nearly everywhere and in all directions excavated by the burrows of' *B. lesueur*, and *I. auratus* was 'very numerous' (Dahl 1897, pp. 201, 205, 210). Floods forced *B. lesueur* out of their burrows, killing many animals (Collett 1897, p. 212; Dahl 1926, p. 319). Was Dahl instead witnessing the commencement of an epizootic?	Collett (1897), Dahl (1897, 1926), Froggatt (1934), Lönnberg (1913)
Before 1895, Niagara district	'In 1869, when I travelled along by Lake Barlee and Mount Margaret [between Leonora and Laverton]…there were abundance of marsupials in that country; but where are they now? [Sir John Forrest had toured the goldfields as far north as Niagara in November 1895] When I asked the Aboriginals what had become of the kangaroos [?wallabies] and other marsupials, they told me that drought had killed them all'.	Forrest (1896)
Before 1896, ?Minderoo, Ashburton district	'Up in the North (Ashburton, for instance) when I went there 23 years ago [1878] there was nothing but a mass of rats, wallabies, mice, and all that kind of thing. For the last five, six, or seven years [1894-6] there is not one to be seen anywhere'.	Forrest (1901, p. 23)
Before 1898, upper and lower Murchison	'It *[M. lagotis]* is one of the few bush animals that survived the drought of a few years ago…they are not numerous, and soon leave a district where cattle or sheep run, probably through their holes being trodden in.'	Drage (1898)
Before 1898, Victoria Plains, i.e. New Norcia-Calingiri district	'*[M. lagotis]* used to be very numerous here at one time, but have disappeared for many years now; as have also the boodies *[B. lesueur]* and opossums *[T. vulpecula]* from this locality'.	Anon. (1898b)

Before *c.* 1898, Dalgaranga	In 1915 on Dalgaranga station, an Aboriginal aged in his late twenties described how Aborigines disturbed the stick nests of *Leporillus* and captured the rats as they fled. He remembered seeing rats as a 'young lad' but had not seen them since. Assuming the Aboriginal was 27 years old and young lad refers to a male younger than 10 years, I tentatively date this disappearance as <1898.	Wellard (1983, p. 130)
1894-9, Kellerberrin district and Avon Valley	*Bettongia lesueur* became extinct in the eastern wheatbelt [Kellerberrin district], as well as along the Avon Valley, in the period 1894-9. *B. penicillata*, *Onychogalea lunata, Lagostrophus fasciatus, Lagorchestes hirsutus*, 'Short Nosed Bandicoot' *[?Potorous platyops]*, *Chaeropus ecaudatus*, *Myrmecobius fasciatus*, *Isoodon obesulus*, *Dasyurus geoffroii* and *Phascogale* aff. *tapoatafa* disappeared from the eastern wheatbelt in 1894-9 (pp. 43, 51). A few of these species later re-appeared. Dalgytes *[M. lagotis]* 'were all gone in 1898' (p. 45). Possums *[T. vulpecula]* and tammars *[M. eugenii]* disappeared from the Kellerberrin district in *c.* 1902 (pp. 43, 49). Based on a discussion with B. Leake, in c. 1895 'all the smaller marsupials disappeared, and have not since been seen there [Kellerberrin district]' (Milligan 1904, p. 220).	Leake (1962)
Before 1897, near Lake Prinsep (now known as Lake Ballard)	'I have never seen one [a "rat"], only their burrows, and these have always shown every appearance of being unoccupied. Most of the burrows that I have seen have been in a low mound, perhaps 30 feet across, of white powdery soil, like gypsum. The only living things that I have seen emerge being a cat…and snakes or lizards.' These remarks are clearly referable to the boodie *[B. lesueur]*.	Carnegie (1898, p. 214)
c. 1897, Mt Magnet district	Possums *(T. vulpecula)* not seen for at least 16 years	Department of Aborigines and Fisheries (1913)
c. 1897, Geraldton-Mullewa district	Settlers were 'not much troubled by…boodie rats *[?B. lesueur]*, opossums *[T. vulpecula]…*'	Lindley-Cowen (1897, p. 197)
c. 1897, near Lennonville	Big hills were riddled with enormous holes 'made by the earthworm', according to a mine manager. These holes are clearly boodie *[B. lesueur]* warrens and evidently they were then unoccupied by boodies.	Vivienne (1901, pp. 323-4)
Late 1890s, Beermullah-Gingin district	Boodies *[B. lesueur]* were remembered as live animals by W. Turner (b. c.1890) in the Beermullah area, whereas F. Wedge (b.1900) and I. Edgar (b.1901) recalled only their burrows 3-5 km north of Gingin.	Roe and Roe (1992)
1898, Mt Morgan near Widgiemooltha	'the only holes discovered being those of native rats *[?Bettongia lesueur]*, these being at least two seasons old and untenanted, as the entrances were covered with herbage and cobwebs'.	Anon. (1898c, p.)
c. 1898, Youndegin	Pig-footed bandicoot *(Chaeropus ecaudatus)* last reported.	Glauert (1928b, p. 6)
1898, 45 miles north-west of Toolinna rockhole near Point Culver	'The plains are dotted all over with deserted rat *[?B. lesueur]* burrows.	H.J. Page in Glyde (1898, p. 8)
c. 1898-*c.* 1903, Balamarra [near Dandaragan]	Numbats *[M. fasciatus]* '…used to be fairly plentiful about here…some 30 years ago, but I have not seen one now for many years. They disappeared about the same time as the 'possum *[T. vulpecula]*, boody rat *[B. lesueur]*, bandicoot *[?M. lagotis]*, etc. Some twenty-five years ago 'possums and boody rats were numerous in this district, but now there is not a boody rat to be found, although there are still a few 'possums…Native cats (spotted) *[D. geoffroii]* and the gnow or mallee hen *[Leipoa ocellata],* which were fairly numerous in this district many years ago, have all gone'.	Green (1928, p. 6)
c. 1898-1905, Coompatine, 12 km north of Katanning	Early disappearance from the Katanning district of several species: *Bettongia lesueuri* (*c.* 1898), *Onychogalea lunata* (1900), *B. penicillata* (1905), *Pseudocheirus occidentalis* ('the early years of the century'), *Isoodon obesulus* ('long before the rabbit or fox came'), and *Perameles bougainville* (no year stated).	Haddleton (1952)
c. 1899	'Some 30 years ago…*[Macrotis lagotis]* disappeared from many of its old haunts, but within recent years it seems to have re-occupied some of them, for it has been caught in rabbit traps in districts where it has not been seen for decades'.	Glauert (1929, p. 40)

c. 1899-1906, Derby district	J. P. Rogers 'tells me that many of the smaller [mammal species] are getting exterminated…there'	G. C. Shortridge, letter to O. Thomas 10 November 1906, in Short (2004, p. 614)
Before 1900-10, Kellerberrin district	When the first agricultural settlers came to the Kellerberrin district in 1900-10, there was practically no game present, in contrast to the 1860s when pastoralists arrived and 20 species of mammals were present (p. 39). An Aboriginal who was born near Coolgardie [*c.* 350 km north-east] stated that many of these 20 species occurred near Coolgardie in *c.* 1878 (p. 44).	Leake (1962)
Before 1902, presumably Depot Hill, south of Kalgoorlie	'In those days [1864] kangaroo, emu and small game of the marsupial variety were fairly numerous. What has caused the disappearance of all this game. I attribute it to the ravages of the domestic cats that have gone wild.'	Anon. (1902a, p. 6)
c. 1903, 'South-West' [?Williams district]	'the boodies *[Bettongia lesueur]* were in hundreds 15 years ago, but to-day they are practically extinct. I have not seen one for years.'	Greig (1918, p. 689)
1903, South Caroling	Report of many skeletons of possums *[T. vulpecula]* in hollows in trees, when the country was being cleared.	Father of H. Hall, H. Hall (pers. comm.)
1903-4, Woogenilup district	Woylies *[B. penicillata]* were plentiful in 1902 at Woogenilup and their stick nests were common in the bush (Pearce 1963, p. 37). They disappeared in 1903-4 ('cause unknown'), but re-appeared in small numbers in *c.* 1929. The ringtail possum *[P. occidentalis]* was plentiful in Woogenilup district in 1902 and was last seen there in 1903.	Pearce (1963, p. 37)
< 1904, Cue district	Last possum *(T. vulpecula)* seen more than nine years previously, at Kalli pastoral station.	Department of Aborigines and Fisheries (1913)
1904, near Tammin	Boodies *[B. lesueuri]* had disappeared from a large warren.	Repton (1999, p. 308)
1905, Wongan Hills-Ballidu district	The earliest settlers 'have never seen an Opossum *[T. vulpecula]* and are only conscious of their [previous] presence by the native toe marks in the old hollow gum trees'.	Ackland (1965, p. 104)
Before 1905, New Norcia-Calingiri district	'nearly all the small marsupials appear to have died out in…[Victoria Plains] district.'	Shortridge (1910, p. 839)
1905-7, north of the Swan River	Boodies *[B. lesueuri]* were noted as 'Not appearing at the present time to exist on the mainland to the north of the Swan River'.	Shortridge (1910, p. 822)
1906, Carnarvon district	'these Rat-Kangaroos [*Bettongia lesueur, Lagorchestes hirsutus* and *Lagostrophus fasciatus*]… are entirely absent from the mainland about here' [in contrast to Bernier Island].	Thomas (1906, p. 773)
1906, Laverton district	'The country is destitute of food for the natives, and the rabbits are not [yet] plentiful enough to enable the blacks to catch them in sufficient numbers to live on'	Anon. (1906, p. 5)
c. 1907-9, Kumminin	'[N]o explanation can be given why…opossums *[T. vulpecula]* and other small animals, practically disappeared from the large tract of country of which Cumminin is part', 1907-9.	Crossman (1909, p. 85)
c. 1910, Dangin	An oldtimer, who lived at Dangin from 1906 to 1918, recalled seeing boodies *[B. lesueur]* alive there in their burrows.	L. McClellan, b. 1906, pers. comm.
1910, Mukinbudin Rocks	Report of boodies *[B. lesueur]* living in burrows there, apparently the last record for Mukinbudin Shire.	Maddock (1987, p. 20)
1911, 'Gracefield', Slab Hut Gully 22 miles south of Kojonup	'he [J. Tunney] cannot account for the disappearance of opossums *[T. vulpecula]* and "other marsupials of no commercial value" from the Kojonup district. He had not seen any dead or dying opossums but he could vouch for that no trapping had been done in their paddocks since trapping was prohibited and Mrs Tunney Sen[ior] told me that they had not seen opossums in their orchard for two years [i.e. since 1911] whereas before they were a veritable pest'. Abjornssen stated that he searched 'undisturbed country off the main road' near Kojonup but failed to find any sign of possum scratchings on trees.	Abjornssen (1913, pp. 10-11)
1911, Margaret River district	Woylies *[B. penicillata]* were obtained 3 years ago [1908] near the Margaret River caves. J. Tunney was sent there ' not long ago to get some…and spent a fortnight in the district, but did not get one'.	Woodward (1911, p. 16)

Before 1912, Broome district	'Opossums *[T. vulpecula]* have been extinct throughout my district for many years'	Department of Aborigines and Fisheries (1912)
c. 1912, northwest of Kojonup	Report of a deserted boodie *[B. lesueuri]* mound near a farmhouse.	Bignell (1997, p. 18)
1912, Gracefield-Deeside (95 km south-west of Gracefield)	'I have not been able to get any [*B. lesueur* or *B. penicillata*] yet although I went 75 miles west [from Gracefield] in search of them…Mr. Muir of Deeside told me that all the smaller marsupials are getting very scarce in the S.W., he says 5 years ago [1907] the rats *[B. penicillata]* and boodies *[B. lesueur]* were a pest and during the last 2 years he has only seen 2 rats though he is always riding about the bush'. Further searches for boodies and woylies were unsuccessful.	Tunney (1912a, 1912b)
1913, Carnarvon district	'there are no opossums *[T. vulpecula]* in the Gascoyne District'	Department of Aborigines and Fisheries (1913)
1913, Frankland River district	'I have been told by a reliable man…that he found in one hollow tree 12 skeletons of opossums *[T. vulpecula]*. That was some months ago'.	Tunney (1913a, p. 15)
1913, Lake Muir district, Gracefield, Cranbrook	'I have returned from a trip in the South West and I am sorry to say I have not been successful. Everywhere I went the Rats *[B. penicillata]* and boodies *[B. lesueuri]* had all left or died out. 12 months ago, there were some about Lake Muir [75 km south-west] but now there are no traces round the Burrows, so I am afraid they must be nearly extinct in the district…I told Mr. Muir of Nabergup [Nerbichup], that if he sent you along a few skins of Boodies you would pay him 10/- for them' (Tunney 1913b). Three boodies were obtained in May 1913 (Tunney 1913c) and another four were collected in June 1913 in a sheep paddock 'about 4 miles' from Gracefield. 'I have offered a reward to all the children around the district so if they catch any I will be sure to get them' (Tunney 1913d). Boodies were reported near Cranbrook [*c.* 30 km south-east] in March 1915 (Tunney 1915), but the WA Museum had no funds available to purchase further specimens owing to the Great War.	Tunney (1913b, 1913c, 1913d, 1915)
1914, Gracefield	Numbats *[M. fasciatus]* 'are about extinct in this part. I have only seen one during the last couple of years around this locality. All the smaller marsupials seem to be getting very scarce, even the Phalangers *[Trichosurus vulpecula]* are scarcer now than when they were being trapped several years ago [1909-10]'.	Tunney (1914)
c. 1915, near Pingelly	About 4 years ago 'mortality amongst opposums *[T. vulpecula]* existing here'.	Tow (1919, p. 44)
c. ?1916, ?Wilson Inlet district	'For some obscure reason, the ring-tailed possum *[P. occidentalis]* has become very scarce in the south coastal districts, in haunts where ten or twelve years ago [i.e. 1914-16] it was plentiful enough. At that period it was quite as common as its relative the grey. But now it is seldom to be seen'. Whitlock, a much travelled ornithological collector, is probably referring to the Wilson Inlet district, where he resided from 1905 to *c.* 1924 (Abbott 2000b).	Whitlock (1926, p. 40)
Before 1919, south Wandering Road, Pingelly district	'Boody rats *[B. lesueur]* & Kangaroo ditto *[B. penicillata]* have entirely disappeared'.	Kemp (1919, p. 63)
Before 1919, Albany district	'some years ago the wallabies & much small ground game died out. Boodie Rats *[?B. penicillata, ?S. brachyurus]* suffered most – they are very scarce here yet '.	Linton (1919, p. 40)
1919, Deepdene near Karridale	'Here, neither rats *[B. penicillata]* or ringtailed opossums *[P. occidentalis]* are as numerous here as a few years ago, – one rarely sees one now especially the ringtailed opossum - while 8 years ago [1911] I could, in an hour get a dozen at any time, out of the blackboys'.	Allnutt (1919, p. 31)
Early 1920s, near Boolading	*B. lesueur* warrens appeared in 1926 to have been recently occupied but no animals were seen. Early settlers stated that they had disappeared suddenly in the early 1920s.	N. Rajander, b. 1918, pers. comm.
Well before 1930, near Latham	'At one time possums *[T. vulpecula]* and boodie rats *[B. lesueuri]* were very common, but they have long disappeared, the warrens of the latter now being the homes of rabbits and stray cats'.	J.H. Turner in Glauert (1930c, p. 36)

collecting effort or technique, as the same party experienced no difficulty in securing many similar species in north-east Queensland in 1913-14 (Lönnberg 1916).

On Barrow Island in 1918, 'wallabies and bandicoots' were noted as 'very plentiful', with the latter recorded as 'quite a nuisance at my camp' (Whitlock 1919, p. 241). These statements should be contrasted with observations made on the mainland by Whitlock (1910, p. 204), cited above.

In 1920 the American collector Charles Hoy twice visited jarrah forest east of Perth but obtained no mammals. He then spent 40 days in the Margaret River district and collected numerous specimens of *T. vulpecula*, *P. occidentalis*, *B. penicillata* and *S. brachyurus* (Short and Calaby 2001, pp. 543-4). This conforms with contemporary observations made in the region between Margaret River and the lower Blackwood River by Perry (1971), but not with those of Allnutt (cited in Table 2) or of Carter and Woodward (cited in Table 3).

Observations of dead quokkas *[S. brachyurus]* in swamps in the early 1920s (G. Gardner in How *et al.* (1987, p. 565) precede the establishment of the fox in Northcliffe district. These dead animals therefore cannot represent surplus killing as suggested by Short *et al.* (2002).

Skeletal remains of rabbits, house mice and numerous native species (e.g. *Phascogale calura, Parantechinus apicalis, Perameles bougainville, Trichosurus vulpecula, Bettongia penicillata, Leporillus apicalis*) have been found in superficial cave deposits at Peak Charles (How *et al.* 1988, p. 82). The rabbit was reported from this area in *c.* 1898 (Abbott submitted.). However, deposits in which bones of rabbits and native mammals both occur may have been mixed with older deposits, as bones of *Sarcophilus harrisii* and *Thylacinus cyanocephalus* are sometimes present (Baynes 1987, p. 139). For this reason, I have not included this type of record in Figures 2, 3 and 5.

Nearly all of the declines documented in this section are consistent with the dates of declines explicitly linked with disease (Figures 2 and 3).

Sometimes the lack of reference to declines helped to clarify the diffusion of the supposed epizootic. For example, near Roebourne 'wallaby' were 'very common' in the period from 1873 to 1888 (Anon. 1888).

Species affected by disease

Most records of species decline explicitly (though speculatively) linked to disease were of the most conspicuous species, namely *Trichosurus vulpecula, Bettongia lesueur, B. penicillata, Setonix brachyurus, Pseudocheirus occidentalis*, and *Myrmecobius fasciatus*. There were also numerous records of early declines of these species without them being linked explicitly to disease. A few records stated that 'all small marsupials', 'marsupials' or 'all rodents' had disappeared as a result of disease. Several other species were recorded as having declined because of disease, but only in one or two accounts: 'bandicoot' [probably *Macrotis lagotis*], dalgyte *[M. lagotis]*, tammar *[Macropus eugenii]*, 'snakes', and 'goannas'. A few sources particularly noted that red kangaroo *[Macropus rufus]*, Western grey kangaroo *[M. fuliginosus]* and euro *[M. robustus]* were unaffected.

Early local or regional declines of several species, before the rabbit or fox arrived, were noted in a few sources without disease being cited as an observed factor: *Lagostrophus fasciatus*, *Lagorchestes hirsutus*, *Onychogalea lunata*, *Macropus eugenii, Dasyurus geoffroii, Macrotis lagotis, Isoodon obesulus, Chaeropus ecaudatus, Perameles bougainville* and *Phascogale* aff. *tapoatafa.* One report implied that 'rats, wallabies, mice' had disappeared.

My retrospective assessment of the degree of apparent immunity or innate resistance of mammal species in WA to the epizootic is summarized in Table 4. Although these categorisations are based on careful assessment of the information recorded above about species affected and how quickly species subsequently recovered their original geographical range, they are deductive, represent informed speculation, and should therefore be considered as tentative.

Persistence of populations in eastern WA, western Northern Territory and western South Australia

Species that declined (apparently affected by disease) in the western half of WA demonstrate widespread persistence to the east of the dashed line (identical to that in Figure 2) up to the 1930s-60s, as well as persistence on islands near Carnarvon and Onslow (Figure 5).

Discussion

Overall evaluation of the evidence for disease as a factor in faunal collapse

In this paper I have assumed that only one disease was involved in the early decline documented, based solely on the application of Ockham's razor (the principle that no more assumptions should be made than are necessary). It is not possible with the inexact descriptive data available to determine whether this disease was viral, bacterial, protozoan, or other.

The major difficulty with identifying a role for disease is that no information on the pathology of the infection is available. Koch's and Evans' postulates (Thrusfield 1995) remain untested, and thus the case for disease as a critical factor cannot be established conclusively on the material available. Although the evidence available about the influence of disease on the mammal fauna of WA is circumstantial and anecdotal, and it is recognised that finding disease in a dying animal does not mean that disease is the cause of death, there are a large number of independent reports of decline stated to be linked to disease. This weight of evidence is consistent with a hypothesis that disease played a significant role for in the early depletion of the WA mammal fauna. I concur with Freeland (1993), who noted that the 'old reports of diseases and epidemics among our native fauna…cannot and should not be dismissed as inconsequential anecdotes'. In addition, most of the reports are independent and free of collusion, as many recorders would not have known of other reports.

Table 4. Hypothetical assignment of native terrestrial mammal species (excluding bats) in Western Australia to various categories of resistance to the epizootic disease discussed in this paper. Species are listed according to the sequence of How *et al.* (2001).

Species showing			
no apparent immunity	partial apparent immunity		total apparent immunity or no apparent contact with disease
	weak	strong	
Sminthopsis psammophila	*Dasycercus cristicauda*	*Antechinomys laniger*	*Tachyglossus aculeatus*
Isoodon auratus	*Dasyurus geoffroii*	*Phascogale* sp. n. aff. *tapoatafa*	*Antechinus flavipes*
Chaeropus ecaudatus	*Dasyurus hallucatus*	*Isoodon obesulus*	*Dasykaluta rosamondae*
Perameles bougainville	*Parantechinus apicalis*	*Macrotis lagotis*	*Ningaui* (3 spp)
Perameles eremiana	*Phascogale calura*	*Setonix brachyurus*	*Planigale* (2 spp)
Bettongia lesueur	*Sminthopsis ooldea*		*Pseudantechninus* (4 spp)
Potorous platyops	*Myrmecobius fasciatus*		*Sminthopsis* (11 spp)
Potorous gilbertii	*Bettongia penicillata*		*Isoodon macrourus*
Lagorchestes hirsutus	*Onychogalea lunata*		*Macrotis leucura*
Lagostrophus fasciatus	*Trichosurus vulpecula*		*Notoryctes* (2 spp)
Leporillus apicalis	*Pseudocheirus occidentalis*		*Lasiorhinus latifrons*
Leporillus conditor	*Pseudomys nanus*		*Lagorchestes* (2 spp)
Notomys amplus	*Pseudomys occidentalis*		*Macropus* (7 spp)
Notomys longicaudatus	*Pseudomys shortridgei*		*Onychogalea unguifera*
Notomys macrotis	*Rattus tunneyi*		*Petrogale* (5 spp)
Pseudomys desertor			*Cercatetus concinnus*
Pseudomys fieldi			*Tarsipes rostratus*
Zyzomys pedunculatus			*Conilurus penicillatus*
			Leggadina (2 spp)
			Melomys burtoni
			Mesembriomys (2 spp)
			Notomys (2 spp)
			Pseudomys (7 spp)
			Hydromys chrysogaster
			Rattus (2 spp)
			Zyzomys (2 spp)
			Canis lupus
(18 species)	(15 species)	(5 species)	(66 species)

Particular features of the decline that favour disease as the primary factor are the suddenness and localised nature of its early appearance, the large area rapidly affected in an identifiable geographical pattern, and its variable impact on species across a broad range of families. A predator, such as the feral cat, should have taken most or all similar-sized prey species in the same genus (e.g. *Notomys, Pseudomys*) in a particular region, otherwise it is difficult to understand why impacts have been highly selective.

Although the decline of 'the small furred animals' in the upper Murchison was linked to drought in 1891 (F. Wittenoom in Lefroy 2003, pp. 38, 41), this is unlikely to have been the first drought in the region. Moreover, the years 1893, 1897 and 1900 had above average rainfall, and animals should have bred up again. If drought were the primary factor, declines should have been reported in the inland parts of other regions of Australia before the cat and fox established. Furthermore, recurrent drought has been a feature of the Australian environment for millennia, and it is difficult to explain why drought should suddenly cause such irreversible decline.

Enervation by drought and nutritional stress may have contributed to the more rapid spread and higher impact of the disease in those parts of WA experiencing low average annual rainfall (cf. Gortázar *et al.* 2006). The aftermath of disease – small, disjunct populations - may have then been intensified by feline predation.

Origin and pattern of spread of disease

The geographical spread of all dated records of early declines of native mammals, particularly those in which disease was implicated, clearly indicates that the decline

began in the north (Figure 2). Its origin is from the coast between Geraldton and Onslow, with Shark Bay most likely as diffusion from this district best fits the dates of declines recorded near Geraldton, Carnarvon and Onslow. The dashed line in Figure 2 represents the limit of the epizootic inland, based on the dated records obtained. There is extensive information available that indicates that many of the species affected persisted to the east of this line until comparatively recent times (Brooker 1977; Burbidge *et al.* 1988; Kitchener and Vicker 1981; Heydon 1996: 458). If drought were the primary cause of this pattern, it is difficult to explain why species survived in these harsh desert regions.

Working back from the 1880, 1886, <1889 and 1894 dates recorded between Geraldton and Onslow, I deduce tentatively that the disease began in *c.* 1875 near Shark Bay.

The single point of origin and subsequent pattern of spread are suggestive of an introduced disease, which appears to have diffused slowly up to 1880 and then spread rapidly during the period 1881-1900 (Figure 4). The epizootic seems to have penetrated only parts of the lower south-west by *c.* 1907 (between Nannup and Bridgetown *c.* 1900-6, Bridgetown *c.* 1901 and 1907, Woogenilup 1904, Ludlow 1905, Deeside 1906). It seems that the least resistant species (those in column 1 of Table 4) declined immediately over their range. Then within a few years the species listed in column 2 of Table 4 were affected.

There are some unusual features of this epizootic. First, it affected a large number of species, across three orders and six families of marsupials, and in one family of rodents. Although the 1889-97 epizootic of rinderpest in Africa affected numerous species (Mack 1970, Scott 1981), all belong to the one order (Artiodactyla). However, rabies affects species across three orders and four families (Sikes 1981), and tularaemia affects mammal species across three orders and six families (Bell and Reilly 1981).

Second, the disease appeared to have caused the extinction of a number of marsupial and rodent species. Usually some individuals in a population survive and eventually the population recovers. Other examples of extinctions of mammal species caused by disease are few. That of *Rattus macleari* on Christmas Island by means of the introduction of trypanosomiasis by *R. rattus* is probably the most convincing, primarily because a pathologist visited the island two years after *R. rattus* was accidentally introduced in a cargo of hay (Pickering and Norris 1996). Other possible disease-linked extinctions relate to frogs and crayfish (Daszak *et al.* 2000, Schloegel *et al.* 2006) and Hawaiian birds (van Riper *et al.* 2002). It has been proposed that the widespread dissemination of European diseases amongst first nations around the world may have been preceded by hyper-virulent and –lethal diseases introduced by first peoples, facilitated by the convergence of 'interlocking conjunctions of novel carriers, diseases, and victims' (MacPhee and Marx 1997).

It is acknowledged that secondary factors such as drought and predation by feral cats may have interacted with disease to have caused extinctions in WA.

Third, most of the extinctions occurred in semi-arid and arid parts of WA. There is a recent parallel with rabbit haemorrhagic disease virus, which was more effective in WA in reducing numbers of the rabbit in areas with low average annual rainfall than in areas with high average rainfall (Bruce *et al.* 2004).

Finally, only one of the affected species eventually recovered, albeit partially: The possum *Trichosurus vulpecula* still occurs over much of its original range to the west of the line depicted in Figure 5, but very much reduced in abundance because of subsequent predation by foxes.

Possible source of the disease

The following conceptual model is proposed to take full account of the facts and interpretations documented above, as well as relevant weather, climatic and historical information.

European settlement of tropical WA did not take place until 1863, when pastoralists introduced sheep from south-west WA by boat to the Roebourne area. From 1857 pastoralists near Geraldton shepherded their sheep inland and gradually occupied the Murchison region in the 1870s. The practicality of droving sheep from Geraldton to the Ashburton River district via the Murchison district was first demonstrated (by E. Hooley) in 1866.

While the pastoral industry was still in its pioneering phase near Roebourne, settlers discovered in 1867 that pearling was a lucrative sideline. Aborigines were employed to beachcomb the extensive areas exposed at low tide for shell. These pearlbeds were quickly over-exploited, and shell was then sought in deeper waters by diving from luggers. This development led to abduction of Aboriginals, particularly women who were well suited to diving. This abuse came to the attention of the Governor, who in 1871 legislated to regulate the hiring and service of Aborigines engaged in the pearl shell fishery.

Pearlers then recruited Malay divers from Batavia for each season. In 1873 there were 46 vessels operating in Shark Bay, with 110 Malays at four camps along an 8 km stretch on the eastern shore of Useless Inlet (McCarthy 1989). In 1874, 225 Malays were employed. In 1875 the Dutch governor at Batavia enacted legislation to curb mistreatment of Malay divers. This action effectively terminated the importation of Malays (989 in 1875, 24 in 1877).

I hypothesise that the twice yearly voyages of luggers between north-west WA and south-east Asia provided the opportunity for the transport of disease-carrying animals, such as pets (monkeys, civet-cats, dogs and cockatoos), food (pigs, poultry), and stowaways (mice and ship rats), to the Shark Bay district. If wind-borne insects were the sole or main transmitting agent, it is difficult to understand why the disease did not arrive much earlier, and why the mammal fauna of the offshore islands was not affected.

An alternative model, based on the introduction of disease by steamships frequently visiting WA from tropical ports, does not fit the timing and pattern of the spread. The

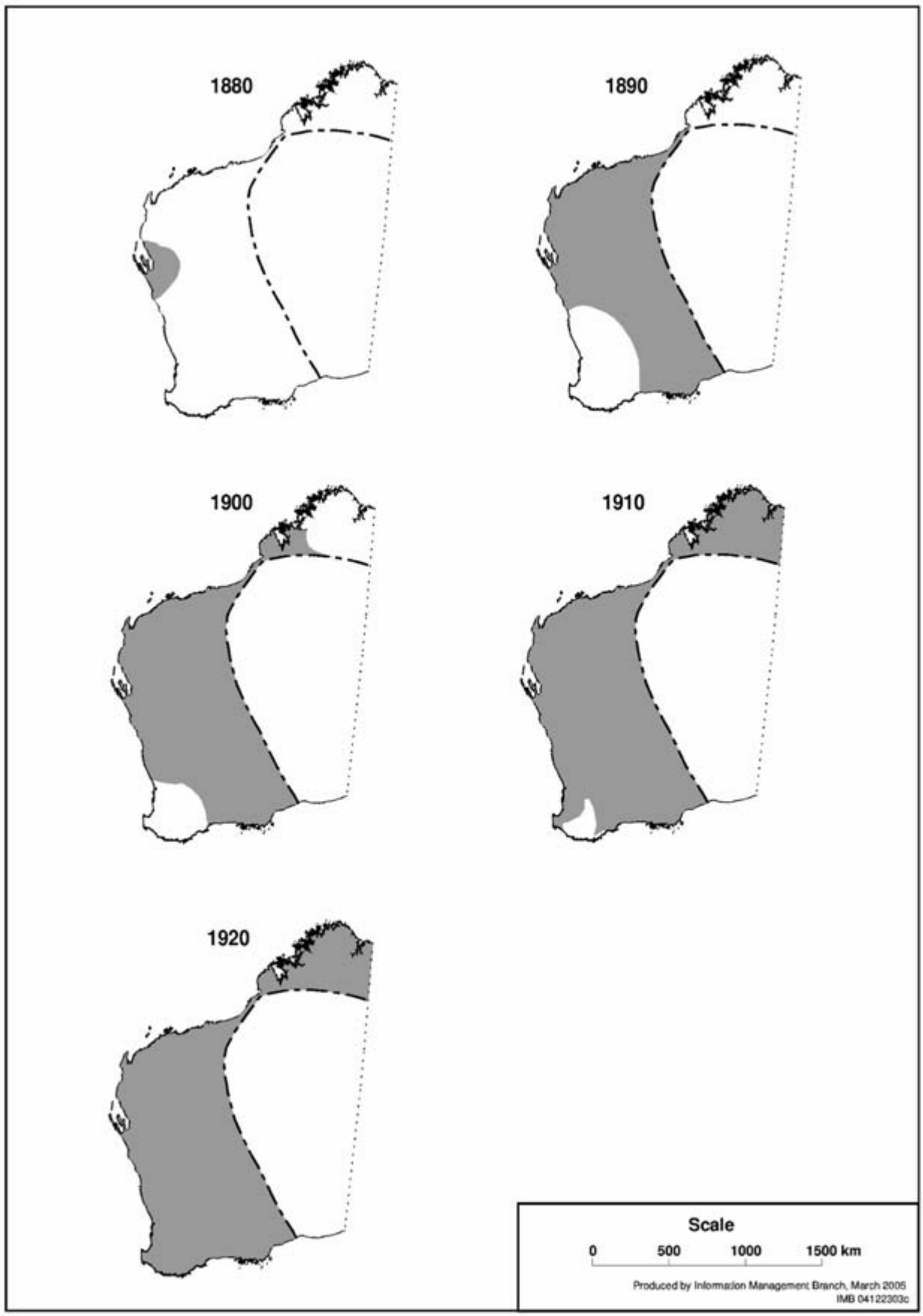

Figure 4. Hypothesised spread of disease, based on the information presented in Figures 2 and 3.

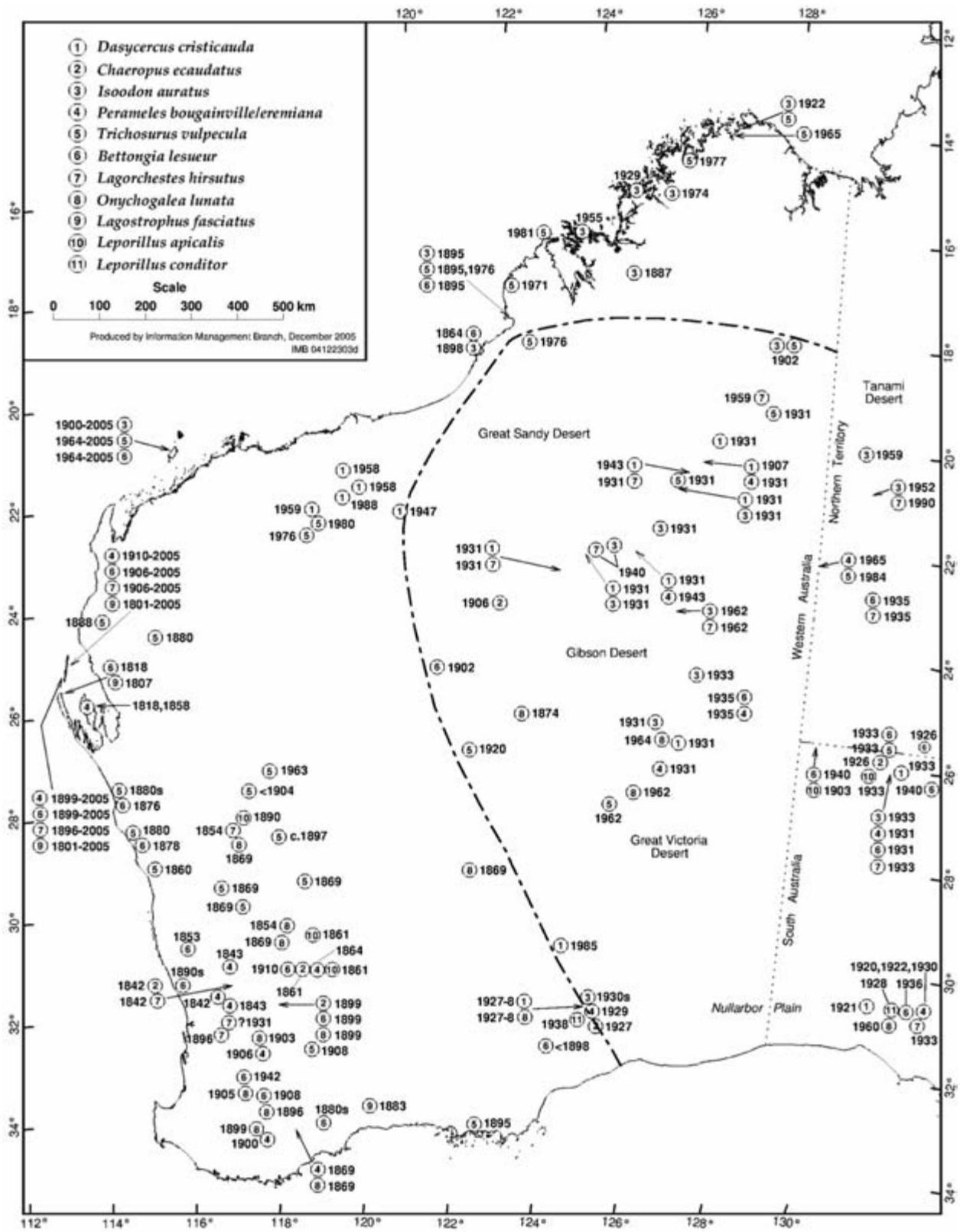

Figure 5. Dated distributional records of widespread mammal species with no or little apparent immunity to the epizootic disease discussed in this paper. (Sources: Abbott submitted, Baynes 1987, Boscacci *et al.* 1987, Brooker 1977, Burbidge *et al.* 1988, Bush 1879, Collett 1897, Copley 1999, Copley *et al.* 1989, David 1995, Donaldson and Elliot 1998, Froggatt 1934, How *et al.* 1991, Johnson and Southgate 1990, Kemper 1990, Kitchener and Vicker 1981, Martin 1864, McKenzie 1983, Ride and Tyndale-Biscoe 1962, Tonkin 2001, Youngson *et al.* 1981).

following information is extracted from Henderson (1977) and *The Victorian Express* newspaper, Geraldton (May 1884-December 1886). A steamship service to WA commenced in 1853, but it was direct from Britain and Albany was the only WA port of call. After the Suez Canal was opened, steamships called at Bombay and Galle before visiting

Albany. It was not until 1884 that a regular steamship route between Singapore, Batavia and WA commenced - with calls every two months at Derby, Cossack, Carnarvon, Shark Bay, Geraldton and Fremantle.

Possible mode of transmission of disease and the testability of the proposed mechanism

Assuming that the disease reached the mainland at Useless Inlet, how did it spread? I hypothesise that the mosquito species *Anopheles annulipes* and *Culex annulirostris* were the main vectors. Both species (probably species complexes) are common and widely distributed, and feed on a wide variety of animals (Liehne 1991). They are also known vectors of arboviruses (arthropod-borne viruses). They are known to use burrows as resting sites and can breed in temporary pools of water.

The role of these mosquitoes in spreading the myxoma virus to rabbit populations in Australia in the early 1950s provides a plausible analogy (Ratcliffe *et al.* 1952). Calaby *et al.* (1960) showed that effective and widespread epizootics of myxomatosis occurred in WA only in areas that had heavy summer, early autumn rains or above average extended spring rains. Between November and March each year several cyclones originate in the Timor Sea or off the north-west coast of WA. They then move in a south-westerly direction parallel to the coast and later in a south-easterly direction. Some move inland between Broome and Onslow and bring heavy and widespread rainfall. I hypothesise that those cyclones that occasionally cross the WA coast and become rain-bearing depressions would provide the climatic conditions for short-term breeding habitat for vector mosquitoes, and provide the conditions for a rapid increase in the food supply of native mammals. Increased populations of mammals (hosts) would then facilitate the spread of disease. Once temporary water bodies dried up, mosquitoes could have maintained some ongoing contact with carriers of disease through their sheltering in mammal burrows, and possibly through the presence of unaffected species acting as reservoir hosts (Gortázar *et al.* 2006). It seems more likely, however, that the disease would have failed to persist once vectors became scarce and susceptible hosts had died.

Reliable records of cyclone tracks exist only from 1909 (Lourensz 1981). Along the subtropical coast of WA they average 0.5 per annum and most commonly occur in March and February (Foley and Hanstrum 1994). Subtropical cyclones are sometimes captured by cold fronts approaching from the west and then cause severe dust storms on their northern side (and thus no breeding habitat for mosquitoes) and floods south of their track. This may explain the differential persistence of some native mammal species east and west of the line marked in Figures 2 and 5.

In the 1880s, agricultural and pastoral settlement did not extend far into the interior of WA, nor had the goldfields been discovered. Meteorological stations are therefore few and records earlier than 1890 are scant. Nonetheless, available rainfall summaries are comprehensive (Bureau of Meteorology 1929) and are suggestive of well above average rainfall, presumably caused by a cyclone, in February 1883 (Northampton), March 1886 (Esperance), February 1887 (Annean), January and February 1888 (Annean and Gabyon), March 1889 (Carnarvon and Annean), February 1890 (Murgoo), March 1892 (Boolardy south to Geraldton, Walebing and Katanning and east to Mangowine, Southern Cross, Bremer Bay and Esperance), March 1893 (Toodyay south to Wagin), March 1894 (Walebing south to Katanning and Bremer Bay and east to Kellerberrin and Esperance), March 1896 (Yatheroo east to Lawlers and Kalgoorlie and south to Kojonup), March 1904 (Beverley south to Kojonup), March 1907 (Kojonup), and March 1911 (Kojonup).

Although rats, mice, fleas, ticks and flies are other possible vectors, the persistence of many native mammal species in the WA deserts (east of the dashed line in Figures 2 and 5) would not be expected if these species were carriers of the disease. *Rattus rattus* and *R. norvegicus* are unlikely to be directly involved in the inland spread of the disease as neither species occurs in the deserts. *Mus musculus* is likely to have been present in the WA deserts by 1890, as it was identified by a scientist as present near Alice Springs in 1895 (Mulvaney *et al.* 2000) and noted at Kanowna in 1893 (Uren 1948, p. 123), at Wiladdie in 1893 (Bridge 1996, p. 55), near Norseman in 1904 (Whitlock 1937), and at Southern Cross, Kurrawang, Laverton and upper Gascoyne in 1905 (Shortridge 1936). It is difficult to conceive of what barrier would have prevented introduction of disease into the deserts if house mice were the primary agent. Flies are widespread because of the presence of dung and carrion. They occur widely in deserts, and some species show annual movements into south-west WA (Matthiessen 1983). If flies were an important vector, disease should have spread much sooner throughout the entire south-west of WA. If fleas, lice or ticks were major vectors, the disease should have spread much more slowly because these arthropods cannot fly and rely on body contact with host animals in order to disperse.

Could livestock and domestic animals have been carriers of the disease? This proposition cannot be decisively rejected but available information is inconsistent with it. Livestock were first brought to WA from Sydney (1826), Britain and Capetown (1829), Java (1829), Timor (1831), and India (1838). It is clear from Figure 2 and Figure 3 that the disease did not enter WA from the major southern ports that were established by 1880. These were the major portals of entry of livestock (sheep, cattle, goats, horses, pigs) and domestic animals (cats, dogs) from 1826 (Albany), 1829 (Fremantle), 1841 (Bunbury) and 1864 (Esperance).

Camels, introduced in 1883 (Gascoyne region), are a possible carrier or vector, but large numbers were not imported until 1892 and 1894 in order to service transport requirements of the newly discovered goldfields. Many camels imported from India had mange (1895 – Thompson 1993, p. 31) and arrangements were made to quarantine animals for 40 days (Stock Department 1897). No mortality was reported.

An Act to prevent the spread of the infectious disease scab (mange) in sheep was legislated in 1844, more than 10 years after the accidental introduction of scab from Van Diemen's Land (Tasmania). Imports of diseased cattle were first regulated in 1865 by an ordinance, which served

to prevent the introduction of infectious or contagious diseases. Regulation of the importation of sheep and pigs occurred in 1873, and these regulations were extended in 1879 to horses, goats, mules, donkeys and dogs. Camels were included in 1885.

Exotic pets such as monkeys are possible carriers. The earliest records found of pet monkeys in WA are: 1858, one on board HMS Herald, which spent 3 months surveying Shark Bay (David 1995, p. 303); early 1870s, at Perth (Adam 1942, p. 15); 1886 at Minilya River (Gunning 1952, p. 96); and 1888 at Cossack (Owen 1936, pp. 39-40). A bear was present at Cossack in 1887, as it escaped from its box during landing (Anon. 1887).

Animals in travelling circuses and associated menageries are considered to be improbable carriers. The earliest records of exotic circus animals in WA are of three tigers, one panther, one elephant, one gazelle, several peccaries, and *c*. 50 monkeys in 1886 (Anon. 1886a; Anon. 1886b), one baboon in 1887 (Carter 1987, p. 57), bears and monkeys in 1896 (Honniball 1968; Flynn 2002, p. 115), and one lion in 1897 (Anon. 1897), all in the south of WA. Circuses would not have been a paying proposition until the 1890s, when the population of WA quadrupled following the discovery of gold, and a rudimentary railway system (opened in 1889, linking Perth to the then major port of Albany) was expanded in 1896 to the goldfields at Kalgoorlie.

The protozoan *Toxoplasma gondii* may have caused declines of some mammal species (Freeland 1993). The mechanism suggested is that animals come into contact by eating herbage contaminated with the faeces of feral cats or by eating animals containing oocysts. However, if cats were responsible, why did declines to the west of the WA deserts occur decades before those in the deserts, as shown by comparison of Figures 2 and 5? Information available on the colonisation of WA by cats (Abbott 2002) does not support this hypothesis. Moreover, a comprehensive sampling program in WA detected *T. gondii* in only one of 11 native mammal species, and only at one locality of the eight sampled. *T. gondii* also had a low prevalence in feral cats (Adams 2003). Wild populations of two other native mammal species had previously been shown to have low prevalence of *T. gondii* in south-west WA (Jakob-Hoff and Dunsmore 1983).

The additional hypothesis that cats in settled parts of WA were kept in check by secondary poisoning from eating prey that ate *Gastrolobium* foliage or seeds (Short 2004) would not explain the earlier decline of native mammal species north of Swan River than south of Swan River. In the 1890s, little clearing of land had taken place north of Swan River. There is also evidence that where foxes have been controlled in jarrah forests lacking any significant presence of *Gastrolobium* species, re-introduced *Bettongia penicillata* have persisted in the presence of feral cats (de Tores *et al*. 1998). In addition, poison peas have a patchy distribution over many south-west landscapes (Havel 1975). It is difficult to see why continual replenishment of feral cats from farms around Dryandra and Perup would not have depleted populations of native mammals over a relatively short period.

Finally, the disease may have been introduced deliberately in an attempt to control 'vermin', i.e. the proliferation of kangaroos, wallabies and other marsupials after settlement by Europeans. This increase followed from lower populations of Aborigines, once influenza, smallpox and measles reached WA. This possibility is not unprecedented - in Queensland, the Government bacteriologist attempted to exterminate flying foxes (Pteropodidae) with chicken cholera (Anon. 1898a).

Inferred ecosystem impacts of disease

The extinction or contraction in geographical range of many mammal species should have disrupted some important ecological processes. The demise of the 'ecosystem engineer' species *Bettongia lesueur* and *Macrotis lagotis*, which create large burrows in the soil, should have altered infiltration of surface water, increasing runoff and erosion. This function was, however, partially restored by the establishment of the rabbit in the period 1894-1930 in much of WA. Even species that dig many small holes seeking food (e.g. *B. penicillata*) are able to increase water infiltration (Garkaklis *et al*. 1998).

The extinction and decline of many native species of rodents which harvested seeds should have led to increased germination of harvested species, perhaps leading to plant successional changes over large scales. The establishment of the house mouse *Mus musculus* in the period 1830-90 may have, however, offset this to some degree. Nonetheless, *B. lesueur* and *B. penicillata* were effective dispersers of seed of *Gastrolobium* spp. and *Santalum acuminatum* (Christensen 1980b; Leake 1961, 1962; Murphy and Garkaklis 2005; Peacock 2003: 28) and their remarkable contraction in range should have impacted on the population ecology of these plant species.

Extinction of the fungivorous *Potorous platyops* and marked decline in the distribution of *P. gilbertii* and *Bettongia penicillata* are likely to have impeded the dispersal of spores of mycorrhizal fungi (Lamont *et al*. 1985), with subsequent detriment to plant species dependent on this symbiosis. Drummond (1843) noted that large numbers of fungi were eaten by 'almost the whole of the marsupial animals…99 out of every 100 are eaten by these creatures. So assiduous are they in watching them that of several sorts which are common in the ground they rarely allow them to appear above the surface'. Reductions in marsupial diversity should have altered the ecology of fungal species.

Nutrient cycling should also have been affected by reductions in the distribution and abundance of mammals. The diggings of *B. penicillata* increase the leaching of soluble nutrients (Garkaklis *et al*. 2000). The decline of the herbivorous, arboreal possums *Trichosurus vulpecula* and *Pseudocheirus occidentalis*, with their small home ranges, should have appreciably reduced the return of nutrients from young foliage to the ground via defaecation. One interviewee (M. Letch) suggested that the local disappearance of *T. vulpecula* had increased the abundance of mistletoe, so that jam, *Acacia acuminata,* now lived less than *c*. 20 years. This is consistent with evidence from elsewhere in Australia that possums can suppress or eliminate mistletoe populations (Reid 1997).

Disease as a possible explanation of other declines

One of the indicators of the usefulness of a new theory is the extent to which it illuminates a range of poorly understood phenomena and refines or even subsumes existing concepts. The following is a brief list of possible examples deserving of more detailed analysis:

- The failure of the two possum species present in south-west WA forests to recover fully from trapping in the context of a great abundance of available hollows and ongoing control of foxes (Abbott and Whitford 2002). Is enzootic disease now the critical limiting factor? Examples of possums with substantial loss of hair, diseased skin and poor body condition are only occasionally encountered (A. Wayne, pers. comm.).
- The wambenger *Phascogale* aff. *tapoatafa* is often brought to the attention of rural residents of south-west WA by domestic cats. Yet, in the forests its distribution is highly localised despite an abundance of suitable hollows (Abbott and Whitford 2002). Was its disappearance from both unlogged and logged forests during a detailed study (Morris *et al.* 2000) related to disease? This species is currently recorded frequently in these and surrounding forests (I. Wilson, pers. comm.).
- The puzzling persistence of *Bettongia penicillata* in three populations (Perup, Dryandra and Tutanning) up to the 1970s has been associated with the occurrence of poison peas (*Gastrolobium*) conferring a significant degree of control of rabbits and domestic stock (Calaby 1971) or fox populations (Christensen 1980a). Alternatively, did these particular populations survive because a particular genetic composition conferred high immunity to disease?
- The ghost bat *Macroderma gigas* has declined in WA (Douglas 1967). Its original breeding/roosting sites (caves) still exist (Bridge 1975) and have increased with settlement (abandoned mine shafts). This species is the only bat in WA that eats small mammals. Was its decline in south-west WA linked to accidental exposure to disease?
- The persistence of small wallaby species on Bernier, Dorre and Barrow Islands is invariably attributed to the absence of foxes and feral cats. However, did the remoteness of these islands (45-55 km from the mainland) prevent the epizootic from reaching them? It is relevant to note that *Bettongia lesueur* disappeared from Dirk Hartog Island sometime after 1818. Its extinction there is usually attributed to sheep and feral cats. However, the island is inshore (being only 1.6 km from the mainland) and it is possible that the epizootic reached the island directly via infected house mice, ship rats, or mosquitoes.
- The potoroo *Potorous gilbertii* was recorded in the 1840s as inhabiting the same vegetation as the quokka *Setonix brachyurus* (Gould 1863, p. 288). Yet, the potoroo persists in only one small population in contrast to the quokka. Is this due to a difference between these species in natural resistance to this disease?
- The Critical Weight Range concept, which links extinction and declines of mammals to body size (Burbidge and McKenzie 1989), overlooks likely differences in susceptibility of species to disease. Most affected species are rodents, bandicoots, possums or small wallabies, and the link with body weight appears coincidental (Freeland 1993). Smith and Quin (1996) concluded that body size alone is not a good predictor of decline in conilurine rodents.
- The study of bones accumulated in owl roosts in caves has indicated the recent occurrence of many of the mammal species that underwent early decline. Few of these deposits have been dated, but there is a presumption that declines commenced in past arid periods and that some species were rare by the time of settlement by Europeans (Main *et al.* 1959; Lundelius 1960; Baynes 1979). The hypothesis advanced in this paper instead states that these declines began more recently, in the period 1875-1925.

Applicability of the disease hypothesis to eastern Australia

Elsewhere in Australia, disease has been suggested as contributing to early declines of native mammals (e.g. Anon. 1861, p. 113; 'Drover' 1900, p. 5; Batey 1907, p. 70; Wood Jones 1923; Le Soeuf and Burrell 1918; Le Soeuf 1923; Froggatt 1927; Finlayson 1934; Guiler 1961; Wakefield 1974; Rolls 1984, p. 365; Smith *et al.* 1993; Low 1999; Gordon and Hrdina 2005) or is implied (Parker 1905; Ratcliffe 1971; Fairbairn 1983). Whether these references to disease are related to the disease that swept through WA is not known.

It is now of course too late to obtain information from early settlers in eastern Australia, but systematic searches are needed of government files, early newspapers and books written by early settlers in order to assemble information comparable to that presented in Table 2.

I offer the following credible mechanism to guide this research. The discovery of gold in New South Wales and Victoria in 1851 resulted in a remarkable increase in population, as men arrived from Europe and North America to try their luck. The marked increase in shipping arrivals at Sydney and Melbourne increased the opportunity for animal disease to be introduced (via dogs, cats, rats, mice etc). The Murray and Darling Rivers were first penetrated by commerce in 1853, when paddle-steamers transported food and equipment from Adelaide to pastoral properties upstream and brought back their wool for export (Lewis 1918).

These inland river systems have experienced six floods between 1852 and 1877 (Russell 1887), before rabbits colonized, and thereby provided the opportunity for transmission of introduced disease by mosquitoes. The mammal fauna of the lower Murray and Darling Rivers was still intact in 1856-7 (Krefft 1866). Major flooding was first reliably recorded in Lake Eyre in 1885 (Kotwicki 1986), six years before rabbits colonized. The mammal fauna of Cooper's Creek was still intact in the early 1880s (Sanger 1884).

Camels imported from Karachi to South Australia in 1866 developed mange and 70 animals died, apparently from surra (trypanosomiasis) (Cleland 1912). However, it seems unlikely that this disease was spread (by biting flies) to marsupials, horses or dogs, as there were no reports of mortality of horses and dogs, for which surra is highly pathogenic (Seddon and Albiston 1966).

Contribution of other factors prior to the incursion of rabbits and foxes

In this study I confined my attention largely to the period before rabbits and foxes established locally or regionally in WA. Therefore, logically, these two factors cannot have contributed to early declines of native mammal species. Experienced observers, early settlers and collectors active in the period 1889-1920 suggested that the following factors were possible causes of early declines of species of native mammals in WA: grazing by sheep (Bain 1975, p. 408; Carter 1987, p. 7); drought (Forrest 1896, p. 130); feral cats ('twice as big as the ordinary cat, and larger than they are anywhere else in the world'), dogs, disease, and shooting (Anon. 1907, p. 7, based on an interview with Shortridge several days before he departed from WA); burning, sheep grazing and clearing (additional factors included in Shortridge 1910, pp. 818-9); and the house mouse (included in Shortridge 1936, p. 748).

Charles Hoy, who visited WA in 1920, emphasised 'fierce bush fires that rage almost every summer…burn out all the under-growth' and feral cats that are 'not uncommon and reach immense sizes' (Short and Calaby 2001).

In his letters to the Curator of the WA Museum, John Tunney (b. 1871) frequently expressed his concern that the Museum Committee would think his collection meagre and by implication would reflect adversely on his competence and perseverance. For example, 'I am sorry to say I am not proving a successful collector but I have done my best. I suppose the Committee are far from satisfied and I am also dissatisfied with myself' (26.3.1896, Carnarvon). The fact that no small or medium-sized mammals were seen or captured must have perplexed Tunney, yet his letters (1896-1903) contain no speculations as to why, except for the following. When at Yeeda station, Fitzroy River, Kimberley, he was told that hundreds of cats live on the river and kill all the small game (8.9.1896). Nevertheless, Tunney did subsequently observe and record disease reducing populations of several species in south-west WA (Tunney 1913a).

Bruce Leake [b. 1880] did not think that drought or sheep grazing were instrumental in the decline of mammals in Kellerberrin district (Leake 1962, p. 43), although he did note that many native mammals 'practically disappeared' during a dry period between 1895 and 1902 (Leake 1961, p. 39). *Macrotis lagotis* returned in 1918 'after three very wet years' (Leake 1962, p. 50) and *Phascogale* aff. *tapoatafa* returned in 1917-18, both wet years (Leake 1962, p. 51). He also mentioned the need to poison *Bettongia lesueuri* because they ate wheat germinants (Leake 1962, p. 45), without drawing a conclusion that poisoning may have contributed to the disappearance of pest species that ate grain. Leake regarded disease as doubtful because it came from the unsettled interior instead of from the west (Leake 1962, p. 44). His last words on the topic were, however, definite and unequivocal: 'Civilisation advances bringing with it virus diseases, which decimate nearly all our small animals' (Leake 1962, p. 52).

Job Haddleton [b. 1879] suggested that agricultural development 'cleared out most of their [i.e. the marsupials'] living places' and that 'most of these small animals were destroyed in the early days when the farmers used to s[o]w poisoned wheat to poison the ringneck parrots that used to be very destructive on the wheat crops' (Haddleton 1952, pp. 96, 100). He did not mention disease.

This diversity of contemporary opinion foreshadows the great variety of theories proposed by later naturalists and scientists in Australia (e.g. Abbott 2001a discusses 15 factors), and reinforces the tendency mentioned in the Introduction of emphasising those obvious factors visible at local scales (Abbott and Christensen 1995). The exaggerated impression that fire made on the two visitors (Shortridge and Hoy) is understandable, but I agree with Short (2004) that this factor cannot explain early declines of mammals. Nor can the scale of clearing on farmland (little of the wheatbelt was cleared before 1915) or the low density of sheep in pastoral country (with few subdivision fences before 1900) logically be major factors (Abbott 2004; Short 2004).

Validity of anecdotal information

Anecdote normally contributes little or not at all to science. Thus, in ecology most practitioners rely on the traditional reductionist techniques of measurement and experiment with replication and a control. During the last decade or so, the science of ecology has become more pluralist, with wider acceptance of other sources of knowledge (Robertson *et al.* 2000). These diverse perspectives include interviews with oldtimers, written records, official archives, adaptive management, and monitoring (regular trapping or observation of populations). All techniques have limitations. For example, statistically well-designed experiments allow strong inference about processes at local scales but are uninformative about landscape-scale processes and historical change. Oral (Aboriginal and settler) and written information is subjective and selective but can be detailed and based on long-term experience and observation and founded on many sources.

Much of the material presented in Tables 2 and 3 represents first-hand observation of what clearly was a spectacular, unexpected and permanent decline of conspicuous and common mammal species. Such clues should not be rejected out of hand on the basis of their failure to satisfy experimental and statistical rigour. Nor should such information be accepted uncritically.

Implications for conservation management

Vigilant quarantine is essential to minimise the risk of animal diseases being introduced to WA. It is important that quarantine policies and laws are seen as legitimately contributing to the protection of the biodiversity of WA, and not as a convenient barrier to trade in order to protect local industries. They should be strengthened and not

relaxed. The illegal introduction of exotic animals is an ongoing issue – e.g. a monkey was reported in December 2003 in coastal sandhills *c*. 25 km north of Geraldton (K. Marshall, pers. comm.).

The role of disease in affecting mammal species in Australia, apart from livestock, pets and pests, is not well investigated. Ecologists have tended to neglect disease in comparison to competition, predation and drought. The bubonic plague epidemic that struck Sydney in 1900 killed wallabies, kangaroos, possums and quolls in the zoo (Curson and McCraken n.d.). In Australia, evaluation of the importance of diseases in wild populations has scarcely proceeded past the necessary first step of compilation of lists of diseases reported (e.g. Arundel *et al.* 1977; Munday 1988; Turni and Smales 2001; Whittington 1992). The highly accidental nature of the introduction of exotic diseases has also hampered study (Dudley 2004). It is also difficult to obtain 'definitive proof' that introduced pathogens have caused historical extinctions (Daszak and Cunningham 1999).

At present, the ongoing conservation of several mammal species is highly dependent on a few island populations, especially Barrow, Bernier and Dorre Islands. Current thinking places great importance in keeping these islands free of cats and foxes. However, attention should also be directed to prohibiting any unauthorised landings on these islands. Improved protection of the WA maritime border from entry of diseases through illegal immigration from Asian ports is also required. Current attempts to repatriate animals from the Shark Bay islands to suitably managed parts of mainland WA should, if successful, reduce the reliance on these islands for conservation. This, together with translocations to suitable islands without native mammals (Abbott 2000a), should help minimise the risk of further extinctions.

Further research

Some of the inferences developed in this paper should be independently testable, for example detection of antibodies or subliminal life-long carriers by serological analysis of surviving populations, or molecular study of material obtained from specimens preserved in museums. In several decades all surviving issues of WA newspapers published since 1830 should have been electronically scanned and put into an archive searchable by keyword. This should generate any overlooked records of disease and mammal declines, both of which can be used to refine historical conclusions drawn in this paper. A systematic search of early records from South Australia, Victoria, New South Wales and Queensland is needed to establish in a more comprehensive way the continental extent of mass mortality of native animals.

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