The potential contribution of kurī (Polynesian dog) to the ecological impacts of the human settlement of Aotearoa New Zealand

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Abstract

The pre-human Aotearoa New Zealand ecosystem was dominated by avian and reptilian species. Prior to first human settlement by East Polynesian colonists, the top predators were two giant raptorial birds. Aside from humans themselves, colonisation also resulted in the introduction of two novel mammalian predators into this naive ecosystem, the kiore (Pacific rat) and kurī (Polynesian dog). While the ecological impacts of kiore are relatively well understood, those of kurī are difficult to assess, and as such kurī have frequently been disregarded as having any meaningful impact on New Zealand's biodiversity. Here we use the archaeological and palaeoecological record to reassess the potential impacts of kurī on this ecosystem. We argue that far from being confined to villages, kurī could have had a significant widespread but relatively localised impact on New Zealand's avian, reptilian and marine mammal (seals and sea lions) fauna as a novel predator of medium-sized species. In this way, kurī potentially amplified the already significant impacts of Polynesian colonists and their descendants on New Zealand's ecosystem, prior to European arrival. As such, kurī should be included in models of human impact in addition to over-hunting, environmental modification and predation by kiore.

Keywords: birds, diet, dog, habitat disturbance, hunting, Māori, predation, Polynesia

Background

Isolated island ecosystems are evolutionary microcosms typically exhibiting high levels of faunal endemicity (Mendelson and Shaw, 2005; Shaw and Gillespie, 2016). They are also often the last places to have been colonised by modern humans, as recently as hundreds to a few thousand years ago (Wilmshurst et al., 2011; Hansford et al., 2021), at times of relative climatic stability (Wanner et al., 2008; Waters et al., 2017). In island ecosystems modern human colonisation is frequently associated with widespread faunal extinctions and environmental modification (Perry et al., 2014; Hansford et al., 2021; Louys et al., 2021; Nogue et al., 2021).

Aotearoa New Zealand presents a unique opportunity to test for anthropogenic impacts on insular biodiversity. Its flora and fauna were shaped by tens of millions of years of isolation and regular long-distance dispersal (Wallis and Jorge, 2018), and exhibit a range of island adaptions including gigantism, flightlessness or flight-reduced terrestrial lifestyles, and slow K-selected breeding strategies (Worthy and Holdaway, 2002). At the time of East Polynesian colonisation in the late thirteenth to early fourteenth centuries CE (Wilmshurst et al., 2008, 2011), the New Zealand fauna was dominated by birds ($\geq$ 217 species), reptiles and marine mammals, specifically pinnipeds (four species of seals and sea lions). The avian fauna ranged from extinct birds such as nine species of giant flightless moa (Dinornithiformes; Bunce et al., 2009) to medium-sized ground-dwelling taxa including moa chicks or juveniles, giant goose (*Cnemiornis* spp.), adzebill (*Aptornis* spp.), and several waterfowl (e.g. Finsch's, blue-billed, musk and pink-eared ducks, and poūwa swan), as well as extant terrestrial birds including takahē, kākāpō and kiwi (Worthy and Holdaway, 2002). Within reptiles, there were at least 110 species of Eugongylinae skinks and Diplodactylid geckos, seven Leiopelmatid frogs and one tuatara (*Sphenodon punctatus*) (Easton et al., 2017; Gemmell et al., 2020; Scarsbrook et al., 2021).

The arrival of Polynesians resulted in the widespread human-driven extinction of around 50% of the vertebrate biodiversity as a result of hunting (Anderson, 1989; Holdaway et al., 2014) and environmental modification (McWethy et al., 2014), in addition to biological turnover events (Rawlence et al., 2017), range-contractions (Salis et al., 2016), population bottlenecks (Rawlence et al., 2015), and significant changes in indigenous forest cover within a few hundred years of initial settlement (McWethy et al., 2014). Polynesians also introduced two exotic predators, the kiore (Pacific rat, *Rattus exulans*) and kurī (Polynesian dog, *Canis familiaris*) (Wilmshurst et al., 2008; Greig et al., 2018). Kurī were also a source of meat and industrial materials (e.g. kahu kurī dog skin cloaks, bone for tools and ornaments) for Māori, the direct descendants of those East Polynesian immigrants (Anderson, 1981; Anderson, 1989; Davidson, 1987; Hartnup et al., 2011).

Much archaeological and palaeoecological research has focused on the direct impacts of humans (i.e., hunting, environmental modification; Anderson, 1989; Holdaway et al., 2014; Perry et al., 2014; Nogue et al., 2021) and predation by kiore - the latter based on modern ecological (Rayner et al., 2007; Ismar et al., 2014) and palaeoecological (Wilmshurst and Higham, 2004; Wilmshurst et al., 2008) studies. In contrast, the potential impacts of kuri in particular on the pre-European contact ecosystem have largely been overlooked as they are difficult to assess, despite the potential of dogs to be a major novel predator in recently colonised ecosystems (e.g. Koungoulos and Fillios, 2020; Hixon et al., 2021). Fleming (1962) stated "*the simplest explanation is to attribute all late Holocene extinction to the profound ecological changes brought about by man with fire, rats and dogs*", while Anderson (1981; 1989) suggested kurī probably contributed to the extinction of moa. In contrast, Holdaway (1999) argued nearly all the known extinctions were due to people and kiore, and not kurī, which "*probably had little effect on the biota*". Worthy and Holdaway (2002) took this idea one step further, boldly stating "*the Polynesian dog can be exonerated: it was kept so close to camps that it is not a factor*".

Our aim is to discuss and reassess the potential ecological impacts of kurī on the pre-European New Zealand ecosystem, including their role in human-driven extinctions, and highlight future research directions that need to be addressed to fully understand the impact that dogs can have on insular island faunas.

Kurī (Polynesian dogs)

An investigation of the impacts of kurī on Aotearoa New Zealand's biota requires an understanding of kurī biology, behaviour and ecology. This is problematic, as by the mid-nineteenth century CE kurī were no longer identifiable as a distinct dog type in Aotearoa New Zealand, due to interbreeding and replacement by European dogs. Dogs were brought to Aotearoa New Zealand around the thirteenth century CE by East Polynesian migrants, the end point of a major trajectory of human colonisation of the islands of the Pacific. Dogs were successfully transported and established on many islands of the region during these migrations. Molecular genetic studies show that Pacific dogs possess a distinctive mitochondrial genetic signature, distinguishable from other lineages, most likely originating from mainland Southeast China (Oskarsson et al., 2012; Greig et al., 2018; Zhang et al., 2021). In the absence of extant populations, the bones, teeth and coprolites (i.e., desiccated faeces) of kurī recovered from archaeological sites now comprise a valuable source of information. Archaeozoological studies and emerging biomolecular techniques can provide data about kurī physical characteristics, diet, mobility, and genetic history. In addition to archaeological remains, there are numerous observations about kurī in early European historical literature, although most accounts focus on physical descriptions, sometimes with a brief comment about the uses of dogs by Māori (for a review see Colenso, 1877), rather than ecological information. In the absence of this type of information, modern studies of free-ranging dog populations and ethnographic data can assist with developing hypotheses for aspects of kurī behaviour.

Kurī feature in Māori mythology, oral histories and art forms, demonstrating their importance in Māori culture (Potts et al., 2013). Legendary kurī are associated with colonising voyages to New Zealand, historical events and the naming of landmarks. In everyday life kurī were kept as companions, watch dogs and hunting dogs, and as a source of meat and industrial materials (bones, teeth and pelts) (Davidson, 1987). Written descriptions in early European accounts tell of a small, fox-like dog, with pricked ears and a bushy tail (Colenso, 1877). Morphometric analysis of skeletal remains indicates an adult shoulder height of slightly under 40 centimetres, and a body weight of 13–15 kilograms (Clark, 1997). This suggests a body shape similar to a small border collie, but more robust and with shorter legs. There is very little geographic and temporal variation in kurī skeletal remains, suggesting that there was no deliberate selection for particular morphological characteristics, such as size, that can be observed in the skeleton (Clark, 1997), despite their importance as a source of food and raw materials. Information about kurī life history, such as reproductive behaviour is extremely limited. Kurī are thought to have reached sexual maturity around 6 to 8 months of age, similar to modern dog breeds (Clark, 1995).

It appears that sizable kurī populations were able to be sustained in early Māori settlements. The results of zooarchaeological analysis of faunal assemblages from early Māori archaeological sites such as Wairau Bar, Shag River Mouth, Kaupokonui and Houhora, for example, have documented substantial numbers of dog bones (Anderson, 1981, 1989; Greig et al., 2018). Some later Māori settlements dating from the sixteenth and seventeenth centuries also appear to have supported high numbers of kurī, for example, Kohika (Horrocks et al., 2002; Horrocks et al., 2003) and the Masonic Tavern site (Wood et al., 2016). During Captain Cook’s second voyage to New Zealand, while anchored in Queen Charlotte Sound, both he and the ship’s scientist Forster commented that they saw plenty of dogs, including those travelling with people in canoes (Colenso, 1877).

Dogs are omnivorous generalists, capable of consuming and surviving on a wide range of food types, ranging from human-derived garbage to animals that may be several times their body mass (Vanak and Gompper, 2009; Hughes and Macdonald, 2013,). Kurī seen by early European travellers were not restrained or tethered (Clark, 1997) and had the freedom to roam throughout settlements and scavenge for food. This freedom would have enabled kurī to forage beyond the close confines of Māori villages (contra Worthy and Holdaway, 2002). Nineteenth century Māori villages often were observed with fenced enclosures or houses to prevent entry by dogs and pigs (the latter introduced by Europeans) (Earle, 1832; Dieffenbach, 1843). Many travellers described 'wata' or 'fata', which were storehouses on poles or stilts several feet above the ground, used to store and protect food such as seed potatoes, or dried fish from roaming animals. Left-over food was kept between meals in baskets on poles, for the same purpose (Earle, 1832). Stages or platforms were also documented to keep important objects away from kurī and kiore (Best, 1916).

Macroscopic analysis of kurī coprolites from archaeological sites suggests a varied diet consistent with a range of faunal components commonly found in correspondingly dated Māori middens (rubbish heaps). Components include small bird, moa, fish, marine shell, as well as charcoal and other plant remains that often do not survive in middens (Clark, 1995, 1997; Irwin, 2004). A recent study of coprolites from the Masonic Tavern site in Auckland used both microscopic and ancient DNA methods, and identified fish, marine shell, charcoal, and wild and cultivated plant taxa (Wood et al., 2016). The contribution of faeces to the diet has also been noted for modern free-ranging dog populations (Butler et al., 2018).

To date, the only published evidence of kurī bones is associated with archaeological evidence for human activities rather than natural sites (e.g. caves, pitfalls, swamps, dunes), creating a taphonomic sampling bias in available data. It is not clear whether kurī formed feral populations, although this is a possibility. There are few truly feral self-sustaining dog populations in the world today, where dogs live in a wild state independently of people. One example is in Australia, where dogs with a similar genetic ancestry to kurī were introduced around 4,000 years ago and subsequently became the dingo (Smith, 2015). Dingoes are an apex predator, and their prey includes a variety of Australian biodiversity, including kangaroos, small mammals, birds, reptiles, fish, crabs, frogs, insects, and seeds, as well as introduced domestic species, including sheep (Smith, 2015). Kurī may have had a similar potential in New Zealand to form feral self-sustaining populations, particularly in warmer northern regions – indeed, recent feral dog populations were observed in Northland (Piper, 2021) and 'wild dogs' were observed subsiding on kakapo, weka and ground dwelling birds in the nineteenth century (Anderson, 1981). The large proportion of dog bones in 'natural' sites (i.e. no clear archaeological context) in northern New Zealand (Table S1) potentially supports this hypothesis (however, see *Breadth and intensity of impacts* below). Populations may have been at low abundance as seen with apex predators (Smith, 2015). Potts et al. (2013) raise the possibility that the monstrous or aggressive dogs in some Māori oral traditions may reflect concerns about kurī that had gone wild and beyond human control.

By the 1830s, with the introduction of European breeds to New Zealand, overall dog numbers appear to have increased to the point of being considered a nuisance. Dogs had been brought to New Zealand by Europeans as early as Captain Cook's voyages in the late eighteenth century (Clark, 1995). Hunting dogs in particular were subsequently introduced relatively quickly by sealers and whalers (Wakefield, 1845). Earle (1832) considered dogs to be the worst introduction by Europeans, due to their rapid increase and the injuries they caused to other animals. Packs of wild dogs present in the mid-19th century appear to be European dogs (e.g. Thomson, 1859) which in the South Island coincide with the arrival of flocks of sheep in central regions. Dieffenbach (1843) observed that a native dog could not bring down a sheep (presumably because of its small size), but that cross-breeds and introduced dogs would do so. By the mid-1800s, kurī were no longer recognisable as a distinct breed, having been subsumed within the burgeoning European dog population (Clark, 1995) through interbreeding and genetic swamping.

Potential impacts of kurī

Direct predation

Studies of free-ranging dog populations from around the world have identified the importance of food derived from human activities in the dogs' diet (Vanak and Gompper, 2009). This includes deliberate feeding, and scavenged food refuse (plants and animals), remains of livestock and other carcasses, and human (and potentially other dogs, and seal and sea lion) faeces. Some studies have documented dogs killing and feeding on wildlife, but as Vanak and Gompper (2009) point out these studies are generally focused on the effects of predation on the prey species, rather than the overall picture of dog foraging ecology. They argue that reliance on human-derived materials is typical, even when wildlife is also killed and consumed.

Even with a possible foraging focus on human-derived food, the presence of flightless or flight-reduced ground-living birds, lizards, and seals and /sea lions with no 'fight or flight' response in New Zealand is likely to have provided a tempting target for kurī. New Zealand birds evolved in the absence of mammalian predators, which hunt by smell. Instead, the top predators in the pre-human ecosystem were raptorial birds (e.g. Haast's eagle and Eyles' harrier) that hunt by sight. Consequently, many New Zealand birds have camouflage plumage (e.g. Rawlence et al., 2009) and freeze when confronted by predators (e.g. kākāpo). In addition, on predator-free islands flighted birds often spend a significant amount of time foraging on the ground (e.g. tīeke saddleback on Tiritiri Matangi Island, kōkako on Hauturu/Little Barrier Island, and kererū New Zealand pigeon on Kapiti Island; NJR and Alan Tennyson pers. obs.). Modern anecdotal evidence from single events suggests the potential severity of the impact of dogs on naïve avifauna. Taborsky (1988) documented the devastating consequences of a single unrestrained dog in the Waitangi State Forest, which killed at least 23 kiwi over a six-month period. The total number killed is thought to have been as many as 500, which represented half of the total population at that time. In Tasmania, a single attack in 2008 by a dog or dogs resulted in the death of 30 little blue penguins (Holderness-Roddam and McQuillan, 2014). Outside of canids, the introduction/translocation of novel mammalian predators to island ecosystems can result in the extinction of local burrowing seabird colonies (e.g. Tasmanian devil introduction to Maria Island; Lu, 2021).

The vulnerability of animals to predation may change throughout their lifetimes. Ground-dwelling kiwi are susceptible to predation by dogs across all life stages (eggs, chicks, juveniles and adults), however, a modern study of introduced mammalian predation of brown and roa great spotted kiwi suggests that the greatest predation of kiwi by dogs takes place on adult birds (McLennan et al., 1996). As with the Waitangi State Forest event, predation by dogs in the forest was found to be unpredictable and episodic, but with drastic results on the breeding population. The rate of dog predation on eggs and adult birds was also found to be much lower than that of chicks and juveniles, although the latter were decimated by mustelids (McLennan et al., 1996). In pinnipeds (seals and sea lions), attacks by dogs are common, even resulting in death (e.g. Boren, 2008; Department of Conservation, 2014; Houseman, 2020; Ker-Lazenby, 2021). While male kekeno fur seals, rāpoka sea lions and ihupuku southern elephant seals would no doubt have been outside the prey size range for kurī, pups and females (especially while nursing) would have been particularly vulnerable to predation. If a female sea lion is killed, it's unborn and dependant pups will also die. Modelling shows these slow-breeding pinnipeds could not withstand even low levels of subsistence hunting or predation resulting in their rapid extinction (Rawlence et al. 2016b; Waters et al., 2017).

As well as immediate fatalities, predatory behaviour can also result in chasing or colony disturbance or abandonment (especially for disturbance prone seabirds), survivable injuries or severe injuries that ultimately result in death sometime after the predation attempt. Studies have demonstrated the negative effects of survivable chasing events, such as behavioural changes and physiological stress (e.g. Lima, 1998; Clinchy et al., 2013).

While it has been hypothesised that kiore had the greatest impact on New Zealand's small avian (e.g. wrens; Tennyson and Martinson, 2007) and reptilian fauna, with human hunting initially focusing on the large megafauna (e.g. moa), it is probable that kurī filled the ecological niche of a predator of medium sized ground-dwelling birds (and in some cases opportunistic predation of ground-foraging volant birds) such as the diverse waterfowl assemblage (goose, ducks, swan), but also moa chicks and juveniles, adzebill, takahē, kākāpō, kiwi, and ground-nesting seabirds like penguins and burrowing petrels. Given the presence of reptiles in the stomach contents of introduced mammalian predators like stoats (McAulay et al., 2020), it is probable that kurī could have also predated on skinks, geckos, frogs and tuatara.

Habitat disturbance

Habitat disturbance by potential predators can also result in behavioural changes in animals, which may ultimately result in lowered reproductive success and negative consequences at a population level (for a review see Twardek et al., 2017). The intensity, frequency and duration of disturbance may result in different types and severity of impacts (Hill et al., 1997). Low level continuous noise, for example, may be tolerated by birds over time, while episodic 'startling' events can result in displacement and ultimately avoidance of a location.

Impacts documented internationally from the presence of modern dogs include increased nest vigilance in coots (Randler, 2006), and changes in spatial distribution of pudu (Silva-Rodrigez and Sieving, 2012) and bandicoots (Carthy and Banks 2012). Even the activity of dog-walkers passing through a woodland area resulted in a 35% decrease in bird diversity and a 41% decrease in bird abundance over time (Banks and Bryant, 2007). Many of New Zealand's seabird, seal and sea lion colonies are prone to disturbance, which can result in colony abandonment and failure of breeding seasons (e.g. Lord et al., 2001; McConkey et al., 2002; Rawlence et al., 2016a, b).

Pathogen transmission

Throughout history, human movement around the world has been associated with the spread of zoonotic diseases, whether viral, bacterial, microbial or parasitic. As humans and commensal animals move into new areas, the chance of zoonotic disease transfer is heightened (e.g. pre-Columbian seal tuberculosis in Amerindian populations (Bos et al., 2014) or the extinction of the endemic Christmas Island rat due to an introduced parasite from black rats; Wyatt et al., 2008). Recent research on the age and transmission of tuberculous in New Zealand suggests than it may have been introduced prior to European arrival, and vectors for transmission could include humans, commensal and wild animals (McDonald et al., 2020).

Assistance with human hunting

The involvement of dogs in human hunting activities has been documented ethnographically in many parts of the world, and this collaborative behaviour may have been part of a complex set of circumstances that contributed to early dog domestication. The participation of dogs in hunts may have enhanced human hunting productivity, but as this behaviour leaves little or no trace in the archaeological record the investigation of such hypotheses is challenging. In Australia, Balme and O'Conner (2016) have suggested that a change in small mammal numbers in mid-Holocene archaeological sites may be related to the introduction and use of dingo for hunting. The use of kurī in moa-hunting activities has also been hypothesised in New Zealand (Anderson, 1981), although there is currently no direct evidence for this.

Ethnographic accounts of dogs and human hunting often assume *a priori* that the presence of dogs has a positive effect on hunting success, but is not demonstrated empirically (Lupo, 2017).

In addition, much of this ethnographic data relates to specialist hunting dogs that have been bred over the last 500-600 years for specific characteristics, such as scent or sight hounds. Not all dogs will possess these enhanced characteristics. Generally hunting with dogs is a non-selective method – dogs may target prey indiscriminately, including non-desirable animals, juveniles or females with young (Koster, 2008; Koster and Noss, 2014).

Lupo's (2017) review of ethnographic evidence for the use of dogs for hunting and the implications for productivity suggests that although dogs can influence hunting productivity in some circumstances, overall this is highly variable and does not apply to all prey types. Dogs' senses and abilities can however complement those of human hunters, resulting in encounter rates that differ from those of hunters working without dogs, particularly the detection of nocturnal or burrowing prey (Koster and Noss, 2014). The circumstances where dogs perform best appear to be where dogs are introduced as novel predators (as in New Zealand), used in packs, or in association with a new technology such as firearms (Lupo, 2017).

Any advantages to human hunting conferred by the presence of dogs in New Zealand are impossible to disentangle, as both species arrived in New Zealand at the same time. It is possible, however, that kurī did increase human hunting productivity, by decreasing search costs and improving encounter rates by finding and flushing out or holding at bay ground-based species (Lupo, 2017), such as kiwi, weka, kākāpo, seals and sea lions, and possibly reptiles. Archaeological evidence certainly suggests Māori hunted the entire ontogenetic size range of sea lions (Rawlence et al., 2016b), and may have utilised kurī for assistance. Indeed, there is ethnographic evidence dating from the second-half of the nineteenth century for the use of dogs to hunt ground birds in New Zealand (e.g. weka, pukeko, kakapo; Beattie, 1920; Beattie, 1939) but the antiquity of this practice is not clear.

Breadth and intensity of impacts

Unlike kiore, which spread rapidly throughout the New Zealand environment (e.g. presence of rat-gnawed seeds in natural palaeoenvironmental archives; Wilmshurst et al., 2004) and have been found in natural subfossil sites (e.g. caves, laughing owl roost sites; Wilmshurst et al, 2008), the distribution of kurī appears to be highly correlated with human settlements and activities. Furthermore, kiore consume a wide range of different flora and fauna, including seeds, plants, invertebrates and birds' eggs, and therefore are hypothesised to have had a much broader impact across the New Zealand ecosystem (Rayner et al., 2007; Tennyson and Martinson, 2007; Ismar et al., 2014). The intensity of impacts of kurī on native biota is therefore likely to have been more restricted than kiore, and to have varied across the country in accordance with underlying patterns of human movement, settlement and land use. There is evidence from macro- and micro-scopic, and genetic analysis of coprolites, for the consumption of cultivated plants, fish and birds by kuri (Clark, 1997; Irwin, 2004; Wood et al., 2016).

During the pre-European colonisation-era, human settlements in New Zealand were predominantly situated on the coast, often in association with river and estuary mouths. Major river valleys were also used to access inland areas in southern New Zealand. Dog bones are numerous in these early Māori sites (Davidson, 1997; Greig et al., 2018). The results of biomolecular analyses of ancient mitochondrial genomes indicate that there was a limited introduction of dogs to New Zealand, but that these dogs and their descendants were transported rapidly around the country (Greig et al., 2018). The impact of kurī is likely to have been intense in the vicinity of these early villages, and possibly along inland routes (i.e. widespread but relatively localised impact compared to widespread non-localised impact by kiore). Following the extinction of moa human population density in southern Aotearoa New

Zealand was markedly reduced until the late 1700s, and human presence was structured around seasonal resource acquisition (Jacomb et al., 2010; Rawlence et al., 2015; Waters et al., 2017).

By the mid-nineteenth century packs of European, and possibly mixed ancestry, feral dogs were becoming a problem in Aotearoa New Zealand. To date, no genetically and morphologically verified kurī remains have been reported outside of archaeological contexts. However, a review of New Zealand natural history collections (specifically fossil vertebrate collections at the University of Auckland Geology Department, Auckland Museum, the National Museum of New Zealand Te Papa Tongarewa, and Canterbury Museum) has identified dog specimens from locations without clearly documented archaeological contexts. It is not known whether these remains are from European or mixed-breed dogs or kurī. The locations comprise predominantly sand dune deposits and some cave deposits (not pitfall traps; Worthy and Holdaway, 2002), the majority of which could be associated with nearby archaeological middens or occupation sites (e.g. Twilight Beach, Ocean Beach, Delaware Bay, and Greville Harbour) (see Appendix 1). It would be expected that if kurī lived independent of humans that their remains could be found in 'natural' subfossil sites. However, potential feral populations may be cryptic in the recent fossil record given hypothesised low population densities.

Future challenges

Our review has identified a variety of potential impacts to indigenous fauna; direct predation, habit disturbance, pathogen transmission, and assistance with human hunting. We hypothesise that, given the close association between kurī and Maorī, these impacts would have been widespread but relatively localised around Maorī settlement or movement patterns (though we cannot discount the possibility of pre-European feral kurī populations), and would have significantly amplified the impact of humans on New Zealand biodiversity. Furthermore, unlike kiore, kurī impacts would have been focused on a sub-set of New Zealand's avifauna, herpetofauna, and seals and sea lions, particularly mid-sized taxa. To obtain a full picture this impact, several avenues of future research need to be undertaken.

(1) Coprolites, attributed to 'kurī' on the basis of size, have been found in numerous midden contexts. The use of ancient DNA is increasingly highlighting its utility as a genetic tool for the study of palaeodiet (e.g. Wood et al., 2020). Multidisciplinary analyses of genetically confirmed kurī coprolites (ancient DNA, macro- and micro-scopic, isotopic, palaeoproteomics) should be used to test hypotheses about geographical and temporal changes in kurī diet (and as a proxy for human diet), and how this reflects wider patterns in the previously recognised ecosystem change in New Zealand. These analyses should be conducted in conjunction with archaeozoological analysis of midden assemblages (including bulk bone metabarcoding of non-diagnostic material; e.g. Seersholm et al., 2018) and regional pre-human palaeofaunal surveys (e.g. Worthy, 1998), especially of understudied taxa (e.g. small birds, herpetofauna), and modelling of Māori movement across the environment through time (e.g. is there a differential decline in ground-nesting birds?). Because kurī are closely associated with people, it may always be difficult to distinguish between hunting versus scavenging.

(2) Ancient DNA analysis of kurī bones and coprolites, focusing on zoonoses, could potentially shed light on this understudied aspect of faunal impact (e.g. did dogs bring zoonoses to Aotearoa, were kurī a vector between seals, sea lions and people for tuberculosis?).

(3) To resolve the debate of whether there were feral pre-European kurī populations, and whether kurī had an independent impact of New Zealand biodiversity, multiproxy genetic, radiocarbon and isotopic analysis of 'natural' dog remains in sites with no clear archaeological context should be undertaken to determine if these are kurī or European dogs, and feral or

human-dependant dogs (e.g. are there differences in diet?). Palaeontological excavations across New Zealand should also be aware of the potential for dogs in these ‘natural’ subfossil sites. It may not be possible to resolve this question but addressing the status of these dogs will allow more informed hypotheses to be drawn about the potential impact of feral kurī.

Conclusion

Kurī have largely been overlooked in contributing to the ecological consequences of Polynesian settlement of Aotearoa New Zealand as these impacts have been difficult to scientifically assess, with the majority of the research focusing on over-hunting, habitat destruction, and predation from kiore. Far from being “*exonerated*” we argue that kurī had the potential for a significant, widespread but relatively localised (*cf.* kiore) impact of New Zealand fauna. Given the behavioural characteristics of much of New Zealand’s avifauna (i.e. terrestrial, flight-reduced or flightless, ground nesting, slow breeding), they would have been highly vulnerable to predation by kurī. In this way, independent predation and as part of hunting trips, kurī mirrored and amplified the impact of people, especially we hypothesise for medium sized birds, herpatofauna, and seals and sea lions. Opportunities for future research will help resolve the remaining gaps in our knowledge of the impact of kurī on New Zealand biodiversity and on insular island ecosystems in general.

Author contributions

KG and NJR devised the study, analysed the data, and wrote the manuscript.

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Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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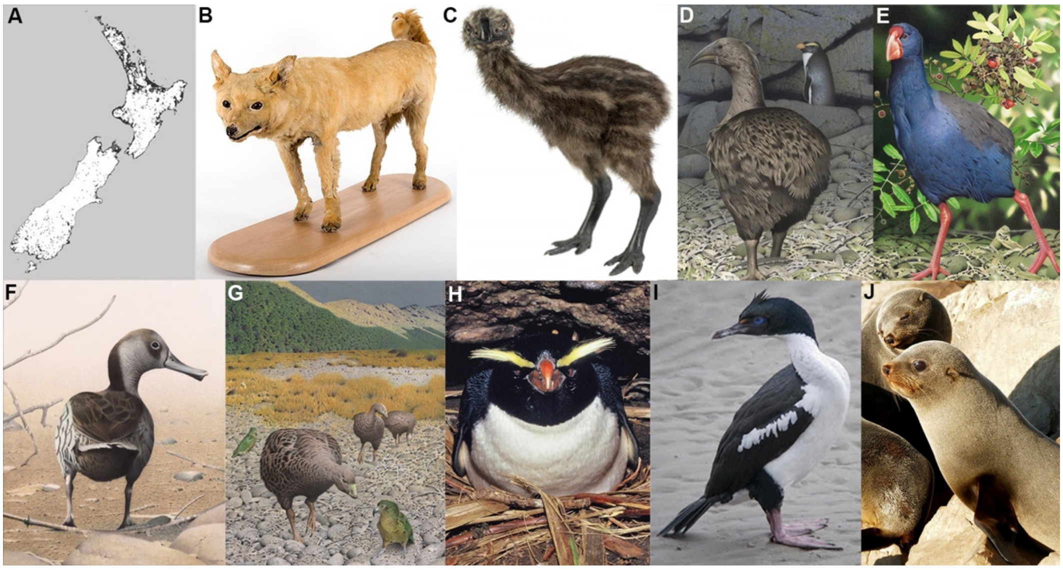

Figure 1 A: Distribution of pre-European contact Māori archaeological sites in Aotearoa New Zealand as a proxy for the human-dependant distribution of kurī (Source: ArchSite. org.nz). **B**: Polynesian dog or kurī (*Canis familaris*). Potential prey of kurī (**C-J**): **C**: extinct flightless moa chicks or juveniles; large flightless rails like the extinct adzebill *Aptornis* spp. (**D**) and the extant takahē/extinct moho *Porphyrio* spp. (**E**); waterfowl including several species of extinct duck (e.g. Scarlett's duck *Malacorhynchus scarletti,* **F**) and the flightless extinct *Cnemiornis* goose (**G**); sedentary seabirds such as cavity or burrow nesting (e.g. extant tawaki Fiordland crested penguin (**H**) *Eudyptes pachyrhynchus*) or sedentary species (e.g. extant blue-eyed shags (**I**) *Leucocarbo* spp.); pinnipeds (especially pups or females) including kekeno fur seals (**J**) *Arctocephalus forsteri*, and extinct lineages of rāpoka sea lions and ihupuku southern elephant seals.

Appendix 1 ‘Natural sites’ where dog remains have been found that are housed in the vertebrate fossil collections at the University of Auckland Geology Department (AU), Auckland Museum (AM), the National Museum of New Zealand Te Papa Tongarewa (NMNZ) and Canterbury Museum (CM). NZ: New Zealand; NI: North Island; SI: South Island.

Site	**Region**	**Museum**	**Subfossil or archaeological assemblages recorded nearby**
Southwest Island, Three Kings Islands	Northern NZ	AM	-
Tapotupotu	Northern NZ	AU	Subfossil + archaeological
Tom Bowling Bay	Northern NZ	AU, AM, NMNZ	Subfossil + archaeological
Waikuku Beach	Northern NZ	AM, CM	Subfossil + archaeological
Wharekawa	Northern NZ	AU	Subfossil + archaeological
Whareana	Northern NZ	AU	Subfossil + archaeological
Te Werahi Beach	Northern NZ	AM	Subfossil + archaeological
Herangi Hill	Northern NZ	AU	Subfossil + archaeological
Twilight Beach	Northern NZ	AM	Subfossil + archaeological
Henderson Bay	Northern NZ	NMNZ	Subfossil + archaeological
Hikurangi	Northern NZ	NMNZ	-
East Beach	Northern NZ	AM	Subfossil + archaeological
Matai Bay	Northern NZ	AM	Subfossil + archaeological
Tokerau Beach	Northern. NZ	CM	Subfossil + archaeological
Waiheke Island	Northern NZ	AM	Archaeological
Auckland	Northern NZ	AU, AM	Subfossil + archaeological
Huriwai Beach	Northern NZ	AU	-
Red Mercury Island	Northern NZ	AM	Archaeological
Port Jackson	Northern NZ	AM	Archaeological
Ocean Beach	Eastern NI	NMNZ	Subfossil + archaeological
Whakaki	Eastern NI	NMNZ	-
Maraekakaho	Eastern NI	NMNZ	-
Poukawa	Eastern NI	NMNZ	Subfossil
Martinborough	Southern NI	NMNZ	Subfossil
Paremata	Southern NI	NMNZ	Archaeological
Otaki	Southern NI	NMNZ	Archaeological
Cape Foulwind	Western SI	CM	Archaeological
Paton’s Rock Cave	Northern SI	CM	Archaeological
Sand Drift Bay	Northern SI	CM	-
Greville Harbour	Northern SI	CM	Subfossil + archaeological
Delaware Bay	Northern SI	NMNZ	Subfossil + archaeological
Lake Grassmere	Eastern SI	CM	Subfossil + archaeological
Rakauteru Cave	Eastern SI	CM	Subfossil
Robinsons Bay	Eastern SI	NMNZ	-
Preservation Inlet	Southern NZ	CM	Archaeological
Stewart Island	Southern NZ	AM, NMNZ	Subfossil + archaeological
Maunganui	Chatham Islands	CM	Subfossil + archaeological