



# The Contribution of Kurī (Polynesian Dog) to the Ecological Impacts of the Human Settlement of Aotearoa New Zealand

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The pre-human Aotearoa New Zealand fauna 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 simultaneous 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 endemism (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 adaptations 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 (>223 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 (*Cnemidornis* spp.), adzebill (*Aptornis* spp.), moho (*Porphyrio mantelli*) and other rails, and several waterfowl (e.g., Finsch's, blue-billed, musk and pink-eared ducks, merganser, and pouwa swan), as well as extant terrestrial birds including takahē (*Porphyrio hochstetteri*), kākāpō (*Strigops habroptilus*) and kiwi (*Apteryx* spp.; Worthy and Holdaway, 2002; Tennyson and Martinson, 2007). The top predators in the pre-human ecosystem were also birds including Haast's eagle (*Aquila moorei*) and Eyles' harrier (*Circus eylesi*; Tennyson and Martinson, 2007). 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 (Figure 1) as a result of hunting (Anderson, 1989; Holdaway et al., 2014; Perry et al., 2014) and anthropogenic environmental modification (McWethy et al., 2014), in addition to biological turnover events (Rawlence et al., 2017a), range-contractions (Salis et al., 2016), population bottlenecks (Rawlence et al., 2015a), and significant changes in indigenous forest cover through widespread anthropogenic burning (McWethy et al., 2014; McConnell et al., 2021). Within a few hundred years of human colonisation, the New Zealand ecosystem had been fundamentally transformed, which has left a clear signature in the archaeological and subfossil record (Holdaway and Worthy, 1996; Tennyson and Martinson, 2007; Holdaway et al., 2014; Perry et al., 2014; Walter et al., 2017; Waters et al., 2017; Rawlence et al., 2019). Polynesians also simultaneously introduced two exotic predators (Figure 1), the kiore (Pacific rat, *Rattus exulans*) and kuri (Polynesian dog, *Canis familiaris*) (Wilmshurst et al., 2008; Greig et al., 2018). Bones and teeth from both are found in colonisation-era archaeological sites throughout the three main islands, and on some but not all offshore islands (e.g., kuri have not been documented in archaeological sites on Rēkohu Chatham Islands ~780 km east of mainland New Zealand but have been inferred, based on chewed bone, to have been present on the sub-Antarctic Auckland Islands ~480 km south of the mainland; Davidson, 1987; Anderson, 2005; Greig and Walter, 2021). Well-documented archaeozoological analysis of early archaeological sites containing kuri bones also shows the presence of numerous extinct prey taxa (e.g., Anderson et al., 1996; Furey, 2002; Worthy and Holdaway, 2002; Scofield et al., 2003). Kuri were also a source of meat and industrial materials (e.g., kahu kuri dog skin cloaks, bone for tools and ornaments) for Māori, the direct descendants of those East Polynesian immigrants (Anderson, 1981, 1989; Davidson, 1987; Hartnup et al., 2011).

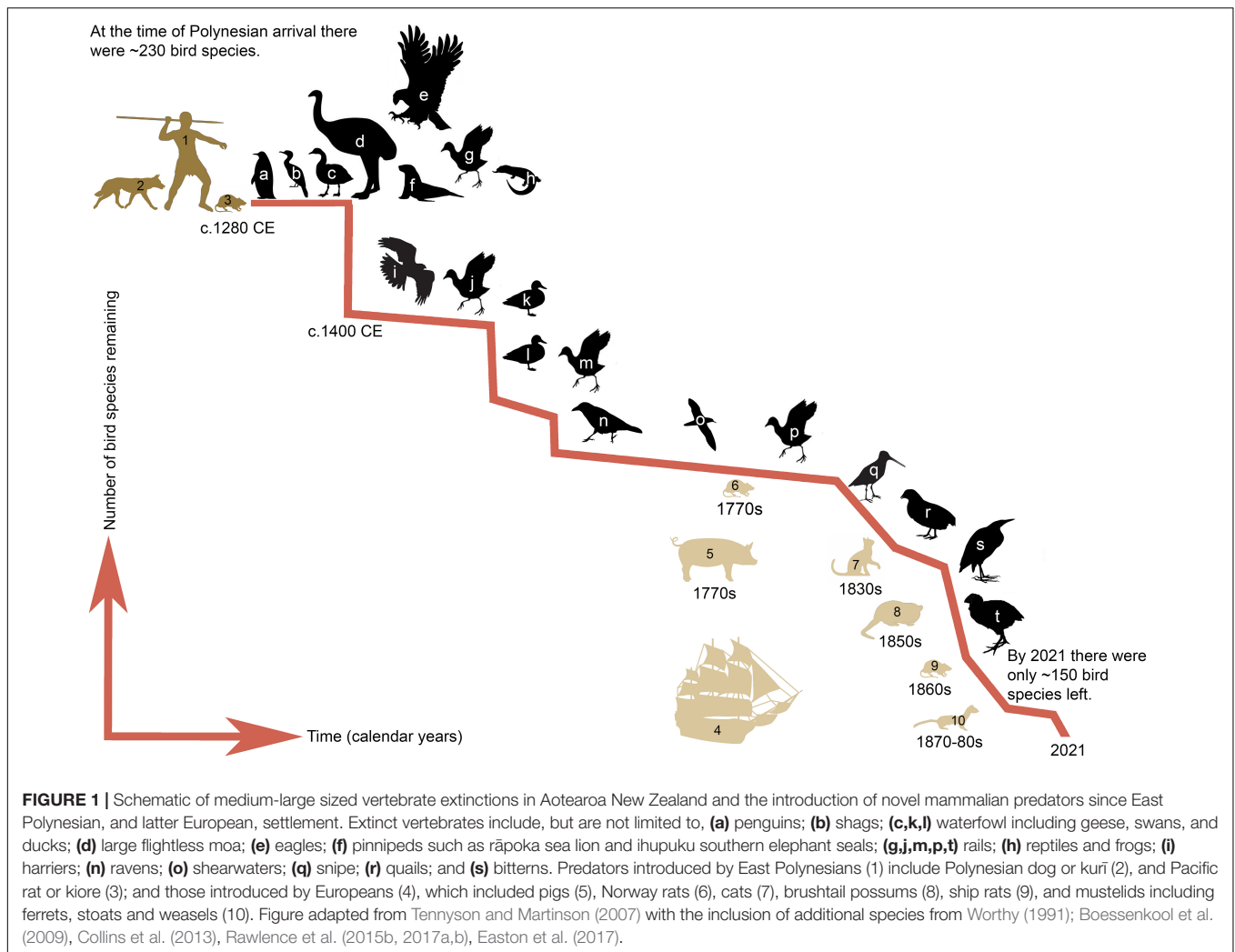
Much archaeological and palaeoecological research has focused on the direct impacts of humans (i.e., hunting, environmental modification; Anderson, 1989; Holdaway et al.,

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 kuri 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 kuri, 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 kuri 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)

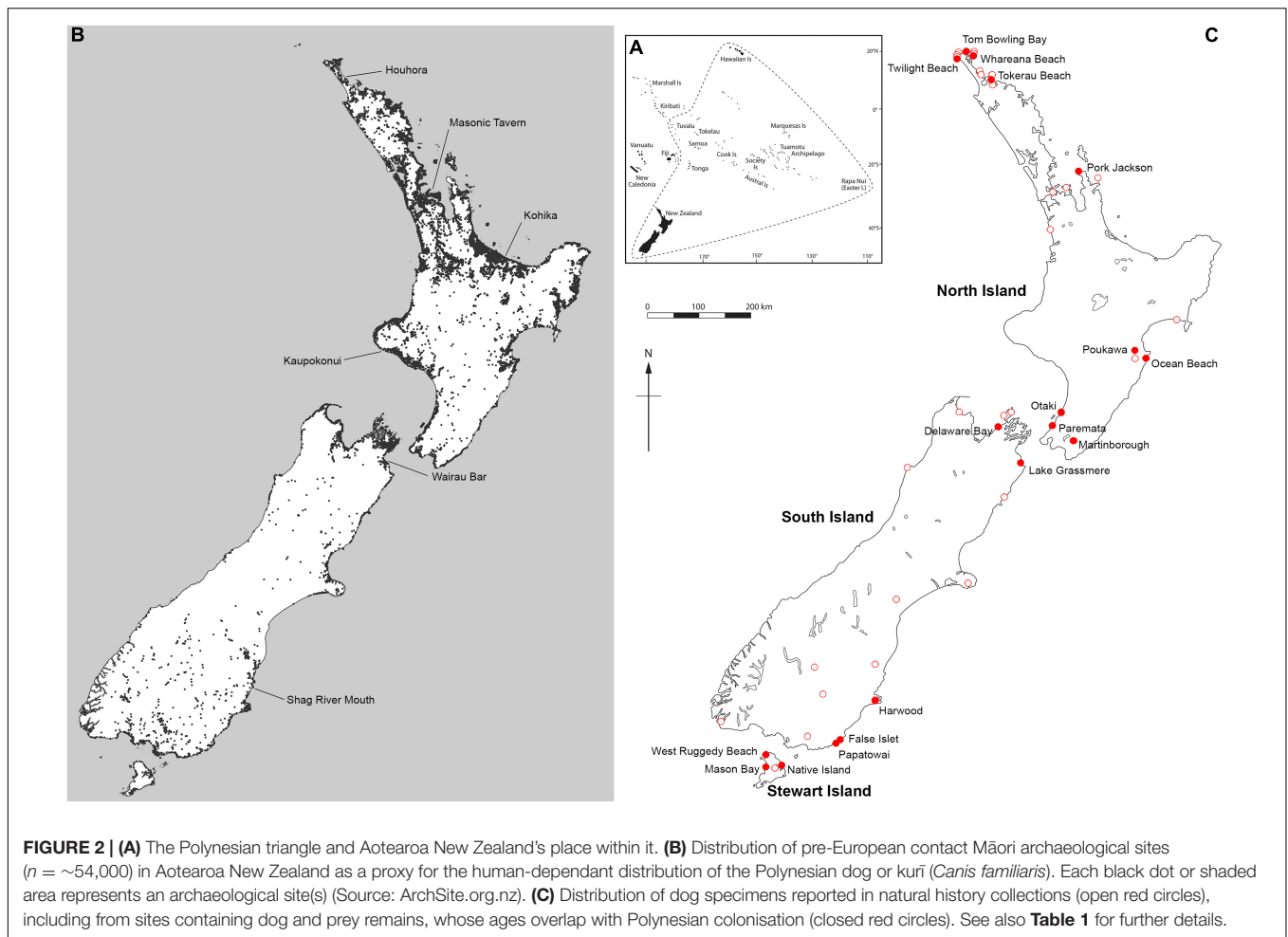
An investigation of the impacts of kuri on Aotearoa New Zealand's biota requires an understanding of kuri biology, behaviour and ecology. This is problematic, as by the mid-nineteenth century CE kuri were no longer identifiable as a distinct dog type in Aotearoa New Zealand, due to interbreeding and replacement by European dogs. Dogs were brought to New Zealand around the late thirteenth century CE by East Polynesian migrants, the end point of a major trajectory of human colonisation of the islands of the Pacific (Greig and Walter, 2021). 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 southern 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 kuri recovered from archaeological sites now comprise a valuable source of information. Archaeozoological studies and emerging biomolecular techniques can provide data about kuri physical characteristics, diet, mobility, and genetic history. In addition to archaeological remains, there are numerous observations about kuri 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 kuri behaviour.



Kuri feature in Māori mythology, oral histories and art forms, demonstrating their importance in Māori culture (Potts et al., 2013). Legendary kuri are associated with colonising voyages to New Zealand, historical events and the naming of landmarks. In everyday life kuri 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 kuri 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 kuri life history, such as reproductive behaviour is extremely limited. Kuri 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 kuri populations were able to be sustained in early Māori settlements (Figures 2A,B). The results of archaeozoological 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 kuri, for example, Kohika (Horrocks et al., 2002, 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 variety 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). Kuri 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 storehouses on poles or stilts several feet above the ground, used to protect food such as seed potatoes, or dried fish from roaming animals (Best, 1916). 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 the range of fauna commonly found in correspondingly dated Māori middens (rubbish heaps). Components include small bird, moa, fish, mollusc 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, terrestrial and marine mollusc 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). Preliminary isotopic analyses of kurī bones using carbon and nitrogen stable dietary isotopes further support a widely varied diet (Leach et al., 2003; Kinaston et al., 2013; Wood et al., 2017) incorporating terrestrial (i.e., similar isotopic compositions to herbivorous moa) and marine components.

To date, the only published evidence of kurī skeletal remains is associated with archaeological evidence for human activities (**Figure 2B**) rather than natural sites (e.g., caves, pitfalls, swamps, dunes), potentially 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 wide variety of Australian fauna and flora, 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,

**TABLE 1** | Sites where dog remains have been found that are housed in the vertebrate fossil natural history collections at the University of Auckland Geology Department (AU), Auckland Museum (AM), the National Museum of New Zealand Te Papa Tongarewa (NMNZ), Canterbury Museum (CM), Otago Museum (OM), the University of Otago Zoology Department (OU), and the Jill Hamel private collection (JH).

Site	Region	Museum	Accession numbers	Natural subfossil and/or archaeological faunal assemblages documented in the vicinity
Southwest Island, Three Kings Islands	Northern NZ	AM	LM859	–
Tapotupotu	Northern NZ	AU	AU6156	Subfossil + archaeological
Tom Bowling Bay	Northern NZ	AU, AM, NMNZ	AU4029, AU4031, AU4033, AU4040-41, AU4054, AM LM697, AM LM802, NMNZ S.39716	Subfossil + archaeological
Waikuku Beach	Northern NZ	AM, CM	AM LM1443, AM LM676, CM 1971.117.745-46, CM NZMA637, CM NZMA665	Subfossil + archaeological
Wharekawa	Northern NZ	AU	AU4032	Subfossil + archaeological
Whareana Beach	Northern NZ	AU	AU4767, AU4769, AU4841	Subfossil + archaeological
Te Werahi Beach	Northern NZ	AM	LM763, LM752	Subfossil + archaeological
Herangi Hill	Northern NZ	AU	AU4646, AU4692, AU4745	Subfossil + archaeological
Twilight Beach	Northern NZ	AM	LM850	Subfossil + archaeological
Henderson Bay	Northern NZ	NMNZ	S.43375	Subfossil + archaeological
Hikurangi	Northern NZ	NMNZ	LM830	–
East Beach	Northern NZ	AM	LM985	Subfossil + archaeological
Matai Bay	Northern NZ	AM	LM701	Subfossil + archaeological
Tokerau Beach	Northern NZ	CM, OM	CM NZMA12, CM NZMA584, OM VT586	Subfossil + archaeological
Waiheke Island	Northern NZ	AM	LM137	Archaeological
Auckland	Northern NZ	AU, AM	AU16902, AM LM313	Subfossil + archaeological
Muriwai Beach	Northern NZ	AU	AU4072	–
Red Mercury Island	Northern NZ	AM	LM138	Archaeological
Port Jackson	Northern NZ	AM	LM1516	Archaeological
Ocean Beach	Eastern NI	NMNZ	LM390	Subfossil + archaeological
Whakaki	Eastern NI	NMNZ	LM383	–
Maraekakaho	Eastern NI	NMNZ	LM381	–
Poukawa	Eastern NI	NMNZ	S.22232	Subfossil
Martinborough	Southern NI	NMNZ	LM387	Subfossil
Paremata	Southern NI	NMNZ	Unregistered	Archaeological
Otaki	Southern NI	NMNZ	LM693/1-693/5	Archaeological
Cape Foulwind	Western SI	CM	FMA2079	Archaeological
Paton's Rock Cave	Northern SI	CM	NZMA664	Archaeological
Sand Drift Bay	Northern SI	CM	NZMA1005	–
Greville Harbour	Northern SI	CM	NZMA471, NZMA742	Subfossil + archaeological
Delaware Bay	Northern SI	NMNZ	S.38474, S.38540, S.38577	Subfossil + archaeological
Lake Grassmere	Eastern SI	CM	FMA688	Subfossil + archaeological
Rakauteru Cave	Eastern SI	CM	NZMA633	Subfossil
Robinsons Bay	Eastern SI	NMNZ	LM382	–
Peel Forest	Eastern SI	OM	D28.348	Subfossil + archaeological
Enfield	Eastern SI	OM	VT053	Subfossil
Harwood	Southern NZ	JH	n/a (see Wood et al., 2017)	Subfossil + archaeological
Hawks Burn	Southern NZ	OM	VT2898	Subfossil + archaeological
Low Burn	Southern NZ	OM	VT2553	Subfossil + archaeological
Mataura Plains	Southern NZ	NMNZ	LM828/1-828/2	Subfossil + archaeological
False Islet	Southern NZ	OM	VT046	Archaeological
Papatowai	Southern NZ	OM	VT2899	Archaeological
Preservation Inlet	Southern NZ	CM	1968.42.640	Archaeological
Stewart Island	Southern NZ	AM, NMNZ	AM LM140	Subfossil + archaeological
West Ruggedy Beach	Southern NZ	OU	2021.6.23	Subfossil + archaeological
Mason Bay	Southern NZ	CM	1972.90.907	Subfossil + archaeological
Paterson Inlet	Southern NZ	OM	VT037	Subfossil + archaeological
Native Island	Southern NZ	NMNZ	S.35949, unregistered	Subfossil + archaeological
Maunganui	Chatham Islands	CM	FMA2034-35	Subfossil + archaeological

Sites containing dog and prey remains, whose ages overlap with Polynesian colonisation are shaded in grey. NZ: New Zealand; NI: North Island; SI: South Island.

recent feral dog populations have been observed in Northland (Piper, 2021) and “wild dogs” were observed subsisting on kākāpō, 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 1**) potentially supports this hypothesis (however, see *Breadth and intensity of impacts* below). Feral 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 kuri 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, kuri 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

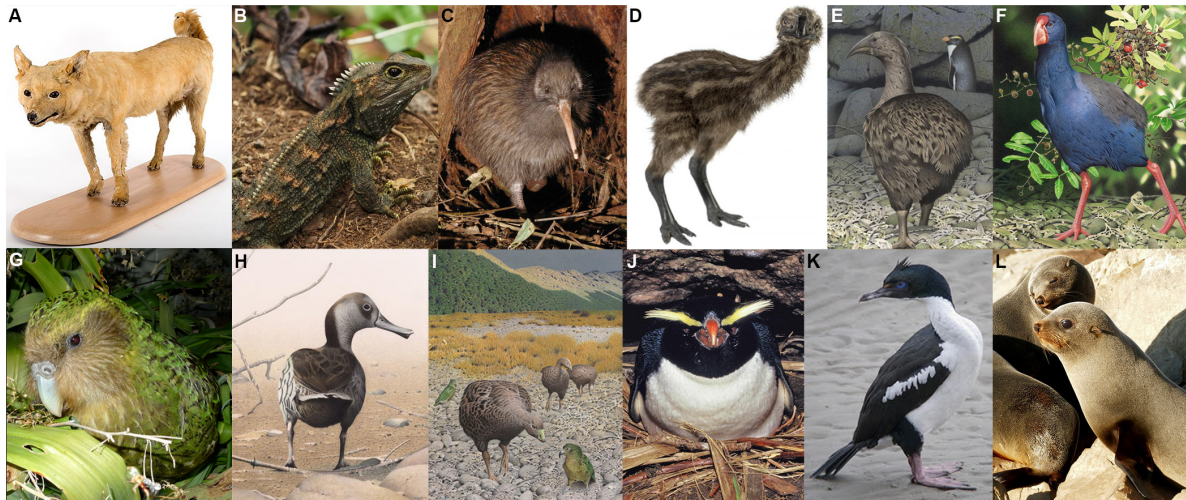
### Predation

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. These human-derived food subsidies can result in long-term negative impacts on direct prey species, which in turn may have indirect flow on effects on the abundance of other species within the ecosystem (Ritchie et al., 2014; Newsome et al., 2015). In New Zealand, kuri were a recent novel predator into a naive ecosystem (**Figure 3**). Subsidising of their food resources through “moa-hunting” activities no doubt resulted in a rapid population increase of kuri, as evidenced by their presence in early archaeological sites across New Zealand (Davidson, 1987; **Figure 2B**). The loss of big game species like moa, seals, and sea lions within a few hundred years of

Polynesian arrival (**Figure 1**) would have potentially exacerbated the effects of kuri on small and medium-sized birds and reptiles, hastening their extinction.

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 kuri (**Figure 3**). 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., kākāpō). In addition, on predator-free islands flighted birds often spend a significant amount of time foraging on the ground (e.g., tieke 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 naive 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). Doherty et al.’s (2017) review of the impacts of dogs on threatened species found that they have contributed to 11 vertebrate extinctions and are a threat to at least 188 species worldwide. Predation is the most frequently reported impact, with the Pacific islands being one of the regions with the most species affected. 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 (**Figure 3**) across all life history stages (eggs, chicks, juveniles, and adults), however, a modern study of introduced mammalian predation of brown kiwi 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; Kerr-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 kuri, pups and females (especially while nursing) would have been particularly vulnerable to predation (**Figure 3**). If a female sea lion is killed, it’s unborn and dependant pups will also die. Modelling shows



**FIGURE 3 |** The Polynesian dog or kurī (*Canis familiaris*) (A) and its potential prey (B–L): Herpetofauna including geckos, skinks, frogs, and tuatara (*Sphenodon punctatus*, B); flightless palaeognathous birds such as kiwi (*Apteryx* spp., C) and extinct flightless moa chicks or juveniles (D); large flightless rails like the extinct adzebill *Aptornis* spp. (E) and the extant takahē/extinct moho *Porphyrio* spp. (F); flightless parrots like the kākāpō *Strigops habroptilus* (G); waterfowl including several species of extinct duck (e.g., Scarlett’s duck *Malacorhynchus scarletti*, H) and the flightless extinct *Cnemiornis* goose (I); seabirds such as cavity or burrow nesting (e.g., extant tawaki Fiordland crested penguin (J) *Eudyptes pachyrhynchus*) or sedentary species (e.g., extant/extinct blue-eyed shags (K) *Leucocarbo* spp.); pinnipeds (especially pups or females) including kekeno fur seals (L) *Arctocephalus forsteri*, and extinct lineages of rāpoka sea lions and ihupuku southern elephant seals. Artwork by Paul Martinson from Tennyson and Martinson (2007) © Te Papa CC BY-NC-ND 4.0. Image of moa chick © Te Papa CC BY 4.0. Image of blue-eyed shag by Philip Griffin (New Zealand Birds Online).

these slow-breeding pinnipeds could not withstand even low levels of subsistence hunting or predation resulting in their rapid extinction (Rawlence et al., 2016a; Waters et al., 2017).

As well as immediate fatalities, predatory behaviour can also result in chasing or seabird 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).

Elsewhere in the world dogs also compete with other carnivores directly for prey and as scavengers for carrion (e.g., Schlacher et al., 2015; Hansford et al., 2021). The pre-human New Zealand situation is different as there were no terrestrial mammalian carnivores, with their roles replaced by flighted and flightless birds including Haast’s eagle, Eyles’ harrier, adzebill, and the New Zealand raven *Corax antipodum* (e.g., Tennyson and Martinson, 2007; Scofield et al., 2017). It is possible that kurī competed with these species for prey and carrion.

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, mergansers, swan), but also moa chicks and juveniles (and potentially the smaller males of some moa species), adzebill, takahē/moho (and other rails), kākāpō, kiwi, and ground-nesting seabirds like penguins, shags and burrowing petrels (Figure 3). This probably also included

predation of the eggs of ground nesting birds. It is likely that kurī contributed to the extinction of at least three seabirds including Waitaha penguin *Megadyptes waitaha* (Boessenkool et al., 2009), Kōhatu shag *Leucocarbo septentrionalis* (Rawlence et al., 2017b) and Scalett’s shearwater *Puffinus spelaeus* (Holdaway and Worthy, 1994). 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 preyed on skinks, geckos, frogs and tuatara (Figure 3) – there are records from the nineteenth century of dogs killing escaped captive tuatara (Cree, 2014). At least one species of giant skink (Worthy, 1991) and three frogs are known to have gone extinct prior to European colonisation, with several species only surviving on offshore islands (e.g., Scarsbrook et al., 2021). Indeed, tuatara were effectively extinct on the mainland before European arrival and now only survive on islands without kiore and dogs (Cree, 2014).

### 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, and seals and sea lions, 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

pus (Silva-Rodriguez and Sieving, 2012) and bandicoots (Carthey 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; Allott, 2021).

## Pathogen Transmission

Throughout history, human movement around the world has been associated with the spread of zoonotic diseases, whether viral, bacterial, microbial or parasitic (Spyrou et al., 2019). 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 trypanosome parasite from black rats; Wyatt et al., 2008]. Recent research on the age and transmission of tuberculosis in New Zealand suggests that it may have been introduced prior to European arrival, and vectors for transmission could include humans, commensal and wild animals (McDonald et al., 2020). To date, eggs from two parasitic helminth taxa (*Caprillaria cf. hepatica* and *Toxocara canis*), whose intermediate hosts also include rats (e.g., Dubinsky et al., 1995), have been found in kuri coprolites (Irwin, 2004).

## 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. Dogs have been used to increase hunting effectiveness across a variety of environments and to target a broad spectrum of prey species, from small rodents, reptiles, ratites, monkeys, marsupials, deer, and boar, to other carnivores [see Kounououlos and Fillios (2020) for a review]. Ethnographic accounts of dogs and human hunting often assume *a priori* that the presence of dogs has a positive effect on hunting success, but this is not demonstrated empirically (Lupo, 2017). In addition, some of this ethnographic data relates to hunting dogs that have been bred over the last 500–600 years for particular characteristics to improve hunting success, such as scent or sight hounds. Although these characteristics may be selectively bred, dogs' hunting performance is also affected by their life experience (Udell et al., 2014). Not all dogs will possess these specialised characteristics. Nonetheless, Kounououlos and Fillios's (2020) review of the use of dingoes for hunting found that although they were not specifically trained to hunt, their general instincts were still beneficial. Hunting with dogs is often 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; Figures 1, 3), 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 (Figure 1). It is possible, however, that kuri 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, kākāpō, seals and sea lions, and possibly reptiles. It may have been more energetically efficient for smaller kuri to hunt these prey than humans, and in turn, they would obtain a greater nutritional benefit in terms of relative body size than larger humans. Archaeological evidence from faunal remains certainly suggests Māori hunted the entire ontogenetic size range of sea lions (Rawlence et al., 2016a), and may have utilised kuri 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, pūkeko, kākāpō; Beattie, 1920, 1939) but the antiquity of this practice is not clear. The use of kuri in moa-hunting activities has also been hypothesised (Anderson, 1981), but as this behaviour leaves little or no trace in the archaeological record the investigation of such hypotheses is challenging. Interestingly, Kounououlos and Fillios (2020) document the use of dingoes in Australia as part of game-drives to hunt large prey such as kangaroos, emu and wallaby. These were collaborative hunts, involving men, woman and children which resulted in large numbers of animals being caught.

## 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 and Higham, 2004) and have been found in natural subfossil sites (e.g., caves, laughing owl roost sites; Holdaway and Worthy, 1996; Wilmshurst et al., 2008), the distribution of kuri appears to be highly correlated with human settlements and activities (Figure 2B). Furthermore, kiore consume a wide range of different flora and fauna, including seeds, plants, invertebrates and birds' eggs, and 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 kuri 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 (Figure 2B). As with their human counterparts, kuri may have undergone a period of adaptation to temperate New Zealand from their tropical East Polynesian homeland. 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 first human colonisation-era, settlements in New Zealand were predominantly situated on the coast, often in association with river and estuary mouths (**Figure 2B**). Major river valleys were also used to access inland areas in southern New Zealand. Dog bones are numerous in these early archaeological sites (that also contain the remains of prey species), suggesting sizable kuri populations (Davidson, 1987; 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 distribution of pre-European archaeological sites, as a proxy for the geographic range of kuri (**Figure 2B**), effectively overlaps with the distribution of potential prey species (Worthy and Holdaway, 2002). Numerous natural subfossil sites contain faunal remains (including moa, medium-sized ground-dwelling birds, seals and sea lions, and tuatara) whose ages overlap with the arrival of Polynesians in New Zealand (e.g., Worthy, 1998a; Brook, 2000; Collins et al., 2013; Rawlence et al., 2017b; Wood et al., 2017; Verry et al., 2021; **Table 1** and **Figure 2C**). However, the co-occurrence or not of dog and prey species within a single site should not be used as evidence for and against potential predation (e.g., Davidson, 2012 *cf.* Surovell and Grund, 2012), given taphonomic biases (e.g., Seersholm et al., 2018), and the geographically widespread overlap of kuri and prey species.

The impact of kuri is likely to have been intense in the vicinity of the early villages, and possibly along inland routes (i.e., widespread but relatively localised impact compared to widespread non-localised impact by kiore). Habitat modification through human-induced changes to indigenous forest cover from widespread burning, particularly in southern New Zealand, with a commensurate increase in grasslands (McWethy et al., 2014) may have also affected the intensity of kuri predation. Habitat changes, including forest fragmentation and increased edge habitats, can facilitate easier access for dogs to hunt in more complex environments (Lacerda et al., 2009; Ritchie et al., 2014). Following the extinction of moa (**Figure 1**) 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., 2015a; Waters et al., 2017).

By the mid-nineteenth century packs of European, and possibly mixed ancestry, feral dogs were becoming a problem in New Zealand (Clark, 1995). To date, no genetically and morphologically verified kuri remains have been reported outside of archaeological contexts. However, our 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, Canterbury Museum, Otago Museum, and the University of Otago Zoology Department) presented here has identified numerous locations where dog specimens have been found without clear archaeological context (see **Figure 2C** and **Table 1**). It is not known whether these dog remains are from European or mixed-breed dogs or kuri. The locations comprise predominantly time-averaged sand dune deposits and some cave deposits (not pitfall traps; Worthy

and Holdaway, 2002), the majority of which could be partially associated with nearby archaeological middens or occupation sites (e.g., Twilight Beach, Ocean Beach, Delaware Bay, and Greville Harbour).

It would be expected that if kuri lived independently of humans in self-sustaining packs, as occurred in Australia with the dingo, 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 (*cf.* sizeable human-dependant populations), especially in isolated areas where taphonomic settings are not conducive to preservation (e.g., high rainfall Fiordland), compared to widespread kiore-gnawed seeds in sediment cores and kiore bones in natural subfossil deposits indicative of high abundance populations (e.g., Holdaway and Worthy, 1996; Wilmshurst and Higham, 2004; Wilmshurst et al., 2008; Wilmshurst and Carpenter, 2020). It may be that in these isolated, rugged areas where human population density was lower (e.g., Jacomb et al., 2010; Waters et al., 2017) that the combined effects of kuri, potentially exhibiting pack hunting behaviour, and kiore, had a greater impact on native species than human hunting ever did.

## FUTURE CHALLENGES

Our review has identified a variety of potential impacts to indigenous fauna; direct predation, competition, habitat disturbance, pathogen transmission, and assistance with human hunting. We hypothesise that, given the close association between kuri and Māori, these impacts would have been widespread but relatively localised around Māori settlement or movement patterns (**Figure 2B**) (though we cannot discount the possibility of pre-European feral kuri populations), and would have significantly amplified the impact of humans on New Zealand's biodiversity. Furthermore, unlike kiore, kuri impacts would have been focused on a sub-set of New Zealand's avifauna, herpetofauna, and seals and sea lions, particularly mid-sized taxa (**Figure 3**). To obtain a full picture this impact, several avenues of future research need to be undertaken.

(1) Coprolites, attributed to "kuri" on the basis of size (and in some cases due to the presence of chewed bone fragments), have been found in numerous midden contexts. However, these coprolites could also be potentially attributed to other carnivores such as sea lions or omnivores like humans, especially given the dietary overlap between kuri and people (e.g., Horrocks et al., 2002, 2003; Wood et al., 2016). The use of ancient DNA is increasingly highlighting its utility as a genetic tool for the study of palaeodiet (e.g., Bon et al., 2012; Wood et al., 2020). Multidisciplinary analyses of genetically confirmed kuri coprolites (ancient DNA, macro- and micro-scopic, isotopic, palaeoproteomics) should be used to test hypotheses about geographical and temporal changes in kuri 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, 1998b), 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 kuri are closely associated with people, it may always be difficult to distinguish between hunting versus scavenging.

(2) Ancient DNA analysis of kuri bones and coprolites, and sedimentary archives from archaeological sites, focusing on the morphological and genetic identification of zoonoses (e.g., Irwin, 2004; Wood et al., 2013; Witt et al., 2021), could potentially shed light on this understudied aspect of faunal impact (e.g., did dogs bring zoonoses to Aotearoa, and were kuri a vector between seals, sea lions and people for tuberculosis?).

(3) To resolve the debate of whether there were feral pre-European kuri populations, and whether and when kuri had an independent impact of New Zealand's biodiversity, multiproxy morphometric, genetic, radiocarbon and isotopic analysis of "natural" dog remains in sites with no clear archaeological context should be undertaken to determine if these are kuri or European dogs (or even hybrids), and feral or human-dependant dogs (e.g., are there differences in diet?) (e.g., Koungoulos, 2020; Runge et al., 2021; Witt et al., 2021; on dogs in other geographical contexts). Palaeontological excavations across New Zealand should also be aware of the potential for dogs in natural (i.e., non-cultural) subfossil sites. Integrated approaches incorporating palaeoenvironmental DNA techniques to detect ancient dog DNA in sedimentary archives should also be investigated (Rawlence et al., 2014; Dussex et al., 2021; Mitchell and Rawlence, 2021). It may not be possible to resolve this question but addressing the status of these dogs will allow more informed hypotheses to be made about the potential impact of feral kuri.

## CONCLUSION

Kuri have largely been overlooked in contributing to the ecological consequences of Polynesian settlement of 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 kuri had the potential for a significant, widespread but relatively localised (*cf.* kiore) impact

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on New Zealand's 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 kuri. In this way, independent predation and as part of hunting trips, kuri mirrored and amplified the impact of people, especially we hypothesise for medium sized birds, herpetofauna, and seals and sea lions. Opportunities for future research will help resolve the remaining gaps in our knowledge of the impact of kuri on New Zealand biodiversity and on insular island ecosystems in general.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

## AUTHOR CONTRIBUTIONS

KG and NJR devised the study, analysed the data, and wrote the manuscript. Both authors contributed to the article and approved the submitted version.

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