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SHORT NOTE

Opportunistic predation of non-native species by pūkeko (*Porphyrio melanotus melanotus*)

AILEEN P. SWEENEY*
KRISTAL E. CAIN
School of Biological Sciences, University of Auckland, Auckland 1010, New Zealand

When species are introduced to, or naturally colonise, new areas they may encounter either novel prey or novel predators or, in some cases, both. Conversely, they may present as either novel prey or novel predators to the local fauna (e.g. McLennan *et al.* 1996; Yorio *et al*. 2020). Whether or not a species establishes a self-sustaining population in a newly invaded region, as well as the impacts they may have on the invaded ecosystem, depends on numerous factors (Williamson 1999; Duncan *et al.* 2003). One of the factors dictating a successful establishment in a new region may be the behavioural flexibility of the introduced species and their responses to novel situations, predators, and prey (Sol *et al.* 2002). For example, an invasion event may involve the partial or total loss of the species native diet, such that, without sufficient dietary flexibility, the establishment of the species may be unsuccessful (Sol & Lefebvre 2000). Therefore, it is reasonable to predict that dietary generalists are better equipped to establish in new regions compared to dietary specialists. Generalist omnivores may be opportunistic feeders and therefore can utilise available novel food sources which specialists cannot. Indeed, some of the most successful and widespread species in the world are opportunistic generalists, for example house sparrows (*Passer domesticus*), common cockroaches (*Periplaneta americana*), and brown rats (*Rattus norvegicus*) (Case 1996; Sax & Brown 2000; Cassey 2001). It is unsurprising that these cosmopolitan species are also associated with humans in both their native and introduced ranges, but it obscures whether their invasiveness is due to diet or being a human commensal (Barrett *et al.* 2019). In other words, successful invaders are often passengers of human driven habitat modification (Grarock *et al.* 2013). However, a number of other very successful invasive species are less dependent on humans, but are still very flexible in diet, such as the Asian carps (a number of species of cyprinid fishes) and cane

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*Correspondence: *aswe261@auckanduni.ac.nz*

toads (*Rhinella marina*), suggesting diet is important.

Non-native species introductions have long been considered one of the main threats to biodiversity and ecosystem composition. Indeed, there are many examples to support this, particularly in New Zealand (Aotearoa) where introduced predators have been responsible for historical extinctions and severe population declines for many endemic species, and are still a driving force in many current population declines (O'Donnell 1996; Dowding & Murphy 2001; Duncan & Blackburn 2004; Innes *et al.* 2010; Tennyson 2010; Remeš *et al.* 2012; Garcia-R & Di Marco 2020). However, it has become increasingly apparent that non-native introductions may have neutral and/or positive effects on native species, particularly if the invading species in question can become prey for natives (e.g. Rodriguez 2006; Goodenough 2010; Pintor & Byers 2015; Carlson *et al.* 2017; Yorio *et al.* 2020). If native predators can take advantage of novel prey (i.e. successfully identify and capture the prey), and if these novel prey become relatively abundant, then the native predators may obtain fitness benefits from the presence of this non-native species (Carlsson *et al*. 2009). In a meta-analysis of introduced species studies, Pintor and Byers (2015) found that the focus on predator-prey interactions involving introduced species is largely one-sided (i.e. focused on introduced predators rather than introduced prey). However, it appears that native predator populations typically increase significantly following the introduction of non-native prey. Thus, introduced prey may indirectly benefit native prey by offering new targets and diluting the risk. Understanding these native predator/introduced prey dynamics may be fundamental in protecting native prey species from severe competition or even displacement by introduced prey species. Native predators may aid in limiting or entirely prohibiting the expansion of introduced prey species populations through biotic resistance (deRivera *et al*. 2005; Cheng & Hovel 2010).

Pūkeko (*Porphyrio melanotus melanotus*) are a highly successful New Zealand subspecies of the purple swamphen. Estimates date their self-introduction from Australia to ~1,000 years ago, and today they are widespread across mainland New Zealand, as well as offshore islands (Worthy & Holdaway 1996; Trewick 1996a, 1996b; 1997; Trewick & Worthy 2001). It was not until the 1800s, during European colonisation, that additional species were introduced to New Zealand, including mammalian predators and various avifauna, particularly British species (see Duncan 1997 for a full list of British passeriforms released in New Zealand).

Pūkeko diet is primarily plant material such as stems, shoots, leaves, and seeds of numerous varieties of grass, sedge, rush, and clover (Carroll 1966; Dey & Jamieson 2013; Rodgers & Cain 2019). In addition, they are also opportunistic feeders and a portion of their diet consists of animal material (Trewick 1996a). However, how large and how frequent a portion is unclear. In one Australian population, animal matter was found in 51 of 234 animal (22%), but made up only 1% of the contents by volume (Norman & Mumford 1985). The animal matter in pūkeko diet is primarily invertebrates. However, reports of larger vertebrate prey exist (Carroll 1966; McKenzie 1967; Fogarty 1968; Wright 1978; Dey & Jamieson 2013). These include New Zealand reports of predation on species such as pied stilt eggs (*Himantopus leucocephalus*), Eurasian blackbird chicks (*Turdus merula*), mallard (*Anas platyrhynchos*) ducklings, pāteke ducklings (brown teal, *Anas chlorotis*), as well as reports in Australia on species such as common starlings (*Sturnus vulgaris*), noisy miner chicks (*Manorina melanocephala*), black swan eggs and cygnets (*Cygnus atratus*), and various waterfowl species ducklings (Van Tets, 1965; Lowe 1966; McKenzie 1967; Fogarty 1968; Wright 1978; Nixon 1983; Egan 1992; Morgan *et al.* 2006; Balasubramaniam & Guay 2008; Rickett 2010). Craig (1974) reported that pūkeko mainly took prey during the breeding season to feed chicks. This presents a unique situation in which pūkeko are a self-introduced (and now considered native) predator *and* prey species. Further, this species has experienced the introduction of further new predator and prey species since this initial colonisation event.

We monitored a North Island population of pūkeko from September 2017 – October 2020 in Māngere, Auckland (36.95052°S, 174.76543°E), as part of a larger project on the species (Sweeney 2022). Regular census counts (on average once a fortnight) and *ad libitum* observations occurred throughout the study period, in addition to other experiments. Over the course of three years, pūkeko were observed opportunistically depredating five non-native species, three avian and two mammalian, involving a total of eight events (Table 1). All events involved significant commotion, with three-nine members of the pūkeko social group involved. The bird which caught the prey typically ran around with it, while other members of the group vocalised loudly and gave chase. In four of the eight observations, we observed the situation immediately preceding the event. In all four cases the depredating bird was not observed "stalking" the prey, instead each event appeared to happen spontaneously (i.e. opportunistically) when the prey item suddenly appeared near the attacking individual. In the case of the European greenfinch *(Chloris chloris)*, it flew to join the pūkeko feeding

Table 1. Non-native species observed being opportunistically predated on by pūkeko (*Porphyrio melanotus melanotus*) from September 2017 – October 2020.

Species	Age	Observations	Time of Year
Brown rat (*Rattus norvegicus*)	Juvenile	1	Breeding Season
Mouse (*Mus musculus*)	Adult	3	Breeding Season
European Greenfinch (*Chloris chloris*)	Adult	1	Breeding Season
European Goldfinch (*Carduelis carduelis*)	Adult	1	Breeding Season
Mallard (*Anas platyrhynchos*)	Duckling	2	Breeding Season

on some grass seed and the pūkeko almost immediately caught it.

It is worth noting that over the course of the study, pūkeko were regularly observed foraging in close proximity to the avian species listed in Table 1, without any attempted predation events being observed. Further, these species did not appear to consider pūkeko a threat; they fly towards them intentionally and do not alarm or engage in any other anti-predator behaviour, until attacked. It is also worth noting that though other observers have reported seeing pūkeko attacking native species, no predation of any native species was observed over the course of this 3 year study, despite many native avifauna species occurring in the area, which is of international importance for migratory species (>35 native species (eBird 2022)).

On one occasion the pūkeko were observed feeding the prey item (a mouse (*Mus musculus*)) to offspring. In all other cases (n = 7), they moved into dense vegetation out of the observers view shortly after capturing the prey, so the fate of the prey item was unknown. However, all observed predation events occurred during the peak breeding season (August – February), which supports Craig (1974) and Wright's (1978) arguments that pūkeko mainly take larger prey opportunistically during the breeding season to provide extra protein to offspring during their critical development stage (growth). Overall, in line with previous studies, pūkeko in the study population were observed to be predominantly herbivorous. However, these observations of predatory behaviour indicate that they are capable of opportunistically exploiting a food source beyond their typical diet range, potentially to benefit their offspring and thereby increase reproductive output.

Behavioural flexibility facilitates rapid responses to novel conditions, and species demonstrating dietary flexibility should be able to exploit novel food resources more readily than specialised species which maintain foraging behaviours from their native range (Sol & Lefebvre 2000; Wyles *et al*. 1983). When a flexible species invades a new region, its ability to modify and develop behaviours should facilitate identifying and utilising novel food resources, and therefore increase its success in establishing a self-sustaining population. The ability of pūkeko to opportunistically depredate non-native prey is further evidence of the species' dietary flexibility. This is perhaps unsurprising given how well established pūkeko have become since self-introduction. Sol *et al.* (2011) predicted that in regions where species often encounter novel feeding opportunities, and where risks associated with native predators are low, the species in question should favour approaching novel resources (neophilia) over avoidance (neophobia). Pūkeko are an excellent example of this process. Though they are a very common species, understanding their behaviour and foraging decisions has important and wide-ranging consequences. A recent paper showcases this possibility, finding that pukeko readily consume native threatened freshwater mussels (*Echyridella spp.* (Farnworth 2021)). Together, these findings illustrate how understanding the diet and behaviour of common species can have very real conservation implications, and that even infrequent food choices may have large effects on prey populations. Perhaps more importantly, it shows us that even our most familiar species still have some secrets for us to learn.

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