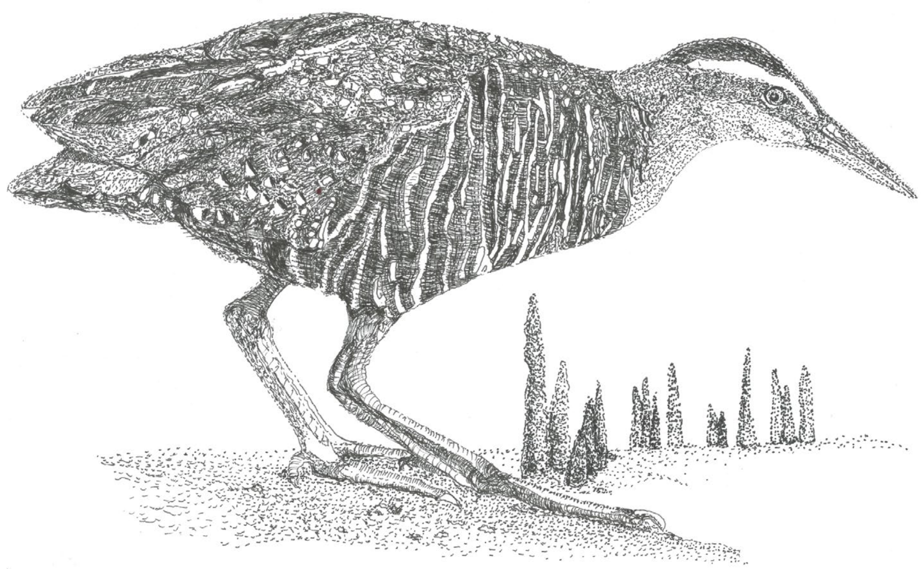
MANGROVE-AVIFAUNA RELATIONSHIPS IN AOTEAROA NEW ZEALAND

Conservation insights from banded rail
(*Gallirallus philippensis*) ecology



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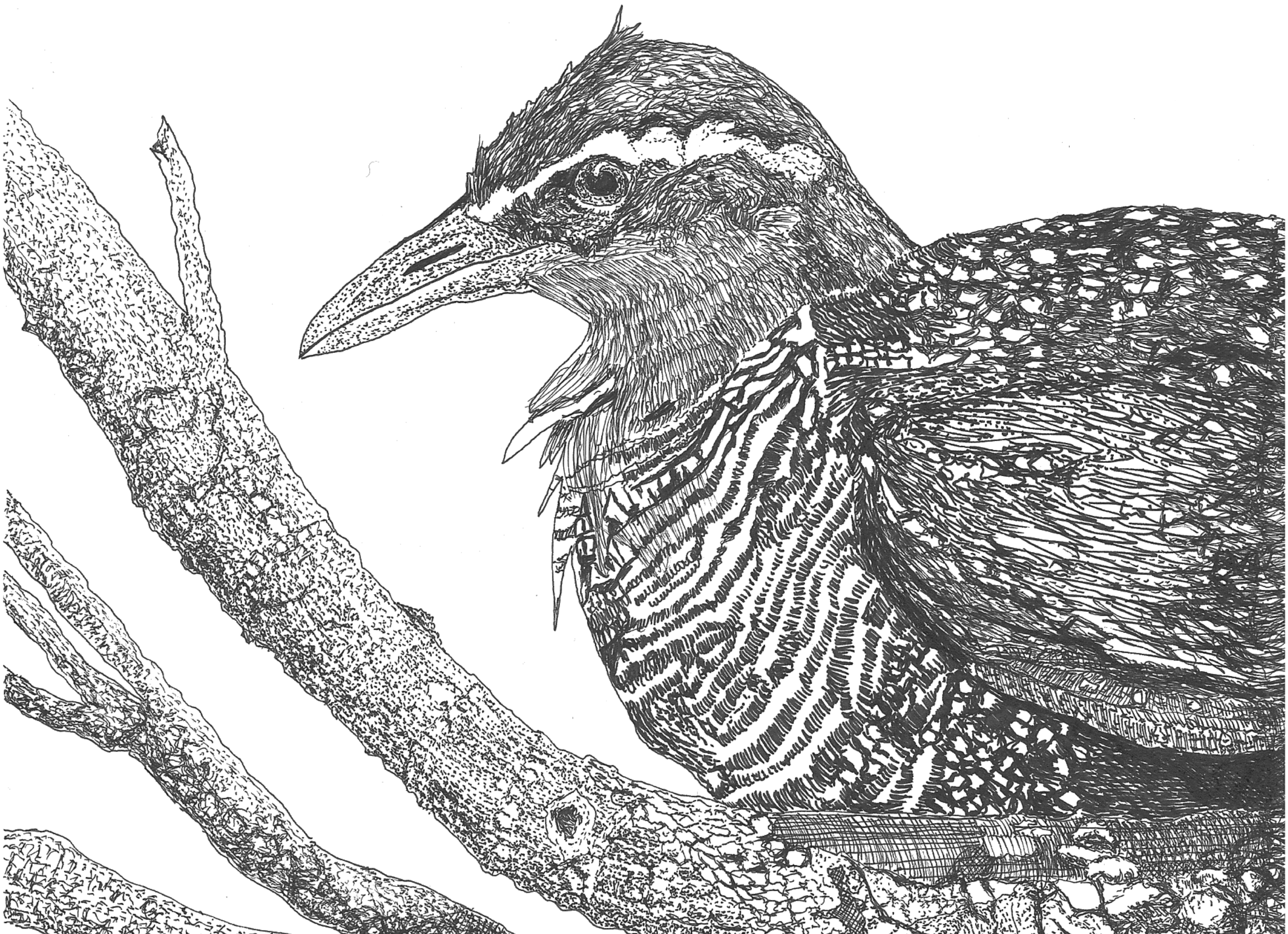

Title page: A New Zealand banded rail, *Gallirallus philippensis assimilis*, stands among the aerial roots of the native mangrove, *Avicennia marina* var. *australasica*. Artwork by Rick de Satgé.

Input page: A banded rail lurks among the pneumatophores and low-hanging branches of a mangrove tree. Artwork by Rick de Satgé.

Thesis abstract

Among terrestrial vertebrates, birds are the most ubiquitous taxa in mangroves globally, using these habitats to breed, roost, and forage. However, within the past half century, the large-scale loss and fragmentation of mangrove forests throughout much of their distribution has corresponded with declines in populations of mangrove-using avifauna. Despite these declines, remarkably little is known about the avifauna that inhabit mangrove forests, nor the ecological relationships that exist between birds and mangrove habitats. The absence of this understanding presents a significant barrier to effective avifauna conservation in mangrove environments.

The ecological relationships between the banded rail (*Gallirallus philippensis assimilis*) and mangroves (*Avicennia marina* var. *australasica*) in Aotearoa New Zealand are poorly understood, reflecting a lack of scientific research addressing mangrove avifauna globally. The study of banded rails has been hindered by their cryptic behaviours and exacerbated by mangroves being logistically challenging habitats to work in because of their intertidal nature, dense vegetation, and muddy substrates. The paucity of research in this field is a concern given that New Zealand's population of banded rails – largely restricted to mangroves in the coastal and estuarine regions lining the northern shores of the North Island – is declining and categorised as 'at-risk' of extinction. Mangroves in New Zealand are globally anomalous, having expanded rapidly in recent decades and having been subject to intensive management predicated on vegetation removal. In this context, understanding the importance of mangrove habitats for banded rails is of ecological interest and conservation concern. This thesis elucidates the ecological relationships between banded rails and mangroves in the context of recent mangrove expansion and contemporary management practices (especially in terms of removals) in New Zealand by (1) reviewing mangrove management practices and their effects on avifauna, (2) determining the relative habitat quality of mangroves for banded rails, (3) establishing and implementing a reliable survey method for banded rails, and (4) quantifying banded rail habitat selection and use in saltmarsh-mangrove complexes of northern New Zealand.

First, to understand the extent, configuration, and repercussions of mangrove removal in New Zealand, I reviewed all legal mangrove removals until 2020, using resource consent documents from relevant regional authorities. I determined that the area of mangrove removed is small relative to mangroves' contemporary area and expansion. Decisions regarding mangrove removal largely prioritised human-centric desires for recreational spaces rather than principles of ecological restoration. In addition, I showed that an ecological understanding of

the repercussions of removal on avifauna is limited by insufficient monitoring. Drawing on limited data, I suggested that mangrove removal creates a conservation trade-off, benefitting species that use open habitats, such as waders and shorebirds, at the expense of mangrove-using avifauna. I then emphasised the importance of addressing the drivers of mangrove expansion rather than its symptoms, situating New Zealand's management response in the theory of invasion biology.

Second, I assessed the habitat quality of New Zealand's mangroves for banded rails, using a resource-based approach. I quantified the abundance and diversity of macrofauna – key food resources to banded rails – collected from a stratified sampling regime across four habitat zones in four saltmarsh-mangrove complexes, determining that old-growth mangroves held the highest abundance and biomass of banded rail food resources. Additionally, I assessed the availability of these resources to banded rails using existing literature and field-based observations, theorising that mangroves provided the highest availability of food resources within saltmarsh-mangrove complexes.

Third, I established and implemented a survey method novel to the study of banded rails (and cryptic marsh birds more broadly). I determined that a combination of camera traps and drift fences (CDF) provides an effective method for surveying banded rails in intertidal habitats, capable of providing both presence-absence data and inferences into banded rail movement patterns. I observed banded rail movements between saltmarsh and mangrove habitats to be correlated with temporal and tidal cycles, the first time banded rail habitat use has been assessed in relation to environmental cues. I explored the applicability and value of the CDF method as a monitoring tool, suggesting the method could support new research avenues for cryptic species and complement monitoring methods used for banded rails in New Zealand.

Fourth, I quantified the habitat selection and habitat use patterns of banded rails at a home-range scale in saltmarsh-mangrove complexes, assessing data from GPS biotelemetry via resource selection ratios and a generalised linear mixed effects model. I determined that banded rail home ranges are largely restricted to saltmarsh and mangrove habitats finding that individuals select for mangrove habitats to support foraging efforts, select for saltmarsh habitats as roosting grounds, and generally avoid open habitats such as mudflats and residential gardens. I showed that habitat use may vary among individuals, noting two individuals that chose to roost in mangrove habitats overnight – a novel observation for this species. Additionally, biotelemetry findings confirmed movement patterns observed by camera traps in that banded rail habitat use was mediated by temporal and tidal cycles. Banded rails were significantly more likely to use mangroves during the day, whereas saltmarshes were primarily used at night and during high tides.

Combining insights from research findings and existing literature, this thesis demonstrates that mangrove habitats play an important role in supporting banded rails. While mangroves are not a prerequisite for the survival of banded rail individuals, mangroves represent preferred habitats and support banded rail behaviours such as foraging and roosting. Viewed from a population perspective, mangroves help maintain banded rail populations by providing habitats to the majority of the country's banded rail population. Three observations from this thesis are particularly relevant to conservationists and coastal managers in New Zealand: (1) mangroves are not uniform habitats; mangrove forests may appear structurally similar, but can be functionally different in their ability to support avifauna populations, (2) mangroves are more important to banded rails than previously understood or quantified; mangroves are preferred as foraging habitat to banded rails, can support roosting behaviours, and may make small patches of adjacent saltmarsh or terrestrial scrub viable breeding habitats, and (3) mangrove removal is likely to adversely affect local populations of banded rail, but more research is required to understand the nuances of these effects.

Acknowledgements

The origins of this PhD thesis can be traced back to Goukamma Nature Reserve and Marine Protected Area, where, as a child, I spent every summer holiday on a rubber-ducky (an inflatable kayak of sorts) watching kingfishers hover above the Goukamma river, herons stalk the gently sloping estuary banks, and spotted grunter splash their tails in the air as they dug, nose first, into the riverbed looking for prawns. I'm almost certain that the magic of that place chartered a course down the river that led me here some 20 years later, handing in a PhD thesis in conservation biology.

Along the way, there have been countless people that have helped me steer the course. During my time at the University of Cape Town (UCT), then HOD Professor Anusuya Chinsamy-Turan let me transfer from a degree in journalism to one in science, giving me a chance to prove myself despite not meeting the pre-requisites for a Bachelor of Science. Others at UCT entrenched and supported my desire to study the natural world; Associate Professor Betty Dawidowitz taught me chemistry during a time where Egyptian hieroglyphs were more relatable than organic compounds, Professor Adam West delivered the best course I've ever attended (Global Change Ecology), and Associate Professor Arjun Amar introduced me, to both my regret and gratitude, to the world of ecological statistics. Moving to Belgium, and the University of Antwerp, for my master's thesis, I have Professor Erik Matthysen and Dr Bogdan Cristescu to thank for their roles in developing my skills as an independent researcher, capable of identifying ecological patterns and their interconnections to human society.

Associate Professor Weihong Ji, my supervisor, took a chance on me. I applied to be her student from a small, kitchen-less flat in Bonn, Germany, having never met her, been to New Zealand, or set foot in a mangrove forest. One of Weihong's greatest strengths is taking brilliantly calculated leaps of faith, in people, research, and life. I'm so grateful Weihong decided to leap with me, providing both the springboard and the crash pad whenever needed. Weihong, thank you for your unflinching belief in me, your recognition that wellbeing enables good research, the example you set in having a balanced life, and your never-ending appreciation of the quirks of nature. You have a talent in guidance, providing me with sage advice always, watching me (without judgement) stumble from one "learning opportunity" to the next, and allowing me to self-correct until I miraculously realign with your original advice. It has been a pleasure being your PhD student and I am so grateful for the opportunity you have given me.

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There's a reason banded rails are so understudied in New Zealand: no-one dares venture into mangrove forests, for fear of mud, stench, and branches to the face. To a select and inspiring group of people, these factors were something to celebrate rather than fear. Covering more than 40 hectares of mangrove forest in search of macrofauna, footprints, lost GPS units, indecipherable noises, and actual banded rails is not something I did alone. During much of my time wading in mud, I was flanked by volunteers, ready to lose a favourite hat, embrace a spiderweb, or manoeuvre 200 meters of plastic netting and steel waratahs through dense bush, in order to see or sniff a banded rail. A massive thank you to Sam, Jeffrey, Kyle, Christine, James, Alex, Samara, Louise, Heshani, Zoë, Suyash, and Maddy for all your help in the field. Without you, I'd probably still be wondering around in the depths of Mangawhai estuary right now. A special mention to interns Gabi Keurntjes, Lucile Fayolle, and Clara Menu for the fantastic work they did in field and lab to advance the study of mangrove avifauna. Also, to DOC's Sarah Wills and Graeme Elliot, as well as Professor Thomas Bodey of the University of Aberdeen, thank you for taking time out of your busy lives to teach me how to handle and band a banded rail (resulting in banded banded rails). Your patience and skill were fantastic in equal measure.

Making sure that my research is relevant and accessible to policymakers, conservation decision-makers, and/or ecological managers has always been a key motivator for me. Thank you to Dame Professor Juliet Gerrard, and her team at the Office of the Prime Minister's Chief Science Advisor, for believing in the relevance of my research to policy and providing a platform to realise my ambitions of reaching policy- and decision-makers in New Zealand. Speaking of whom, a particular thank you to Jimmy Matthew, Alan Moore and Megan Carbines of Auckland

Council, Hamish Dean and Josie Crawshaw of Bay of Plenty Regional Council, Paul Maxwell, James Griffin and Sharon Callaghan of Northland Regional Council, and Dean Allen and Andrew Hammond of Waikato Regional Council for providing access to regional council data and information on coastal policies that helped inform Chapter 3 of this research. Further thanks to Helen Kettles of the Department of Conservation, and Associate Professor Carolyn Lundquist and Dr Daniel Hikuroa of Auckland University for helping to frame the questions asked in Chapter 3. Lastly, thank you to Chris Wedding and Graeme Don (Bioresearches) and Tim Martin (Wildlands) for your time in explaining practices around banded rail monitoring.

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The greatest credit I can give to my friends in New Zealand and abroad – you know who you are – is that you've put up with me throughout my PhD, in particular its latter stages. Thank you for your support and patience. If you're reading this, I promise to be more social and involved in your lives.

It's no exaggeration to say that my family has traversed oceans to help me get this thesis over the line. Ma, your contribution to this thesis is hidden in plain sight: the carefully checked sentences, the (hopefully) error-free grammar, the cross-referenced figures. It's a fair reflection of your support during my PhD; you've always been there, in the background, keeping me and the family ticking over. Thank you for your unyielding love and support. Da, your vat-hom-flaffie attitude has been just the tonic I've needed so often during this thesis. I'm so glad I can reflect the care and love you have shown me in the drawings that mark each chapter. Boeta, thank you for putting up with my absence and for squeezing normality into my life between thesis chapters. You've always had my back, through thick and thin. Claudia, my mother-in-all-but-law, thank you for being a wonderful Omi and creating the space to write my final thoughts.

Without a shadow of a doubt, this thesis would not have seen the light of day without the support of my partner, Lisa. For every hour that has gone into this thesis, Lisa has put two into our children. She has been our household's breadwinner. She has risen above, time and time again, all while keeping her sanity intact. If anyone is deserving of a dissertation, it is her. Lisa, a few sentences in an acknowledgements section can never repay the effort, support, and consideration you've poured into my PhD journey. Your grace and kindness continue to astound me. Thank you for all you have done. Following your advice, I'll keep this to a minimum – I'd rather spend time with you than writing about you.

Lastly, to my children, Louie and Malea, thank you for giving me the push I needed to finish my PhD. I once thought of my PhD as my baby, but then I had you and realised what a frivolous comparison that was. I love you both, endlessly.

Permits and ethics

Banded rail fieldwork, including recording, capture, banding, and GPS tagging, across multiple field sites was undertaken with the permission of local iwi or hapu (including Ngāti Manuhiri, Te Uri O Hau, Te Kawerau a Maki, and Ngāti Whātua o Kaipara), the New Zealand Department of Conservation (74169-RES), and the Massey University Animal Ethics Committee (19/04).

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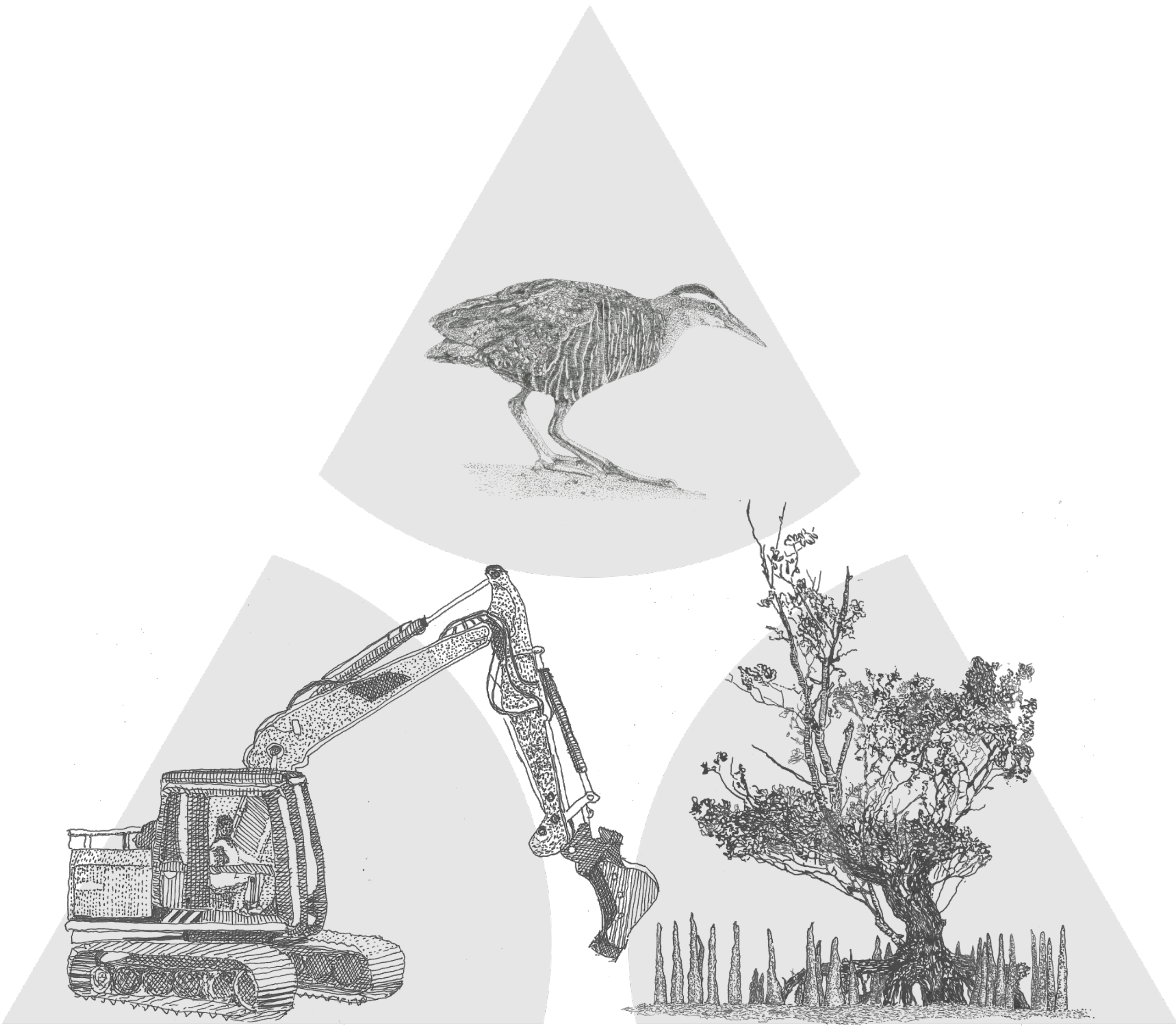
CHAPTER 1

GENERAL INTRODUCTION



<u>Chapter 1 cover image</u>: A banded rail (*Gallirallus philippensis assimilis*), a mangrove tree (*Avicennia marina* var. *australasica*), and a digger represent the interactions between species, habitat, and people used as a guiding framework for this PhD. Artwork by Rick de Satgé.

1.1 Background

Mangrove forests in Aotearoa New Zealand (henceforth New Zealand) are rapidly expanding, fuelled by anthropogenic increases in terrigenous sediments and nutrients in estuaries (Horstman *et al.* 2018). This expansion, in stark contrast with global mangrove declines (FAO 2007; Spalding *et al.* 2010; Giri *et al.* 2011), has sparked debate about the value of mangrove ecosystems and raised concerns about changes to the habitat composition, ecosystem functioning, and recreational value of estuaries in New Zealand (Thrush *et al.* 2004; Harty 2009; Makowski & Finkl 2018).

In response to mangrove expansion in the past half century, regional authorities in northern New Zealand have removed substantial areas of mangrove vegetation throughout its distribution (Lundquist *et al.* 2014, 2017) despite a limited understanding of the ecological ramifications of these actions (Morrisey *et al.* 2010; Lundquist *et al.* 2014) and at odds with international efforts to restore mangrove forests (Spalding *et al.* 2014; UNEP *et al.* 2014). Consequently, New Zealand's mangroves have drawn intensive academic scrutiny (Horstman *et al.* 2018), including research on sediment processes (Nichol *et al.* 2000; Thrush *et al.* 2004; Jones 2008; Morrisey *et al.* 2010), invertebrate communities (Ellis *et al.* 2004; Alfaro 2006, 2010), carbon dynamics (Bulmer *et al.* 2016, 2020; Perez *et al.* 2017), nutrient fluxes (Lovelock *et al.* 2007; Bulmer *et al.* 2017b), mangrove management (Harty 2009; Morrisey *et al.* 2010; Lundquist *et al.* 2014, 2017; Stokes *et al.* 2016), and mangrove removal as a restoration tool (Stokes *et al.* 2016; Bulmer *et al.* 2017a). Despite this extensive research, remarkably little study has addressed the importance of mangroves as habitats for native birds (Lundquist *et al.* 2014; Bell & Blayney 2017b; Makowski & Finkl 2018) and avifauna are often omitted when evaluating the restoration success of mangrove removals (Stokes *et al.* 2016). A lack of mangrove-avifauna research is noteworthy given that biologists have studied the relationships between birds and their habitats for decades (Block & Brennan 1993), often situating these studies in the context of rapidly changing environments (Morrison *et al.* 2006; Saltz & White 2013; Seifert *et al.* 2018).

Although just 30–35 bird species are considered endemic to mangroves globally, almost 800 avifauna species or subspecies are thought to have distinct populations that are primarily found and reproduce in mangrove ecosystems (Luther & Greenberg 2009; Huang *et al.* 2019). New Zealand does not have any bird species considered endemic to mangrove forests (Crisp *et al.* 1990) but multiple species regularly use mangroves to roost, breed, and forage (Cox 1977). The lack of scholarship on the value of mangroves as habitats to birds, both in New Zealand and globally, can be largely attributed to difficult working conditions and the cryptic nature of many species that inhabit coastal wetlands (Marchant & Higgins 1993; Macintosh & Ashton 2002; Kutt 2007; Williams 2016). This thesis seeks to rectify this knowledge gap by improving ecological understanding of the relationships between the banded rail (*Gallirallus philippensis assimilis*) and mangrove forests in New Zealand, situating this research in a framework that evaluates the species, its habitats, and socio-political context that influences conservation and habitat management.

The banded rail is of particular interest because it is classified as 'at-risk' of extinction and undergoing decline in New Zealand (Robertson *et al.* 2021), while its population has undergone a substantial range contraction over the last century (Elliott 1983). Moreover, banded rails are frequently associated with mangroves in New Zealand, by biologists and birdwatchers alike (Bell & Blayney 2017a). An estimated 80-90% of New Zealand's banded rail population occurs in or adjacent to mangroves (Bellingham 2013; Bell & Blayney 2017a) and the species has been promoted as a flagship for mangrove and wetland conservation (National Wetland Trust 2021; Forest and Bird 2022a). Despite this status, data collected on banded rails are sparse (Robertson *et al.* 2017) and inferences about their habitat selection and use are limited (Elliott 1987, 1989; Botha 2011; Beauchamp 2015, 2022). The banded rail's 'at-risk' conservation status, as well as their close association with mangrove habitats subject to intensive management interventions, highlights a pressing need to understand the relationships between banded rails and mangrove habitats in order to inform effective conservation strategies.

1.2 Theoretical framework

The foundational objective of this PhD is to elucidate the ecological relationships between banded rails and mangrove habitats. As has long been the case for ecological study, I situate these relationships within habitat theory as I evaluate banded rail habitat selection, use, and quality in this thesis. While an understanding of the associations between animals and their habitats is a prerequisite for effective conservation (Luck 2002; Morris 2003; Morrison *et al.* 2006; Seifert *et al.* 2018), Giles (1978), author of the book *Wildlife management*, emphasises the importance of recognising the societal context in which ecological relationships and conservation take place. Giles visualises the relationships between wildlife, habitat, and people in a triad, presenting these separate elements as interactive. This viewpoint resonates with the intersectionality of conservation biology, a scientific field that draws on multiple disciplines, including social sciences, biological sciences, and resource management (Soulé 1985; Dyke 2008; Van Dyke & Lamb 2020).

Adapting Giles' triad concept, this thesis adopts a theoretical framework that examines the ecology of banded rail-mangrove relationships in the context of habitat management and conservation biology (Figure 1.1). While the bulk of this thesis examines the relationships between banded rails and mangrove forests through the lens of habitat theory (Chapters 4-6), it also evaluates mangrove management in New Zealand (Chapter 3) and explores the conservation implications of research findings throughout. In the following chapter (Chapter 2), I provide a comprehensive review of the species (banded rail, *Gallirallus philippensis*), the habitat (mangroves, *Avicenia marina* var. *australasica*), and the socio-political context ('people') that make up the three corners of the theoretical framework triad (Figure 1.1). The interaction of these three areas is critical as is indicated by the bi-directional arrows in Figure 1.1.

1.2.1 Ecological study: habitat theory

Much of this thesis evaluates the ecology of banded rails, i.e., the relationships between a species and its environment (Block & Brennan 1993). Here, I summarise the habitat theory that frames these relationships and apply this theory to the study of banded rails in mangrove habitats of New Zealand.

1.2.1.1 Functional and structural habitat

As researchers have assembled increasing knowledge on animals and the environments in which they live, the concept of 'habitat' has played a key role in interpreting how individuals interact with their surroundings (Block & Brennan 1993; Morrison *et al.* 2006). The habitat concept is a cornerstone of ecological study and wildlife management (Krausman 1999), and has been applied in a wealth of studies (Morrison *et al.* 2006). While this has aided the development of the concept, it has also resulted in loose terminology and a varying set of definitions related to habitat (Block & Brennan 1993; Krausman 1999; Jones 2001; Gaillard *et al.* 2010). As per Gaillard *et al.* (2010), this thesis recognises two inherently different, but complementary definitions for the term 'habitat' – the 'functional' definition and the 'structural' definition (described in detail below).

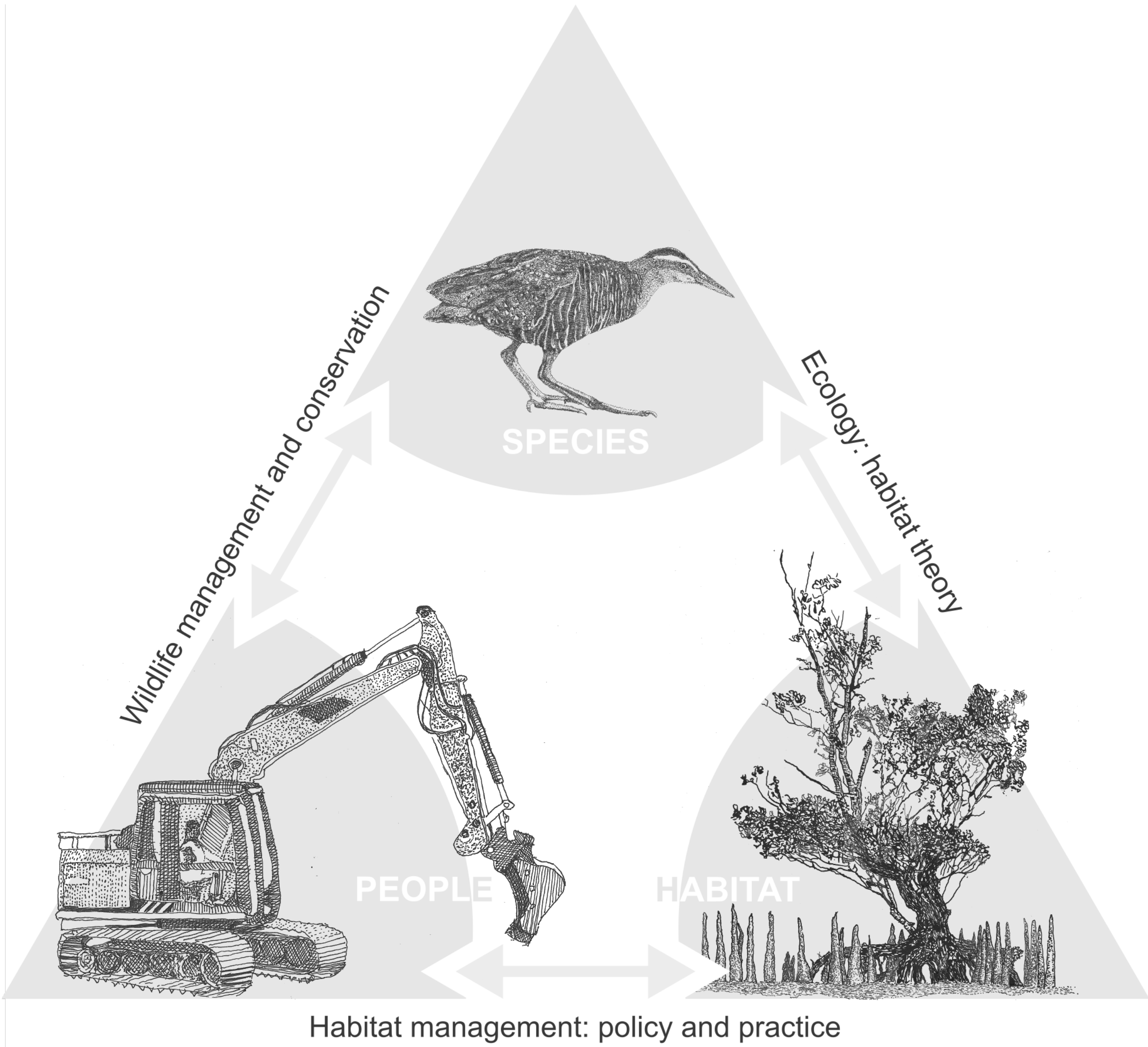


Figure 1.1 A visual depiction of the theoretical framework for this thesis. Based on Giles' (1978) triad concept of the interconnected relationships between wildlife, habitat, and people, this thesis is structured by a theoretical framework which studies the ecological relationships between the banded rail (top) and mangrove habitats (bottom right) in the context of their relationships with people (bottom left) through the lens of habitat management and conservation. In this visual representation of the theoretical framework, 'people' are depicted as a digger (being driven by a human), because people frequently use heavy-machinery during the removal of mangrove forests – an intervention that has come to define contemporary mangrove management in New Zealand.

A habitat is, in its simplest form, the place where an organism lives (Odum 1971). While useful, this simple definition does not enlighten the relationship between organism and place. The concept of the 'niche' – the suite of biotic and abiotic factors that permit an animals existence in an environment, and the manner in which an animal exploits these factors (Hutchinson 1957; James *et al.* 1984; Block & Brennan 1993) – links occupancy with environment, and is the theoretical backbone of the 'functional' habitat concept (Gaillard *et al.* 2010) exemplified by multiple authors (Block & Brennan 1993; Hall *et al.* 1997; Krausman 1999; Sinclair *et al.* 2005). Thus, the functional habitat concept (FHC) defines habitats as the subset of resources and conditions – a distinctive set of physical and environmental factors – which result in occupancy, including survival and reproduction, by a given organism (Block & Brennan 1993; Krausman 1999).

While vegetation is an important component of the FHC, it only makes up part of the sum of specific resources that are needed by organisms (Cody 1981; Krausman 1999). These resources are traditionally viewed to consist of food, water and cover (Leopold 1933), while more recent theory includes a wide variety of environmental factors (Morrison *et al.* 2006) such as temperature, precipitation, topography, species interactions (e.g., predation and competition), and further organism-specific factors (Krausman 1999). Thus, habitat is a series of components unique to the organism in question. The dispersion of these components in space and time determines the distribution, density, structure and productivity of wildlife populations (Morrison *et al.* 2006). Gaillard *et al.* (2010) coin FHC as 'functional' as this conceptualisation of habitat can be functionally linked with aspects like animal survival or reproductive success (Pulliam 2000).

Using this functional interpretation of habitat, the presence and persistence of banded rail in mangroves (or other habitats) is likely related to a suite of factors, including (but not limited to) the structure and diversity of the vegetation (Elliott 1989; Botha 2011), the distribution of food resources (Elliott 1987), predation (Parker & Brunton 2004), competition, and the availability of fresh water (Elliott 1983).

'Structural habitat' (SHC) provides an alternate "common-sense resource-based" definition of habitat (Gaillard *et al.* 2010) defined by spatially contiguous, homogenous, and physiognomically distinct categories of vegetation communities (Hutto 1985; Gaillard *et al.* 2010). While more restrictive than FHC, Hutto (1985) argues that dominant plant species extensively alter environments such that important subsets of species are coincident in their distributions, and that habitat types correspond well with biome types or plant community types (Whittaker 1975; Ricklefs 1979; in Hutto 1985). Habitat categories might therefore include saltmarsh, mangrove, grassland, pine forest, and so forth, with more refined categories (e.g. rush saltmarsh) possible if they are spatially and physiognomically distinct (Hutto 1985). The shortcomings of this definition are that it is not species-specific, does not account for spatial and temporal scales, and its quality to a given animal is difficult to measure (Gaillard *et al.* 2010). Nevertheless, the application of SHC has high relevance to wildlife management, as conservation policy is often shaped by a corresponding view of the environment (Morrison *et al.* 2006; Gaillard *et al.* 2010).

In New Zealand, coastal policy and concomitant management practices adopt a structural habitat definition of mangrove forests. Mangrove vegetation is 'managed' on the basis of its identity (a species of vegetation), rather than its functional value to other species (Harty 2009). For example, mangrove removal projects in New Zealand target the mangrove species, *Avicennia marina* var. *australasica*, while adjacent habitats comprising other species such as rush saltmarsh (e.g. *Juncus kraussii* subsp. *Australiensis*) are left in place (Morrisey *et al.* 2010; Lundquist *et al.* 2014). Similarly, where mangroves are monitored as a habitat for banded rails (e.g., Beauchamp 2015; Don 2015; Don & Wedding 2016), this habitat is viewed structurally, with the assumption that banded rails are coincident in the distribution of a dominant vegetation type (Hutto 1985; Heather & Robertson 2005).

1.2.1.2 Habitat quality, use and selection

When studying how animals use and select their environments, researchers typically attempt to quantify habitat quality and availability. For populations to persist within an area, habitats must be of sufficient quality (also referred to as 'suitability') – i.e., provide the conditions or resources suitable for survival, reproduction and population persistence (Block & Brennan 1993). Habitat quality can be seen as a continuous variable; ranging from low (i.e. resources only available for survival), to median (resources support reproduction), to high (resources available for population persistence) (Block & Brennan 1993; Hall *et al.* 1997; Krausman 1999).

Understanding the distribution and availability of resources in mangrove habitats can provide insight into the quality of these habitats for banded rails (Johnson 2007). Specifically, understanding the abundance and distribution of banded rail food resources – typically benthic macrofauna (Elliott 1983) – in mangrove environments can yield insight into their relative habitat quality. Although macrofauna have been studied in mangrove environments in New

Zealand (Ellis *et al.* 2004; Alfaro 2006, 2010), their distribution and abundance have not been used as a measure of habitat quality for birds, nor linked to habitat use patterns of species such as the banded rail. In Chapter 4 of this thesis, I quantify the distribution and abundance of macrofauna in order to assess the habitat quality of mangroves for banded rails.

In addition to assessing habitat quality, this thesis also seeks to quantify habitat selection and use by banded rails using camera traps (Chapter 5) and GPS biotelemetry (Chapter 6). 'Habitat use' refers to the "manner in which a species uses a collection of environmental components to meet life requisites" (Block & Brennan 1993, p. 38). Habitat use can be broken down into specific needs such as foraging, denning, breeding, roosting or other life history traits (Block & Brennan 1993; Krausman 1999). These categories can divide habitat into use-based areas (e.g. nesting habitat or foraging habitat), but more than one category can exist in a given area (Krausman 1999). For example, an area used for foraging may also illustrate the physical characteristics that facilitate roosting, cover behaviours or both (Kong *et al.* 2018). As discussed in more detail in coming chapters, mangroves may facilitate multiple life requisites for banded rails (Botha 2011; Beauchamp 2015; Bell & Blayney 2017a).

'Habitat selection' is often equated (or used interchangeably) with 'habitat use', despite being a distinct concept within habitat theory (Jones 2001). Habitat selection refers to the innate and learned behaviours that allow an animal to distinguish environmental components; these behaviours result in a disproportionate use of habitats to influence survival and fitness (Block & Brennan 1993; Jones 2001). Thus "when resources are used disproportionately to their availability, use is said to be selective'' (Manly *et al.* 2002, p. 1). Habitat selection implies that individuals actively understand and respond to complex environmental and behavioural processes, meaning habitat-use patterns are the product of habitat-selection processes (Krausman 1999; Jones 2001).

Habitat selection by banded rails has not been studied in New Zealand (or elsewhere), although banded rail habitat use has received minor attention. Elliott (1987) quantified habitat-use patterns of banded rails in saltmarsh habitats near Nelson on the New Zealand South Island, suggesting that banded rails preferred vegetation that provided adequate aerial cover without impeding their movement along the ground. Elliott's (1987) study was restricted to sites on the South Island, some of the few locations where banded rails occupy areas of rush saltmarsh in the absence of mangroves. In saltmarsh-mangrove complexes on the North Island – home to an estimate 80-90% of New Zealand's banded rail population (Bellingham 2013) – little is known about banded rail habitat use or selection. Observations from grey literature (Botha 2011; Richardson *et al.* 2019) and scientific study (Beauchamp 2022) suggest that banded rails select for mangrove habitats to support foraging behaviours, but this has long remained a working hypothesis. This thesis addresses this hypothesis in Chapter 6, where I used GPS biotelemetry to determine the habitat use and selection of banded rails among habitats at a home range scale.

1.2.1.3 Habitat scale

When evaluating wildlife-habitat relationships, it is imperative that researchers recognise that their perceptions are scale-dependent (Hall *et al.* 1997). Johnson's (1980) seminal work on hierarchical habitat selection defines four spatial scales at which selection takes place: first-order selection that takes place at a geographic scale, i.e. the distribution of a species; second-order selection for a home-range, i.e. where animals conduct their activities; third-order selection for specific components or patches within of their home-range; and fourth order selection for specific sites (e.g., nest) or item (e.g., food) within a given habitat component (Hall *et al.* 1997; Gaillard *et al.* 2010). These scales are often grouped as macrohabitat – landscape-scale features that correlate with the distribution or abundance of species; and microhabitat – specific, recognisable features of the environment such as patches of habitat or a tree that corresponds with the presence of individuals (Block & Brennan 1993).

In this thesis, I evaluate habitat selection by banded rails at the second-order scale only (Chapter 6) as plans to evaluate selection at first- and fourth-order scales were scuppered by multiple Covid-19 lockdowns in 2020 and 2021[1]. However, I outline future pathways for this research in Chapter 7.

[1] The Covid-19 pandemic had significant repercussions for the scope of this thesis. Frequent and unpredictable regional border closures meant that study sites outside the Auckland region were inaccessible at key times, included during fieldwork sessions that had been planned months in advance. Moreover, due to DOC permit restrictions, biotelemetry fieldwork could not be undertaken without a licensed, rail-qualified DOC Officer – of which there are ca. 5 in the country, none of whom live in the Auckland region. Given inter-regional travel was banned for months at a time, this prevented several planned fieldwork sessions from going ahead. In addition to affecting this thesis' scope, Covid-19 had negative effects on the research environment, for students and their supervisors alike. The loss of both the tangible and intangible aspects of being a PhD student – including academic community, lab meetings, field excursions, in-person interactions with colleagues, impromptu brainstorming sessions and collaboration opportunities, conferences, teaching opportunities, access to lab equipment, a quiet and comfortable working environment, among others – took a significant toll on my ability, and the ability of others, to meet research objectives and stick to pre-pandemic timelines. In the case of this thesis, I required an additional year to undertake additional fieldwork and meet adjusted goals.

1.2.2 Contextualising ecological relationships

As do many scholars, Giles (1978) argues that wildlife-habitat relationships interact with, and are influenced by, people. As such, understanding how society perceives and interacts with species or habitats is a fundamental part of effective conservation (Dickman 2010; Saltz & White 2013; Colléony *et al.* 2017; van Eeden *et al.* 2020). In New Zealand, policy, management, and public perceptions of coastal habitats and their birds (Harty 2009; Lundquist *et al.* 2014; Stokes *et al.* 2016) have the potential to influence the ecological relationships between banded rails and mangrove forests, both positively and negatively. Here, I discuss the tensions in policy and public perception and highlight the importance of providing this context when examining banded rail-mangrove relationships.

1.2.2.1 Conservation policy and perception in New Zealand: birds

New Zealand has a well-established and internationally renowned conservation ethic (Clout 2001; PCE 2017) and is particularly known for its pioneering work in bird conservation (Clout & Craig 1995; Miskelly & Powlesland 2013), its mission to eradicate invasive mammalian predators (Russell *et al.* 2015), and its extensive network of conservation areas (Craig *et al.* 2000; Norton 2000). Public support for conservation efforts in New Zealand is generally high (Craig *et al.* 2000; Seabrook-Davidson & Brunton 2014; Peters *et al.* 2015) and public awareness campaigns for avifauna protection, such as Forest and Bird's 'Bird of the Year' (started in 2005), are popular and regularly receive international attention. Most indigenous bird species are protected under the 1953 Wildlife Act, a policy decision that has driven the expansion New Zealand's conservation estate in recent decades (PCE 2017). Today, more than a third of New Zealand's land area lies within a network of national parks, wildlife areas, conservation areas, reserves and private sanctuaries (Clout 2001; Department of Conservation 2022). Following the Wildlife Act, the conservation of bird species was further entrenched by the 1991 Resource Management Act (RMA) that made the protection of "significant habitats of indigenous fauna" a matter of national importance, and later mandated that regional authorities "maintain indigenous biological diversity" (PCE 2017, p.22). National and regional authorities have poured huge sums of money into conservation efforts (Cullen *et al.* 2005), most notably in supporting the 'Predator Free 2050' ambition to rid mainland New Zealand of invasive mammalian predators by 2050 (Russell *et al.* 2015).

As part of New Zealand's avifauna conservation efforts, the Department of Conservation (founded in 1987) established the New Zealand Threat Classification System (NZTCS) in 2001, creating a systematic approach for assessing the conservation status of birds within New Zealand and its coastal waters (Townsend *et al.* 2008; Robertson *et al.* 2021). In the NZTCS, birds are assigned one of four high-level threat rankings based largely on estimates of population size and ongoing or predicted population trends: extinct, threatened, at risk, or not threatened (Townsend *et al.* 2008). In the most recent NZTCS assessment, approximately 80% of New Zealand's resident native bird species are described as either 'at risk' or 'threatened' (Robertson *et al.* 2021). The threat status of taxa in the NZTCS is complemented by 'qualifiers', critical pieces of information about a taxon's listing, status, and management (Townsend *et al.* 2008). In the most recent NZTCS (2021), banded rails were classified as 'At Risk – Declining' with an estimated population of 5,000 – 20,000 individuals and a low ongoing decline forecasted to lead to a 10 – 30% population reduction within the next ten years (Robertson *et al.* 2021). This threat classification is accompanied by multiple qualifiers, including 'Climate Impact' (the species is known or predicted to be adversely affected by long-term climate trends and/or extreme events), 'Conservation Research Needed' (the causes of decline and/or solution for recovery need further research), 'Data Poor Size' (there is a lack of data on population size), 'Data Poor Trend' (there is lack of data on population trends), and 'Range Restricted' (confined to substrates, habitats, or geographic areas of less than 1,000 square kilometres).

Echoing the data-poor qualifiers that describe the banded rail's threat classification, the species is not widely known to the New Zealand public – probably as a result of the banded rail's reclusive nature (Elliott 1983; Marchant & Higgins 1993) and lack of academic study. In the 2022 edition of the 'Bird of the Year' competition, Forest and Bird assigned the banded rail to the 'underbird' category, a list of 20 "overlooked" birds identified using an algorithm that took into account the birds' popularity in previous iterations of the competition, media coverage, and conservation status (Forest and Bird 2022b). This category is indicative of a broader trend in conservation: animals that are not deemed attractive, charismatic, and/or highly endangered tend to go largely unnoticed by the public and are understudied by scientists (Clucas *et al.* 2008; Smith & Sutton 2008; Veríssimo *et al.* 2009, 2017; Colléony *et al.* 2017). In the 2021 and 2022 editions of Bird of the Year, the banded rail was the subject of small-scale advocacy campaigns by the National Wetland Trust and the Office of the Prime Minister's Chief Science Advisor, but the species failed to make the top ten in the final vote count in both years.

1.2.2.2 Conservation policy and protection in New Zealand: mangroves

In 1995, the Ministry for the Environment set the goal of maintaining and enhancing the net area of New Zealand's remaining indigenous forests and enhancing the ecological integrity of other remaining indigenous ecosystems to counteract the extensive loss of forest cover (70% lost) and wetlands (90% lost) since human colonisation of New Zealand some 800 years ago(MfE 1995). This goal catalysed legislative and attitudinal changes in the late 1990s that saw a shift away from bush clearance towards preservation of native habitats, resulting in most public indigenous forests falling under the protection of the Department of Conservation (Davis & Cocklin 2001). As a result, the rate of indigenous land cover loss has slowed substantially in recent decades (MfE & Stats NZ 2022), although estimates suggest that there has been a small net loss of indigenous land cover (native forest, scrub, shrubland, and grasslands) between 2012 and 2018. Motivation for forest preservation and restoration in New Zealand extends beyond ecologically-oriented goals as native forests are considered important to people, promoting wellbeing and a sense of place as well as providing economic benefits and recreation opportunities, and contributing to New Zealand's national identity (Masterson *et al.* 2017; Department of Conservation 2020; Dunball 2020; MfE & Stats NZ 2022).

While inland forests in New Zealand are protected and valued by people and policy alike, coastal mangrove forests are often perceived differently. Similar to inland forests, mangrove forests underwent significant declines with the arrival of European settlers, as coastal areas were subject to coastal development, grazing, and reclamation for ports and agriculture (Morrisey *et al.* 2007; Horstman *et al.* 2018). Implementation of the 1977 New Zealand Harbour's Amendment Act and the 1994 New Zealand Coastal Policy Statement granted mangroves protected status, given they are an indigenous vegetation (Harty 2009; Morrisey *et al.* 2010; Stokes *et al.* 2016). In addition, mangrove forests are protected under the RMA under the mandates to protect "areas of significant indigenous vegetation and significant habitats of indigenous flora" and to prevent disturbance or destruction to coastal areas in "a manner likely to have an adverse effect on the foreshore or seabed, or on plants or animals or their habitat" (New Zealand Government 1991, RMA sections 6 and 12e). Unlike inland forests, mangrove forests have rebounded substantially since their early decline, primarily as anthropogenically-induced increases in sediment have facilitated the rapid seaward expansion and densification of mangroves (Lundquist *et al.* 2014; Swales *et al.* 2015; Suyadi *et al.* 2019). As a result, coastal policies allow the removal of mangrove seedlings and mature forests at small scales (Environment Waikato 2012; Auckland Council 2019; Bay of Plenty Regional Council 2019; Northland Regional Council 2020), while removal at larger scales is possible (and common – see Chapter 3) with a resource consent from a regional authority (New Zealand Government 1991, RMA section 12e). This approach is in alignment with the RMA mandate to provide for "the maintenance and enhancement of public access to and along the coastal marine area" (New Zealand Government 1991, RMA section 7).

The expansion of mangrove forests in New Zealand has fuelled significant social debate, resulting in polemic viewpoints regarding mangrove protection (as applied to inland forests) and mangrove removal (as applied to invasive vegetation). In many coastal communities, mangroves are unwanted, perceived as eyesores, odorous, and detrimental to coastal ecosystems and recreational activities (Harty 2009; Dencer-Brown *et al.* 2018). This viewpoint is a far-cry from the wider appreciation of inland indigenous forests (MfE & Stats NZ 2022) despite the array of ecosystem services provided by mangroves (Barbier *et al.* 2011; Dencer-Brown *et al.* 2018) and a push for mangrove restoration in other parts of the world (Spalding *et al.* 2014; UNEP *et al.* 2014).

In New Zealand, mangrove management has become synonymous with vegetation removal, reflecting the general approach taken for invasive vegetation (Nackley *et al.* 2017). In Chapter 3 of this thesis, I situate New Zealand's mangrove management practices within the theory of invasion biology, arguing that mangrove expansion in New Zealand meets the theoretical prerequisites of a native invasion (Valéry *et al.* 2009; Simberloff 2010) and is perceived and managed accordingly. In Chapter 3, I discuss the differences between management of alien and native invasions and highlight the importance and complexities of addressing the drivers of mangrove expansion in New Zealand.

1.2.2.3 Tensions in policy and perception

The perceptions and policies surrounding mangroves and birds such as the banded rail yield several tensions. First, and most pertinently, banded rails are deemed an 'at risk' species undergoing population decline (Robertson *et al.* 2021), yet the habitats they are most commonly associated with (Bell & Blayney 2017a) – mangrove forests – are actively removed in New Zealand. Second, New Zealand society at large appreciates avifauna and prioritises their conservation but may undervalue species that are less well known or not charismatic. Third, mangrove forests that provide an array of ecosystem services do not seem to hold the same value for communities as inland native forests do, despite both being protected under national and regional conservation frameworks. And fourth, contradictory policies at a national and regional level mean that mangroves are simultaneously valued as indigenous vegetation, but also viewed as an obstruction to public access in coastal areas.

Ultimately, these tensions prompted the overarching question that has guided the direction and development of this thesis:

In the context of mangrove removal practices in New Zealand, what is the importance of mangrove forests as habitats for the banded rail?

1.3 Thesis aim and objectives

The overarching aim of this thesis is to improve the ecological understanding of the relationships between the banded rail (*Gallirallus philippensis assimilis*) and mangrove forests in New Zealand.

In addressing this aim, I set the following research objectives:

1. (i) Determine the extent of mangrove removal in New Zealand, and
   (ii) its potential effects on banded rail populations
2. Determine the relative quality of mangrove habitats to banded rails in saltmarsh-mangrove complexes
3. Establish and implement a reliable method for monitoring banded rails in intertidal environments
4. Quantify banded rail habitat selection and habitat use in saltmarsh-mangrove complexes

These objectives are investigated in Chapters 3 to 6, respectively, and have been designed to create intersectional insights into banded rail ecology and conservation.

1.4 Thesis structure

This thesis is organised into seven chapters, comprising four research chapters (Chapters 3 – 6) that are written in a publication format and are in preparation for imminent journal submission. This format has resulted in some unavoidable repetition, particularly in context setting and study site descriptions. Nevertheless, I have kept duplication to a minimum wherever possible.

In Chapter 1, this chapter, I provide a brief overview of mangroves and banded rails in New Zealand, highlighting the importance of understanding the ecological relationships between habitat and bird. In addition, I introduce the theoretical framework adopted by this thesis; a triad that visualises the relationships between wildlife, habitat, and people (Figure 1.1) and I expand on the ecological theory and social context underpinning these relationships. In Chapter 2, I establish the research context by providing a review of literature relating to mangroves and their avifauna, both globally and in New Zealand.

In Chapter 3, I investigate mangrove management practices in New Zealand, with a view to contextualising the ecological relationships between banded rails and mangroves. Additionally, I collate existing monitoring data to assess the known effects of mangrove removal on avifauna in general and banded rails in particular.

In Chapter 4, I assess the relative habitat quality of mangrove habitats within saltmarsh-mangrove complexes. In this chapter, I use the distribution and abundance of food resources (macrofauna) as an indicator of habitat quality and assess the composition and diversity of macrofauna communities among habitats used by banded rails.

In Chapter 5, I present and implement a novel method of surveying ground-dwelling avifauna, namely the use of camera traps in combination with drift fences. Using data derived from this survey approach, I assess the inter-habitat movement patterns of banded rails in relation to environmental cues.

In Chapter 6, I quantify the habitat selection and use patterns of banded rails in saltmarsh-mangrove complexes. In addition, I discern banded home ranges using data from GPS biotelemetry.

In the final chapter, Chapter 7, I present the key findings of all research chapters, highlight their contributions to scientific knowledge and their implications for conservation, and I make recommendations for areas of future research both within each research component and for the interlinked research as a whole.

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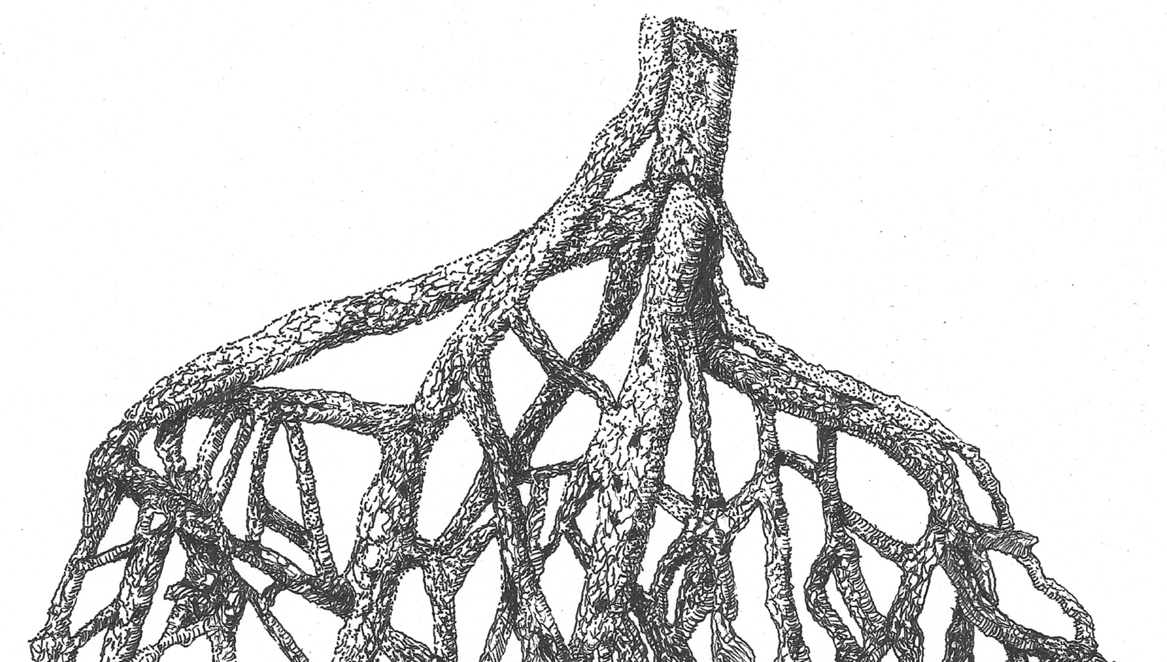
CHAPTER 2
LITERATURE REVIEW



This chapter reviews literature relevant to this thesis' overarching research question and theoretical framework (Chapter 1). Thus, this chapter (1) provides an overview of the state of mangrove forests, both globally and in New Zealand, (2) reviews mangrove management practices in New Zealand, (3) summarises scientific literature on mangrove avifauna, both globally and in New Zealand, and (4) introduces the model species of this thesis, the banded rail *Gallirallus philippensis assimilis*. Additionally, I show how knowledge gaps within the literature relate to the structure of this thesis.

Chapter 2 cover image: an artistic impression of the aerial roots of the red mangrove *Rhizophora mangle* which is distributed in tropical and subtropical areas in both hemispheres, extending to near 28˚ N to S latitude. Artwork by Rick de Satgé.

2.1 Mangroves

In this section (2.1), I address objectives 1 and 2 of this review by providing a definition of mangroves, exploring the diversity, distribution, and decline of mangroves globally, and describing the state of New Zealand's mangroves and concomitant management practices in the country.

2.1.1 Mangrove definition

Mangroves are distinctive plant communities that occupy the intertidal zones of low-energy coastal and estuarine environments (Morrisey *et al.* 2007). The term 'mangrove' has been used to refer to the constituent plants of these (sub-) tropical intertidal forest communities or to the community itself (Tomlinson 2016). The constituent plants are further classified into 'true mangroves' and 'mangrove associates' (Tomlinson 2016). True mangroves show unique adaptations to intertidal environments (e.g. physiological salt exclusion or aerial roots), and, unlike mangrove associates, only occur in mangrove ecosystems and do not extend into terrestrial communities (Spalding *et al.* 2010; Tomlinson 2016). Hence, true mangroves are defined by their shared traits that allow them to live successfully, and largely exclusively, in stressful intertidal environments (Morrisey *et al.* 2010).

For clarity, this literature review will use the term 'mangrove' to refer to true mangrove plant species – halophytic (salt-tolerant) trees and shrubs, typically woody and taller than half a meter, which grow above mean sea level in the intertidal zone of coastal or estuarine environments (Duke 1991, 1992). To avoid confusion, mangroves and their associated microbes, fungi, plants, and animals will be referred to as the 'mangrove community' or 'mangal' (Macnae 1968; Kathiresan & Bingham 2001), while the 'mangrove ecosystem' refers to the mangal and its associated abiotic factors (Kathiresan & Bingham 2001).

2.1.2 Mangroves globally: diversity, distribution, and decline

Globally, there are approximately 70 species of true mangroves within 19 families (Morrisey *et al.* 2010), found between ±32˚N and ±38˚S (Quisthoudt *et al.* 2012) in more than 118 countries and territories (Spalding *et al.* 2010; Giri *et al.* 2011). As observed in other taxa, mangrove species richness is highest at the equator and decreases with increasing latitude (Ellison 2002). Mangroves are not distributed evenly across the globe, with south-east Asia (33.8%) and Africa (20.9%) accounting for over half of the global mangrove forest extent (Thomas *et al.* 2017). The latitudinal distribution of mangroves is primarily driven by temperature, and moderated at local scales by aridity and disturbance (Morrisey *et al.* 2010; Quisthoudt *et al.* 2012; Tomlinson 2016). Mangroves are largely restricted to climates where mean air temperatures of the coldest months are above 20˚C (Morrisey *et al.* 2010). Thus, mangroves predominantly occur in the tropics, although outlier mangrove communities – referred to as 'temperate mangroves' – do occur at higher latitudes (Morrisey *et al.* 2010). The poleward extent of mangroves is limited by ground frost and generally coincides with the winter position of the 20˚C seawater isotherm (Duke *et al.* 1998; Horstman *et al.* 2018). Examples of temperate mangrove forests include mangroves in New Zealand (see section *Mangroves in New Zealand*), South Africa, southern Florida, southern Australia, and southern Japan (Morrisey *et al.* 2010).

Worldwide, mangroves forests are restricted to narrow strips along coastlines, covering an estimated total area of 137,000–152,000 square kilometres (Spalding *et al.* 2010; Giri *et al.* 2011). For reference, this represents less than 0.4% of the global total forest area, and less than 1% of the total area of tropical forests (Spalding *et al.* 2010; FAO 2015). Hence, despite the wide latitudinal range of mangrove forests, their limited total area makes them a relatively rare forest type (Spalding *et al.* 2010; Quisthoudt *et al.* 2012). This rarity has been emphasised by historical and ongoing losses of mangrove forest. An estimated 20–35% of mangrove forest area was lost between 1980 and 2005 (Agardy & Alder 2005; FAO 2007), translating to an average annual rate of mangrove loss of 0.8–2% over this period (Valiela *et al.* 2001; FAO 2007; Spalding *et al.* 2010). This rate of loss was greater than or equal to declines in adjacent coral reefs or tropical rainforests over the same period (Duke *et al.* 2007). More recent estimates of mangrove loss suggest that the *rate* of mangrove loss is declining (Spalding *et al.* 2010; Hamilton & Casey 2016; Richards & Friess 2016; Goldberg *et al.* 2020). Between 2000 and 2005, mangroves were lost at a rate of 0.66% per annum – a notable reduction but nevertheless three to four times higher than estimates of the rate of global forest loss over the same period (FAO 2007; Spalding *et al.* 2010). The most recent estimate of mangrove loss, measured between 2000 and 2016, indicates mangroves were lost at an annual average rate of 0.13%, corresponding to 3,363 square-kilometres or approximately two percent of the global mangrove area (Goldberg *et al.* 2020).

Importantly, the proportion of mangrove loss varies substantially by global region. For example, south-east Asia lost almost 27%(16,900 km^2) of its mangrove forest area between 1980 and 2005, while Australasia lost just 0.6% (90 km^2) over the same time period (Spalding *et al.* 2010). South-east Asia has remained the epicentre of mangrove losses in more recent estimates; the vast majority (nearly 80%) of mangroves lost globally to anthropogenic causes between 2000 and 2016 occurred in six nations: Indonesia, Myanmar, the Philippines, Thailand, Malaysia and Vietnam (Goldberg *et al.* 2020).

Global mangrove declines have been driven by multiple factors, including clearance for aquaculture and urbanisation, overexploitation, erosion, coastal infill, and deterioration as an indirect effect of pollution and upstream land use (Duke *et al.* 2007; UNEP *et al.* 2014). A recent assessment by Thomas et al. (2017) of changes in mangrove extent between 1996 and 2010 found the most frequent cause of mangrove decline to be the conversion of mangrove forests to aquaculture or agriculture, followed by logging. Natural processes of erosion and sediment deposition can exacerbate mangrove decline by prompting mangrove retreat, but can conversely also allow for regrowth and colonisation (Thomas *et al.* 2017; Goldberg *et al.* 2020). Erosion can cause mangrove decline by removing substrate that mangroves grow on or can result in mangrove growth by yielding sediment for new deposition in sheltered coastal environments. Indeed, several areas of temperate mangrove forests have seen localised expansions in recent decades (Morrisey *et al.* 2010), most notably in New Zealand (Horstman *et al.* 2018). However, mangrove regrowth and expansion has not compensated for ongoing mangrove losses at a global scale (Thomas *et al.* 2017), as evidenced by net mangrove losses in global mangrove extent (FAO 2007; Spalding *et al.* 2010; Goldberg *et al.* 2020).

The declining rate of annual mangrove losses has been the result of international action to conserve mangrove forests and a lack of remaining mangroves viable for conversion to coastal agriculture (Goldberg *et al.* 2020). In response to historical and ongoing mangrove losses, mangrove management strategies in many countries have been defined by restoration and rehabilitation efforts (Spalding *et al.* 2014; UNEP *et al.* 2014), with numerous international and national targets seeking to reforest significant areas of mangroves (Lovelock *et al.* 2022). Mangrove conservation efforts are considered particularly important given the ecosystem services these habitats provide, with their role in protecting coastlines from extreme climate events deemed an urgent global need (Lovelock *et al.* 2022).

2.1.3 Ecosystem services

The global loss of mangrove forests is of concern because they provide an array of ecosystem services, including carbon sequestration, water purification, coastal protection, erosion control and sediment trapping, nutrient cycling, heavy metal absorption, and the provision of fuelwood, timber and fisheries resources (Kitchen *et al.* 1999; Agardy & Alder 2005; Barbier *et al.* 2011; Mukherjee *et al.* 2014; Yessoufou & Stoffberg 2016; Bulmer *et al.* 2017; Selig *et al.* 2018).

Additionally, mangroves forests provide energy, organic matter (debris), and a diversity of microhabitats – from canopy through to substratum – which support both aquatic (marine and freshwater) and terrestrial fauna (Nagelkerken *et al.* 2008; Lundquist *et al.* 2017). Epibionts (e.g. tunicates, sponges, algae, and bivalves) anchor themselves to mangrove roots, macrofauna (infauna and epifauna) species live in the soft substratum within mangrove forests, motile fauna such as fishes, prawns and crabs find food and shelter between mangrove roots, while insects, mammals, reptiles and birds (see section *Mangrove avifauna*) also make use of mangrove forests (Agardy & Alder 2005; Nagelkerken *et al.* 2008). Species present in mangrove communities range from being wholly dependent on mangroves to opportunist visitors from neighbouring habitats (Macintosh & Ashton 2002).

2.2 Mangroves in New Zealand: a case study

2.2.1 Diversity and distribution

The mangrove genus *Avicennia* has the largest latitudinal range of all mangroves, from 32˚N in Bermuda to 38˚S in Australia and New Zealand (Horstman *et al.* 2018). *Avicennia* in New Zealand, also known as mānawa, represents one of the southern-most mangrove forests in the world, and is likely the relict population of a greater poleward mangrove distribution during a warmer period in the past (Duke *et al.* 1998; Morrisey *et al.* 2007; Horstman *et al.* 2018). New Zealand's mangrove forests comprise a single species: *Avicennia marina* var. *australasica*, previously known as *Avicennia marina* var. *resiniferai* (Horstman *et al.* 2018). Mangrove presence in New Zealand has been dated back to 19 million years BP (Sutherland 2003) and pollen records indicate that *Avicennia marina* has been present from around 14,000 years BP (Pocknall *et al.* 1989). *Avicennia marina* var. *australasica* is also found in south-eastern Australia, New Caledonia and Lord Howe Island (Duke 1991).

New Zealand's mangrove forests cover approximately 26,000 ha (Spalding *et al.* 2010) and are restricted to the northern coastlines of the North Island (Figure 2.1). Mangroves start as low forest in the far north of New Zealand (34˚27'S in) and gradually become low scrub towards their southern limit at Kawhia Harbour on the west coast (38˚05'S) and Ohiwa Harbour on the east coast (38˚03'S) (de Lange & de Lange 1994; Morrisey *et al.* 2007; Tomlinson 2016). Expansion of mānawa southwards is limited by several factors: low winter temperatures and frosts that depress physiological functioning (Morrisey *et al.* 2007; Lundquist *et al.* 2014b); dispersal barriers (unsuitable coastline); and unfavourable ocean currents that prevent establishment in suitable microclimates further south in New Zealand (de Lange & de Lange 1994; Morrisey *et al.* 2007).

2.2.2 Changes in mangrove extent

In line with global trends, loss of mangrove habitat occurred in New Zealand prior to the 1960s, driven by coastal development, grazing, pollution and land reclamation for ports and agriculture (Morrisey *et al.* 2007, 2010; Stokes *et al.* 2016). The extent of this loss has not been quantified as it largely occurred before aerial photographic surveys began in the 1930s (Morrisey *et al.* 2010). However, mangrove losses were substantially reduced with the implementation of New Zealand's Harbours Amendment Act in 1977, which made it illegal to reclaim seabed for agricultural purposes (Morrisey *et al.* 2010). In addition, mangroves were granted protected status under the 1994 New Zealand Coastal Policy (Harty 2009), meaning mangrove clearance could only be approved by local regulatory bodies (regional councils) through a formal resource consent process (Stokes *et al.* 2016).

While early European settlement saw large-scale loss of mangroves (Morrisey *et al.* 2007; Horstman *et al.* 2018), subsequent anthropogenic changes to the New Zealand landscapes have facilitated a rapid expansion of mangrove forests (Lundquist *et al.* 2014b). Large-scale deforestation of river catchments, conversion of forest to pasture, and rapid urban development over the last 50 years have accelerated sedimentation in estuarine environments in New Zealand (Swales *et al.* 2009). The concomitant increase in fine terrigenous sediments has caused estuary infilling and built extensive tidal flats, which, coupled with increased nutrient inputs, warming climate, and structural modifications to estuarine environments (Schwarz 2003; Nicholls *et al.* 2004; Lovelock *et al.* 2007; Morrisey *et al.* 2007, 2010) have created additional suitable habitat for mangroves (Swales *et al.* 2009; Lundquist *et al.* 2014b; Horstman *et al.* 2018). Subsequently, mangroves have colonised seawards across bare mudflats (Lundquist *et al.* 2014b; Swales *et al.* 2015). In addition, there is evidence of limited landward encroachment by mangroves in New Zealand (Suyadi *et al.* 2019), although this is not thought to contribute significantly to overall mangrove spread (Saintilan *et al.* 2014; Suyadi *et al.* 2019). Aerial photography records indicate that mangroves have expanded their range in New Zealand at an average rate of 4% per year since the early 1940s (Morrisey *et al.* 2010; McBride *et al.* 2016).

The future expansion of New Zealand's mangrove forests will likely be determined by the pace of sea-level rise relative to rates of sedimentation (Swales *et al.* 2009; McBride *et al.* 2016). Recent modelling of mangrove expansion in the Firth of Thames (in Waikato, New Zealand) suggests that current or increased levels of sedimentation will see an increase in mangrove distribution in the region, irrespective of sea-level rise scenarios (0.3–1m rise). However, if sedimentation does not keep pace with sea-level rise, mangrove stands may be displaced from intertidal flats but retained in the tidal creeks with higher elevation (Swales *et al.* 2009; McBride *et al.* 2016).

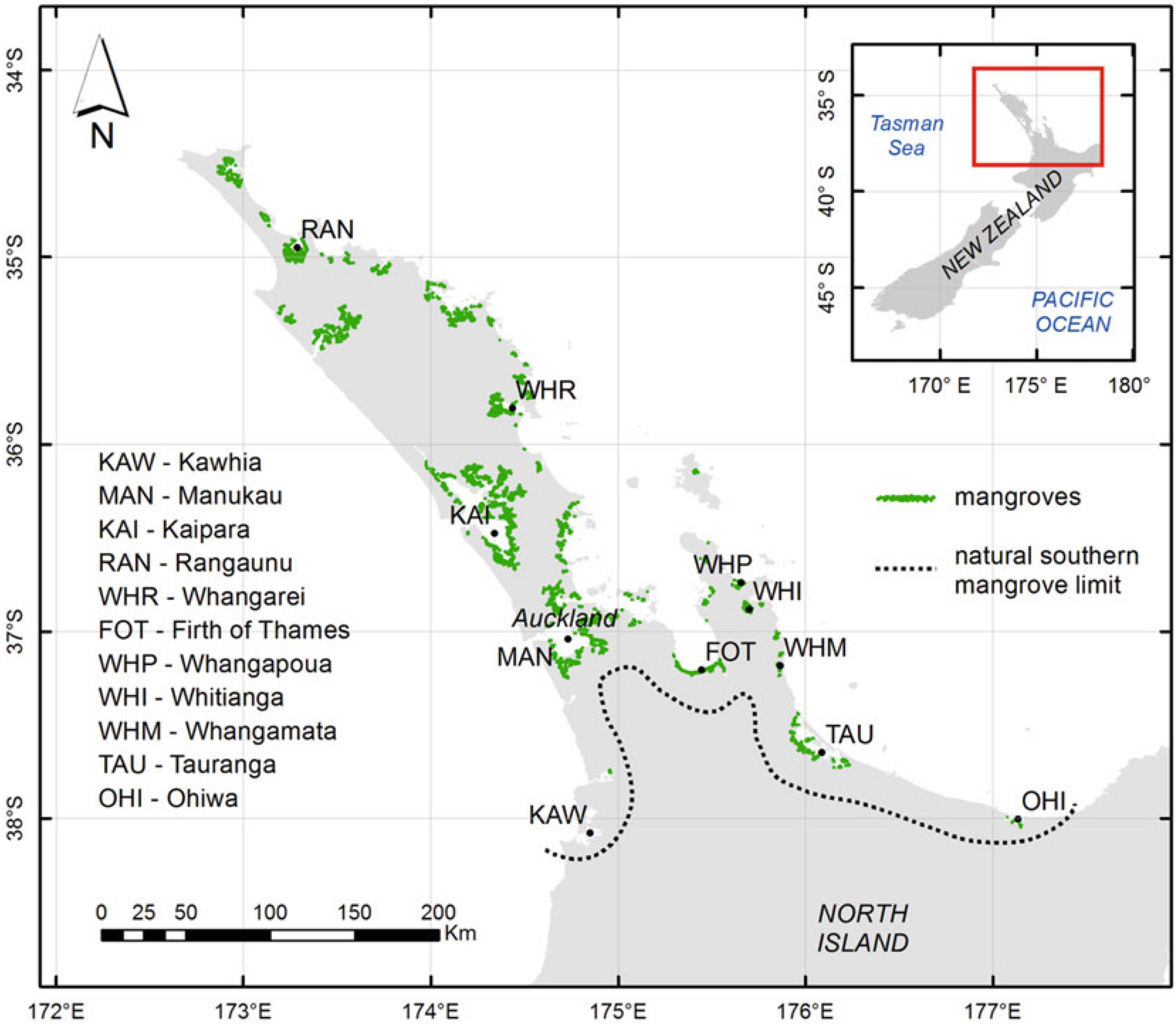


Figure 2.1 Mangrove distribution in New Zealand, as per Horstman *et al.* (2018). Mangrove distribution data from Spalding *et al.* (2010). The names of several harbours provided for reference.

2.2.3 Repercussions of expanding mangroves

The expansion of mangrove forests in New Zealand has wide-ranging repercussions for coastal areas, including changes to ecosystem services, habitat composition, and the perceived amenity value of estuarine environments (Horstman *et al.* 2018).

An increase in mangrove area will likely increase the ecosystem services in New Zealand associated with these habitats, including carbon storage (Gladstone-Gallagher *et al.* 2014; Bulmer *et al.* 2016a, b, 2020; Perez *et al.* 2017), water filtration (Barbier *et al.* 2011; UNEP *et al.* 2014), heavy metal trapping (Bastakoti *et al.* 2018), nutrient input and redistribution (Spalding *et al.* 2010; Horstman *et al.* 2018) as well as coastal protection and erosion control (Harty 2009; Lundquist *et al.* 2017).

However, mangrove expansion comes at the expense of alternate habitats (Morrisey *et al.* 2007), which in turn increases the homogeneity of estuarine environments and reduces ecosystem resilience (Thrush *et al.* 2004). As mangroves expand their reach down shore, they can replace adjacent habitats such as intertidal flats or seagrass beds (Turner & Schwarz 2006; Battley *et al.* 2007; Lundquist *et al.* 2017). However, it is likely that adjacent habitats are already adversely affected by high rates sediment deposition in those estuaries and harbours where mangroves are spreading rapidly (Ellis *et al.* 2004; Morrisey *et al.* 2007). While mangroves readily spread seawards, little documented evidence exists of substantial landward incursions by mangroves in New Zealand (Morrisey *et al.* 2007). Despite substantial losses of coastal saltmarsh in Australia due to landward mangrove expansion (Saintilan & Williams 2000; Wilton 2002; Saintilan *et al.* 2009; Saintilan & Rogers 2013), New Zealand landward mangrove incursions are usually limited to areas of sparse saltmarsh or where channels facilitate the dispersal and establishment of mangrove propagules (Park 2004). Neither saltmarsh nor wetland habitats adjacent to mangrove forests in New Zealand appear to have suffered substantial losses due to landward mangrove expansion (Saintilan *et al.* 2014), although this finding may be an artefact of limited study (Morrisey *et al.* 2007).

Changes in estuarine habitat composition inevitably have knock-on effects for associated fauna. The expansion of mangrove forests in New Zealand has resulted in additional habitat for numerous invertebrate and vertebrate species that use mangroves, including distinct groups of macrofauna (Ellis *et al.* 2004; Alfaro 2006; Morrisey *et al.* 2007), eels and juvenile fish (Morrisey *et al.* 2007; Swales *et al.* 2009; Lundquist *et al.* 2017), and up to 48 species of bird (Crisp *et al.* 1990; Bell & Blayney 2017b). However, the shift from open coastal habitats to mangrove forests may deprive wading birds of feeding and roosting areas (Veitch & Habraken 1999; Melville & Battley 2006; Battley *et al.* 2007; Morrisey *et al.* 2007), and potentially reduce the diversity and abundance of benthic macrofauna (Alfaro 2006; Morrisey *et al.* 2007). While a loss of habitat diversity likely causes an overall loss of biological diversity, it is important to note that this may be caused by the factors that lead to mangrove spread (Ellis *et al.* 2004) – such as increased sediment deposition or nutrient inputs (Ellis *et al.* 2004; Horstman *et al.* 2018) – rather than by mangrove plants themselves.

2.2.4 Mangrove management in New Zealand

Increased rates of sedimentation in estuaries and the concomitant rapid expansion of mangroves have raised concerns about the loss of habitat diversity and associated decline of ecosystem functioning in New Zealand estuaries (Thrush *et al.* 2004; Harty 2009) as well as declines in recreational and amenity values (Harty 2009; Lundquist *et al.* 2014b; Horstman *et al.* 2018). As a result, mangrove removal has been a common management response to mangrove expansion (Lundquist *et al.* 2014b). Typically, the primary management objective of removal operations is to restrict mangrove forests to a desired reference state or dateline (Stokes *et al.* 2016) and to restore open sandflat habitats by either partially or entirely removing mangrove forests (Lundquist *et al.* 2014b; Horstman *et al.* 2018).

Removing mangroves requires consent from those regional councils under whose jurisdiction mangroves are found in northern New Zealand, although illegal removal is not uncommon (Morrisey *et al.* 2007; Horstman *et al.* 2018). The total area of removed mangroves in New Zealand has not been measured; information on legal removals is siloed among regional authorities, while illegal removal has not been officially tracked. To provide an indication of mangrove removal extent, Lundquist *et al.* (2014a) listed 40 mangrove removal sites in the Auckland region which totalled some 117 hectares. Similarly, large removal operations have cleared at least 113 hectares and 24 hectares of mangroves in Tauranga and Whangamata harbours respectively (Lundquist *et al.* 2014b).

While the aim of mangrove removal operations is to restore sandflats that may have been historically present (Harty 2009; Horstman *et al.* 2018), there is little scientific evidence to suggest that muddy substrate will consistently return to sandflat habitat following mangrove clearance (Stokes 2009; Stokes *et al.* 2010; Lundquist *et al.* 2012, 2014b). This process relies on natural, site-specific factors that remove fine silt (e.g. high wind/wave exposure) but do not deposit further sediment (Lundquist *et al.* 2014b). Successful restoration via mangrove removal is typically seen in sites already dominated by sandy substrate, although sandier removal sites represent only a very small proportion of all removal sites (Lundquist *et al.* 2014b; Horstman *et al.* 2018).

Removal sites that do not return to a desired sandy state may develop unwanted phenomena such as macroalgal blooms, anoxic sediments, lower levels of oxygen in the water column, and macrofauna communities dominated by opportunist species (Lundquist *et al.* 2014b; Bulmer & Lundquist 2016). With respect to avifauna, further scientific study is required to assess how mangrove removal affects bird species that make use of mangrove habitat for breeding, foraging and roosting (Horstman *et al.* 2018). Particular research attention is required for those species considered to be closely associated with mangrove forests, such as the banded rail *Gallirallus philippensis assimilis* (Bell & Blayney 2017a, see section *Mangrove avifauna*).

Ultimately, the expansion of New Zealand's mangrove forests in recent decades has resulted in a polarity of public attitudes towards mangrove habitats (Morrisey *et al.* 2007; Dencer-Brown *et al.* 2018) and increasing numbers of consent applications to facilitate the removal of mangroves (Lundquist *et al.* 2014b). In concluding their review on managing mangrove expansion in New Zealand Lundquist *et al.* (2014b) stated:

> *"The relationship between people and mangroves in New Zealand is complex and driven by emotional responses to historical changes in estuarine habitats that are a symptom of catchment land-use practices. In managing mangrove expansion, a balance must be found between maintaining people's values and maintaining any valuable ecosystem services that mangroves provide. This requires careful and informed management of mangroves to ensure that firstly what people desire from mangrove removal is achieved and secondly that mangrove areas of ecological and functional importance are also maintained. In the absence of adequate information we run the risk of ad-hoc, unsuccessful removals doing more harm than good, and threatening ecosystem services and biodiversity in New Zealand estuaries."*

2.3 Mangrove avifauna

In this section (2.4), I address the third objective of this review by summarising the scientific literature on mangrove avifauna, both globally and in New Zealand.

2.3.1 Global patterns

Globally, mangrove fauna have been poorly studied relative to mangrove flora (Macintosh & Ashton 2002; Nagelkerken *et al.* 2008). Reviews of mangrove faunal diversity (e.g. Macintosh & Ashton 2002; Nagelkerken *et al.* 2008; Luther & Greenberg 2009) are reliant on patchy data, primarily because several mangrove regions – such as the west coast of the Americas and the west and east coasts of Africa – remain severely understudied (Macintosh & Ashton 2002). In addition, mangrove environments in other areas may be excluded from ecological studies due to difficult or dangerous working conditions (Kutt 2007).

Luther & Greenberg (2009) undertook a systematic review of literature on terrestrial vertebrates in mangroves around the globe, searching for terrestrial species, subspecies and distinct populations that are primarily found and reproduce in mangrove ecosystems. These authors found 853 terrestrial vertebrates in total, including 790 birds, 40 mammals, 20 reptiles, and 3 amphibians. Of these, just eight percent (n=69: 39 species, 16 subspecies, and 14 distinct populations) were classified as 'mangrove endemics', whereby their life histories are "tied to and dependent on mangrove habitat" (Luther & Greenberg 2009, p. 604). Of the mangrove endemic group, 70 percent were birds (n=48; 22 species, 12 subspecies, and 14 distinct populations) including 5 different species of rail. More recently, Huang *et al.* (2019) reached a similar tally, finding 32 species or sub-species of birds considered endemic to mangrove ecosystems.

The majority of mangrove-endemic bird species are found in north-western Australia and south-east Asia, corresponding with the largest and most taxonomically diverse areas of mangrove on the planet (Noske 1996; Tomlinson 2016). The floristically less diverse mangals of Africa and South America each have just one bird species considered endemic to this habitat (Haverschmidt 1965; Noske 1996), although this may be an artefact of limited study (Macintosh & Ashton 2002). While global-scale patterns indicate a positive relationship between the richness of mangroves and the richness mangrove-endemic avifauna (Noske 1996), this relationship becomes less clear at a regional scale (Mohd-Azlan *et al.* 2012). For example, the floristically rich mangroves of north-eastern Australia have fewer avian endemics than the less diverse mangroves of north-western Australia (Noske 1996; Nagelkerken et al. 2008), yet in Western

Australia species richness of avian mangrove specialists declines with decreasing species richness and structural complexity of mangrove plants (Mohd-Azlan *et al.* 2012).

Most bird species found in mangroves are also found in other habitats (Nagelkerken *et al.* 2008), and mangroves support fewer bird species that are obligate habitat specialists – i.e., species that are restricted to a particular habitat type – relative to other forest types (Buelow & Sheaves 2015; Buelow *et al.* 2018). This apparent lack of mangrove specialists may be a result of the structural and floristic simplicity of mangrove ecosystems, relative to more complex ecosystems such as rainforests (Mohd-Azlan *et al.* 2014). However, a lack of mangrove endemics does not preclude the value of mangroves to avifauna, primarily as mangroves support species that do not use mangrove resources exclusively (Kutt 2007). For example, of some 200 bird species observed in Australian mangroves, 14 passerines are confined to mangroves (i.e. mangrove endemics), while a further 71 species use mangroves frequently or seasonally (Noske 1996). This latter group represents birds that use mangrove habitat to forage – food types include juvenile fish, insects, and infauna such as bivalves, crustaceans and worms – but also for breeding, roosting and as refuge habitat during migration, winter seasons, drought, or due to coastal development (Hutchings & Recher 1982; Schodde *et al.* 1982; Hutchings & Saenger 1987; Kutt 2007). Thus mangrove environments play an important supporting role for the wider avian community (Macintosh & Ashton 2002).

Importantly, the global loss of mangrove forests has ramifications for the continued existence of bird populations reliant on these habitats (Spalding *et al.* 2010). Huang *et al.* (2019) quantified the effects of mangrove loss on mangrove-endemic bird populations globally: of 99 separate metapopulations restricted to mangroves, 94 inhabited areas where mangrove cover declined from 2000–2015. Of these 94 populations, 85 saw a decrease in metapopulation capacity, a trend driven primarily by the loss and fragmentation of large patches of mangrove habitat.

2.3.2 Mangrove avifauna in New Zealand

In this section, I summarise available literature on the relationships between birds and mangroves in New Zealand. Importantly, this drawing conclusions from this summary is difficult and should be approached cautiously, given the minimal academic study that has addressed mangrove-avifauna relationships (Macintosh & Ashton 2002; Morrisey *et al.* 2007; Bell & Blayney 2017b). For example, a recent review of mangrove biodiversity in New Zealand by Dencer-Brown *et al.* (2018) cites just four sources (of which just two are peer-reviewed) pertaining to avian diversity in New Zealand's mangroves. Similarly, another recent report on mangrove avifauna in New Zealand heeds caution when interpreting its findings, stating that the review "heavily relies on individual statements of evidence, and anecdotal one-off observations" (Bell & Blayney 2017b, p. 4). A Master of Science thesis by Cox (1977) – deemed the "most comprehensive assessment" of birds inhabiting mangroves to date (Dencer-Brown *et al.* 2018, p. 8) – remains a key reference for multiple sources on NZ mangrove avifauna (e.g., Crisp *et al.* 1990; Morrisey *et al.* 2007; Win *et al.* 2015; Bell & Blayney 2017b; Dencer-Brown *et al.* 2018). An absence of scientific literature indicates a lack of progression in this field of study. In the 42 years since Cox's (1977) study, few academic articles with direct links to mangrove avifauna have been published. While a valuable resource, Cox's research was largely restricted to study of a single harbour over two years (1976-1977) and is therefore to unlikely to comprehensively describe mangrove-avifauna associations.

Cox (1977) recorded 23 bird species in New Zealand's mangroves, the majority of which were observed during seasonal surveys in Kaipara Harbour. Of these 23 species, 6 species were observed to breed in mangroves, while a further 8 species used mangroves for roosting, foraging or both. Crisp *et al.* (1990) list 48 bird species classified as utilising estuarine habitat, including mangroves. Many of these records appear to be sourced from a combination of Cox's (1977) study and government wildlife surveys, although specific reference material is not provided. Neither Cox (1977) nor Crisp *et al.* (1990) describe any bird species as entirely restricted to mangroves (i.e., mangrove endemics) in New Zealand.

An apparent lack of mangrove endemics in New Zealand is unsurprising. New Zealand's mangal is structurally and floristically simple – mangrove forests in New Zealand comprise just one species (*Avicennia marina* var. *australasica*) – a pattern that likely explains the relatively low species richness of mangrove avifauna (Mohd-Azlan *et al.* 2012). In addition, mangrove endemism in birds appears to be a relatively rare phenomenon (Luther & Greenberg 2009); even the highest levels of such endemism (15% in parts of Australia; Nagelkerken *et al.* 2008) are substantially lower than proportions of terrestrial forest-dependent birds (e.g., 61% in Madagascar; Watson *et al.* 2004; Buelow & Sheaves 2015). Moreover, New Zealand has far fewer mangrove-using bird species (ca. 48) than high-endemism areas like Australia (ca. 200) (Crisp *et al.* 1990; Noske 1996; Kutt 2007).

Given the apparent absence of mangrove endemic bird species in New Zealand, several authors argue that mangroves represent marginal habitats for all bird species, native or introduced (Cox 1977; Crisp *et al.* 1990; Morrisey *et al.* 2007). No species of bird is deemed dependent on New Zealand's mangrove ecosystems (Morrisey *et al.* 2007), with the possible exception of the banded rail *Gallirallus philippensis assimilis* (Bell & Blayney 2017a). However, mangroves undoubtedly support a variety of bird species who use mangrove forests for food, shelter, nesting areas and roosting sites (Cox 1977; Crisp *et al.* 1990). This includes 'threatened' species (Bell & Blayney 2017b; Robertson *et al.* 2017) such as the 'nationally critical' New Zealand fairy tern *Sternula nereis davisae* (Ismar *et al.* 2014), the 'nationally endangered' Australasian bittern *Botaurus poiciloptilus* (Miller & Miller 1991), the 'nationally vulnerable' lesser knot *Calidris canutus rogersi* and caspian tern *Hydroprogne caspia*, as well as five further species deemed 'at risk' of extinction (New Zealand Threat Classification System, Robertson *et al.* 2021). The banded rail represents one of these 'at risk' bird species, and is frequently referred to in New Zealand literature on mangroves given it commonly occurs in these habitats (Bellingham 2013; Beauchamp 2015, 2022). As the focal species of this PhD, it is discussed in further detail below to meet this literature review's fourth and final objective.

2.3.3 Study species - the banded rail

The banded rail *Gallirallus philippensis*[1], also known as the buff-banded rail, is a medium-sized, intricately patterned member of the Rallidae family (Figure 2.2; Figure S2.1 – Supplementary Material). The species is widely distributed across south-east Asia, Australasia, and the southwest Pacific (Figure 2.3) and is thought to comprise ~20 subspecies (Taylor & van Perlo 1998; Garcia-Ramirez *et al.* 2017). The New Zealand subspecies, moho-pererū *Gallirallus philippensis assimilis,* was once widely distributed across both the North and South Island (Elliott 1983), but underwent substantial range contraction in the early 1900's following extensive habitat loss and the introduction of mammalian predators (Heather & Robertson 2005). Recent estimates suggest that 80-90% of the New Zealand banded rail population – thought to be a total of 5,000–20,000 individuals (Robertson *et al.* 2021) – is restricted to saltmarsh-mangrove complexes in the North Island estuaries of Northland, Auckland, Waikato and Bay of Plenty, while further sub-populations inhabit offshore islands and the saltmarshes in Nelson and Marlborough on the South Island (Figure 2.4) (Bellingham 2013). Estimates of the banded rail's distribution (Bellingham 2013) are largely based on survey data collected from

[1] There has been some taxonomic instability in the genus name for banded rails, with *Hypotaenidia* now mostly used rather than *Gallirallus*. However, this thesis retains *Gallirallus* to reflect New Zealand databases like eBird and New Zealand Birds Online, as well as recent New Zealand literature, and The Clements Checklist of Birds of the World.

1999-2004 for the New Zealand Bird Atlas. Notably, recent occupancy modelling of all of NZ's land birds excludes banded rails given the low number of observations for this species (Walker & Monks 2018).

Banded rails are a cryptic species and therefore difficult to study. Much scholarly understanding of the life history of *G. p. assimilis* is informed by qualitative studies of other banded rail subspecies across Oceania (Dunlop 1970, 1975; Clark 1994; Wiley & Goldizen 2003; Manson 2004; Clark & Harris 2016) and complemented by research on banded rail habitat use in New Zealand (Fagan 1954; Elliott 1987, 1989; Beauchamp 2015, 2022). In New Zealand, banded rail research is somewhat limited, comprising government-commissioned reports (Botha 2011; Bell & Blayney 2017a; Martin & Richardson 2018) and academic research based on footprint surveys (Elliott 1983, 1987; Botha 2011), call counts (Beauchamp 2015), nest examinations (Parker & Brunton 2004), and visual observations (Beauchamp 2022). The limited data on banded rails in New Zealand, in combination with their restricted range, has determined their status of 'At Risk – Declining' (Robertson *et al.* 2021), whereby their population is predicted to undergo a decline of 10-30% in the next 10 years (Townsend *et al.* 2008; Robertson *et al.* 2017).

With respect to habitat selection and use, banded rails show preference for dense clumps of sedges, rushes or long grass for breeding and roosting (Marchant & Higgins 1993; Botha 2011). On the New Zealand mainland this breeding habitat largely corresponds with the upper reaches of saltmarsh habitats (Elliott 1983). Breeding pairs are thought to remain on their territories all year, with females laying (multiple) clutches of 3–8 eggs from September to December (Marchant & Higgins 1993; Heather & Robertson 2005). Incubation lasts between 19–25 days (Marchant & Higgins 1993). Chicks are led from the nest within 24 hours of hatching, staying with both parents for ~60 days to fledging (Heather & Robertson 2005). While moult regimes are poorly known, banded rails are likely to have two moults per year (Bell & Blayney 2017a), one of which is a complete post-breeding adult moult that may render adult birds flightless for >30 days in January–March (Elliott 1983; Marchant & Higgins 1993).

The banded rail's diet consists mostly of crustaceans, molluscs, worms and insects (Elliott 1983). Banded rails are typically diurnal and crepuscular foragers, and usually feed under cover, rarely venturing far from the edge of dense vegetation (Botha 2011; Beauchamp 2015). Mangrove forests provide dense cover and are considered important foraging habitats for banded rail (Elliott 1983; Botha 2011; Beauchamp 2015; Bouma 2016), particularly in the North Island where banded rails are typically restricted to saltmarshes with adjacent mangroves (Bellingham 2013;

Beauchamp 2015). Mangrove forests exhibit a dense canopy but low structural complexity at ground level. These structural traits may provide banded rails with cover from potential aerial predators, but allow for unimpeded foraging for benthic macrofauna (Marchant & Higgins 1993; Botha 2011; Bell & Blayney 2017a). The potential preference for this habitat structure is also observed in areas without mangroves (Bell & Blayney 2017a); in rush saltmarsh environments in the South Island, banded rail used rush *Juncus kraussii* subsp. *australiensis* more frequently than other rush species, a pattern potentially explained by *Juncus*' superior aerial cover but clearer access at ground level (Elliott 1987).

Figure 2.2 The banded rail *Gallirallus philippensis*, as per the plate in Marchant and Higgins (1993). Image numbers: 1 Adult, subspecies *mellori* ;2 Adult, subspecies *assimilis*;3 Downy young;4 Juvenile, subspecies *mellori;* 5, 6 Adult subspecies *mellori*

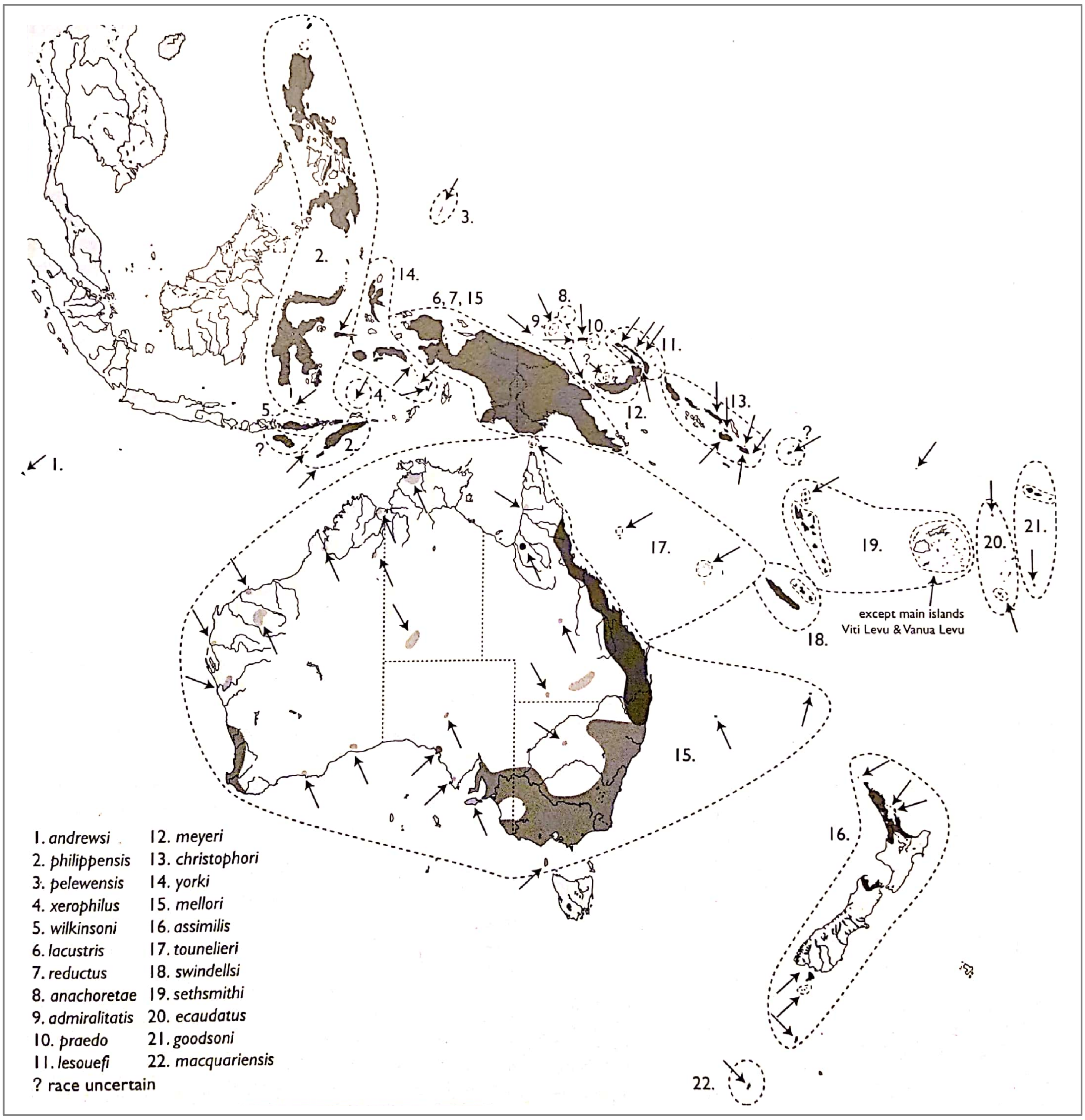


Figure 2.3: The global distribution of *Gallirallus philippensis* with subspecies indicated by number. Figure as published in Taylor and van Perlo (1998). Note, subspecies diversity is indicative; counts differ among authors.

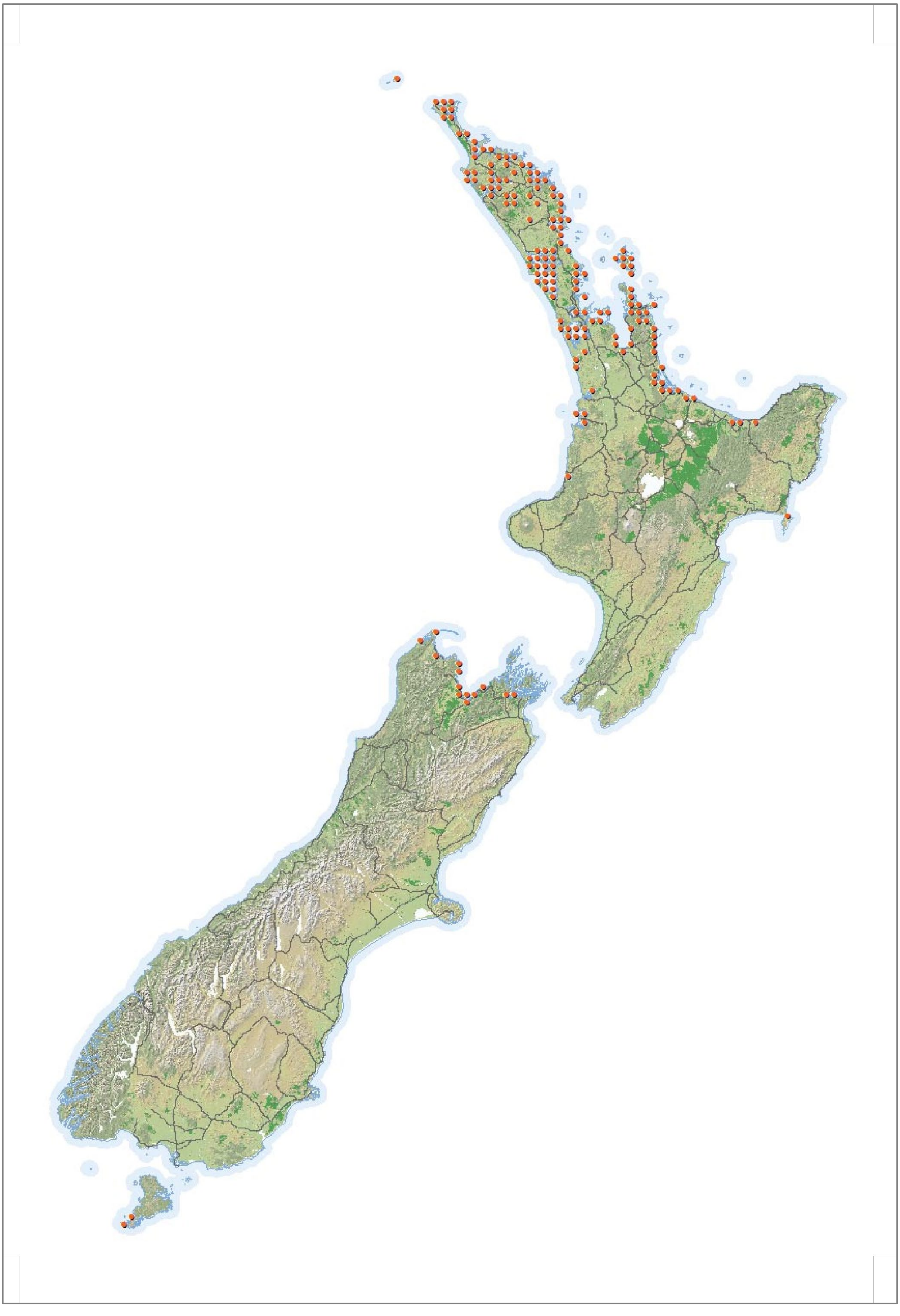


Figure 2.4: Banded rail *Gallirallus philippensis assimilis* distribution in New Zealand (Robertson et al. 2007). Red dots indicate banded rail observations within 10km grid square surveys undertaken as part of the Atlas of Bird Distribution in New Zealand 1999-2004.

New Zealand's banded rail does not illustrate a "natural obligate dependency" on mangrove habitats (Bell & Blayney 2017a, p. 8). The banded rail's distribution in New Zealand includes areas that do not contain mangroves, including saltmarsh habitats around the Nelson-Golden Bay area and Marlborough Sounds (Elliott 1983, 1989), on Stewart Island/Rakiaura and smaller surrounding islands (Robertson *et al.* 2013), and a range of non-mangrove habitats on Great Barrier Island/Aotea (Beauchamp 2015). However, the banded rail may be dependent on mangrove habitat for their continued survival in the North Island, where the majority of their population is found (Bellingham 2013; Bell & Blayney 2017a). Historical habitat loss and increased predation pressure has restricted banded rail to, outside of occasional records, a distribution that matches the current distribution of mangroves in New Zealand (Figures 2.1 and 2.4 respectively). Within this North Island distribution, limited evidence suggests that banded rails use mangroves as foraging grounds (Botha 2011) and that banded rails may be restricted to saltmarsh habitats (breeding habitat) in close proximity to mangroves (Beauchamp 2015). However, researchers recognise that further scientific study is required to quantify banded rail habitat selection, use as well as their dependency on mangroves (Bell & Blayney 2017b, a).

The predicted decline of banded rails and their close association mangrove habitats is brought into sharp relief by ongoing debates about the value of mangrove forests in New Zealand. The consequences of mangrove removal for avifauna such as the banded rail are poorly understood, largely because detailed information on the associations between banded rails and mangrove ecosystems is lacking. Little is known about how and why banded rails use mangrove forests, as evidenced by a string of future research aims identified in existing literature. These include, but are not limited to suggestions for: an evaluation of mangroves as ecological corridors (Botha 2011), the quantification of banded rail movement, feeding patterns and territory sizes in mangrove and saltmarsh habitats (Giles 2014; Bouma 2016), and an understanding of home-range sizes and the ways in which rails use different habitats within their home-range (Beauchamp 2015).

2.4 Knowledge gaps addressed in this thesis

Despite the anomalous nature of New Zealand's expanding mangrove forests and the scrutiny paid to mangrove management practices, few academic studies have examined mangrove-avifauna relationships in New Zealand. Here, I present four knowledge gaps relevant to the ecological understanding of mangrove forests, the conservation of banded rails, and the management of expanding mangrove forests in New Zealand:

1. **Mangrove management**: the extent of mangrove removal in New Zealand has not been quantified. Moreover, the effects of mangrove removal on banded rail populations – and avifauna generally – have not been formally studied.
   → This knowledge gap is addressed in Chapter 3.
2. **Habitat quality**: the relative quality of mangroves as foraging habitats to banded rail is poorly understood.
   → This knowledge gap is addressed in Chapter 4.
3. **Monitoring**: existing monitoring methods for banded rail are often unreliable and yield limited information; accordingly, little is known about basic banded rail behaviours, including their circadian rhythms and activity patterns.
   → This knowledge gap is addressed in Chapter 5.
4. **Habitat selection and use**: the cryptic nature of banded rails has hindered study of their ecology; estimations of the home range sizes remain uncertain, while their habitat selection and use at a home-range scale in mangrove environments is unknown.
   → This knowledge gap is addressed in Chapter 6.

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2.6 Supplementary material

Figure S2.1 Photographs of banded rails *Gallirallus philippensis assimilis* captured, tagged, and released in Mangawhai estuary, New Zealand.

Chapter 3

Managing an invasive native species: challenges and ecological repercussions

In this chapter, I examine the management of New Zealand's mangrove forests. I determine the spatial extent and configuration of mangrove removal in New Zealand and assess the ecological repercussions of mangrove removal on avifauna, including the banded rail. In addition, I determine rationales for mangrove removal and discussion challenges facing mangrove management in New Zealand if it is to transition towards addressing the drivers of mangrove expansion. This chapter addresses the first research objective of this thesis:

Objective 1: Determine the extent of mangrove removal in New Zealand and its potential effects on banded rail populations

An earlier version of this chapter has been published as a report aimed at policymakers in New Zealand, in association with the Office of the Prime Minister's Chief Science Advisor. The full report is available for download at https://bit.ly/OPMCSA-mangrove-management, while a summary of the report's findings and policy recommendations can be found in Section 3.7 – Supplementary material. The report can be cited as: de Satge, J (2021) Mangrove management in Aotearoa New Zealand: a bird's eye review. Prepared in association with: The Office of the Prime Minister's Chief Science Advisor. Massey University, Auckland, New Zealand.

Chapter 3 cover image: a lone mangrove tree (*Avicennia marina* var. *australasica*) stands among a bed of its pneumatophores. Artwork by Rick de Satgé.

3.1 Abstract

The rapid expansion of a native species driven by human-induced changes to ecosystems is seldom characterised as a biological invasion, despite invasion theory offering great value for framing such expansions and determining effective management interventions. In New Zealand, native mangroves have rapidly expanded in the past half century, fuelled by wide-scale human-mediated changes to river catchments; a set of conditions that arguably renders mangroves as a native invader. The expansion of mangroves has triggered a management response premised on vegetation removal, as local communities seek permission – mediated by permits called resource consents – from regional authorities to restore open habitats in coastal areas where mangroves have spread. Using data collated from municipal resource consent documents, this study quantified the spatial extent and configuration of mangrove removal in New Zealand and assessed the ecological repercussions of mangrove removal for avifauna. The area of mangrove vegetation legally removed in New Zealand was small (>330 ha) relative to its contemporary area (>26,000 ha) and recent expansion. Mangrove removals seldom adhered to best-practice guidelines and were primarily motivated by human-centric desires for recreation rather than by ecological restoration. Notably, mangrove removal projects inadequately considered the repercussions of mangrove removal for avifauna communities, as evidenced by the poor standard and infrequent nature of avifauna monitoring in resource consents. Limited data from monitoring reports at 14 removal sites suggested mangrove removal adversely affected mangrove-using avifauna, in particular the banded rail, but benefited species that use open habitat such as waders. Resource consent data provided evidence of a ‘symptom-oriented’ approach to mangrove management in New Zealand, whereby removal of mangrove vegetation is prioritised over interventions addressing the drivers of mangrove spread. Transitioning to a driver-oriented management presents a long-term and ecologically appropriate response to mangrove expansion in New Zealand but faces several challenges, including policy that does not reflect ecosystem processes, public perception of native invasive species, insufficient monitoring practices, and knowledge gaps in the study of native invasions.

3.2 Introduction

Invasion science examines the human-mediated proliferation, spread, and dominance of species that have expanded their range into novel areas (Richardson & Pyšek 2008; Valéry *et al.* 2008; Nackley *et al.* 2017). Invasive species are drivers of global change (Vitousek *et al.* 1996; Wilson & Pinno 2013) capable of reducing biodiversity and altering ecosystem functioning in terrestrial, freshwater, and marine environments (Molnar *et al.* 2008; Clavero *et al.* 2009; Doherty *et al.* 2016; Gallardo *et al.* 2016; Maxwell *et al.* 2016; Linders *et al.* 2019). In management contexts, invasive species are typically associated with the damage they cause to recipient ecosystems (Blackburn *et al.* 2011; Mačić *et al.* 2018), however, in ecological theory invasive species are defined by the extent of their spread rather than their impacts (Richardson *et al.* 2000).

While prominent frameworks of invasion biology are limited to invasive alien species (IAS) (Williamson & Fitter 1996; Richardson *et al.* 2000; Blackburn *et al.* 2011), natives species can also become invasive (Valéry *et al.* 2008, 2009; Nackley *et al.* 2017) with significant ecological and economic consequences (Valéry *et al.* 2004; Simberloff *et al.* 2012; Anadon *et al.* 2014). Invasions by native and alien species share numerous characteristics (Nackley *et al.* 2017), including changes to population distribution (Stevens *et al.* 2017) and ecosystem functioning (Valéry *et al.* 2004; Ravi *et al.* 2009; Anadon *et al.* 2014), as well as deleterious effects on biodiversity (Ratajczak *et al.* 2012; Mollot *et al.* 2017) and ecosystem services (Asner *et al.* 2004; Angassa 2005).

Native invasions and natural colonisations by range-expanding native species are functionally analogous (Hoffmann & Courchamp 2016), but can be distinguished by the driver of their expansion – the spread of native invasive species is mediated by human actions, intentional or unintentional, whereas natural colonisations are not. Thus, distinguishing between natural colonisers and invasive native species acknowledges the role of human actions in driving regime changes and shifting habitat composition at broad spatial scales. Importantly, native invaders are considered ‘invasive’ when the species spreads beyond its natural past or present range (Nackley *et al.* 2017), although the spatial and temporal thresholds for spread remain unclear.

Human activities have created three pathways to invasion for native species (Simberloff 2010; Carey *et al.* 2012). In the first pathway, the intentional establishment of new populations of species in novel areas within their native range – for example, fish stocking – results in local invasions that do not expand the outer boundaries of these species’ native ranges (Hirner & Cox

2007; Carey *et al.* 2012). In the second pathway, populations of range-restricted native species are supplemented with introductions of species from afar that have new genotypes, and these genotypes, or their recombinants, become invasive (Lavergne & Molofsky 2007; Simberloff 2010). In the third pathway, anthropogenic changes to the environment facilitate the population growth and/or competitive ability of native species (Goodrich & Buskirk 1995; Didham *et al.* 2007; Valéry *et al.* 2008) resulting in their expansion and dominance in novel communities (Nackley *et al.* 2017; Essl *et al.* 2019). Although not explicitly situated in invasion theory, Essl *et al.* (2019) describe species that follow the third pathway to native invasion as 'neonative', but only where the latitudinal range expansion distance exceeds 100 kilometres.

An increase in invasive native species (INS) appears inevitable as ongoing human-mediated changes to the environment raises the risk of biological invasions (Ricciardi *et al.* 2017). This increase occurs as significant anthropogenic changes to climate, nutrient, fire, hydrological, and sediment regimes (Davis *et al.* 2011; Lundquist *et al.* 2011; Simberloff *et al.* 2012; Thompson *et al.* 2017) restructure communities by allowing species to invade and persist under novel environmental conditions (Nackley *et al.* 2017). Environmental change is driving a wave of range expansions among native species (Heyerdahl *et al.* 2006; Chen *et al.* 2011; Pinsky *et al.* 2013; Lenoir & Svenning 2015), often with novel and/or negative effects on recipient ecosystems (Buitenwerf *et al.* 2012; Peng *et al.* 2013; Stevens *et al.* 2017). Such expansions have profound implications for biogeography, ecology, conservation policy, and management of invasive species (Essl *et al.* 2019).

3.2.1 Mangroves in New Zealand: a case study

In New Zealand, the rapid expansion of mangrove forests presents a case study for exploring the challenges and repercussions of INS management. In stark contrast with global mangrove declines in recent decades (Giri *et al.* 2011), New Zealand's native mangroves *Avicennia marina* var. *australasica* have expanded their total area at an average rate of 3-4% per year since the mid-1940s (Swales *et al.* 2009; McBride *et al.* 2016; Suyadi *et al.* 2019), with mangrove forests in some estuaries undergoing increases of >20% per year (Horstman *et al.* 2018). Recent estimates suggest mangrove cover exceeds 26,400 hectares in New Zealand (LINZ 2022), stretching from 34˚27'S in the country's far north to 38˚05'S at Kawhia Harbour on the west coast and 38˚03'S at Ohiwa Harbour on the east coast (Crisp *et al.* 1990; de Lange & de Lange 1994). In New Zealand, mangrove expansion has been driven by a rapid increase in nutrient-rich mudflats in infilling estuaries, a phenomenon caused by human-mediated increases to sedimentation and eutrophication rates in river catchments (Swales *et al.* 2015; Horstman *et al.* 2018; Suyadi *et al.* 2019). Increases in sediment and nutrients are largely the result of large-scale deforestation of river catchments, conversion of forest to pasture, and rapid urban development over the last 50 years (Swales *et al.* 2009). Spatially, mangrove expansion occurs within and between estuaries, over hundreds of meters (Swales *et al.* 2009, 2015; Horstman *et al.* 2018), with anecdotal evidence suggesting potential southwards expansion beyond known latitudinal boundaries.

Given ambiguity in ecological theory applied to range-expanding native species, New Zealand's mangroves could be labelled as natural colonisers, encroachers, or native invaders (Valéry *et al.* 2009; Simberloff *et al.* 2012; Saintilan *et al.* 2014; Hoffmann & Courchamp 2016; Essl *et al.* 2019) as these terms find common ground in describing native species that have expanded into new territory. However, this study contextualises mangrove expansion within an invasion biology framework; a rationale justified on theoretical and practical grounds. Theoretically, mangrove expansion meets many, if not all, of the prerequisites of a biological invasion (Valéry *et al.* 2009; Simberloff 2010; Nackley *et al.* 2017), particularly given their expansion is driven by human-mediated changes to the environment (Nackley *et al.* 2017; Horstman *et al.* 2018). Practically, framing mangrove expansion within an invasion context is highly relevant to contemporary mangrove policy in New Zealand and corresponding management interventions that mirror strategies to counteract alien invasive spread (Harty 2009; Lundquist *et al.* 2014b).

Similar to many invasive species, mangrove expansion in New Zealand presents a conservation paradox as their spread offers advantages and disadvantages (Hershner & Havens 2008; Schlaepfer *et al.* 2011; Mačić *et al.* 2018). As mangroves expand into novel coastal territory, they provide a range of ecosystem services, including increased capacity for carbon storage (Bulmer *et al.* 2016, 2020), coastal hazard protection (Lundquist *et al.* 2014b), and habitat provisioning to several rare and threatened species (Bell & Blayney 2017; Dencer-Brown *et al.* 2020). Conversely, mangrove spread raises concerns about biodiversity and habitat loss, changes to ecosystem functioning, and the loss of open, sandy habitats for recreation and amenity (Thrush *et al.* 2004; Alfaro 2010; Lundquist *et al.* 2017; Makowski & Finkl 2018).

Community concerns regarding the potential deleterious effects of mangrove expansion have prompted regional authorities in New Zealand to remove mangrove vegetation in several areas as a form of coastal restoration (Stokes *et al.* 2016). This 'symptom-oriented' approach to mangrove management targets mangrove vegetation rather than increases in sediment that drive change and has drawn academic scrutiny (Morrisey *et al.* 2010; Lundquist *et al.* 2014b;

Stokes *et al.* 2016; Bulmer *et al.* 2017) and social debate (Dencer-Brown 2019; PCE 2020). Mangrove removal projects aim to restore open habitats and reinstate recreational values associated with sandier substrates (Harty 2009; Lundquist *et al.* 2014b), a goal in conflict with efforts to retain ecosystem services provided by mangroves (Huxham *et al.* 2017; Dencer-Brown *et al.* 2018) and conserve native fauna that use mangrove habitats (Cox 1977; Beauchamp 2015; Bell & Blayney 2017). Despite this conflict and a spate of recent research on mangrove removal in New Zealand (Lundquist *et al.* 2012, 2014a; Stokes *et al.* 2016; Bulmer *et al.* 2017), knowledge of the spatial extent of mangrove removal efforts and their ecological repercussions remains limited.

Mangrove forests are protected under national law in New Zealand (Harty 2009), and their removal is regulated by regional councils using resource consents (henceforth ‘consents’). Consents require an evaluation of the ecological effects of removal, although published reports are primarily limited to evaluations of biophysical conditions – including changes to water oxygen levels, nutrient availability, sediment condition, and erosion levels (Alfaro 2010; Lundquist *et al.* 2012, 2014b; Bulmer *et al.* 2015, 2017) – and communities of benthic macrofauna (Alfaro 2010; Lundquist *et al.* 2014a). These evaluations focus on changes to the benthic environment, and seldom account for impacts on other mangrove-using fauna.

Mangroves and surrounding estuarine and coastal areas are important habitats to many bird species(Cox 1977; Crisp *et al.* 1990); open-habitat species like waders and shore birds forage and roost on sandflats (Riegen & Sagar 2020), while forest birds and cryptic birds such as the banded rail (*Gallirallus philippensis assimilis*) make extensive use of mangroves (Cox 1977; Beauchamp 2015, 2022; Bell & Blayney 2017). However, remarkably little is known about avifauna in mangrove environments (Bell & Blayney 2017) and mangrove-removal policy seldom acknowledges birds as a component of mangrove ecosystems (Environment Waikato 2012; Auckland Council 2019; Bay of Plenty Regional Council 2019; Northland Regional Council 2020). In addition, mangrove removal creates a conservation trade-off for birds in coastal areas, whereby open habitats gained by removing mangroves favours populations of coastal birds at the cost of habitat to mangrove-using birds. This trade-off is seldomly considered in evaluations of restoration success following mangrove removal (Stokes *et al.* 2016; Horstman *et al.* 2018), a surprising omission given that avifauna are often used as indicators of ecological change (Piatt *et al.* 2007; Ogden *et al.* 2014).

3.2.2 Study aims

In reviewing literature on mangrove management practices in New Zealand, I have identified several knowledge gaps that inhibit our understanding of the process of mangrove removal in New Zealand and its ramifications for avifauna.

Knowledge gaps pertaining to mangrove removal include:

1. The spatial extent of mangrove removal
2. The spatial configuration of mangrove removals
3. The methods of mangrove removal stipulated by consents
4. The implementation of sediment mitigation measures in mangrove removal consents
5. The societal rationales for mangrove removal

Knowledge gaps pertaining to avifauna include:

1. The extent to which avifauna are included in ecological assessments of mangrove removals
2. The type of assessments undertaken for mangrove avifauna
3. The reported effects of mangrove removal on avifauna

In this study, I collate data from resource consents to address these knowledge gaps. In so doing, this study aims to review mangrove removal in New Zealand as a case study in managing an invasive native species. I show that the area of mangrove vegetation removed is modest relative to its contemporary area and recent expansion but suggest that mangrove removals seldom adhere to best-practice guidelines or consider trade-offs for avifauna communities. In addition, I show that mangrove removals are primarily motivated by human-centric desires for recreation in estuarine environments and seldom by conservation or ecological restoration objectives. More broadly, I argue that mangrove management in New Zealand is not aligned with the ecology of native invasions as it follows a symptom-based approach that fails to address the drivers of invasion. Considering these shortcomings, I propose that mangrove management pivots towards a ‘driver-oriented’ approach and discuss the challenges in making this shift.

3.3 Methods

3.3.1 Data collection

To address the knowledge gaps identified in this study, I sourced 148 consent documents for legal mangrove removals from the four local authorities in New Zealand whose jurisdictions cover the distribution of *Avicennia marina* in New Zealand: Auckland Council (AC), Bay of Plenty Regional Council (BOPRC), Northland Regional Council (NRC), and Waikato Regional Council (WRC) (Figure 3.1). Documents were obtained by Official Information Requests (OIRs) to each council in November 2020. Each OIR requested the resource consent document, staff report, application document, environmental effects (AEE) report, and any avifauna monitoring reports for each mangrove removal project on record. To control for search effort among regional councils, I requested councils provide all consents files containing the keyword ‘mangrove’ in the title or description for all digital and hardcopy records on file. Thereafter, I assessed each file individually to ensure they pertained to mangrove removal.

3.3.2 Mangrove removal

I determined the location and spatial extent of mangrove removal by sourcing the co-ordinates of each removal area from consent documents. The total area of mangrove removal granted by each consent was verified by comparing present-day and historical satellite imagery in Google Earth Pro (version 7.3.4.8248) using the polygon tool to delineate and measure removed areas. Expanding on definitions by Lundquist et al. (2017), I classified the spatial configuration of each mangrove removal site, defining eight different spatial configurations in total (Table S3.1, Supplementary material).

I reviewed consent stipulations to determine the duration of the consents (the timeframe granted for removal and maintenance of mangrove removal), the methods of mangrove removal, and the types of mangrove vegetation removed. Mangrove removal methods were classified into three groups: ‘heavy machinery’ (diggers and bulldozers), ‘hand-held machinery’ (chainsaws and brushcutters), and ‘hand tools’ (loppers and secateurs). The type of vegetation removed was classified into two groups based on mangrove height (Auckland Regional Council 2010): ‘mature vegetation removal’ (mangrove plants >60cm tall) and ‘sapling/seedling removal’ (mangrove plants <60cm tall). In addition, I used application documents and staff reports to collate applicant rationales for removal.

For comparative purposes, I classified consents that granted removal of >1000m^2 of mature mangrove vegetation as ‘large removals’ and consents that granted <1000m^2 as ‘small removals’. For large removals, I assessed consent stipulations to determine whether sediment monitoring was required during and/or after removal, and whether sedimentation mitigation strategies were required as part of mangrove removal works.

3.3.3 Avifauna

I determined the extent to which avifauna are assessed in mangrove removal projects using consent stipulations and AEE reports from large removals. I recorded and categorised all consent stipulations relating to avifauna and determined the frequency of avifauna-targeted stipulations among all consents. Using AEE reports, I categorised the bird species assessed into three groups: ‘coastal birds’ – defined as birds observed in open habitats (often referred to as wading- or shorebirds in reports), ‘mangrove-using birds’ – defined as forest and ground-dwelling birds observed in mangrove habitats, and a ‘banded rail’ group for assessments specific to the species *Gallirallus philippensis* (thus, banded rails were excluded from mangrove-using birds’ group). Banded rail assessments were summarised separately to mangrove-using birds as they were monitored using different methods to other species and given their particular relevance to this thesis. In addition to these avifauna categories, I recorded all instances where AEE reports did not include avifauna assessments.

I determined the type of avifauna assessments by collating monitoring methods used in AEE reports. I sorted these methods into three groups: ‘formal monitoring’ – repeatable, standardised monitoring (as per Dowding 2012) that generated abundance and/or richness estimates of avifauna populations, ‘informal monitoring’ – non-standardised, non-repeatable surveys that provided a basic assessment of avian diversity, and ‘no monitoring’ – cases where no on-site monitoring of any kind took place.

To assess the reported effects of mangrove removal on avifauna, I summarised the report conclusions from AEE reports for each bird group. I categorised report conclusions into three groups: ‘positive effects’ – reports that predicted mangrove removal would increase the abundance and/or richness of a given bird group, ‘negative effects’ – reports that predicted mangrove removal would decrease abundance and/or richness of a given bird group, and ‘no effect’ – reports that predicted mangrove removal to have no effect on abundance and/or richness of a given bird group.

As AEEs are written in advance of mangrove removal (and are therefore predictive), I identified fourteen consents where avifauna monitoring was undertaken both before and after mangrove removal (henceforth: 'case study' sites) to assess the effects of mangrove removal on avifaunae reported retrospectively. Using monitoring reports for each case study, I summarised reported changes to species richness and/or abundance for each bird group as for AEE reports.

Banded rails were monitored using footprint surveys at all case study sites, and monitoring reports provided raw data from these surveys for thirteen of fourteen sites. I used this data to determine the average number of footprints found before and after mangrove removal events, correcting for survey effort, and used a paired sample *t*-test to determine whether these pre- and post-removal counts differed.

3.4 Results

In total, OIRs yielded 148 resource consents and >600 affiliated documents on legal mangrove removal from all the regional councils in New Zealand whose jurisdictions contain mangrove forests – Auckland Council, Bay of Plenty Regional Council, Northland Regional Council, and Waikato Regional Council.

3.4.1 Mangrove removal

From consent documents, I identified 161 discrete areas of mature mangrove removal (Figure 3.1, Table 3.1), totalling 333.0 hectares of felled mangrove forest (Figure 3.2), granted by resource consents between 1994 and 2020. The largest total area of mangrove removal granted by a single consent was 75 hectares, while the smallest was two square-metres. On average, consents for mangrove removal throughout New Zealand were granted for periods of 18± 1.1 years (Table 3.1). Fifty-six consents were identified as large removals (>1000m^2), while ninety-two consents were small removals (<1000m^2).

Almost ninety percent of consents permitted the removal of adult mangrove plants, while just seven percent targeted only saplings or seedlings only. Mangroves were most frequently removed in large-contiguous patches (22% of all consents), followed by pathway-style clearances (17%) and in-shore clearances (15%) (Figure 3.3).

More than a third of all removals (37%) used hand-held machinery or hand tools to fell mangroves, 17% of removals used heavy machinery, a combination of methods was used for 12% of all removals, while the remaining consents did not specify a method for mangrove removal.

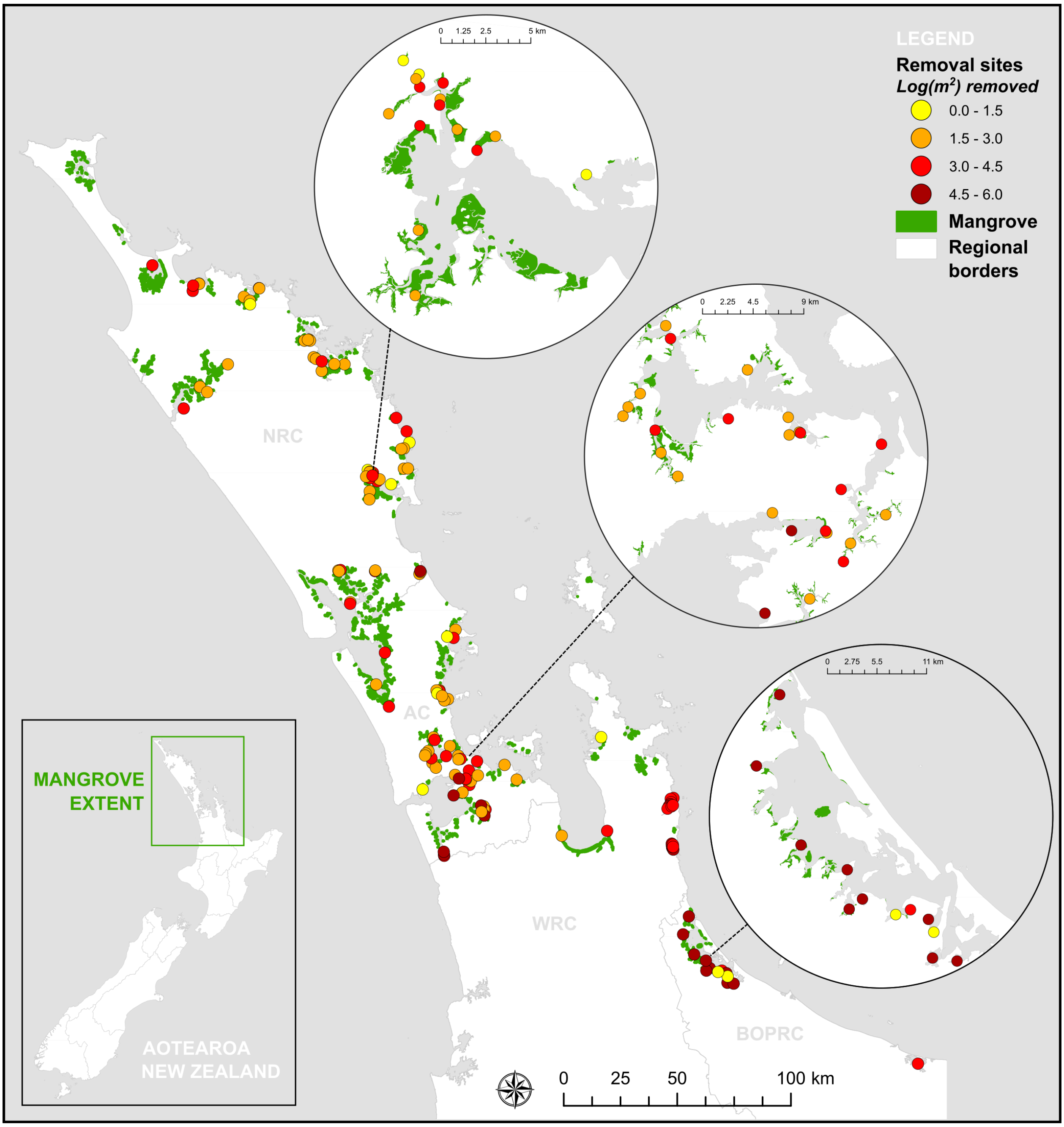

Figure 3.1 The distribution of mangrove forests (green areas) and mangrove removal sites (coloured circles, not to scale) in northern New Zealand. Large circles show enlarged views of removal sites in major cities, including Whangarei (top), Auckland (middle), and Tauranga (bottom). Colours of removal sites indicate the area of mangrove removed, presented on a log scale.

Table 3.1 An overview of mangrove removal resource consents granted by four regional councils in New Zealand. Mangrove area data sourced from LINZ Data Service (2022)

	Auckland	Bay of Plenty	Northland	Waikato	All sites
Total mangrove area, ha (% of total)	8,256 (31)	1,126 (4)	14,213 (54)	2,879 (11)	**26,474**
Consents granted (sites)	56 (56)	16 (16)	65 (65)	11 (24)	**148 (161)**
Consents by removal size					
0-500m^2	24	2	32	2	**60**
500-1000m^2	5	0	6	0	**11**
1000-10,000m^2	13	0	14	4	**31**
>10,000m^2	8	11	4	2	**25**
Total area removed (ha)	151.3	109.1	27.0	45.6	**333.0**
Proportion removed (%)	1.8	9.7	0.2	1.6	**1.3**
Average removal size (ha ± SE)	3.2 ± 1.6	8.4 ± 1.9	0.5 ± 0.3	5.7 ± 3.6	**2.4 ± 0.7**
Most frequent removal shape (n)	Large contiguous (14)	Seaward strip (10)	Pathway & Inshore (13)	Large contiguous & Juvenile (2)	**Large contiguous (33)**
Avg. consent duration (years ± SE)	17 ± 2	11 ± 1.7	20 ± 1.6	17 ± 3.8	**18 ± 1.1**

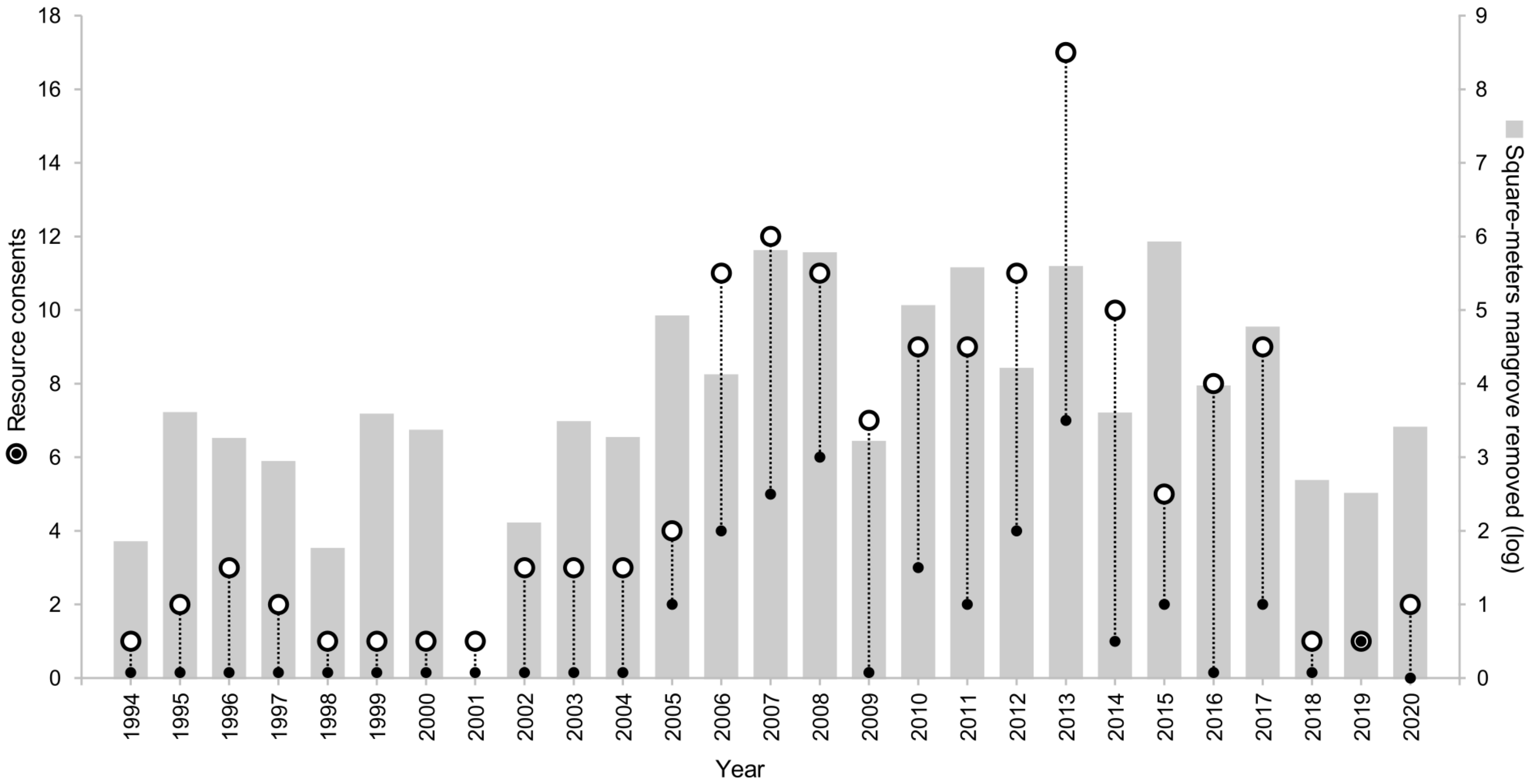

Figure 3.2 A comparison of resource consents granted annually (white circles) since 1994 with the amount of mangrove removal granted by consents in the same year (grey bars). Dotted lines indicate the disparity between all consents (white circles) and those containing avifauna-relevant stipulations (black circles)

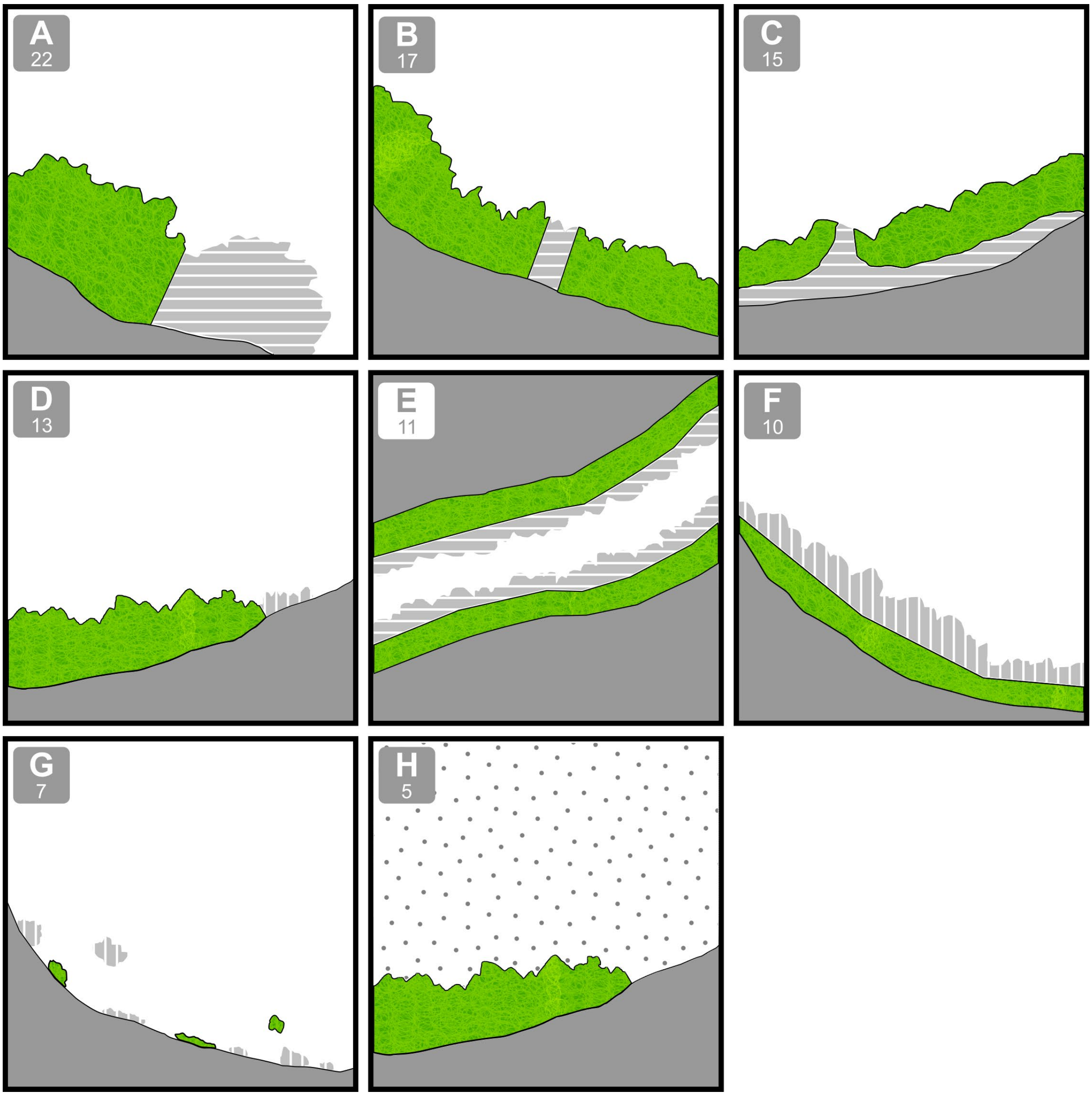

Figure 3.3 Mangrove removal spatial configurations (letters) ordered by their respective frequencies in the collated data set (numbers, indicating percentage): A = large-contiguous; B = pathway; C = inshore; D = small-contiguous; E = channel; F = seaward-strip; G = patchwork; H = seedling-only. Green areas indicate mangroves, grey-striped areas indicate mature mangrove removal, and grey dots indicate seedling removal. Clearance shapes adapted from Lundquist et al. (2017) and expanded upon.

Of the 330 hectares of cleared vegetation, 147 hectares were removed from the coastal marine area (CMA) after clearance (44% of all felled mangroves across 97 sites), 122 hectares were mulched on site and left to be dispersed by tidal action (37%, n=14), and a further 17 hectares were burned on site (5%, n =16).

Among large removals (n=56), just 21 consents (38%) required monitoring of sediment levels during and/or after mangrove removal, while only 9 consents (16%) required the implementation of a long-term sediment mitigation strategy as a condition of removing mangroves. Sediment mitigation strategies consisted exclusively of on-site coastal or riparian planting.

Application documents indicated that more than half of all large removals were motivated, in part, by community desires for improved coastal amenity and recreation values. Ecological restoration and bird conservation were cited as a rationales in 18% and 7% of applications for large removals respectively, but neither were cited for small removals (Figure 3.4).

3.4.2 Avifauna

3.4.2.1 Consent stipulations

Avifauna-targeted stipulations were found in fewer than a third (27%) of all resource consents. Additionally, the incidence of avifauna stipulations increased proportionately to the increase in consents granted since 1994 (Figure 3.2). The most common avifauna stipulation among consents specified the condition that removal work take place outside of the avian breeding season (21% of all consents), followed by stipulations requiring post-removal bird surveys (12%) and pre-removal bird surveys (7%).

3.4.2.2 AEE reports

In total, I identified fifty AEE reports from large removal consents (n=56), but just 68% of these reports considered avifauna in their assessments. The majority of AEE assessments predicted that mangrove removal would have no effect on either banded rails or mangrove-using birds, and a positive effect on coastal birds (Table 3.2). However, AEE assessments were seldomly informed by formal monitoring of relevant avifauna groups (Table 3.2).

3.4.2.3 Case studies

I identified fourteen case study sites in four major harbours (Table 3.3). The area of mangroves removed in these case study sites totalled 156.4 hectares, accounting for almost half of all removal identified in this study. Banded rails were monitored at all case study sites using footprint surveys, but other avifauna were poorly represented by comparison. Mangrove-using birds were monitored at three sites using five-minute point counts, and coastal birds were monitored at one site using census counts.

Analysis of data from banded rail footprint surveys (n=13) indicated significantly fewer footprints in post-removal surveys relative to pre-removal surveys ($P < 0.05$, $t = 2.39$, $df = 12$). Just two case studies reported a decline in banded rail abundance, two case studies reported no change to banded rail abundance, and the remaining nine case studies said results were inconclusive (Table 3.3) as footprint declines may reflect a decline in banded rail abundance or poor substrate conditions following mangrove removal.

Monitoring of coastal birds in a large-contiguous removal site in Auckland reported an increase in absolute abundance and avifauna richness following mangrove removal (Table 3.3). Mangrove-using birds were not monitored at the same site, and the effects of a large-contiguous mangrove removal on this bird group remain unquantified. However, monitoring from three seaward-strip removal sites in Whangamata (Table 3.3) reported no significant changes to the abundance of 33 species of mangrove-using birds following mangrove removal. Relatively minor declines in abundance were reported for seven species – all classified as either Not Threatened or Introduced (Robertson et al. 2017) – but these declines were attributed to differences in sampling effort and seasonal timing rather than removal effects.

Table 3.2 An overview of findings made by Assessment of Environmental Effects (AEE) reports regarding the predicted effect of mangrove removal on three bird groups, as well as the types of monitoring methods used to inform these predicted effects. Monitoring methods were classed as formal where repeatable, standardised monitoring was used to quantify abundance or richness, while informal methods were non-repeatable and non-standards assessments of diversity.

Bird group	AEE reports (n)	Predicted effect of removal (% of reports, n)		Monitoring method (%, n)	
Coastal birds	20	Negative:	10% (2)	Formal:	10% (2)
		No effect:	5% (1)	Informal:	45% (9)
		Positive:	85% (17)	None:	45% (9)
Mangrove-using birds	21	Negative:	29% (6)	Formal:	10% (2)
		No effect:	71% (15)	Informal:	29% (6)
		Positive:	0% (0)	None:	62% (13)
Banded rail	25	Negative:	44% (11)	Formal:	28% (7)
		No effect:	56% (14)	Informal:	28% (7)
		Positive:	0% (0)	None:	44% (11)

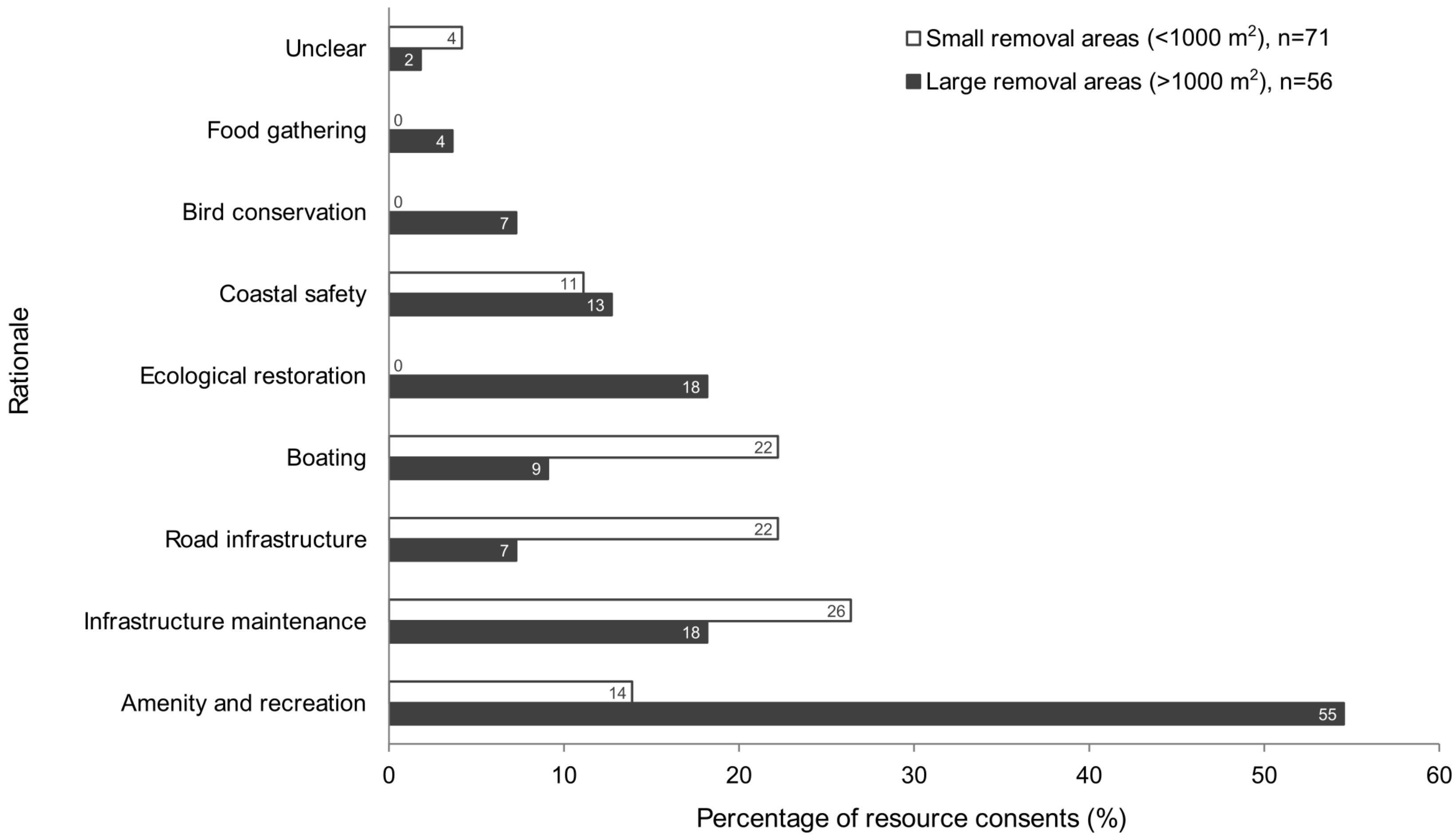

Figure 3.4 A summary of applicant rationales for mature mangrove removal among large and small removal sites, as determined by application documents for mangrove removal

Table 3.3 The reported changes to abundance and/or richness of three avifauna groups – coastal birds, mangrove birds, and banded rail (BR) – in response to mangrove removal in fourteen case study sites. The number of surveys undertaken before ('pre') and after ('post) mangrove removal is indicated for each site. For banded rail, the average number of footprints observed by monitoring surveys before (pre) and after (post) mangrove removal is also indicated. '-' symbols indicate that abundance and/or richness was not measured.

Council[1]	Location	Removal area (ha)	Clearance type	Surveys		Reported change to abundance (*A*) or richness (*R*)			Average BR prints	
				Pre	Post	Coastal birds	Mangrove birds	Banded rail	Pre	Post
AC	Pahurehure Inlet	26.8	Large contiguous	3	4	Increase (*A,R*)[1,2]	-	Decrease (*A*)[2,3,4,5]	*No data*	*No data*
BOPRC	Matua	2	Seaward strip	2	2	-	-	Unclear (*A*)[6]	29	17
BOPRC	Waikareao	6.5	Seaward strip	2	2	-	-	Unclear (*A*)[6]	28	8
BOPRC	Wainui	12.4	Seaward strip	2	2	-	-	Unclear (*A*)[6]	23	19
BOPRC	Te Puna	16.9	Seaward strip	2	2	-	-	Unclear (*A*)[6]	19	17
BOPRC	Welcome Bay	7.4	Seaward strip	2	2	-	-	Unclear (*A*)[6]	17	10
BOPRC	Waikaraka	8	Seaward strip	2	2	-	-	Unclear (*A*)[6]	17	12
BOPRC	Athenree	24.2	Seaward strip	2	2	-	-	Unclear (*A*)[6]	9	8
BOPRC	Uretara	11.9	Seaward strip	2	2	-	-	Unclear (*A*)[6]	5	4
BOPRC	Omokoroa	12.3	Seaward strip	2	2	-	-	Unclear (*A*)[6]	5	7
WRC	Whangamata (i)	0.1	Seaward strip	1	4	-	No change (*A,R*)[7]	Decrease (*A*)[7]	8	2
WRC	Whangamata (ii)	3.2	Seaward strip	1	10	-	No change (*A,R*)[7]	Decrease (*A*)[7]	7	7
WRC	Whangamata (iii)	2.9	Seaward strip	1	10	-	No change (*A,R*)[7]	No change (*A*)[7]	6	6
WRC	Tairua	21.8	Seaward strip	1	6	-	-	No change (*A*)[8]	0	3

Reports: (1) Don et al. 2008 (2) Don 2015 (3) Southey 2009 (4) van Winkel & Wedding 2010 (5) van Winkel & Wedding 2012 (6) Rowson 2012 (7) Richardson & Wium 2019 (8) Wium 2019
[1]Councils: Auckland Council (AC), Bay of Plenty Regional Council (BOPRC), and Waikato Regional Council (WRC)

3.5 Discussion

The expansion of mangrove forests in New Zealand has influenced the habitat composition of numerous estuaries and fuelled demand for mangrove removal in many coastal communities. Using data collated from resource consents – documents issued by local authorities to regulate the removal of mangroves – this study shows that >330 hectares of mangrove forest have been removed since 1994. This represents the first estimate of the extent of legal mangrove removal in New Zealand. In addition, results from consent-associated monitoring reports suggest that removal is likely to benefit coastal bird species that prefer open habitat but at a cost to populations of mangrove-using avifauna such as the banded rail.

Here I discuss the ongoing management of expanding mangroves in New Zealand as a case study in managing an invasive native species. Broadly, I argue that contemporary management strategies are misaligned with the ecology of native invasions as they prioritise the symptoms of invasion (symptom-oriented management) rather than its drivers (driver-oriented management). I argue that a removal-centric, symptom-oriented approach is unlikely to reverse mangrove expansion, optimise restoration success, or mitigate the negative effects of removal on mangrove-using avifauna. Considering these shortcomings, I propose that mangrove management should better reflect the ecological theory of native invasions and pivot towards a 'driver-oriented' management, while acknowledging the challenges in making this shift.

3.5.1 Mangroves as native invaders

Mangrove expansion in New Zealand occurs at the interface of two theoretical concepts: natural range-expansions (native colonisers) and native invasions (native invaders). While these concepts can both be explained by the mechanisms of colonisation (Hoffmann & Courchamp 2016), distinguishing between them is necessary for informed habitat management and policy. Neither 'natural coloniser' nor 'native invader' concisely describe *Avicennia marina*'s expansion in New Zealand. While mangroves are a native species undergoing expansion, they are not natural colonisers given their reliance on human-mediated changes to coastal regions. Given that mangrove expansion can be explicitly linked to human actions (Swales *et al.* 2015; Horstman *et al.* 2018), they can be considered native invaders (Simberloff 2010; Simberloff *et al.* 2012; Nackley *et al.* 2017), yet whether mangroves have spread beyond their "natural past or present range" (Nackley *et al.* 2017) is subjective. Within and between numerous estuaries in New Zealand, mangroves have expanded significantly over hundreds of meters and arguably beyond their "present" range. Moreover, *Avicennia marina* has expanded its latitudinal range in other parts of its global distribution, steadily moving southwards with warming temperatures (Saintilan *et al.* 2014). Conversely, *A. marina* in New Zealand has not expanded beyond its past natural range – pollen in sediment cores from Sponge Bay and Awapuni suggests mangroves previously occurred some 140 kilometres south of its present distribution (Morrisey *et al.* 2007), with local extinctions in this region as recently as 6,500 years ago (Mildenhall 2001).

Although not a perfect conceptual fit, the rapid expansion of mangroves in New Zealand bears the hallmarks of a native species invasion. Mediated by human-induced changes to the environment mangroves have proliferated rapidly, overcome natural obstacles to their expansion through human intervention, and become dominant in novel areas (Valéry *et al.* 2009; Nackley *et al.* 2017). Mangroves have expanded their range at an estimated 3-4% per year in New Zealand since the mid-20th century, corresponding to an increase from 2,313 ha in 1940 to 10,483 ha in 2014 in the Auckland region alone (McBride *et al.* 2016; Suyadi *et al.* 2019). Importantly, framing mangroves as native invaders emphasises the underlying drivers of their expansion and provokes evaluation of the source of their ecological impacts.

Although invaders are defined by the scale of their spread and not their impact on recipient ecosystems (Richardson *et al.* 2000), invasive species are often associated with deleterious effects on biodiversity, ecosystem functioning, and ecosystem services (Valéry *et al.* 2009; Blackburn *et al.* 2011). While the rapid expansion of mangroves is unmistakable, their effects on biodiversity and ecosystem functioning are often misconceived by the public (Harty 2009). Contrary to public perception, declines in habitat (e.g., seagrass meadows or shellfish beds) and macrofauna diversity that have accompanied mangrove expansion are not driven by mangrove vegetation, but rather by human-induced increases in sediment supply and deposition that precede, and enable, mangrove growth (Ellis *et al.* 2004; Thrush *et al.* 2004; Swales *et al.* 2015). However, mangroves can influence biophysical conditions such that estuarine regions become favourable environments for further sediment deposition (Stokes *et al.* 2010; Horstman *et al.* 2018), thereby reinforcing sedimentation effects.

The impact of expanding mangroves on New Zealand's coastlines has ignited a value-laden debate that has shaped New Zealand's management response. Mangrove proliferation has increased the coastal capacity for nutrient, sediment, and heavy metal trapping (Barbier *et al.* 2011; Bastakoti *et al.* 2018), enhanced the capacity for carbon storage (Bulmer *et al.* 2020), improved erosion mitigation and coastal safety (Lundquist *et al.* 2014b), and created additional habitats for species that use mangrove forests (Nagelkerken *et al.* 2008; Dencer-Brown *et al.* 2020). However, these ecosystem services are the result of a transition from open, sandy habitats to closed, muddier habitats – a transformation that has diminished the societal and cultural value of coastal environments to many human communities (Harty 2009) and reduced the local availability of sandy habitat required by several species of shorebirds. Thus, while mangroves are not responsible for the deleterious effects of sedimentation, their establishment has contributed to changing the functioning and make-up of coastal ecosystems and has prompted a management response defined by vegetation removal.

3.5.2 Contemporary mangrove management: a symptom-oriented approach

3.5.2.1 Political context

Policy on native invasive species is caught at the junction between native and invasive species management. In New Zealand, political perspectives on mangroves have changed over time, swinging between protecting and removing mangroves in response to changing mangrove distribution and public perceptions of coastal environments. During the late 1800s and early 1900s, mangrove forests in New Zealand declined as European settlers reclaimed coastal land for ports and agriculture (Morrisey *et al.* 2007, 2010). To prevent further reclamation, the Harbours Amendment Act made seabed reclamations for agricultural purposes illegal in 1977. Later, the 1994 New Zealand Coastal Policy (NZCPS) granted mangroves protected status, citing it as “significant indigenous vegetation and significant habitat [to] indigenous fauna”. Correspondingly, relatively few consents were granted for mangrove removal prior to the mid-2000s (Figure 3.2). However, facing pressure from local communities to counteract expanding mangrove forests (Harty 2009), national and regional policies were increasingly amended to enable mangrove removal (PCE 2020), resulting in a substantial increase in removal projects in the mid- to late-2000s (Figure 3.2).

Today, mangrove management in New Zealand is synonymous with mangrove removal (Harty 2009), addressing the symptom (mangrove vegetation) not the driver (excess sediment), of mangrove expansion. Since the regulation of mangrove removal in 1994, I estimate >330 hectares of mangrove forest in New Zealand have been removed (Table 3.1), primarily in the vicinity of coastal towns and cities (Figure 3.1). However, this estimate does not capture the full extent of mangrove removal in New Zealand; this study ignores mangroves removed before 1994 and does not account for illegal removal of mangroves, which may account for half of all removals (C. Lundquist, personal communication, August 2021). Taking illegal removal at this scale into account, more than 660 hectares of mangrove forest have likely been removed since 1994, corresponding to an average rate of removal of 25 hectares per year. However, this rate is substantially lower than mangrove expansion in recent decades (Suyadi et al. 2019), and, barring substantial reductions in sediment supply, mangroves are expected to continue expanding their distribution (McBride et al. 2016).

3.5.2.2 Drivers of symptom-oriented management

Despite the established link between mangrove expansion and increased rates of sedimentation (Swales *et al.* 2015; Horstman *et al.* 2018), mangrove removal remains the principal management response to mangrove expansion in New Zealand. I suggest two reasons for this continued response: first, mangrove removal satisfies community objectives for open habitats, and second, a removal-led management approach is easier to implement than an approach that addresses catchment-wide drivers.

The rationales for mangrove removal (Figure 3.4) highlight a discrepancy between the objectives of coastal managers and those of consent applicants. Coastal managers implement mangrove removal as a habitat restoration tool, often using biophysical- and macrofauna-targeted monitoring to assess restoration success (Stokes *et al.* 2010, 2016). In contrast, consent applicants – often community groups – typically prioritise mangrove removal that meets human-centric criteria – such as improvements to amenity and recreation – over objectives that prioritise ecological restoration or conservation purposes (Figure 3.4). Thus, while mangrove removals consistently fall short of objectives for ecological restoration (Lundquist *et al.* 2014a), they meet community objectives for open habitat. Mangrove removal is therefore effective in meeting common community goals and retains pressure on local authorities to continue with a removal-centric mangrove management strategy.

A symptom-oriented strategy for mangrove management represents a simpler management pathway than a driver-oriented strategy, albeit less effective in establishing long-term solutions. The management of invasive alien species (IAS) is an established example of symptom-oriented management with the simple of objective of removing unwanted species based on their the origins (Davis *et al.* 2011; Nackley *et al.* 2017). While this approach may provide practical tools to INS management (Nackley *et al.* 2017), INS pose a more complex challenge as the management end-goal is not eradication but ecosystem balance (typically to restore the landscape to a historical state). Although the effects of INS expansions are comparable to those of IAS (Valéry *et al.* 2009; Hoffmann & Courchamp 2016; Nackley *et al.* 2017), INS are integral to the functioning of their resident ecosystems. Thus, instead of exclusively pursuing a short-term partial-eradication approach, INS management strategies should target the drivers of invasion (Carey *et al.* 2012) – typically large-scale human-mediated changes to the environment (Didham *et al.* 2007; Valéry *et al.* 2008; Simberloff 2010).

Mangrove management in New Zealand has become misaligned with the theory of native invasions as it fails to connect mangrove traits with environmental change and ecosystem processes. Mangrove removal represents a relatively simpler management strategy than addressing catchment-scale drivers: mangrove removal is quick, has an established regulatory framework, and involves local stakeholders. In contrast, managing river inputs such as sediment and nutrients at a catchment scale is time-intensive, is subject to multiple legal frameworks, and requires input and collaboration from numerous stakeholders with conflicting viewpoints (PCE 2020). In this regard, mangrove management represents a ‘wicked problem’, whereby a multitude of conflicting perspectives and objectives render strategies difficult to characterize, let alone implement (Woodford *et al.* 2016). However, without reducing rates of sedimentation, mangrove growth is unlikely to slow down (McBride *et al.* 2016), leaving mangrove growth to remain a point of contention in coastal areas. Moreover, mangrove removal has a poor track record as a restoration tool (Lundquist *et al.* 2014b; Stokes *et al.* 2016; Bulmer *et al.* 2017) and given its wide-ranging ecological repercussions (Lundquist *et al.* 2014a; Horstman *et al.* 2018) it is clear that coastal managers must find a balance between managing the symptoms of mangrove invasion and addressing its drivers.

3.5.3 Repercussions of symptom-oriented management

3.5.3.1 Mangrove removal and restoration

Mangrove removal in New Zealand is frequently characterised as a tool for habitat restoration (Stokes *et al.* 2016; Bulmer *et al.* 2017; Horstman *et al.* 2018) with the goal of transitioning substrate conditions, the balance of ecological communities, and ecosystem services towards the characteristics of sandflat habitats (Horstman *et al.* 2018). Globally, mangrove removal has rarely been considered a restoration technique (Stokes *et al.* 2016) and there is limited understanding of its short- and long-term ecological effects (Lundquist *et al.* 2014a).

Although mangrove removals successfully create open habitats, they seldom meet habitat restoration objectives (Lundquist *et al.* 2014a; Bulmer *et al.* 2017). Reinstating sandflat-type habitats is dependent on local conditions and removal techniques (Lundquist *et al.* 2014b, 2017; Bulmer & Lundquist 2016); transforming muddy substrates to sandier ones relies on natural site-specific factors that remove fine silt – such as high wind and/or wave exposure – but do not deposit further sediment (Lundquist *et al.* 2014b). Successful restoration of sandflats is typically seen in sites already dominated by sandy substrate, although sandier removal sites represent only a limited proportion of all removal sites (Lundquist *et al.* 2014b; Horstman *et al.* 2018). Moreover, removal sites are more likely to recover where non-mechanical removal techniques are used, smaller areas are cleared, and mangrove cuttings are removed from the coastline (Lundquist *et al.* 2014a). This study shows that these conditions are infrequently met. Analysis of resource consent documents found that mechanical methods were commonly used to remove mangroves (particularly among large removal sites), that large-contiguous clearings were the most frequent removal configuration observed (Figure 3.3) and that mulching of felled vegetation was undertaken across >130 hectares, triggering macroalgal blooms and declining oxygen concentrations in the water column at several removal sites (Lundquist *et al.* 2014a; Stokes *et al.* 2016). While smaller removal areas can exhibit faster trends towards recovery – i.e., loss of muddy sediments – this process can take decades and is highly unlikely in sheltered locations not exposed to strong coastal erosion (Lundquist et al. 2014a). Counter to the ecological objectives of mangrove removal projects, mangrove clearance, particularly at large scales, seldom guarantees a transition to sandier habitats and can have several repercussions for coastal ecosystems (Lundquist *et al.* 2014a; Stokes *et al.* 2016; Bulmer *et al.* 2017).

3.5.3.2 Ecological repercussions

Although the ecological repercussions of mangrove removal are potentially wide-ranging, existing research focuses on the benthic environment. Results from this study indicate that these repercussions may extend to avifauna; evidence from banded rail monitoring reports (Table 3.3) indicates this species may suffer localised declines following mangrove removal. However, coastal bird communities likely benefit from mangrove removals as in the case of Pahurehure Inlet, a large-contiguous mangrove removal in the Auckland region (Table 3.3), which saw wading- and shorebird communities increase in both richness and abundance. Importantly, limited data to date prevents a comprehensive understanding of changes to populations of avifauna.

Limited evidence from case studies suggests that the configuration and scale of mangrove removal may influence its repercussions on banded rail populations, as well as other mangrove-using avifauna. For example, monitoring reports from a large-contiguous removal site in Auckland found that banded rail population declined by >50% following removal (Southey 2009), disappearing entirely in localised areas (Don 2015). In sites where mangroves were cleared in seaward strips, available monitoring reports inferred that banded rail populations remained following removal, albeit seemingly restricted to remaining mangrove patches (Table 3.3). This comparison between large-contiguous removals and seaward-strip clearances requires further study, but limited data from case study sites suggests that the seaward-strip removals may minimise the conservation trade-off between different avifauna groups by retaining habitat for mangrove-using species and reinstating habitat for coastal birds.

Inferences into the ecological repercussions of mangrove removal on avifauna are limited by a small sample size – this study identified just twelve relevant case-study consents – and inadequate monitoring practices. For example, declines in banded rail footprint numbers following removal events may be an artefact of poorly designed surveys that did not consider substrate condition or survey repeatability (see Table S3.2, Supplementary material for recommended improvements to footprint surveys). More generally, a lack of avifauna monitoring may be the result of high financial costs; Lundquist *et al.* (2017) estimate that the costs of monitoring removal areas (including abiotic changes, macrofauna communities, and avifauna) can reach $125,000 NZD for harbour-wide removal operations. Additionally, regional councils may not require monitoring based on AEE report recommendations. As shown by this study, AEE assessments frequently predicted that mangrove-using birds and banded rails would be unaffected by mangrove removals, despite seldomly using formal monitoring to inform these assertions (Table 3.2).

3.5.4 Shifting to driver-oriented management

The majority of native invasions are caused by human mediated changes to the environment (Carey *et al.* 2012) therefore addressing the roots of these changes is key to managing invasive native species. To halt the spread of expanding mangroves and minimise the ecological impacts of symptom-oriented management, coastal managers in New Zealand must address the drivers of mangrove expansion.

Adopting driver-oriented management requires policymakers, managers, and communities to recognise that native invaders are connected to, and result from, changes in their wider environment. Scientists drawing on Western perspectives explain and make recommendations using earth-system sciences and emerging ecological theory on native invasions (Nackley *et al.* 2017). In a New Zealand context, a driver-oriented perspective to mangrove management can learn from and reflect the tenets of *mātauranga* Māori (henceforth mātauranga), the continuum of distinct knowledge with Polynesian origins that includes Māori worldviews, values, culture and cultural practices (Hikuroa 2017; Clapcott *et al.* 2018). Mātauranga has long recognised the natural world as an interconnected system whose parts respond to and rely on one another and are best interpreted as a whole (Harmsworth & Awatere 2013; Salmond *et al.* 2019).

Adopting driver-oriented management to tackle mangrove expansion in New Zealand requires adaptive, multi-faceted strategies that test the theoretical constructs of invasion science (Nackley *et al.* 2017). It also requires overcoming challenges that span political, societal, and scientific spheres of thinking (Carey *et al.* 2012) and changing attitudes to the allocation of financial and management resources. The expansion of mangroves in New Zealand provides a case study to understand the challenges posed by INS and highlight the first steps to implementing a driver-oriented management approach. More broadly, the challenges posed by mangrove management in New Zealand extend beyond issues of practicality, scale, and implementation, requiring a shift in thinking that acknowledges that the natural world is comprised of multiple, co-dependent parts – a fundamental principle with mātauranga and the concept of *taiao* (Harmsworth & Awatere 2013; Salmond *et al.* 2019; Hikuroa 2021).

Transitioning both policy and perceptions of mangrove environments to reflect their connection to catchment-scale process presents a multifaceted challenge (PCE 2020). Here, I name and discuss four challenges that currently inhibit a transition to driver-oriented management of mangroves in New Zealand.

3.5.4.1 Challenge 1: Poorly designed policy

Despite the well-established link between mangroves and sediment, contemporary mangrove policy in New Zealand seldom targets sediment inputs at a catchment scale. In regional policies on mangrove management, mangrove clearance regulations are defined in detail (Auckland Council 2019; Bay of Plenty Regional Council 2019; Northland Regional Council 2020), while sediment mitigation methods are, at best, vaguely defined. This policy imbalance is reflected in management actions: among mangrove removal consent conditions for large removals (n=56), the review in this study identified just nine consents that required sedimentation mitigation measures to mitigate release of sediments when mangroves are removed, all being riparian planting in the immediate vicinity of removal sites, rather than at wider catchment scales.

A lack of sediment-oriented interventions (e.g., riparian planting, bank stabilisation, or reforestation) at catchment scales as part of mangrove management reflects a disconnect between freshwater policy and catchment-scale processes. Estuaries in New Zealand are currently managed under as many as eight distinct statutory frameworks, several of which manage estuarine and freshwater systems separately despite their physical interconnections (PCE 2020). Mangrove management falls under the framework for the coastal marine area (CMA), resulting in management practices that is focused on mangrove plants without accounting for their drivers (sediment and eutrophication) as these fall under upstream statutory frameworks. Thus, a fragmented resource management framework is a key challenge to driver-oriented management, given that the need to redefine mangrove policy and management to reflect catchment processes is key to addressing mangrove spread and restoring ecosystem health at multiple spatial scales (Peacock *et al.* 2012; Lundquist *et al.* 2014b; Swales *et al.* 2015).

3.5.4.2 Challenge 2: Changing societal views

Public perception of invasive species is a key determinant of management responses (Jarić *et al.* 2020) and in New Zealand has resulted in a mangrove management strategy that prioritises human-centric objectives over ecological restoration and/or health (Lundquist *et al.* 2014b, Figure 3.4). Of the eight different rationales this review identified for mangrove removal, just two were based on ecological considerations (Figure 3.4). Moreover, mangroves in New Zealand are frequently regarded by communities as unattractive and of little value to coastal regions (Harty 2009; Dencer-Brown 2019). If community perceptions of mangroves remain generally negative, it is unlikely that regional councils will gain public support to transition towards management strategies focused on sediment reduction rather than mangrove removal.

A negative perception of mangroves in local communities may be rooted in the misconception that coastal changes are caused by mangroves rather than by sediment (Harty 2009). This perception has caused an opinion-based debate about mangrove management in New Zealand, unsupported by peer-reviewed or even by documented evidence (Morrisey *et al.* 2007), resulting in conflict between communities, regional authorities, and local conservation organisations. In this context, it is possible that framing mangroves as native invaders – as proposed by this study – may further entrench a negative social perception of mangrove forests in New Zealand. 'Invasive' is a loaded term, typically associated with alien species that cause widespread damage to recipient ecosystems (Valéry *et al.* 2009; Blackburn *et al.* 2011), despite invasive species being defined (in invasion theory) by their spread and not their impacts (Richardson *et al.* 2000). As mangroves continue to expand, use of the term 'neonative' (Essl *et al.* 2019) to describe *Avicennia marina* may mitigate negative perceptions associated with 'invaders' while retaining the ecological nuance to inform management actions.

To ensure informed management outcomes, resource managers must, of course, acknowledge public perceptions of INS in planning and implementing management actions (Jarić *et al.* 2020). In a mangrove management context, this may require a balance between implementing driver-oriented and symptom-oriented management. Thus, while reducing sedimentation should be the primary objective of mangrove management, this could be complemented by limited mangrove removal in areas where mangrove presence interferes with high-value public recreation areas or encroaches upon rare or threatened ecological communities (Harty 2009; Lundquist *et al.* 2014b). However, implementing a balanced approach to mangrove removal will require collaboration and engagement among scientists, managers and affected local communities to establish joint management goals (Fischer *et al.* 2014; Crowley *et al.* 2017; Novoa *et al.* 2018).

3.5.4.3 Challenge 3: Improving monitoring

Mangrove removals in New Zealand lack a standardised national monitoring framework, resulting in differing monitoring practices among regional councils and hindering inter-site comparison as well as assessments of restoration success. For example, this review identified numerous consents that used a variety of informal survey methods to evaluate avifauna populations. In this instance, monitoring efforts would be easily improved by adopting the habitat- and species-specific methods guidelines set by the Department of Conservation (Dowding 2012).

While this review has addressed avifauna monitoring, a variety of abiotic and biotic factors should also be considered to inform mangrove management decision-making. Stokes *et al.* (2016) identify multiple parameters – physical, chemical, and biological – and define monitoring targets and timeframes to inform decision-making around mangrove removals in a cost-effect and site-specific manner. Implementation protocols like those proposed by Stokes *et al.* (2016) are key to an effective adaptive management approach in mangrove environments, an approach that incorporates research into action (Salafsky & Margoluis 2003) by treating management actions as experiments to monitor and learn from (West *et al.* 2019).

3.5.4.4 Challenge 4: Furthering invasion science

A shortfall in invasion science is the exclusion of native species from prominent theoretical frameworks of invasion (e.g., Williamson & Fitter 1996; Richardson *et al.* 2000; Blackburn *et al.* 2011). Moreover, a framework to guide management of native invasions remains a work in progress as the ecology of native invasions is poorly characterised (Nackley *et al.* 2017). Native invasions are understudied and scientists remain hard-pressed to explain why, when, and where native species will become invasive, or to quantify the impacts of established INS on recipient ecosystems (Carey *et al.* 2012).

Without studying the mechanisms and effects of native invasions, it is difficult to devise appropriate management strategies. The bias in invasion science towards IAS means that tried-and-tested strategies for countering IAS are readily available to managers, yet these solutions are potentially ill-suited to the problems posed by INS. Although native and alien invasions share multiple characteristics (Nackley *et al.* 2017), they should elicit different management responses given their root causes and unique pathways to invasion. Scientific study of such INS invasion pathways should inform management strategies for INS, particularly where INS have deleterious effects on biodiversity and/or ecosystem functioning.

Scientific research to address and frame native invasions has begun, although it is in its infancy. For example, Nackley *et al.* (2017) lay out guidelines for when, where, and how to manage INS in their discussion of the nebulous ecology of native invasions; their recommendations are wide-ranging, including the need to develop mechanistic models of ecosystem dynamics, define strategies to address both *in situ* and *ex situ* drivers, and cherry-pick from methods used to control alien species. As illustrated by mangrove expansion in New Zealand, there is a clear need for further research in this area and to test applications of such guidelines in real-world management scenarios.

3.5.5 Concluding remarks

Managing the consequences of biological invasions in the face of rapid environmental change is a priority among conservationists (Ricciardi *et al.* 2017, 2021) and more attention must be paid to invasive native species. This study of mangrove forests in New Zealand provides a case study of INS management and highlights the repercussions of managing the symptoms of invasion rather than the drivers. It offers an example of the potential of mātauranga for understanding and addressing a local scientific and community contestation. Pivoting towards management strategies that target the drivers of native invasions presents an opportunity to reverse environmental change and mitigate its deleterious effects, but to do so requires driver-oriented policy, collaboration among stakeholders, and a cohesive adaptive management framework.

3.6 References

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3.7 Supplementary material

Table S3.1 Definitions for the spatial configurations of mangrove removal, as determined by this study.

Code[1]	Name	Definition
A	Large-contiguous	Uninterrupted clearance of a patch of mature mangrove forest mangrove exceeding 500 square meters in area, whereby mangroves are removed entirely from their seaward to landward edge.
B	Pathway	A linear clearance of mangroves, often perpendicular to the shoreline, implemented to allow access to the waterfront. Mangroves on either side of the clearance (parallel to the shoreline) are retained.
C	Inshore	A linear clearance of mangroves along their landward edge in parallel to the coastline. Mangroves on the seaward side of the clearance are retained, although additional narrow perpendicular pathways may provide access to the waterfront.
D	Small-contiguous	Uninterrupted clearance of a patch of mature mangrove forest mangrove exceeding 500 square meters in area, whereby mangroves are removed entirely from their seaward to landward edge.
E	Channel	Clearance along the channel-facing edges of mangrove forests. Clearance type typically associated with dredging for improved drainage.
F	Seaward-strip	Clearance along the seaward edge of a mangrove forest, typically in parallel to the shoreline. The landward side of mangroves are retained.
G	Patchwork	Clearance of multiple disconnected patches of mangrove forests.
H	Seedling-only	Clearance of juvenile or seedling mangrove plants, typically defined as unbranched plants <60cm tall. Occasionally, juveniles are considered mangrove plants <1m tall. Mature mangrove plants are retained.

[1]Code as used in Figure 3.3

Table S3.2 Recommendations for establishing standardised banded rail (BR) footprint surveys which enable consistent temporal and spatial comparisons of banded rail presence or absence.

Recommendation	Description
Sampling method	Choose a scientifically recognised sampling method for finding and counting footprints and maintain this method over the course of the study. Listed below are two options:
1) Transects	Establish transects of equal length within mangroves, along their outer edge, and on adjacent mudflats or within a mangrove removal area. Record all footprints within 1 meter on each side of the transect line. It is important to keep the location of these transects consistent over time to allow for temporal comparisons. Transects along mangroves' outer edges should be adjusted accordingly as/if mangroves are removed. The inclusion of a transect within mangroves is important; recent research has indicated that BR footprints are more likely to be found within mangrove stands than along their outer edge.
2) Stratified-random	Allocate sampling points randomly within mangroves and adjacent mudflats or removal areas. Ensure that the number of sampling points allocated within each habitat is proportional to the habitat size or area of habitat sampled. At or near each randomly allocated sampling point, conduct a search for footprints within a 2x2 meter square quadrat.
Substrate condition	Note the condition or quality of substrate when sampling as the ability of substrate to retain footprints affects their detectability. Create a scoring system for substrate quality, for example, 2 = excellent (substrate retains full footprint), 1 = good (retains partial or faint footprints), 0 = poor (substrate retains little or no footprints as it is too hard/soft/wet). For transect sampling, provide a score of substrate quality at set intervals (e.g., every 5-10 meters). For stratified-random sampling, provide a score for each sampling point. Where possible, select for good and excellent substrates when sampling.
Tide timing	Start searches for footprints at low tide. This allows time between high tides for banded rails to leave footprints behind and time for observers to find prints before the tide comes in again.
Time of day	Note the time of day the survey is undertaken. While it is preferable to keep this standardised over the course of the study, tide timing should be prioritised.
Weather	Avoid performing footprint surveys during or after periods of heavy rainfall. This is likely to degrade substrate quality and in turn decrease the detectability of banded rail footprints.
Observer	Keep a record of the observer undertaking the survey. Different observers may identify footprints inconsistently and it is important to account for this bias.
Correct footprint identification	Accurately determine which footprints belong to BR. As per Elliott (1983), BR footprints are between 36 and 47 mm long and can be confused with footprints from oystercatchers, spur-winged plovers, pied stilts, crakes and young wekas. However, several key differences make BR prints distinguishable from these species. The footprints of waders (oystercatchers, spur-winged plovers, and pied stilts) are more asymmetrical than those of BR, whose prints are mostly symmetrical. Crake prints are usually smaller than BR, although the largest crakes' prints may overlap with the smallest BR prints. Young wekas have similar prints to BR but are likely to be accompanied by adult wekas and their much larger prints. For further guidance on footprint identification on a variety of coastal bird species, see https://www.nztracker.org/.

The following material is an excerpt from the report:

de Satge, J (2021) Mangrove management in Aotearoa New Zealand: a bird's eye review. Prepared in association with: The Office of the Prime Minister's Chief Science Advisor and Massey University. Auckland, New Zealand.

The full report, published in association with the Office of the Prime Minister's Chief Science Advisor in 2021 is available for download at https://bit.ly/OPMCSA-mangrove-management . Here, the report's summary and policy recommendations are presented:

Report summary

Aotearoa New Zealand's mangroves are expanding rapidly, fuelled by human-induced changes to river catchments. Mangrove expansion has prompted communities to remove mangrove vegetation, a process controlled by regional councils using resource consents. This review synthesises data from these consents, highlighting the extent of mangrove removal and its potential effects on avifauna.

In total, this review synthesised data from 148 resource consents granted since 1994 by relevant regional councils. Regional councils granted a total of 330 hectares of mature mangrove removal, a fraction of the area of mangroves gained over the same period. Resource consents predominantly targeted the removal of mature mangrove stands and the average duration of consents – the time during which mangrove removal was permitted and maintained – was 18 years. Most mangrove removal was in Auckland and Bay of Plenty, removing 1.8 and 9.7 percent of their current mangrove forest areas respectively.

The predominant rationale for large-scale mangrove removals ($>1000m^2$) was the restoration and improvement of recreational and amenity values in coastal environments. By contrast, small-scale removals ($<1000m^2$) were typically undertaken for the development and/or maintenance of coastal or road infrastructure.

Avifauna were poorly represented among consent conditions and assessment of environmental effects (AEE) reporting was seldom informed by scientifically rigorous monitoring. Review findings highlight the lack of adequate monitoring processes associated with mangrove removals, particularly for large removals. In this respect, this review has quantified the depth of the mangrove-avifauna knowledge gap, rather than filled this gap. Nevertheless, a limited number of case studies indicated that some coastal birds are likely to benefit from mangrove removal, and few adverse effects were documented for mangrove-using birds (excluding banded rails) in removal sites where large areas of mangroves were retained. Contrastingly, available evidence suggests that banded rail populations may decline after mangrove removal. However, mangrove-avifauna findings should be interpreted cautiously; case studies are context-specific, and insights are limited by a small sample size. The implementation of standardised monitoring protocols for resource consents would serve to deepen this evidence and lead to improved management practices.

The paucity of standardised monitoring in mangrove forests has hindered effective adaptive management of these habitats, while a complex statutory framework does not reflect the catchment-scale drivers of mangrove expansion. Reorienting policies to mandate monitoring and reflect large-scale ecological processes is a priority for mangrove management in Aotearoa New Zealand.

Policy relevance

Report findings have several implications for the direction and scope of mangrove-relevant policies (note, for functional hyperlinks, please view the full report):

1. ***Improving monitoring***
   1.1. *Issue identified*: Mangrove removals lack a standardised monitoring framework, hindering the ability to track the restoration success of removal projects. Monitoring of avifauna is seldom mandated by resource consents (*see* Figure 4), monitoring practices differ among regional councils and removal sites, and monitoring practices for assessment of environmental effects (AEE) reporting are typically informal, lacking standardised methodologies.
   1.2. *Policy shift*: Regional council policies should facilitate standardised monitoring of mangrove removal projects, particularly for large-scale removals. Standardising monitoring allows for informed management decisions, measurable results, and inter-council comparisons of management outcomes. While this report focuses on avifauna, standardised monitoring practices should encompass a range of abiotic and biotic factors.
   1.3. *Recommended action*: Regional councils need to collaborate to define monitoring targets, standardised techniques, and timeframes to inform evidence-based mangrove

management. A conceptual framework is provided by Stokes *et al.* (2016), while avifauna-specific recommendations are provided here and in Table A2.

2. ***Adopting adaptive management***

2.1. *Issue identified*: The management and removal of large areas of mangroves does not follow a consistent management framework. Different regional councils undertake mangrove removal and disposal via different methods, implement different monitoring strategies, and infrequently make use of monitoring-based decision-making.

2.2. *Policy shift*: Mangrove removal should follow the principles of adaptive management, incorporating standardised monitoring, trial removals, and control sites to inform a stepwise, evidence-based management process. While a broad management framework is needed, decision-making should be tailored to individual sites given site-specific differences to important abiotic and biotic factors.

2.3. *Recommended action:* Regional councils need to collaborate to define an adaptive management framework for large-scale mangrove removals. A conceptual starting point is provided here (see Figure 7).

3. ***Following a holistic approach***

3.1. *Issue identified:* Current policy, both regionally and nationally, presents conflicting messages on mangrove removal and conservation. More importantly, policies largely fail to account for the interconnected nature of estuarine systems. As such, the removal of mangrove stands within estuaries targets the outcome of catchment-scale processes (mangrove growth) rather than the processes themselves (sedimentation and eutrophication).

3.2. *Policy shift*: In Aotearoa New Zealand, mātauranga Māori provides a compelling lens with which to view mangrove ecosystems and shape future policy such that management reflects the interrelated nature of estuaries' component parts. To tackle long-term changes, coastal policy needs to address estuaries holistically and target drivers of change. In the short term, mangrove management decisions should occur on a site-specific basis, but must recognise that this is not a sustainable solution to mangrove expansion.

3.3. *Recommended action*: Within national resource management policy, estuaries need to be recognised as connected to and part of river catchments and placed under the same policy framework. Within regional policies, local-scale mangrove management must be complemented by catchment-scale initiatives to reduce sedimentation and eutrophication in waterways.

4. ***Prioritising restoration success***

   4.1. *Issue identified*: Currently, mangroves are most frequently removed in large contiguous patches (see Figure 3) despite evidence suggesting this form of removal is unlikely to meet restoration objectives and may have adverse ecological effects.

   4.2. *Policy shift*: Mangrove removals that focus on preventing further expansion and retain some mangrove habitat should be preferred to large contiguous removals. Available evidence suggests this form of management is more likely to see recovery of sandy substrates and retain a variety of habitats for avifauna.

   4.3. *Recommended action*: Regional council policy should prioritise the retention of longshore mangrove strips in large removal areas (i.e., seaward-strip clearances – see Figure 3), while accounting for site-specific variance in biotic and abiotic factors.

Chapter 3, Statement of Contribution:

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GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.

Student name:	Jacques de Satge
Name and title of main supervisor:	Associate Professor Weihong Ji
In which chapter is the manuscript/published work?	Chapter 3
What percentage of the manuscript/published work was contributed by the student?	95%

Describe the contribution that the student has made to the manuscript/published work:

Jacques developed the manuscript's design and research questions, sourced the data, analysed the data, and wrote the manuscript in its entirety. Weihong provided guidance in establishing the manuscript's research design and editorial input on the final draft of the manuscript.

Please select one of the following three options:

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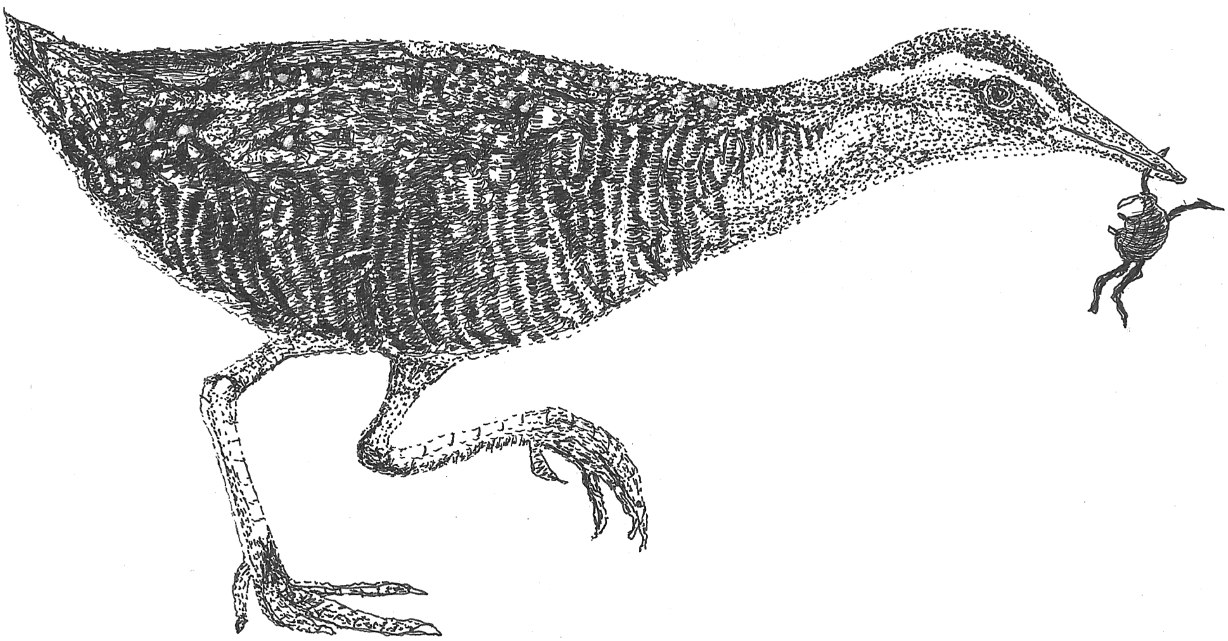
Student's signature:	Jacques de Satge — Digitally signed by Jacques de Satge Date: 2023.03.09 10:38:58 +13'00'	Main supervisor's signature:	Weihong Ji — Digitally signed by Weihong Ji Date: 2023.03.08 14:56:41 +13'00'

This form should be placed at the beginning of each relevant thesis chapter.

CHAPTER 4

ASSESSING HABITAT QUALITY FOR A CRYPTIC MARSH BIRD



In this chapter, I assess the relative habitat quality of mangroves for banded rails. To do so, I quantify the abundance and diversity of macrofauna – a key food resource for banded rails – across multiple habitat strata within saltmarsh-mangrove complexes in northern New Zealand containing established populations of banded rails. Additionally, I evaluate the community structure of macrofauna among different estuarine habitat types. This chapter addresses the second research objective of this thesis:

Objective 2: Determine the relative quality of mangrove habitats to banded rails in saltmarsh-mangrove complexes

Chapter 4 cover image: a banded rail (*Gallirallus philippensis assimilis*) holds a mud crab (*Austrohelice crassa*), a preferred species of prey, in its bill. Artwork by Rick de Satgé.

4.1 Abstract

Understanding habitat quality for birds is important to effective conservation management but it can be difficult to assess quality when species are cryptic and when they occupy dense, logistically challenging habitats. Assessing a habitat's resources, rather than birds themselves, presents a practical and useful method for evaluating habitat quality. In New Zealand, little is known about the quality of mangroves (*Avicennia marina* var. *australasica*) as habitats for avifauna, even for species that extensively use these coastal ecosystems such as the banded rail (*Gallirallus philippensis assimilis*). This is a significant knowledge gap given that banded rail populations are in decline and mangrove forests are routinely removed by regional authorities. To assess the habitat quality of mangroves for banded rails, macrofauna samples were collected in a stratified sampling regime across four sites and four habitat strata (saltmarsh, saltmarsh-mangrove interface, mangroves, and mangrove-mudflat interface) in saltmarsh-mangrove complexes in Mangawhai Harbour, northern New Zealand. The abundance and diversity of macrofauna – a significant food resource to banded rails – were modelled in relation to habitat type and the age of mangrove forests. The abundance and biomass of macrofauna was found to be highest in old-growth mangrove forests, whereas new-growth forests had the second lowest abundance of macrofauna and the lowest biomass of banded rail prey species among all habitats. Contrary to expectations, mangroves had the highest species richness among habitats, although differences in absolute taxa numbers between habitats were marginal. However, mangroves were not observed to hold a unique set of species relative to adjacent habitats. Study findings suggest that mangroves, in particular old-growth forests, can provide high quality foraging habitats to banded rails, contingent on the availability of their resources being high – an assertion this study hypothesises to be true. Accordingly, coastal managers in New Zealand will need to acknowledge the value of mangrove habitats to banded rails, while recognising that mangroves can vary in the resources they provide.

4.2 Introduction

Variation in resources and environmental conditions within and among habitats influences the reproduction, distribution and survival of individual animals and contributes to the regulation of animal populations (Bernstein *et al.* 1991; Krausman 1999; Pulliam 2000). Consequently, measuring habitat quality – the ability of the environment to provide conditions appropriate for survival, reproduction, and population persistence (Block & Brennan 1993) – is a fundamental component of ecological study and wildlife management (Van Horne 1983; Hall *et al.* 1997).

There are two general approaches to measuring habitat quality: 'resource-based' assessments measure habitat quality by measuring habitat attributes directly, while 'species-based' assessments measure individuals or populations (including their demography, density, and/or distribution) to reveal variation in habitat quality (Krausman 1999; Johnson 2007). Although the concept of habitat quality is rooted in demography (Block & Brennan 1993; Hall *et al.* 1997; Krausman 1999), measuring habitat features directly can provide a feasib le assessment of habitat quality in some systems (Johnson 2007) and bypasses difficulties in measuring demographic parameters (Pérot & Villard 2009). In addition, measures of particular habitat attributes, like food availability or vegetation structure, can provide information on the quality of habitats in supporting specific animal behaviours, such as foraging, nesting, or denning (Rodenhouse *et al.* 2003; Chabot *et al.* 2014; Li *et al.* 2019).

Measuring habitat resources, rather than demographic parameters, is a practical approach to assessing the habitat quality of 'cryptic' species – animals that are difficult to detect due to their secretive behaviours and use of inaccessible habitats (Thompson 2004; Durso *et al.* 2011). Monitoring cryptic species is inherently challenging (Williams *et al.* 2018; Crawford *et al.* 2020); monitoring efforts typically yield proxy, and often highly uncertain, measures of species presence, absence, or abundance, and seldom provide robust estimates of survival, reproduction, density, or distribution (Thompson 2004; Vögeli *et al.* 2008; Durso *et al.* 2011). By comparison, the habitat resources that facilitate species' survival and persistence may be simpler to measure than cryptic species themselves, and thus allow resource-based assessments of habitat quality (Johnson 2007). For example, Barnes *et al.* (1995) assessed habitat quality for Northern Bobwhites (*Colinus virginianus*) – an elusive, ground-dwelling bird native to North America – by quantifying food abundance (insects), grass forage quality, and availability of cover. Similarly, Arbeiter *et al.* (2020) measured food abundance (invertebrates) and vegetation structure to assess habitat quality for Corncrakes (*Crex crex*) in relation to meadow management in north-eastern Germany.

Food availability is a key component of habitat quality, linking habitats with demographic parameters such as reproductive performance (Block & Brennan 1993; Mettke-Hofmann *et al.* 2015; Grüebler *et al.* 2018). In studies of avifauna, increases in food availability have been positively correlated with bird abundance, survival, reproductive success, and nestling growth (Marciniak & Nadolski 2007; Moorman *et al.* 2012), while limited food resources can result in fewer nesting attempts, reduced nest provisioning, and significant declines in reproductive success (Champlin *et al.* 2009; Amrhein 2014). Thus, measuring food resources within habitats can provide a proxy of habitat quality (Barnes *et al.* 1995; Isaksson & Andersson 2007; Wilkin *et al.* 2009), particularly when researchers consider the ecological conditions and relationships – including predation, competition, habitat selection, and accessibility – that constrain food availability (Block & Brennan 1993; Lyons 2005; Morrison *et al.* 2006; Johnson 2007).

The banded rail (*Gallirallus philippensis*) is a medium-sized cryptic marsh bird species with a wide distribution spanning south-east Asia, Australasia, and the southwest Pacific, with as many as 20 subspecies recognised across the region (Taylor & van Perlo 1998; Garcia-Ramirez *et al.* 2017). The New Zealand subspecies, moho-pererū *G. p. assimilis*, was once widely distributed across the North and South Island, inhabiting both freshwater and coastal wetlands. However, in recent decades New Zealand's population of banded rails has undergone a significant range-restriction, driven by habitat loss and predation by introduced mammalian predators (Elliott 1983, 1987; Heather & Robertson 2005). Although small populations remain in coastal saltmarshes in the Nelson bays (<200 individuals) and on several offshore islands (Elliott 1983; Heather & Robertson 2005), the majority of New Zealand's remaining banded rail population – an estimated 80-90% – is restricted to the saltmarsh-mangrove complexes (SMCs) along the northern coastlines of the North Island (Bellingham 2013). These complexes are characterised by a tidal gradient whereby the rush saltmarsh-dominated upper reaches are less frequently flooded by the tide than the lower reaches, which are dominated by the mangrove species *Avicennia marina* var. *australasica.*

Within saltmarsh-mangrove complexes, saltmarsh habitats are thought to provide banded rails with nesting and roosting sites, as well as food resources in the form of benthic macrofauna, while mangroves are thought to provide food resources only (Elliott 1987; Heather & Robertson 2005; Beauchamp 2015). Mangroves are hypothesised to be preferred foraging habitats for banded rails within SMCs (Botha 2011; Beauchamp 2022) despite research indicating that mangroves may comprise fewer and less diverse benthic macrofauna than adjacent estuarine habitats (Elliott 1983; Ellis *et al.* 2004; Alfaro 2006). Although macrofauna are also found in open mudflats beyond the seaward edge of mangrove forests, banded rails are seldom seen far (>10m) from cover vegetation (Botha 2011; Beauchamp 2015).

The habitat quality of mangrove habitats is of conservation concern. Not only do these habitats help support the vast majority of New Zealand's banded rail population, but they are also subject to rapid environmental change and intensive management practices. Within the last two decades, regional authorities have removed several hundred hectares of mangrove forest from multiple harbours (Lundquist *et al.* 2014, Chapter 3) in response to the rapid, huma-mediated spread of mangroves across intertidal mudflats in northern New Zealand over the past half century (Harty 2009; Lundquist *et al.* 2014; Suyadi 2019). Although the scale of mangrove removal is small relative to the area of mangroves gained in recent decades (Suyadi 2019, Chapter 3), mangrove removal can have adverse effects on coastal ecosystems (Lundquist *et al.* 2014), although little is known about its effects on coastal avifauna (Horstman *et al.* 2018). Estuary-scale observations suggest that local banded rail populations may decline (Southey 2009, Chapter 3) following removal of mangroves in saltmarsh-mangrove complexes, but evidence to support such assertions is limited, context-specific, and often anecdotal.

The secretive behaviour of banded rails has hampered study of their life history and demography (Marchant & Higgins 1993) and renders species-based evaluations of mangrove habitat quality highly impractical. However, banded rail food resources in saltmarsh-mangrove complexes can be feasibly measured (Ellis *et al.* 2004; Alfaro 2010) and studies of banded rail habitat use provide insight into the relative importance of these resources (Elliott 1983) and the factors that may govern their use (Elliott 1987; Parker & Brunton 2004; Botha 2011; Beauchamp 2015, 2022). Although the persistence of banded rail populations in saltmarsh-mangrove complexes suggests these environments are of high quality (Hall *et al.* 1997), measuring specific habitat factors, like food abundance, allows an assessment of the variation in quality among the component habitats of saltmarsh-mangrove complexes (Johnson 2007).

In this study, I assess the relative quality of mangroves as foraging habitats for the banded rail by comparing the abundance and diversity of macrofauna communities in four intertidal habitat zones (saltmarsh, saltmarsh-mangrove interface, mangrove, and mangrove-mudflat interface) in old-growth (mangrove established prior to 1946) and newer-growth (mangroves established in the late 1970s or early 1980s) saltmarsh-mangrove complexes known to contain persistent populations of banded rails. Given multiple observations of mangroves holding less diverse and lower density macrofauna communities relative to adjacent coastal habitats (Ellis *et al.* 2004; Alfaro 2006, 2010), I hypothesised that mangroves would exhibit the lowest abundance and diversity of banded rail food items among measured habitat zones. Additionally, I hypothesised that older mangrove forests would exhibit a higher macrofauna diversity and abundance than younger mangrove forests. Lastly, I hypothesised that mangroves would not hold a unique community of macrofauna in comparison with adjacent habitats, given similar findings in other studies (Butler *et al.* 1977; Morrisey *et al.* 2007).

4.3 Methods

4.3.1 Study sites

Four study sites in two inlets in Mangawhai Harbour were selected, northern inlet sites A1 and A2 and southern inlets sites B1 and B2 (Figure 4.1). Each site was characterised by a saltmarsh-mangrove complex that contained established populations of banded rails (present and reproductively active for >3 years, de Satgé unpublished data). Satellite photography – sourced from historical image resource Retrolens and the Mangawhai Harbour Restoration Society – was used to identify SMCs with mangrove stands of different ages, namely SMCs containing mangrove forests that had been established prior to 1946 ('old' sites: A1 and B1) and SMCs where mangroves had established over the course of 1977-1983 ('new' sites: A2 and B2). Thus, each inlet represented a replicate comparison of an old and a new site. Within each site, saltmarsh-mangrove complexes were delineated into habitat zones along a tidal gradient (Table 4.1) transitioning from saltmarsh (least frequently flooded) to saltmarsh-mangrove interface (SMI), to mangroves, to mangrove-mudflat interface (MMFI) (most frequently flooded). At old sites, the seaward edge of mangrove forests ended in a narrow muddy bank before descending steeply into a tidal channel, whereas in new sites the mangrove edges were fringed by a wider area of intertidal mudflats.

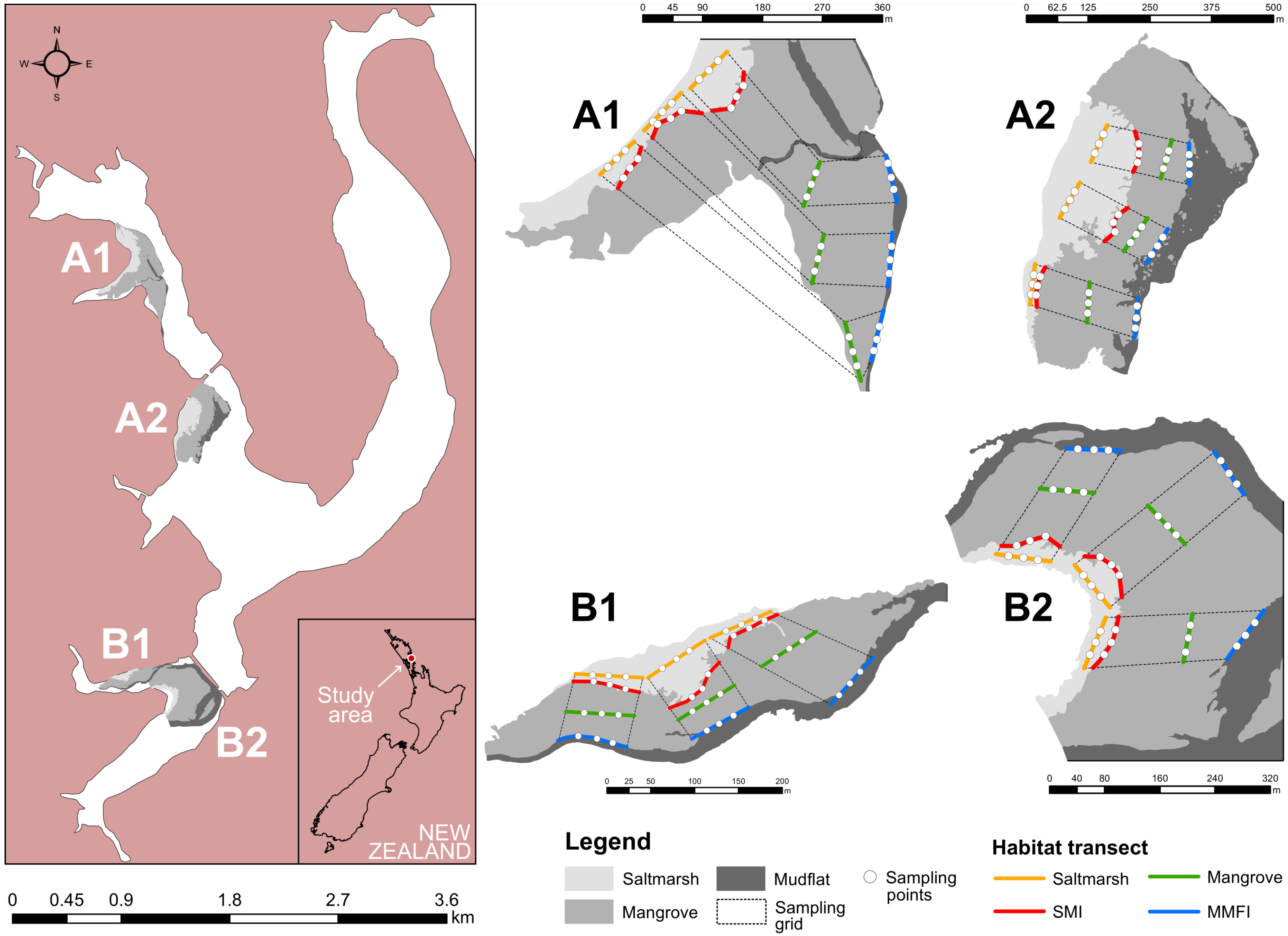


Figure 4.1 Study site locations of saltmarsh-mangrove complexes (SMCs) in Mangawhai estuary, New Zealand (left panel); sites A1 (old growth mangrove forest) and A2 (new growth) are located in the estuary's northern inlet (A), and B1 (old growth) and B2 (new growth) in the southern inlet (B). Enlargements of SMC sites (right panel) show sampling grids (dotted lines) and their corresponding sampling transects (coloured lines) in four habitat zones - saltmarsh, saltmarsh-mangrove interface (SMI), mangrove, and mangrove-mudflat interface (MMFI).

Table 4.1 Description of habitat zones within the saltmarsh-mangrove complexes (SMCs) which characterise study sites A1, A2, B1, and B2. Descriptions of tidal inundation timings for each habitat zone are illustrative, based on on-site observations rather than targeted measurements of tidal height, showing the tide-habitat gradient from least flooded saltmarshes to most-flooded MMFI.

Habitat	Description
Saltmarsh	Dense rush-marsh dominated by sea rush *Juncus krausii* and jointed wire rush *Leptocarpus similis.* Shallowly inundated at the peak of high tide for 0-2 hours (varies by site and tide height) but subject to the lowest frequency of tidal flooding among SMC habitat zones as it is found at the highest elevation.
Saltmarsh-mangrove interface (SMI)	A narrow strip (ca. 1-2 metres wide) of sparsely vegetated ground demarcating the ecotone between saltmarsh and mangrove habitats. Bare ground occasionally punctuated by low-growing rush grasses, mangrove seedlings, glasswort *Salicornia europaea*, and mangrove pneumatophores. Inundated at the peak of high tide for 0.5-2.5 hours (varied by site and tide height).
Mangrove	Dense, low-growing (<5 meters tall at our study sites), salt-tolerant trees comprising a single species, *Avicennia marina* var. *australasica* (previously known as *Avicennia marina* var. *resinifera*). Inundated for 1-4 hours around high tide (varied by site and tide height).
Mangrove-mudflat interface (MMFI)	A ten-meter-wide strip demarcating the ecotone between the seaward edge of mangrove forests and adjacent mudflats. Bare mudflat punctuated by mangrove pneumatophores and occasional isolated mangrove trees. Inundated for 2-4.5 hours around high tide (varied by site and tide height) and subject to the highest frequency of tidal flooding among SMC habitat zones as it is found at the lowest elevation.

4.3.2 Sampling and macrofauna extraction

To determine the diversity and abundance of potential food items for banded rails, epifauna and infauna (henceforth macrofauna) were collected from all habitat zones in all four study sites over two months in December 2016 - January 2017. Macrofauna sampling took place within three 80m-wide sampling grids in each site (Figure 4.1); each grid extended from the centre of the saltmarsh habitats to five meters beyond the seaward edge of the mangrove forest. Each sampling grid contained an 80m-long transect in each habitat zone in the SMC: saltmarsh, SMI, mangrove, and MMFI. A minimum of three substrate samples were collected at 20m intervals along each habitat-oriented transect line. Each substrate sample (13 × 13 × 8 cm) was extracted using flat-edged spades. Samples were washed through a fine net sieve (mesh size of 1 × 1 mm) on site and transferred to labelled sampling bags. Bags were stored in a -20˚C freezer prior to fauna extraction in a laboratory.

In the laboratory, samples were defrosted and rinsed through a fine sieve (1 × 1mm) again to remove excess sand, mud, and/or silt. Samples were sorted in shallow sorting trays containing water and Rose Bengal stain, the latter added to increase sorting accuracy by aiding identification of small animals among shell casings and plant material (Rumohr 2009). To ensure that all macrofauna specimens were extracted from the samples, I examined each sample under a dissecting microscope and identified macrofauna to the lowest taxonomic group possible (Table S4.1, Supplementary material). Once removed from sample-assigned sorting trays, macrofauna were stored in sample-specific vials in 70% ethanol.

4.3.3 Data collation

I collated the identified macrofauna specimens into a dataset comprising every sample (n = 154), the taxa it contained, and their respective abundances (the 'all species' dataset; n = 30 taxa). I created a subset of this data restricted to higher-value food items (the 'prey species' dataset, n = 18 taxa), defined as taxa found in >10% of banded rail faecal samples in the only formal study of banded rail dietary items to date (Elliott 1983). In addition, I calculated the total biomass of the most common species found by Elliott (1983) in banded rail faecal samples, defined as species occurring in >50% of faecal samples and comprising >30% of faecal matter: the mud snail *Potamopyrgus estuarinus*, a small gastropod *Pleuroloba costellaris*, and the tunneling mud crab *Austrohelice crassa*. I calculated the total biomass of *P. estuarinus*, *P. costellaris*, and *A. crassa* within each sample by multiplying their respective abundances with their average dry weight (in grams), as determined by Elliott (1983) for each species.

4.3.4 Statistical analyses

I analysed created four generalised linear mixed effects models (GLMMs) in RStudio (version 2022.02.03-492) with package *lme4* version 1.1-29 (Bates *et al.* 2015) to assess variation in species richness, species abundance, prey abundance, and biomass respectively. GLMMs were fitted by restricted maximum likelihood estimation and specified with normal distributions. Model residuals were assessed for normality using quantile-quantile plots and residual versus fitted values plots (Zuur *et al.* 2009). Richness and abundance models, despite using count data, were confirmed as being normally distributed.

Response variable ‘species richness’ was calculated as the sum of unique taxa within each sample in the all-species dataset. ‘Species abundance’ was calculated as the sum of species abundances in each sample in the all-species dataset, and resulting values were log-transformed. ‘Prey abundance’ was calculated as per species abundance calculations but limited to taxa in the prey species dataset. Finally, response variable ‘biomass’ was defined as the square-root of summed biomass values for *P. estuarinus*, *P. costellaris*, and *A. crassa*.

Each response variable was regressed against the same explanatory variables in a GLMM: fixed effect ‘habitat’ (factor variable with four levels: saltmarsh, SMI, mangrove, and MMFI), fixed effect ‘age’ (factor variable with two levels: old site and new site), and the interaction term between habitat and age. In addition, three random variables were fitted to each model to account for potential variation explained by the sampling design: ‘inlet’ (A or B, reflecting northern and southern sites – see Figure 4.1), ‘sampling grid’ (n = 12), and ‘transect’ (n = 48). I dropped interaction terms from models if they did not explain significant variation in the response variable (as assessed by ANOVA Type III with Satterthwaite's method) and did not interact significantly with other model terms. Additionally, to keep model structures simple, I dropped random effects from models if they did not explain additional variation.

In addition to GLMM analyses, I tested for differences in community composition among habitat zones of different ages. I used function ‘vegdist’ in package *vegan* (version 2.6-2) to calculate two resemblance matrices for species in the all-species data set. The first matrix was calculated using Bray-Curtis dissimilarity of square-root transformed species abundances where data reflected species richness weighted by abundance. The second matrix was calculated using Jaccard dissimilarity of binary species data where data reflected species richness without abundance (i.e., presence-absence data). I used function ‘betadisper’ to calculate multivariate dispersions from each resemblance matrix, grouped by habitat zone and site age. For each set of dispersions (Bray-Curtis and Jaccard), I assessed whether one or more groups was more variable than others, using ANOVA of the distances to group centroids. I examined differences between paired habitat-age combinations by calculating Tukey’s Honest Significant Differences between groups.

4.4 Results

In total, 154 substrate samples were collected: seventy-eight in new sites and seventy-six in old sites. Thirty invertebrate taxa were identified (Table S4.1, Supplementary material) from samples collected across four habitat zones – saltmarsh, SMI, mangrove, and MMFI. Half of all macrofauna taxa was identified to a species level (n=15), while remaining taxa were identified to their taxonomic order (n=11) or class (n=4).

4.4.1 Species richness

I identified 30 unique taxa among all study sites (Table S4.1, Supplementary material). Mangrove habitats comprised the highest total species richness (21 taxa), containing two more species than the least species rich habitat, saltmarsh (19 taxa). The average species richness (±SE) within a sample, irrespective of habitat or age, was 5.7±0.2 taxa (range: 1–12, n=154).

Habitat zones explained significant variation in species richness, whereas the age of sites and the habitat-age interaction did not (Table 4.2). Least-squares estimates from the richness model suggested significantly higher species richness in mangroves relative to saltmarsh and MMFI habitat zones but showed no difference in richness between old and new sites (Table 4.3; Figure 4.2). On average, mangrove samples contained 6.6±0.3 taxa (range: 3-10, n=39), whereas saltmarsh contained 5.2±0.2 taxa per sample (range: 2-7, n=38) and MMFI contained 4.7±0.3 taxa per sample (range:1-9, n=39).

Table 4.2 Analysis of variance for fixed effects habitat, age, and their interaction for GLMM models of species richness, species abundance, prey abundance, and biomass. Significant terms shown in bold

	Richness			Abundance			Prey abundance			Biomass		
Fixed effects	df	*F*	p	df	*F*	p	df	*F*	p	df	*F*	p
Habitat	3	8.40	**<0.001**	3	6.61	**0.001**	3	5.88	**0.002**	3	0.45	0.713
Age	1	0.83	0.384	1	7.11	**0.026**	1	19.87	**<0.001**	1	9.24	**0.014**
Habitat × Age	–	–	–	3	2.10	0.120	3	2.61	0.065	3	4.49	**0.010**

Table 4.3 Estimates of fixed effects for GLMM models of species richness, species abundance, prey abundance, and biomass. Transformations applied to response variables are indicated in parentheses. Variance and SD of random effects shown for each model. Habitat 'mangrove' and site age 'new' were set as reference categories within models.

	Richness				Abundance (log)				Prey abundance (log)				Biomass (square-root)			
Fixed effects	Est.	SE	*t*	p	Est.	SE	*t*	p	Est.	SE	*t*	p	Est.	SE	*t*	p
Intercept	6.41	0.37	17.32	**<0.001**	3.86	0.33	11.58	**0.001**	3.33	0.36	9.14	**0.003**	0.86	0.16	5.27	**0.002**
Habitat																
MMFI	-1.85	0.43	-4.36	**<0.001**	-0.59	0.34	-1.74	0.092	-0.61	0.36	-1.71	0.096	0.08	0.19	0.41	0.681
Saltmarsh	-1.40	0.43	-3.27	**0.003**	0.49	0.34	1.42	0.165	0.46	0.36	1.27	0.211	0.37	0.19	1.97	0.059
SMI	-0.34	0.43	-0.79	0.436	0.28	0.34	0.82	0.421	0.51	0.36	1.43	0.161	0.50	0.19	2.63	**0.014**
Age																
Old	0.34	0.38	0.91	0.384	1.14	0.35	3.26	**0.002**	1.56	0.36	4.36	**<0.001**	0.82	0.20	4.19	**<0.001**
Habitat × Age	–	–	–	–												
MMFI × Old					-0.68	0.48	-1.41	0.169	-0.64	0.51	-1.26	0.216	-0.33	0.27	-1.24	0.223
Saltmarsh × Old					-1.21	0.48	-2.50	**0.018**	-1.32	0.51	-2.61	0.013	-0.78	0.27	-2.91	**0.007**
SMI × Old					-0.67	0.48	-1.39	0.174	-1.08	0.51	-2.12	0.040	-0.86	0.27	-3.20	**0.003**

Random effects	Variance	SD	Variance	SD	Variance	SD	Variance	SD
Inlet	–	–	0.101	0.318	0.138	0.312	0.016	0.125
Grid	0.149	0.387	0.015	0.123	–	–	0.009	0.095
Transect	0.229	0.479	0.214	0.463	0.224	0.473	0.060	0.244

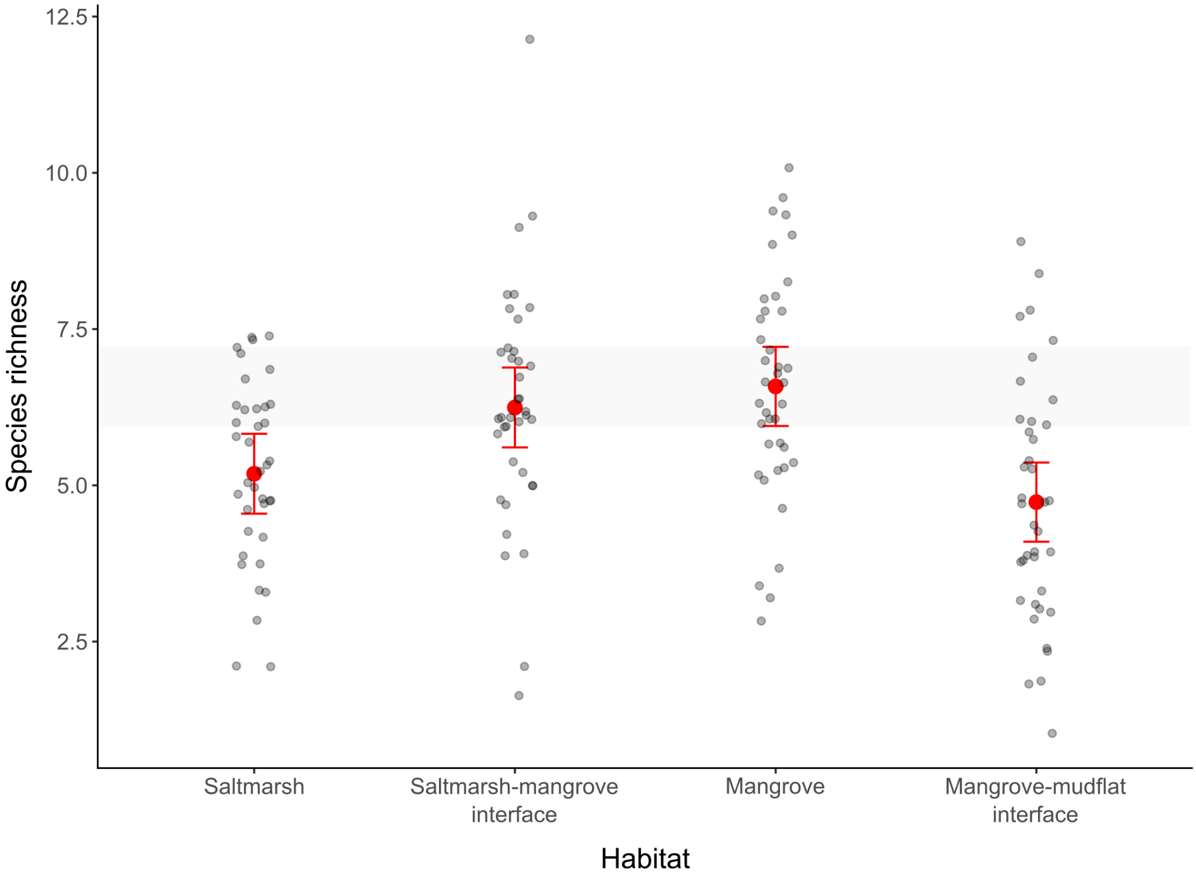


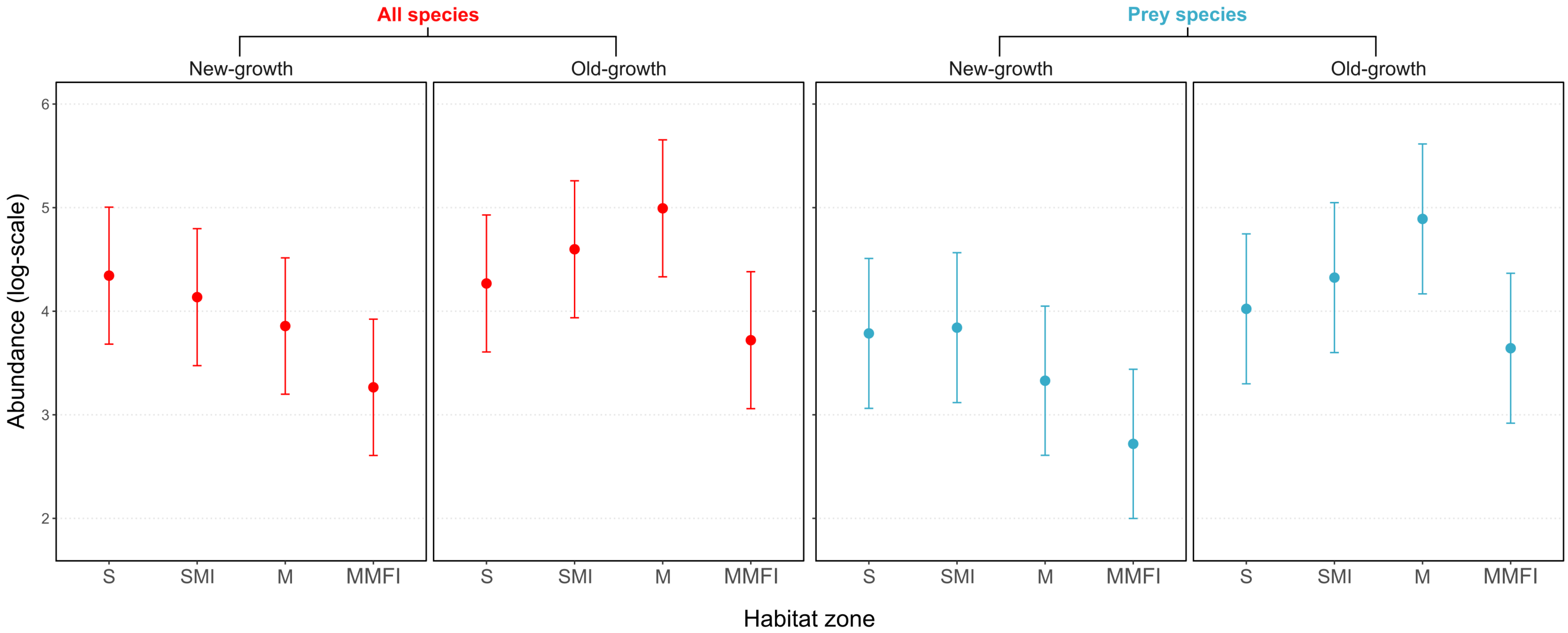
Figure 4.2: Model-predicted estimates and their standard errors (red points with error bars) of species richness for four habitat zones, overlaid on raw species richness values of all samples. Grey horizontal bar corresponds with the predicted standard error range of mangrove species richness.

4.4.2 Species abundance

The number of individuals found in samples varied widely: on average there were 90.2±6.3 (mean±SE) individual invertebrates per sample, but samples ranged from 2 – 517 individual macrofauna (median = 72.5). The mud snail *Potamopyrgus estuarinus* was the most abundant taxa observed across all sites and in all habitat zones; its median among all samples was 42.5 individuals (range: 0–384). Among habitat types, mangroves had the highest density of invertebrates (81.5 individuals dm^{-3}), while the mangrove-mudflat interface contained the lowest density of invertebrates (35.3 individuals dm^{-3}; Table S4.2, Supplementary material).

Habitat and site age explained significant variation in abundance of all taxa (Table 4.2). Least-squares estimates indicated that old sites contained a significantly higher abundance macrofauna individuals than new sites (Figure 4.3). Although the interaction between habitat and age did not explain significant variation in abundance (Table 4.3), there was a significant, near three-fold difference in the average abundance of invertebrates in new (62.2±11.7 individuals) and old mangroves (161.2±20.1 individuals) (Figure 4.3).

Figure 4.3: Log-scale estimates (and standard errors) of species abundance in four habitat zones - saltmarsh (S), saltmarsh-mangrove interface (SMI), mangrove (M), and mangrove-mudflat interface (MMFI) - in new-growth and old-growth study sites, as predicted by GLMMs for all species (red) and prey species (blue) respectively.



The prey-abundance model (limited to high-value prey species, n=18) produced comparable results to the abundance model (all species, n=30): habitat and site age explained significant variation in abundance of prey species, while the habitat × age interaction term was near significant (Table 2). Interaction effects were most evident in mangrove habitats of different ages, with a four-fold difference in the abundance of prey species in new mangroves (34.3±4.9 individuals per sample) and old mangroves (143.2±15.2 individuals per sample) (Figure 4.3). Correspondingly, mangroves in old sites contained the highest abundances of prey species among all habitats, whereas mangroves in new-growth sites contained the second-lowest prey abundances among all habitats (Figure 4.3).

4.4.3 Species biomass

Each sample contained an average (±SE) of 1.9±0.1 grams of biomass (in dry weight) from three prey species *P. estuarinus*, *P. costellaris*, and *A. crassa*. Among all samples in the biomass dataset, the mud snail *P. estuarinus* accounted for the most biomass (198.4g), followed by the tunnelling mud crab *A. crassa* (77.0g) and the small gastropod *P. costellaris* (11.4g).

The interaction between habitat and site age explained significant variation in biomass (Table 4.2). Least-square estimates indicated that biomass in mangrove and MMFI habitat zones was significantly lower in new sites relative to old sites, while biomass in saltmarsh and SMI habitat zones did not vary with site age (Figure 4.4). Mangrove samples taken from old sites averaged 2.9±0.3g of biomass, compared with 0.9±0.2g in samples taken from new sites. By contrast, the average biomass in saltmarsh samples remained consistent between old(1.9±0.4g) and new sites (1.8±0.3g).

4.4.4 Community composition

Community composition calculated by Jaccard's dissimilarity (species presence/absence) for different habitats, sorted by old and new sites, showed limited evidence of differences among groups (df = 7, F = 1.96, p = 0.065), as reflected by overlapping group dispersions in principal component space (Figure 4.5A). Post-hoc Tukey tests provided weak evidence for differences in community compositions between new-SMI habitats and new-MMFI habitats (p = 0.065) but indicated no differences among other pairwise habitat comparisons. In contrast, community composition calculated by Bray-Curtis' dissimilarity (species relative abundances) showed significant differences among habitat groups (df = 7, F = 2.91, p = 0.006), reflected by greater separation in group dispersions, particularly as habitat zone new-MMFI diverged from other habitats along the primary principal component axis (Figure 4.5B). Post-hoc Tukey tests indicated that macrofauna communities in new-SMI habitats were significantly different from communities in new-MMFI sites (p = 0.029), as were communities in old-mangrove habitats relative to those in new-MMFI sites (p = 0.002). Additionally, communities in old-SMI sites showed a near-significant difference to community composition in new-MMFI sites (p = 0.060).

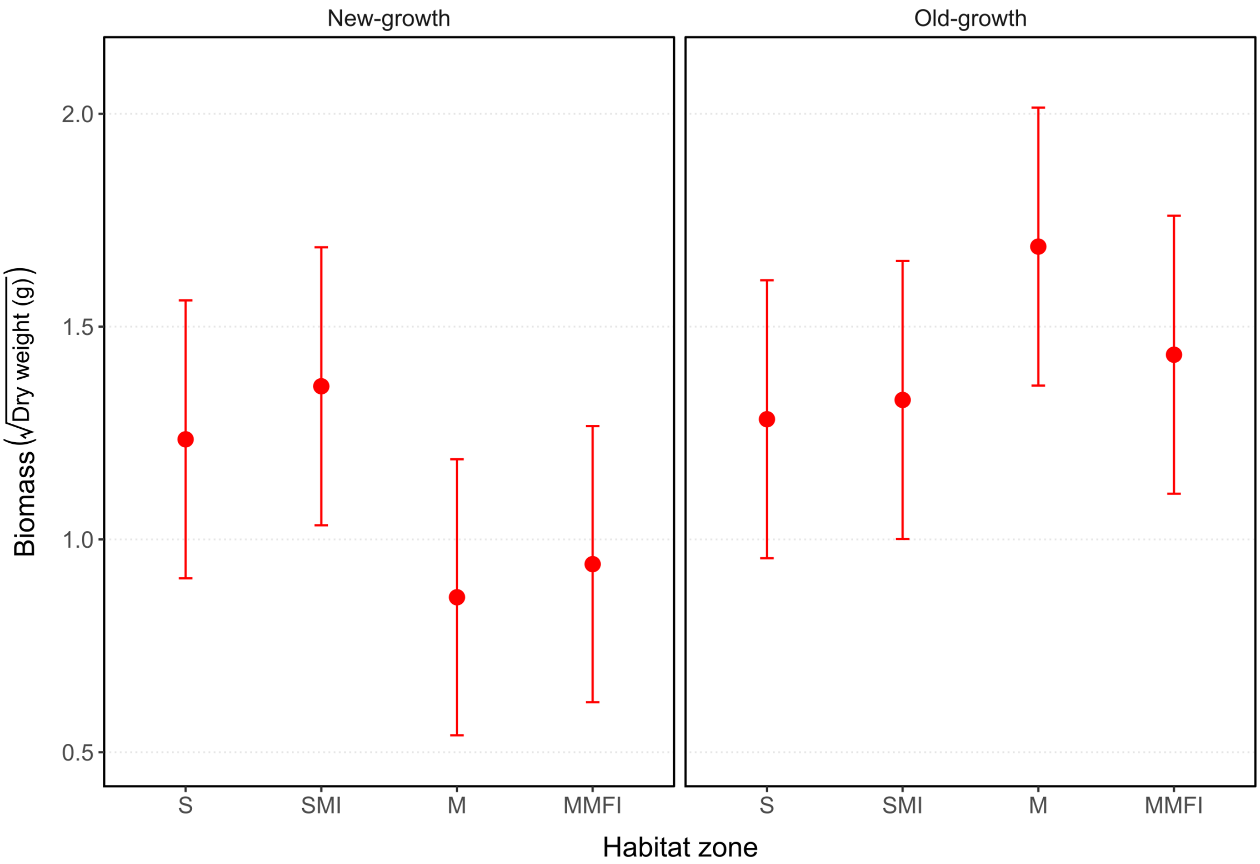


Figure 4.4 Model-predicted estimates and their standard errors (red points with error bars) of the biomass of three prey species - *Potamopyrgus estuarinus*, *Pleuroloba costellaris*, and *Austrohelice crassa* - expressed as the square root of species' average dry weight. Model predictions are shown for four habitat zones - saltmarsh (S), saltmarsh-mangrove interface (SMI), mangrove (M), and mangrove-mudflat interface (MMFI) in new-growth (left panel) and old-growth (right panel) sites.

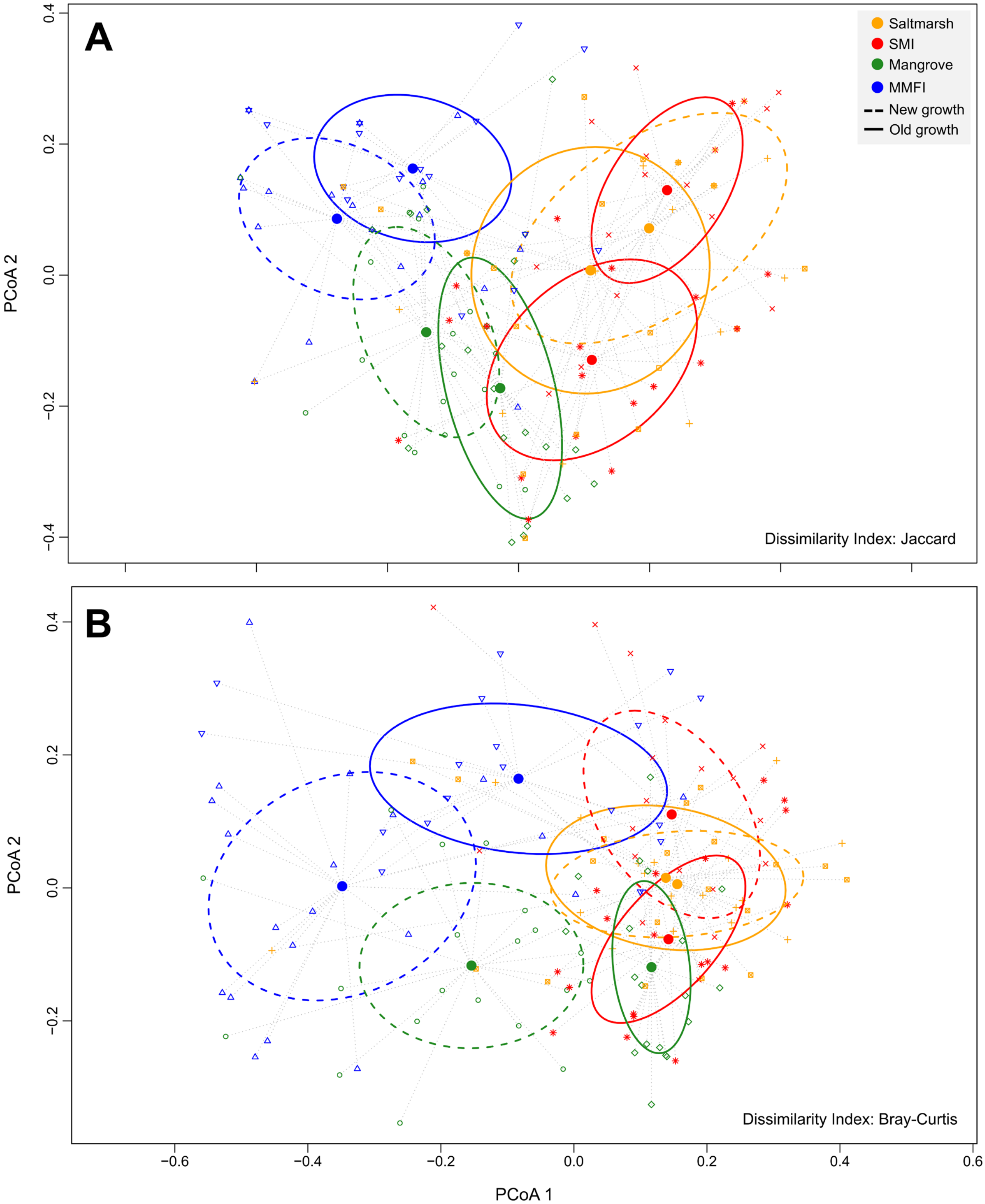


Figure 4.5 Ordination plots of multivariate dispersions (Anderson 2006) of macrofauna communities from four habitat types - saltmarsh (orange), saltmarsh-mangrove interface (SMI, red), mangrove (green), and mangrove-mudflat interface (blue) categorised by sites of two age classes (old = dashed ellipsese, new = solid-line ellipses). Group spatial medians (coloured circles - see legend) are encircled by standard deviation confidence ellipses (coloured ovals). Distances between individual sample values (coloured shapes radiating from spatial medians) and group spatial medians are shown in principle component space, reduced from a resemblance matrix of Jaccard (panel A) or Bray-Curtis dissimilarity (panel B) values of square-root transformed samples.

4.5 Discussion

Measuring habitat resources directly can provide insight into habitat quality (Johnson 2007). This study found that food resources used by banded rails *G. philippensis* in saltmarsh-mangrove complexes vary among habitat zones (saltmarsh, saltmarsh-mangrove interface, mangrove, and mangrove-mudflat interface). Contrary to expectations, the abundance and biomass of banded rail food items (macrofauna) was highest in mangrove forests, but only in old sites (mangroves established pre-1946). Surprisingly, mangroves also showed the highest species richness among habitat zones, although differences in absolute taxa numbers between habitat zones were marginal (range among habitats: 19-21 species). In line with expectations, mangrove forests in new sites (mangroves established 1977-1983) had the second lowest abundance of macrofauna and the lowest biomass of common prey species among all habitats. As hypothesised, mangroves did not hold a unique set of macrofauna; analyses of macrofauna communities among habitat types suggested that inter-habitat differences in community composition were a result of differences in relative abundance rather than species identity.

4.5.1 Habitat comparisons: food abundance and availability

Based on the abundance and biomass of important food resources, results from this study suggest that old-growth mangrove forests provide higher quality foraging environments to banded rails than other habitat zones they use – including saltmarsh, SMI, and MMFI. Contrarily, new-growth mangrove forests, along with the mangrove-mudflat interface, provide the lowest food resources to banded rails. These relationships remained consistent across different measures of food for banded rails, including the abundance of all macrofauna (Figure 4.3), the abundance of high-value prey items (Figure 4.3), and the biomass of the three macrofauna species most frequently found in banded rail faecal samples (Figure 4.4).

Crucially, food abundance does not equate to food availability: habitats comprise more than the resources surrounding an animal (Krausman 1999; Johnson 2007). It is important to account for ecological constraints that restrict resource use, including predation pressure, competition, and the physical accessibility of resources (Morrison *et al.* 2006; Johnson 2007). Although I did not measure these factors, I can speculate on their influence on food availability in field sites (Table 4.4). Relative to adjacent habitats, mangrove habitats in Mangawhai may present the best availability of food resources, providing banded rails with aerial- and ground cover from predators, low competition for resources from other birds, and a vegetation structure that does not impede visual foraging or movement. By contrast, I suggest that the mudflat-mangrove interface is the lowest quality foraging habitat for banded rails in this study, as low food abundances are compounded by the limited availability of these resources (Table 4.4).

Table 4.4 The hypothetical availability of food resources – classed as low, moderate, and high – to banded rails in habitat zones in this study, expressed for three ecological factors which influence the availability of food resources. Availability levels are defined relative to other habitats, not in absolute terms (as these were not measured by this study).

Habitat	Predation	Competition	Accessibility
Saltmarsh	**Moderate availability**: Rushes provide dense cover from terrestrial predators[1] but limited cover from aerial predators[2]. Predation by terrestrial mammals presents a big threat to nesting birds[2,3]	**Moderate availability**: Main competitors for resources are pukekos *Porphyrio melanotus* and bitterns *Botaurus poiciloptilus*, (larger-bodied), and marsh crakes *Zapornia pusilla* (smaller-bodied)[4,5]	**Moderate availability**: Seldom flooded by high tides exceeding foraging depths[1]. Dense vegetation at ground-level may inhibit foraging and movement, especially in oi-oi (*Apodasmia similisi*) dominated patches[2]
Saltmarsh-mangrove interface (SMI)	**Low availability**: Little to no cover from aerial or terrestrial predators cover given sparse vegetation[1]. Open habitat presents natural wildlife trial*, used by mammalian predators[6]	**Low availability**: Several competitors for resources, including white-faced herons *Egretta novaehollandiae*, pukekos, bitterns, and marsh-crakes[6]	**High availability**: Only flooded during high-tide peaks. Little to no vegetation to impede movement or foraging[1]
Mangrove	**High availability**: Mangroves provide good cover from aerial predators[1]. Mangroves do not exclude terrestrial predators[5,7,10] but may be less preferred by larger mammalian predators than more terrestrial habitats[7,8]	**High availability**: Few direct competitors in mangrove habitats[10]. Potential competition from herons, bitterns, or pukekos more likely in taller and less dense mangrove stands[8]	**Moderate availability**: Flooded during high tide, but only fully flooded for ca. 1-4 hours during diurnal hours[1]. Ground-level vegetation is not overly dense and does not impede visual foraging or movement[10]
Mangrove-mudflat interface (MMFI)	**Low availability**: Very limited cover from ground- or aerial predators[8]	**Low availability**: Numerous wading birds make use of open habitats and channels adjacent to mangroves[8]. High prevalence of white-faced herons along mangrove edges[1]	**Moderate availability**: Flooded for ca. 2-4.5 hours during diurnal hours. Open habitat does not impede foraging or movement[1]

[1]On-site observation [2]Elliott (1983) [3]Parker & Brunton (2004) [4]Hill *et al.* (2015) [5]Dencer-Brown *et al.* (2020) [6]de Satgé, unpublished data (see Ch. 5) [7]Johnston-González & Abril (2019) [8]Cox (1977) [9]Riegen & Sagar (2020) [10]Beauchamp (2022). *A clear pathway through mangroves and/or saltmarsh which lacks substantial undergrowth, maintained by intertidal water flows and the frequent passage of animals.

4.5.2 Age as a mediator of mangrove habitat quality

Macrofauna abundances in mangrove and MMFI habitats were markedly different in sites of different ages: old sites showed substantially higher macrofauna abundances than new sites for all species and high-value prey species (Figure 4.3). In contrast, macrofauna abundance in saltmarsh and SMI habitats remained consistent in sites of different ages (Figure 4.3). This latter result is expected: saltmarsh habitats are, to the best of my knowledge, similar in age and at least as old as old-growth mangrove forests in this study.

Importantly, differences in macrofauna abundance among habitats were mirrored by differences in prey biomass (Figure 4.4), a measure of food abundance that accounts for the relative value of prey species. The combined biomass of three prey species key to banded rails – the mud snail *Potamopyrgus estuarinus*, a small gastropod *Pleuroloba costellaris*, and the tunnelling mud crab *Austrohelice crassa* – varied significantly in mangrove and MMFI habitats of different ages, with significant increases in biomass in old sites relative to new ones (Figure 4.4). As observed for macrofauna abundance, biomass of key species in saltmarsh and SMI habitats did not vary with site age (Figure 4.4). The increased biomass of key species in old-growth mangroves echoes existing research in another harbour in New Zealand; Morrisey *et al.* (2003) found significantly more mud snails in old-growth mangrove stands relative to new-growth stands in Manukau Harbour, and equal numbers of tunnelling mud crabs among sites of different ages.

The comparison of ‘new’ and ‘old’ mangroves by this study provides an interesting but limited comparison of the stages of mangrove establishment. While >30 years separate the new- and old-growth mangroves of this study, ‘new-growth’ as defined here does not capture mangroves that have established within the last 40 years (a period when mangrove spread has been particularly rapid - Suyadi *et al.* 2019). Notably, this excludes establishing mangroves, i.e., saplings and seedlings, which are regularly removed as part of harbour management plans in northern New Zealand. Theoretically, the expansion of mangroves has provided banded rails with significant additional habitat, yet the quality of recently established and establishing mangroves to banded rails remains unclear. As such, determining the quality of mangroves established more recently than those assessed by study presents should be prioritised by future research.

4.5.3 The mangrove macrofauna community

The composition of macrofauna communities in mangroves was not significantly different to communities in other habitats, echoing research in Australia and New Zealand that suggests that mangrove habitats lack a distinct community of macrofauna (Butler *et al.* 1977; Morrisey *et al.* 2007). Analysis of macrofauna community composition suggests that differences in macrofauna communities among SMC habitats are driven by the relative abundances of species (Figure 4.5B), rather than species identity (Figure 4.5A). This finding, in combination with GLMM results, suggests that saltmarsh-mangrove complexes offer a common suite of prey species to banded rails across habitat zones, but that the quantity of these food resources may vary with site age and habitat zone. In addition, the accessibility of these resources is likely to be different among habitat zones (Table 4.4).

Studies comparing macrofauna communities in New Zealand's mangrove forests with adjacent saltmarsh have consistently found mangroves to hold a lower diversity and density of macrofauna (Alfaro 2006, 2010) – a consensus this study's findings disrupt. Two theories have been proposed to explain the relatively low diversity and density of mangrove macrofauna communities. Several authors argue that mangroves hold few macrofauna as a result of the high proportion of tannins from mangrove detritus and mud associated with mangrove habitats (Alongi & Christoffersen 1992; Alongi *et al.* 2000; Alfaro 2006), whereas Ellis *et al.* (2004) argue that increases in sediment results in lower macrofauna diversity and abundance in New Zealand's mangrove habitats, irrespective of the presence or absence of mangroves themselves. This study's findings provide little support for the theory that tannins from mangrove detritus reduce macrofauna diversity or abundance; given mangrove detritus increases with mangrove age (Morrisey *et al.* 2003) I would expect lower macrofauna diversity and/or abundance in older forests relative to younger ones, a predicted outcome opposite to the findings of this study.

While the findings of this study do not support the theory that mangrove detritus decreases macrofauna densities, they are consistent with studies that suggest that increases in mud-dominated sediment can have deleterious effects on macrofauna communities (Thrush *et al.* 2003, 2004; Ellis *et al.* 2004). For example, Thrush *et al.* (2003) observed declines in the total density of benthic invertebrates with increasing mud content along a sand-mud gradient on intertidal flats in multiple New Zealand estuaries. Similarly, Smith & Kukert (1996) observed that increases in sedimentation rates in Kane'ohe Bay, Hawaii, were negatively correlated with the total biomass of the bay's macrofauna community. Although I did not quantify sedimentation rates in this study sites, it is logical to assume that sedimentation in new sites is more recent than in old sites, given mangrove growth tracks sediment deposition over time (Lundquist *et al.* 2014; Swales *et al.* 2015). If this assumption is true, I would expect higher amounts of mud-dominated sediment in newer mangrove forests (Morrisey *et al.* 2003; Ellis *et al.* 2004) and a concomitant reduction in macrofauna abundance. Theoretically, the negative effects of sediment deposition should decrease with time in mangrove forests; as mangroves mature, sediment is likely to become more compact and contain more organic material (Morrisey *et al.* 2003), potentially providing a more stable environment for macrofauna. However, without knowing the historical and ongoing dynamics of sedimentation among study sites, the effects of sediment on macrofauna communities – and, in turn, banded rail food sources – remain hypothetical.

4.5.4 Study limitations

Assessments of habitat quality that measure habitat attributes directly, as opposed to demographic attributes of individuals or populations, rely on the assumption that researchers understand which resources and ecological constraints govern species fitness (Block & Brennan 1993; Johnson 2007). Resource-based assessments of habitat quality are best suited to species whose demography, habitat use, and life histories are well understood (e.g., Barnes *et al.* 1995; Wilkin *et al.* 2009). Given banded rails are an understudied species, a resource-based assessment of their habitat quality is reliant on sparse data and generates uncertainty in this study's findings. However, the alternative approach to the study of habitat quality – using demographic measures such as abundance, distribution, or reproductive performance – presents significant challenges for cryptic species such as the banded rail. For banded rails living in saltmarsh-mangrove complexes, obtaining demographic measures is logistically challenging and time-consuming. Moreover, it may require invasive forms of monitoring (e.g., nest disturbance or habitat destruction) because frequently used visual and/or acoustic monitoring techniques (e.g., five-minute point counts or distance sampling) provide poor estimates of banded rail density (Elliott 1987; Beauchamp 2015). In acknowledging the limitations of a resource-based assessment of habitat quality, this study highlights the conundrum of assessing habitat quality for cryptic species: a resource-based approach requires simple measures of habitat features but is limited by the ecological understanding of the study species, whereas a species-based approach requires demographic information which is unfeasible or highly impractical to obtain but can provide an absolute measure of species fitness relative to habitats.

Importantly, this study's assessment of habitat quality within saltmarsh-mangrove complexes does not quantify the absolute habitat quality of these environments but illustrates the relative contribution of their component habitat zones to their quality. As distinct environments, SMCs in this study can be considered 'high quality' habitats as they provide the conditions for individual and population persistence (Hall *et al.* 1997; Krausman 1999); banded rails have been established and breeding at all sites for at least three years (de Satgé, unpublished data) and likely much longer (Robertson *et al.* 2004). Thus, the finding that new-growth mangroves provide lower quality foraging habitats than old-growth mangroves does not necessarily imply that new-growth mangroves lack appropriate resources to support banded rail populations in absolute terms, but that new-growth mangroves contribute less to the overall quality of SMCs than old-growth mangroves. As evidenced by long-term observations in Mangawhai (de Satgé, unpublished data), new-growth mangroves can support persistent populations of banded rails, but whether this is because they contain available food resources (in absolute terms), or because resource availability in other habitats compensates for their lower resources, is unclear.

A notable limitation of this study is that it did not capture seasonal variation in food resources; this study's assessment of habitat quality reflects a brief time-period in summer – coinciding with the banded rail's breeding season. Although work by Alfaro (2006) suggests that differences in macrofauna abundance among intertidal habitats are largely consistent among seasons, the abundance, size, and availability of important food items such as *Austrohelice crassa* and *Potamopyrgus estuarinus* may vary seasonally in mangrove, saltmarsh, and estuarine environments in New Zealand (Nye 1977; Jones 1980; Elliott 1983; Alfaro 2006). The timing of sampling meant this study assesses habitat quality during a key phase of a banded rail's life history – during chick rearing and fledging (Marchant & Higgins 1993; Beauchamp 2022). To determine whether the quality of SMC habitats remains consistent over time would require sampling among multiple seasons – an area of for potential future research.

4.5.5 Conservation implications

As evidenced by this study, mangrove habitats within these SMCs are of value to banded rails, providing a species-rich set of highly available food resources that includes important prey species (Elliott 1983). Importantly, the findings of this study suggest that old-growth mangroves hold the highest abundance of macrofauna, as well as the greatest biomass of key prey species to banded rails, among all SMC habitat zones. Contrary to the view of mangrove habitats as low-diversity habitats (Ellis *et al.* 2004; Alfaro 2006, 2010), this study found mangroves to hold the highest diversity of macrofauna among habitat zones.

The findings of this study suggest that mangroves are not uniform habitats, even within the same estuary. This is of particular importance to contemporary mangrove management practices, which only differentiate mangrove vegetation based on an arbitrary metric of vegetation maturity ('mature' plants >1m tall, or saplings and seedlings <60cm tall; Chapter 3) and not on other characteristics such as its age, the diversity of its macrofauna or avifauna, its potential habitat quality, or structural features like density and height. While this rule-of-thumb approach is practical for management purposes, it neglects inherent variation in mangrove habitats. As such, mangrove removal efforts – the defining feature of New Zealand's mangrove management approach – are unlikely to be discerning and may unknowingly clear habitats that support a high diversity of benthic macrofauna, and that hold high value to mangrove-using avifauna such as banded rails. Given that the vast majority of New Zealand's declining banded rail population is restricted to SMCs in the North Island (Bellingham 2013; Robertson *et al.* 2021), it is counterintuitive (from a conservation perspective) to remove valuable mangrove habitats that hold an abundance of highly available food resources for banded rails.

Undertaking a species-based assessment of habitat quality – an approach that links habitats to species demography (Johnson 2007) – presents a logical next step in determining variation in the absolute quality of mangrove forests to banded rails. However, this likely to be a challenging as it requires measuring parameters such as breeding success, survival rates, or population abundance that are notoriously difficult to quantify for cryptic species (Williams 2016; Colyn *et al.* 2019). Quantifying these parameters for banded rails is contingent on the development of reliable, and preferably non-invasive, survey methods.

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4.7 Supplementary material

Table S4.1: List of macrofauna taxa collected in study sites. Macrofauna are identified to their taxonomic class and lower where specimen quality allowed.

Taxa #	Phylum	Class	Order	Family	Genus/Species
1	Annelida	Polychaeta	Phyllodocida	Nereididae	
2	Annelida	Polychaeta			
3	Annelida	Polychaeta			
4	Arthropoda	Arachnida	Araneae	Tetragnathidae	*Tetragnatha extensa*
5	Arthropoda	Hexanauplia	Thoracicalcarea	Chthamalidae	*Chamaesipho brunnea*
6	Arthropoda	Insecta	Diptera	Chironomidae	
7	Arthropoda	Insecta	Diptera	Chironomidae	
8	Arthropoda	Insecta	Diptera	Dolichopodidae	
9	Arthropoda	Insecta	Hemiptera	Veliidae	*Microvelia macgregori*
10	Arthropoda	Insecta	Hemiptera		
11	Arthropoda	Insecta			
12	Arthropoda	Insecta			
13	Arthropoda	Malacostraca	Mysida	Mysidae	
14	Arthropoda	Malacostraca	Mysida	Mysidae	
15	Arthropoda	Malacostraca	Amphipoda	Talitroidea	
16	Arthropoda	Malacostraca	Amphipoda		
17	Arthropoda	Malacostraca	Amphipoda		
18	Arthropoda	Malacostraca	Decapoda	Alpheoidea	*Alpheus richardsoni*
19	Arthropoda	Malacostraca	Decapoda	Hymenosomatidae	*Halicarcinus whitei*
20	Arthropoda	Malacostraca	Decapoda	Varunidae	*Austrohelice crassa*
21	Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	*Sphaeroma quoianum*
22	Arthropoda	Malacostraca	Isopoda	Sphaeromatidae	
23	Arthropoda	Malacostraca	Isopoda		
24	Mollusca	Bivalvia	Venerida	Veneridae	*Austrovenus stutchburyi*
25	Mollusca	Gastropoda	Ellobiida	Ellobiidae	*Pleuroloba costellaris*
26	Mollusca	Gastropoda	Littorinimorpha	Tateidae	*Potamopyrgus estuarinus*
27	Mollusca	Gastropoda	Neogastropoda	Tudiclidae	*Buccinulum vitattum*
28	Mollusca	Gastropoda	Pylopulmonata	Amphiboloidea	*Amphibola crenata*
29	Mollusca	Gastropoda	Trochida	Trochidae	*Diloma subrostratum*
30	Mollusca	Gastropoda	*Unassigned*	Batillaridae	*Zeacumantus subcarinatus*

Table S4.2: Density of invertebrates (per cubic decimetre) collected in saltmarsh, saltmarsh-mangrove interface (SMI), mangrove, and mangrove-mudflat interface (MMFI) habitat zones (highlighted in bold) across study sites in Mangawhai estuary. Density of invertebrates for different site ages ('Old' and 'New') indicated for each habitat type.

Habitat	Invertebrates	Samples	Density (dm^{-3})
Saltmarsh	**3755**	**38**	**73.09**
Old	1609	19	62.64
New	2146	19	83.54
SMI	**3830**	**38**	**74.55**
Old	2265	19	88.17
New	1565	19	60.92
Mangrove	**4299**	**39**	**81.53**
Old	3058	19	119.04
New	1241	20	45.89
MMFI	**1859**	**39**	**35.26**
Old	1130	19	43.99
New	729	20	26.96

Chapter 4, Statement of Contribution:

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STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.

Student name:	Jacques de Satge
Name and title of main supervisor:	Associate Professor Weihong Ji
In which chapter is the manuscript/published work?	Chapter 4
What percentage of the manuscript/published work was contributed by the student?	95%

Describe the contribution that the student has made to the manuscript/published work:
Jacques completed the lab work, statistical analyses of the data, and write up of the manuscript in its entirety. Weihong established the research design, facilitated sample collection, and provided editorial input on the final draft of the manuscript.

Please select one of the following three options:

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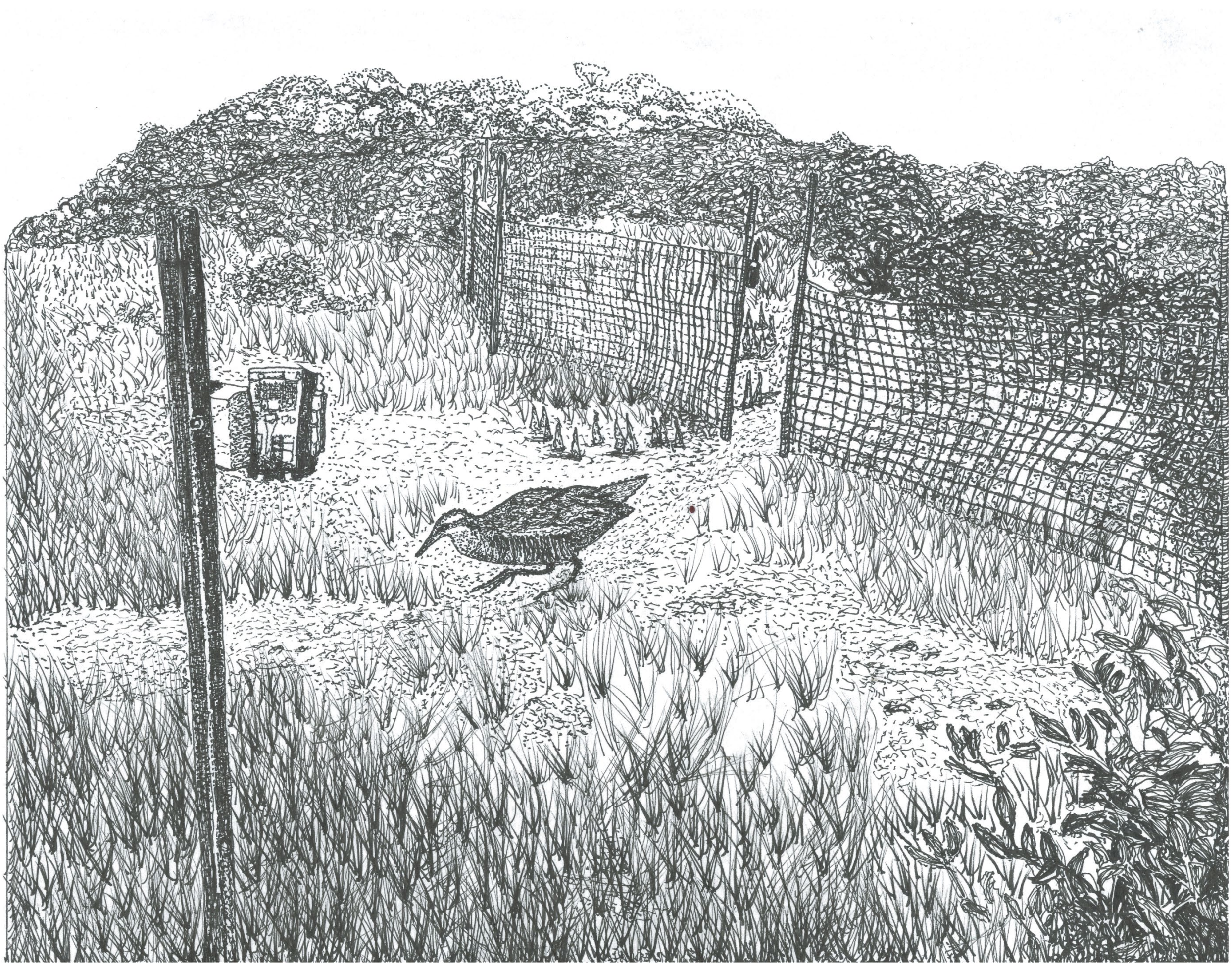
Student's signature:	Jacques de Satge Digitally signed by Jacques de Satge Date: 2023.03.09 10:39:20 +13'00'	Main supervisor's signature:	Weihong Ji Digitally signed by Weihong Ji Date: 2023.03.08 14:58:03 +13'00'

This form should be placed at the beginning of each relevant thesis chapter.

Chapter 5

A novel approach to cryptic avifauna monitoring: combining camera traps and drift fences



In this chapter, I establish and trial a survey method novel to both the study of banded rails and cryptic avifauna more broadly. Using a combination of camera traps and drift fences, I successfully survey banded rails in three saltmarsh-mangrove complexes in Mangawhai, and capture data on their movement between saltmarsh and mangrove habitats. I evaluate these movement patterns relative to tidal and temporal cycles. Finally, I discuss the value and wider application of using camera traps in conjunction with drift fences. This chapter addresses the third research objective of this thesis:

Objective 3: Establish and implement a reliable method for monitoring banded rails in intertidal environments

<ins>Chapter 5 cover image</ins>: A banded rail is caught on camera as it crosses a fence line separating saltmarsh and mangrove habitats. Artwork by Rick de Satgé.

5.1 Abstract

Cryptic species are difficult to detect and monitor, undermining efforts to conserve and study them. However, camera traps provide a non-invasive, versatile, and cost-effective method for surveying species that are not easily observed; such species include a variety of avifauna. Moreover, the efficacy of camera traps in surveying cryptic species can be improved by complementary trapping infrastructures, such as drift fences, designed to increase detection likelihoods. In New Zealand, the study of the banded rail *Gallirallus philippensis assimilis* – a medium-sized cryptic marsh bird in decline – has been hindered by the species' reclusive nature, its use of logistically challenging habitats such as mangrove forests, and a lack of reliable monitoring methods. Overcoming these hindrances, this study successfully used a combination of camera traps and drift fences to survey banded rails in three saltmarsh-mangrove complexes in Mangawhai Harbour, northern New Zealand – the first time this method has been used to target cryptic avifauna. By installing drift fences along the saltmarsh-mangrove interface of study sites, data collected by camera traps captured directional movement of banded rails. Modelling this data suggested that banded rail movements between saltmarsh and mangrove habitats were correlated with both temporal and tidal cycles. Banded rails were significantly more likely to move into mangroves in the early morning, whereas movement into saltmarsh habitats was most common during dusk hours. Having a reliable method for surveying banded rails is fundamental to both their ecological study and effective conservation. In this regard, the camera-drift fence setup developed and implemented in this study provides an effective and versatile method for monitoring banded rails and similar cryptic avifauna.

5.2 Introduction

Camera traps have become a widespread and effective survey tool in the field of ecological study (O'Connell *et al.* 2011; Rovero *et al.* 2013; Meek *et al.* 2015). Camera trapping is a cost-effective, replicable, efficient, and non-invasive means of studying wildlife (Tobler *et al.* 2008; Rovero *et al.* 2013; Meek *et al.* 2015; Colyn *et al.* 2017; McLean *et al.* 2017) capable of addressing a wide variety of research objectives (Cutler & Swann 1999; Caravaggi *et al.* 2017; Delisle *et al.* 2021). Enabling diverse research interests is an array of camera trap methodologies and study designs that optimise species detection and allow data collection tailored to different research goals (Rovero *et al.* 2013; Sollmann 2018). For example, camera traps can be deployed in grids or random arrays over large areas to assess species richness, occupancy, and detection rates of mammals (Kays *et al.* 2020), installed in trees to target arboreal species (Moore *et al.* 2021), baited to attract elusive species (Mills *et al.* 2019), or built into additional infrastructure such as fencing (Dupuis-Désormeaux *et al.* 2016; Welbourne *et al.* 2017) or nest boxes (Surmacki & Podkowa 2022) to assess patterns of animal movement or improve detection of small, bait-averse and/or ectothermic species.

Although the majority of camera trap studies has focused on mammals (O'Brien & Kinnaird 2008; Murphy *et al.* 2017; Delisle *et al.* 2021), there is a long history of using cameras to study birds (Cutler & Swann 1999) and avian-focused camera trap studies have become more predominant in recent years (Burton *et al.* 2015; Delisle *et al.* 2021). Many of these studies use camera traps to document species occurrences or assess avian diversity (e.g. Dinata *et al.* 2008; Seki 2010; Samejima *et al.* 2012; Beaudrot *et al.* 2016; Beirne *et al.* 2017; Colyn *et al.* 2017) often making use of 'by-catch' data where avifauna are not explicitly targeted (e.g. Dinata *et al.* 2008; Mugerwa *et al.* 2013; Ehlers Smith *et al.* 2017b; Murphy *et al.* 2017; Brooks *et al.* 2018). However, camera traps are also more often being used to study avian ecology (O'Brien & Kinnaird 2008; Delisle *et al.* 2021), including to research habitat use (Kuhnen *et al.* 2013; Ehlers Smith *et al.* 2017a; Colyn *et al.* 2019); occupancy, abundance, and density (Thornton *et al.* 2012; Suwanrat *et al.* 2015; Beaudrot *et al.* 2016; Ehlers Smith *et al.* 2017b; Murphy *et al.* 2017; Drouilly *et al.* 2018; Hunt *et al.* 2020); nest predation (Bolton *et al.* 2007; Krüger *et al.* 2018; Ribeiro-Silva *et al.* 2018; Anto *et al.* 2020); breeding status and behaviour (Huffeldt & Merkel 2013; Znidersic *et al.* 2019; Colyn *et al.* 2020); activity patterns (Li *et al.* 2010; McRoberts *et al.* 2011; Kuhnen *et al.* 2013; Mere Roncal *et al.* 2019); seed dispersal (Bartlow *et al.* 2011), and feeding behaviours (Kapfer *et al.* 2011; Campos *et al.* 2012; Blake *et al.* 2013).

The success of camera traps in avian ecological study is partly attributable to their ability to collect ecological data where other methods cannot. In surveys of cryptic (i.e., difficult to detect) avifauna, species characteristics and habitat conditions can render a multitude of established survey methods ineffective (Ehlers Smith *et al.* 2017a); auditory surveys have limited application to species that are not highly vocal or have inconspicuous calls (Colyn *et al.* 2017, 2019), call-broadcast surveys may make certain species less detectable by inducing cryptic responses (Conway & Gibbs 2005; Beauchamp 2015), point counts cannot be relied upon for reclusive species that are generally silent (Fletcher *et al.* 2000), while invasive techniques used to flush birds can yield poor results for species that are reluctant to take flight (Colyn *et al.* 2020). Additionally, species that use dense or logistically challenging habitats are difficult to survey with visual-based approaches (Fletcher *et al.* 2000; Ehlers Smith *et al.* 2017a). Where other methods have failed, camera traps have proven effective at surveying elusive species of avifauna despite difficult habitat conditions (Huffeldt and Merkel 2013, Znidersic 2017, Hand et al. 2019), as demonstrated by studies of cryptic ground-dwelling birds (e.g., Kuhnen *et al.* 2013; Suwanrat *et al.* 2015).

The habits and habitats of Rallidae – a diverse assemblage of ground-dwelling birds poorly represented in ornithological research (Taylor & van Perlo 1998; Conway & Gibbs 2005; Colyn *et al.* 2017; Znidersic 2017) – are well suited to the use of camera traps for ecological study. Rails are secretive birds that typically inhabit wetlands and marshlands (Taylor & van Perlo 1998; Znidersic *et al.* 2019). Additionally, rails call infrequently – particularly outside of the breeding season – and are rarely directly observed as individuals remain concealed in dense vegetation (Conway & Gibbs 2005; Hand *et al.* 2019). These characteristics make rails challenging to monitor using conventional approaches, meaning population declines may go unnoticed (Znidersic *et al.* 2019). As such, studying this avian family with camera traps provides unique opportunities for insights into their ecology and conservation (Znidersic 2017; Colyn *et al.* 2019; Znidersic *et al.* 2019).

The banded rail *Gallirallus philippensis* comprises as many as twenty recognised subspecies across south-east Asia, Australasia, and the southwest Pacific (Marchant & Higgins 1993; Garcia-Ramirez *et al.* 2017), yet remarkably little is known about this species throughout its distribution. The New Zealand subspecies, moho-pererū *Gallirallus philippensis assimilis*, was once relatively common across both New Zealand's North and South Islands (Elliott 1983), but is today largely restricted to coastal pockets of saltmarsh and mangrove in the upper North

Island (Marchant & Higgins 1993; Bellingham 2013; Beauchamp 2015). This range restriction has been driven by habitat loss and predation by introduced mammalian predators (Elliott 1983, 1987; Heather & Robertson 2005) and explains the banded rail's threat status as 'at risk of extinction – declining population' (Robertson et al. 2021).

Insights from a limited pool of research (namely, Elliott 1987, 1989; Botha 2011; Beauchamp 2015, 2022) suggest that banded rails roost, nest, and forage in saltmarsh habitats, while adjacent mangroves are typically considered foraging habitat only. Importantly, observations of banded rail habitat use to date have relied on proxy measures of banded rail presence, including calls (Beauchamp 2015) and footprints (Elliott 1983, 1987; Botha 2011), or limited visual observations (Beauchamp 2022). While banded rails have been captured on camera as part of a biodiversity surveys (Dencer-Brown et al. 2020), camera traps have not been used explicitly to study banded rail ecology in New Zealand or elsewhere.

In New Zealand, there is an urgent need for ecological insight into banded rail-habitat relationships given ongoing changes to coastal environments. In recent decades, saltmarsh habitats have become progressively reduced through land reclamations (Walker *et al.* 2008; Saintilan *et al.* 2014), whereas mangrove forests have rapidly expanded seawards across intertidal flats, fuelled by anthropogenically driven increases in terrigenous sediment in estuaries and along coastlines (Morrisey et al. 2010, Horstman et al. 2018). The expansion of mangrove forests has raised concerns about the loss of recreation value in estuaries (Chapter 3) and the ecological repercussions of increasing habitat homogeneity in coastal areas (Morrisey et al. 2007; Harty 2009; Lundquist et al. 2014). In response to these concerns, management interventions to remove areas of mangrove have occurred in numerous estuaries throughout northern New Zealand (Chapter 3), typically justified as a means to preserve cultural, aesthetic, and recreational values of open intertidal flats (Harty 2009; Lundquist et al. 2014, Chapter 3). However, the ecological consequences of this mangrove removal are poorly understood (Stokes et al. 2016), particularly for mangrove-using species such as the banded rail. Without understanding how *G. p. assimilis* makes use of saltmarsh and mangrove habitats, little can be done to develop effective strategies for the banded rail's conservation and recovery (Morris 2003; Morrison *et al.* 2006; Seifert *et al.* 2018).

The objectives of this study were two-fold. First, I sought to establish and trial a survey method novel to the study of banded rails, namely the use of camera traps and drift fences (CDF). While camera traps have been used in conjunction with drift fences to optimise detection of reptiles and small cryptic mammals (Welbourne *et al.* 2017; Hohnen *et al.* 2019; Neuharth *et al.* 2020), this study is the first to show that this method is an effective survey method for ground-dwelling birds such as the banded rail. Second, I aimed to improve ecological understanding of the banded rail's use of habitats in coastal environments, using the CDF method to survey banded rails in saltmarsh-mangrove complexes in several study sites in Mangawhai Harbour, northern New Zealand. To do so, I installed camera traps and drift fences along the mangrove-saltmarsh interface (MSI) of study sites to determine inter-habitat movement patterns of banded rails and correlate these with local environmental conditions.

This study used the CDF survey method to test three hypotheses on banded rail movement across the MSI. First, I hypothesised that birds would move into mangrove habitats in the early morning and return to saltmarsh habitats in the evening (diurnal state hypothesis). Second, I hypothesised that birds would move into mangroves on outgoing tides and return to the saltmarsh on incoming tides (tide state hypothesis). Third, I hypothesised that tidal amplitude would influence the relationship between movement direction (towards saltmarsh or mangrove) and tide state, whereby larger high tides would result in greater movement towards saltmarsh habitats (tidal amplitude hypothesis). These hypotheses reflect the prediction that banded rail movement between coastal habitats is not random and is, in-part, mediated by temporal and tidal cues.

5.3 Methods

5.3.1 Study design and site selection

Three study sites (A, B, and C) consisting of rush-saltmarsh and mangrove habitats were selected in Mangawhai estuary (Figure 5.1). Sites were selected to maximise the likelihood of observing banded rail movement between saltmarsh and mangrove habitats; thus, sites exhibited a clear delineation between saltmarsh and mangrove habitat types and the presence of banded rail populations was confirmed (de Satgé, unpubl. data). For practical purposes, site selection within Mangawhai estuary was restricted to areas accessible from land.

A combination of camera traps, guide-netting, netting gaps, and cage traps (henceforth 'trapping infrastructure') was installed at each study site with two objectives: first, to monitor banded rail movement between two coastal habitat types (rush-saltmarsh and mangrove forest) – the objective of this study – and second, to trap banded rails as part of a biotelemetry study (see Chapter 6).

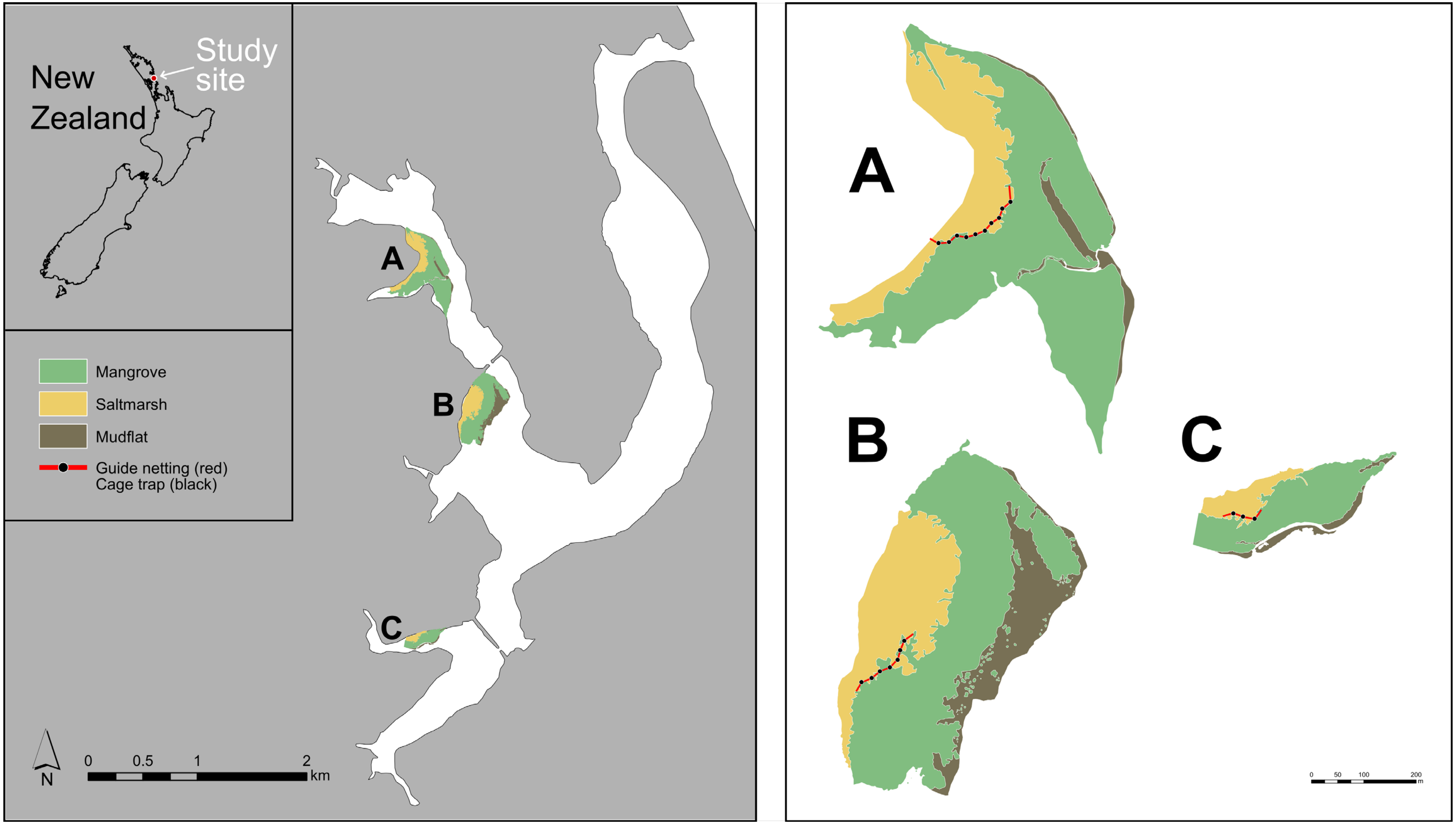


Figure 5.1 *Left panel* - The location of camera trap study sites in Mangawhai estuary (shown in white) in northern New Zealand (inset). *Right panel* - Enlargements of each study site (A, B, and C) show the position of drift fence lines (red) and cameras (black dots) along the mangrove-saltmarsh interface at each site.

5.3.2 Camera trapping

In 2020 and 2021, drift fences were installed at three study sites to intercept and funnel banded rails past camera-monitored fence gaps as birds moved between saltmarsh and mangrove habitats (Figure 5.2). Drift fences were built using plastic mesh fencing secured to steel stakes to a height of 90cm. A mesh size of 5x5cm was chosen to prevent banded rails from walking through fences, while allowing smaller animals such as fish, crabs, and smaller birds to pass through mesh holes. Fence gaps measuring 50cm wide were located at 20-30m intervals along drift fence lines, ensuring that >2 gaps would fall within the expected foraging range of a pair of banded rails based on conservative home range estimates in intertidal saltmarshes (Elliott 1983).

All fence gaps, as well as fence endpoints in Sites B and C, were monitored using a Bushnell Trophy Cam HD wildlife camera (henceforth 'camera trap'). To optimise for detection of rails and other small-bodied animals, each camera was mounted to a metal stake at a height of 1.2 metres above ground two meters from each netting gap, and angled to align the entrance of each netting gap with the centre of the camera's detection zone (Meek *et al.* 2014a; Colyn *et al.* 2017). Camera placement relative to netting gaps was dictated by vegetation presence and density, but always a ensured a clear line of sight between cameras and netting gaps. Cameras were motion-triggered by passive infra-red sensors, set to high motion sensitivity, and programmed to capture three still images upon each trigger, with no capture delay between triggers.

Drift fence length, netting gaps, and the total number of cameras varied among study sites (Table 5.1) but trapping infrastructure at each site was designed and implemented consistently among sites using the same fundamental design. In addition to camera traps and drift fences, double-door walk-through cage traps were installed in netting gaps in preparation for a biotelemetry study requiring live-capture (Chapter 6) which would follow the camera trapping. In 2020, cage traps were placed between netting gaps after ten days of camera monitoring and left in place for the remainder of the study (a further 9-10 days; Table 1), whereas in 2021, cage traps, drift fences, and camera traps were installed simultaneously. During camera trapping in both 2020 and 2021, cage traps were left open and unset, and did not impede banded rail movement between saltmarsh and mangrove habitats (Figure 5.2). To improve detection likelihoods, the timing of camera surveys (January-March, Table 5.1) coincided with the period adult birds may be flightless during a complete post-breeding moult (Elliott 1983; Marchant & Higgins 1993). However, banded rails are highly reluctant fliers even when capable (Marchant & Higgins 1993; Heather & Robertson 2005).

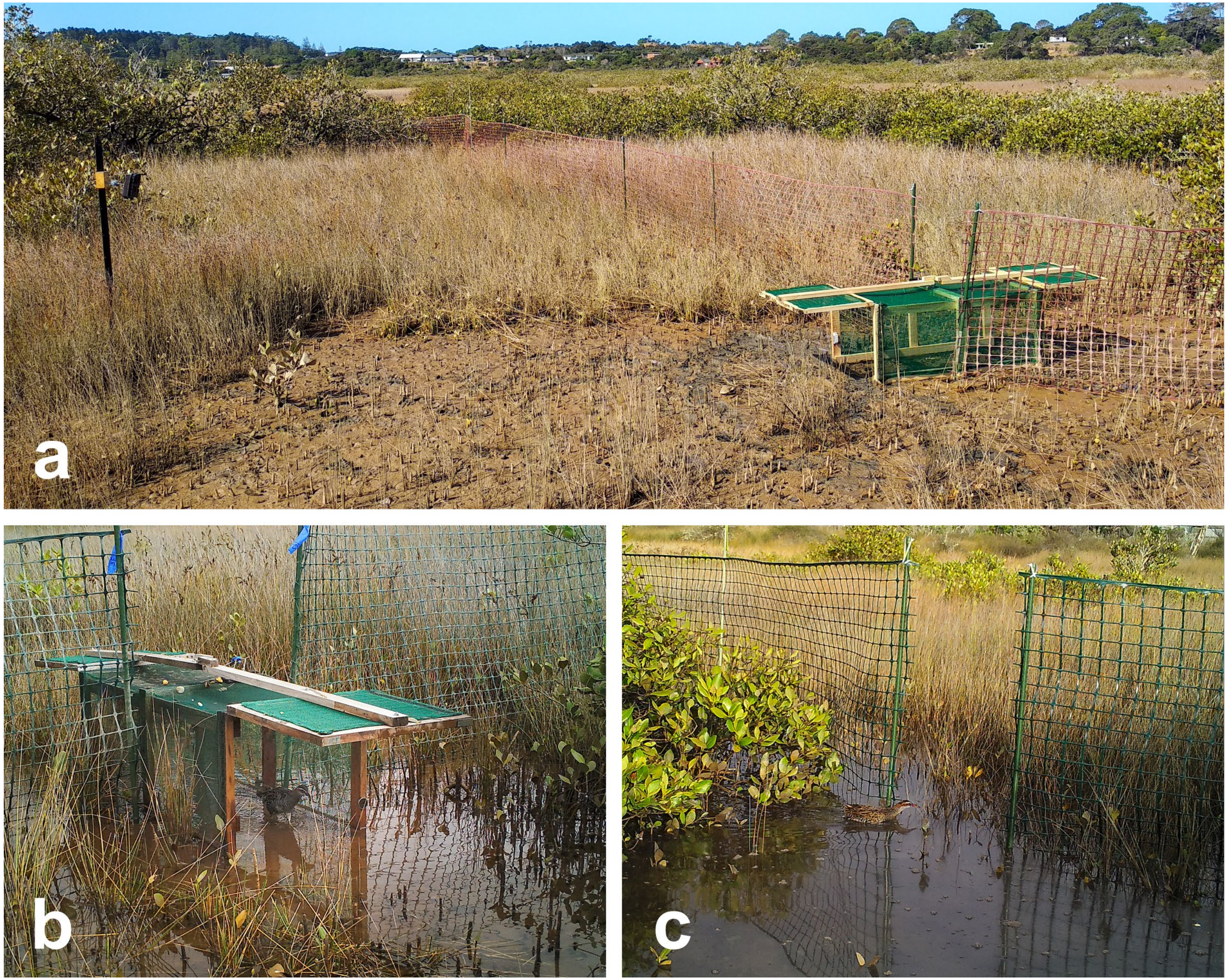


Figure 5.2 (a) Image showing the drift fence-camera configuration, with a camera trap monitoring an open cage trap located in a fence gap along the mangrove-saltmarsh interface **(b)** A camera trap image of a banded rail walking through an open, unset cage trap towards mangroves **(c)** A camera trap image of a banded rail walking through a fence gap towards rush saltmarsh.

Table 5.1 Habitat features and trapping infrastructure in three camera trapping study sites

	Site A	Site B		Site C	*Total*
Habitat features					
Saltmarsh area (m^2)	46,960	46,200		7,870	147,230
Mangrove area (m^2)	133,290	105,230		27,480	371,230
MSI length (m)	860	510		240	2,120
Trapping infrastructure					
Year	2021	2020	2021	2020	
Dates installed	19-31 Jan	29 Jan-18 Feb	19-31 Mar	30 Jan-18 Feb	
Fence length (m)	240	160	240	80	720
Fence gaps	10	7	10	3	30
Fence length : MSI	0.28	0.31	0.47	0.33	
Camera traps	10	9	10	5	34
Camera trap days	120	180	120	95	515

5.3.3 Photo processing

Photographs were processed using Timelapse2 software (Greenberg 2021) that automatically extracted the time, date, and camera ID of each photograph. Photographs were manually identified and sorted to separate banded rail photographs from other wildlife and wind-triggered photographs. Photographs of banded rails were then assessed for the number of individuals, behaviour (walking, foraging, or other), positioning and walking direction relative to mangrove and saltmarsh habitats. Only the first image – of three in succession – of each motion-trigger event was retained, unless the first image was of poor quality. The study design intentionally increased the likelihood of capturing banded rail on camera as birds had to pass through bottlenecks (i.e., fence gaps or cage traps) created by drift fences, a concentration method used to improve detection rates by camera traps (Welbourne *et al.* 2017). Thus, I expected multiple individuals to pass the same camera over short time frames, so, when calculating camera events (as per Meek *et al.* 2014a) multiple images taken of banded rail by one camera in the same minute or successive minutes (up to three minutes) were treated as a single event, unless different individuals were demonstrably present (Znidersic 2017). Bird size, height, shape, orientation, and colouration were evaluated to ensure different individuals were marked as independent events, within the three minute threshold (Znidersic 2017). Only photographs of birds walking were retained for analyses of inter-habitat movement as the direction of travel of banded rails could not consistently be determined from photographs of foraging or preening behaviours.

5.3.4 Statistical analyses

I built two generalised linear mixed effect models (GLMMs) using the *lme4* package ver.1.1-26 (Bates *et al.* 2015) in RStudio ver.1.3.1056 (RStudio Team 2020) to test hypotheses on the effects of tidal and diurnal cycles on banded rail inter-habitat movement. For both models, I used a dataset restricted to photographs of banded rails crossing the MSI, either walking towards mangroves or saltmarsh (n = 167), but not parallel to either habitat (i.e., along the fence line). Using this restricted movement dataset, I parameterised a response variable 'Direction' with binomial outcomes 'mangrove direction' (0) and 'saltmarsh direction' (1) indicating the orientation of walking banded rails as they crossed the MSI.

To test the tide- and diurnal-state hypotheses, I built a 'tide-diurnal model' that regressed response variable 'direction' against explanatory variables 'tide state' (TS), 'time of day' (TD), the interaction of TS and TD, and a random effect 'Trap ID' (the unique identity of each camera's physical location). In addition, to test the tidal amplitude hypothesis, I created a 'tidal-amplitude model' by adding the fixed effect 'tide height' (TH) term to the tide-diurnal model, as well as interaction terms for all fixed effects. Both GLMMs were fitted by restricted maximum likelihood estimation and specified with a binomial distribution. Models were tested for misspecification by examining scaled residuals in quantile–quantile plots and histograms (Zuur *et al.* 2009) using package DHARMa ver. 0.3.3.0 (Hartig 2020). Model fit for both models was compared the using Akaike information criterion (AICc) (Burnham & Anderson 2002) with package MuMIn (Bartoń 2016).

Tide state (TS) was defined as a factor variable with two levels - whether the tide was 'incoming' or 'outgoing' relative the time of each photograph. Time of day (TD) was defined as an integer variable to reflect the three broad phases in visible solar irradiance – dawn, day, and dusk – over the course of daylight hours (Spitschan *et al.* 2016). For TD, 'dawn' was defined as the period between 05:00 AM and thirty minutes after sunrise, 'dusk' as the period from thirty minutes before sunset to 10:00 PM, and 'day' as the hours between dawn and dusk. Given the relatively small sample size of this study's data set (n = 168), TD was parameterised as a continuous integer by assigning values '-1', '0', and '1' to temporal periods dawn, day, and dusk respectively to retain degrees of freedom and aid model convergence. Tide height (TD) was defined as a continuous variable comprising the average daily height of high tide in meters, reflecting a range of tidal heights (2.2 – 3.6 meters) over the course of the study.

Neither of the GLMMs controlled for differences among study sites; all sites were located within the same estuary and comprised near-identical habitat composition, hence I assumed inter-habitat movement behaviour would remain consistent among sites. Additionally, models did not control for inter-annual variation; data were captured within the same temporal window (post breeding season) over consecutive years, and I did not expect differences in movement behaviour among years.

5.4 Results

Camera traps were active for a total of 515 camera days across three study sites in 2020 and 2021, capturing a total of 490 photos of nine different species, including banded rail *Gallirallus philippensis* (n = 308), Norway rat *Rattus norvegicus* (59), mallard *Anas platyrhynchos* (31), mouse *Mus musculus* (22), white-faced heron *Egretta novaehollandiae* (22), sacred kingfisher *Todiramphus sanctus* (18), pukeko *Porphyrio melanotus* (4), song thrush *Turdus philomelos* (2) and stoat *Mustela erminea* (2).

Photographs of banded rail were captured at an average rate of 0.60 photos per camera day, but this varied substantially among study sites. The vast majority of banded rail photos were taken at Site B (n = 287) at an average rate of 1.59 banded rail photos per camera day, substantially higher than Site C (n = 11) and Site A (n = 10) with 0.12 and 0.08 photos of banded rails per camera day. Similarly, photo capture rates for mammals were highest in site B (0.30 photos of mammals per camera day, n = 38), followed by site A (0.19 photos per camera day, n = 23) and site C (0.06 photos per camera day, n = 6). Mammal photos at Site B and Site C were exclusively of rodents, while Site A had rodents and a species of mustelid (*Mustela erminea).*

During the study period, the photograph of banded rails taken earliest in the day was taken at 05:40 AM and the latest at 09:07 PM. All photographs were of adult or sub-adult banded rails, and only on eight occasions were more than one banded rail observed in the same photograph. The average time interval between successive photographs of a banded rail at the same camera station was 430 minutes (range of 0 - 13,940 minutes). Of banded rail photographs, 96% (n = 295) were of birds walking, while just 2% (n = 6) were of birds actively feeding, and a further 2% (n = 7) were classified as ‘other’ (preening, flapping, or craning). Of photographs classified as walking, 27% (n = 84) were of birds moving towards saltmarsh, 27% (n = 83) towards mangroves, and 46% (n = 128) parallel to both habitats as birds walked along fence lines.

Banded rails crossed the MSI continuously during daylight hours but did so most frequently during dawn and dusk hours (Figure 5.3). Time of day (TD) explained significant variation in direction of banded rail movement in the tide-diurnal GLMM (Chi-sq 4.4036, df = 1, p = 0.03), as banded rail movement into mangroves was significantly more likely during dawn hours than during the day or at dusk (Table 5.2). The correlation between Direction and TD was weakly influenced by Tide State (Chi-sq 3.3909, df =1, p = 0.07). During outgoing tides banded rails were just as likely to move into mangroves or saltmarsh irrespective of TD, whereas banded rails were far more likely to move towards saltmarsh with the incoming tide during dusk hours than during dawn hours (Figure 5.4).

The tidal-amplitude GLMM (deviance = 196.4, residual df = 159, R^2 = 0.35, AICc = 215.5) represented a marginally poorer fit to the data (ΔAICc = 3.1) than the tide-diurnal GLMM (deviance = 202.1, residual df = 163, R^2 = 0.31, AICc = 212.4). The tidal-amplitude GLMM indicated that Tide Height may interact with Tide State in explaining variation in Direction; although I observed only weak evidence of this interaction (Chisq = 2.71, df = 1, p = 0.09). However, raw data suggested that tide height may limit the incidence of MSI crossings, irrespective of their direction, during larger tides as no photographs were captured at, or within 115 minutes of, high tide when tides were higher than 3.1m on average (Figure 5.5).

Table 5.2 ANOVA summary and model estimates of tide-diurnal GLMM fitted to banded rail MSI bi-directional movement data

Explanatory variables	Estimate ± SE	df	χ^2	*p*
Time of day	1.34 ± 0.48	1	4.40	**0.04**
Tide state (outgoing)	-0.56 ± 0.38	1	1.38	0.24
Time of day × Tide state	-1.19 ± 0.64	1	3.39	0.07

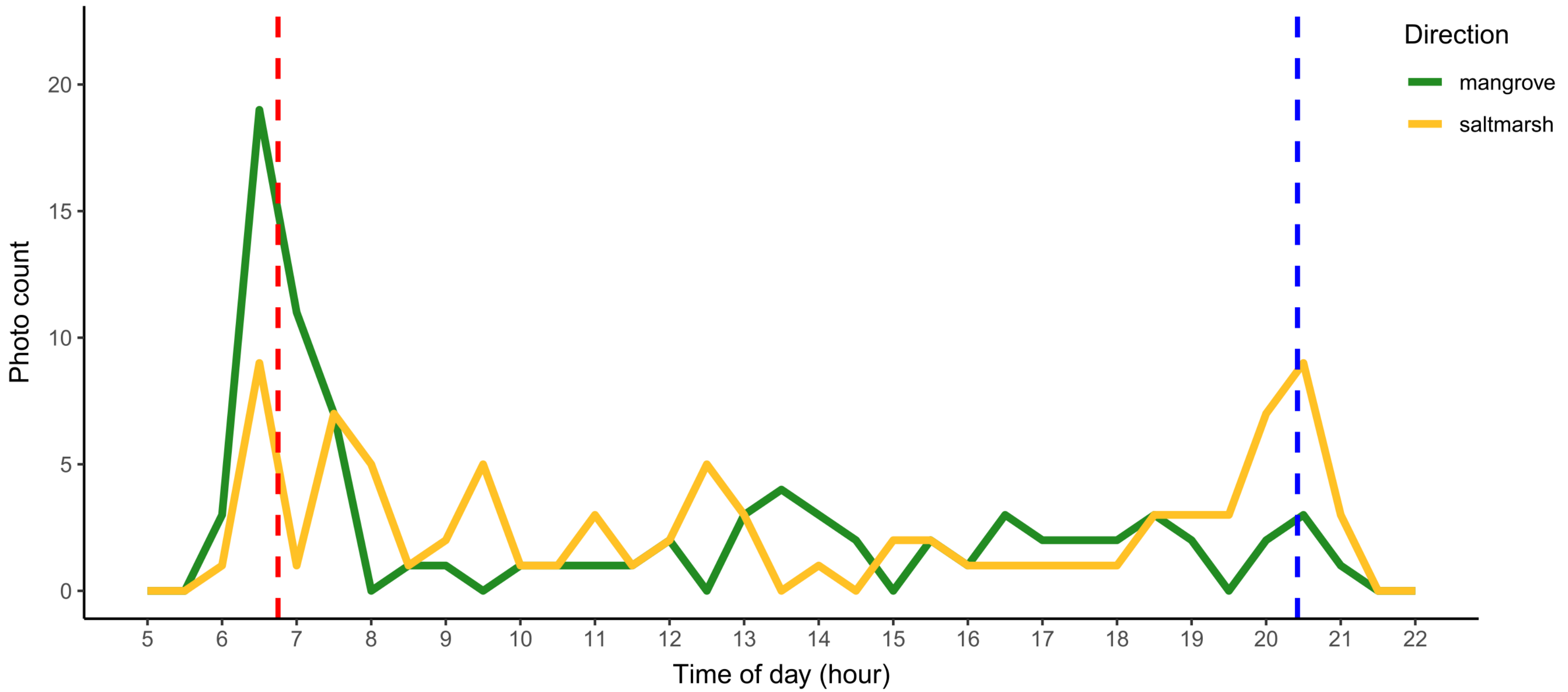


Figure 5.3 Hourly photo counts of banded rail movements across the mangrove-saltmarsh interface, as depicted by photos capturing walking behaviour toward mangrove (green) or saltmarsh (yellow) throughout the day. Red and blue dashed lines indicate the average sunrise and sunset times over the course the study, respectively.

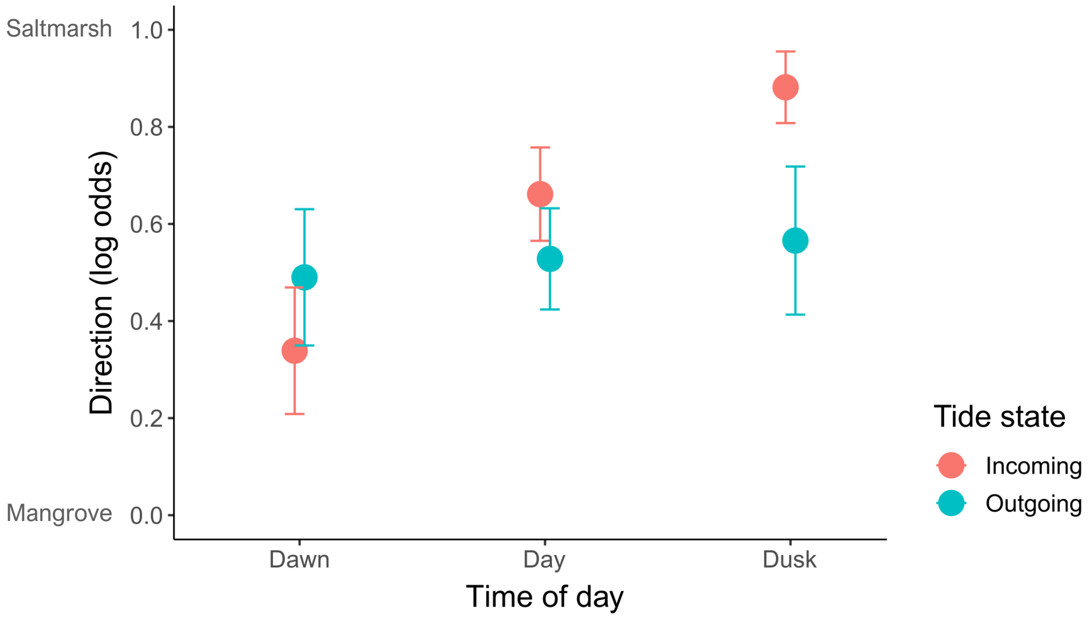


Figure 5.4 The tide-diurnal GLMM predictions (expressed as log odds) of banded rail movement across the mangrove-saltmarsh interface, where logit odds >0.5 indicate a saltmarsh direction and logit odds <0.5 indicate a mangrove direction. Probabilities are expressed relative to the time of day and the tide state.

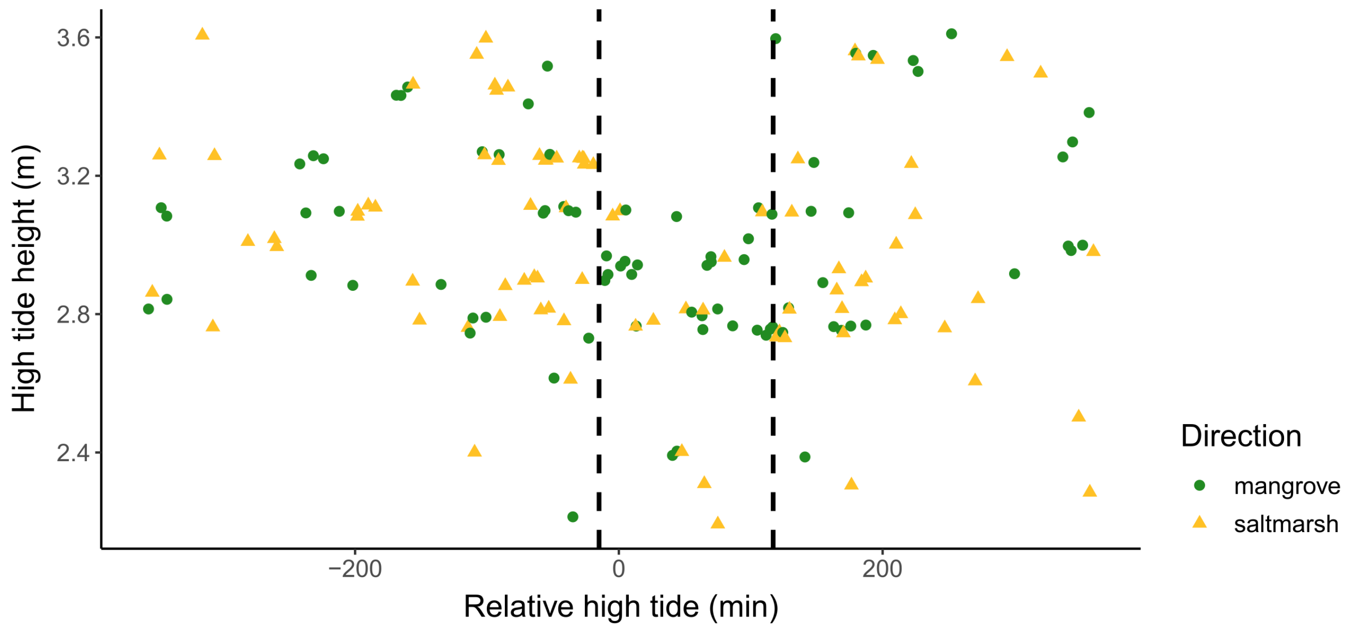


Figure 5.5 Photograph occurrences of banded rails (jittered, coloured points) relative to high tide time and high tide height. The tidal cycle (x axis) is expressed in minutes relative to high tide: values = 0 indicates the exact point of high tide, whereas values <0 indicate an incoming tide, and values >0 indicate an outgoing tide. Point colours/shapes indicate banded rail walking direction; mangrove direction = green circles, saltmarsh direction = yellow triangles. Black dotted lines indicate tidal times where no MSI crossings were recorded at tide heights >3.1m.

5.5 Discussion

Camera traps provide a reliable, versatile and cost-effective method of surveying wildlife that are not easily observed (Rovero & Zimmermann 2016; Caravaggi *et al.* 2017), including a variety of avifauna (O'Brien & Kinnaird 2008; Znidersic 2017; Colyn *et al.* 2019, 2020). This study is the first to use a CDF survey approach for a cryptic, ground-dwelling bird by observing the habitat use patterns of the elusive banded rail *Gallirallus philippensis assimilis*. Using a combination of drift fences and camera traps installed along the interface between mangrove and saltmarsh habitats in three coastal sites in Mangawhai, northern New Zealand (Figure 5.1), this study has successfully tested three hypotheses relating to banded rail habitat use. First, this study has shown that banded rails are most likely to move between different habitats during crepuscular hours (diurnal state hypothesis), moving into mangroves in the early morning, and returning to saltmarsh habitats during dusk hours (Figure 5.3). Second, study results provide weak evidence that banded rail movement between saltmarsh and mangrove habitats is mediated by the tidal cycles (tidal state hypothesis, Figure 5.4), which in turn may be influenced by tidal amplitude (tidal amplitude hypothesis). Following this successful trial of the CDF method, I discuss the merits, drawbacks, and potential novel applications of combining camera traps with drift fences for ecological study.

5.5.1 Banded rail ecology

Despite being widespread globally, remarkably little is known about the banded rail *Gallirallus philippensis* (Garcia-Ramirez *et al.* 2017; Robertson *et al.* 2021). In New Zealand, banded rail populations are largely restricted to saltmarsh-mangrove complexes (Bellingham 2013; Beauchamp 2015) but their cryptic nature and habitation of logistically challenging environments has hindered study of their ecology (Marchant & Higgins 1993; Bell & Blayney 2017). This lack of understanding is reflective of the challenges of studying Rallidae populations around the world – particularly in wetland and coastal environments (Znidersic 2017; Hand *et al.* 2019) – as species of this family are generally poorly suited to commonly used visual- and acoustic-based survey methods (Colyn *et al.* 2020). A consequent lack of data on rails has inhibited effective strategies for their conservation globally (Morris 2003; Morrison *et al.* 2006; Robertson *et al.* 2017; Seifert *et al.* 2018).

The findings of this study shed new light on banded rail ecology, in particular banded rails' use of saltmarsh and mangrove habitats in New Zealand. Data from camera traps confirm that banded rails use both saltmarsh and mangrove habitats, echoing results from previous studies based on footprint surveys and acoustic monitoring (Elliott 1987; Botha 2011; Beauchamp 2015). Additionally, this study suggests that banded rails are not nocturnally active but are active during crepuscular hours as they move between saltmarsh and mangrove habitats (Figure 5.3).

The timing of banded rail movements between saltmarsh and mangrove habitats (Figure 5.3) suggests that banded rails primarily use mangrove habitats during diurnal hours, likely as foraging grounds (Dencer-Brown *et al.* 2020; Beauchamp 2022), and use saltmarsh habitats as roosting sites during nocturnal hours. However, these assertions are inferential; banded rail individuals are not identifiable from photographs, therefore I cannot be certain whether the same individuals are moving back and forth between habitats. However, the even split between photographs of rails moving into saltmarsh (n = 84) and into mangroves (n = 83), supports the assumption that banded rails move into mangroves in the morning and return to saltmarshes at night. If this is the case, camera trap data suggest that mangroves play an important role in the daily habitat use patterns of banded rail in these study sites, particularly as banded rails are seldom observed using open mudflats on the seaward edge of mangroves (Botha 2011; Beauchamp 2015).

5.5.2 Conservation implications

The findings of this study have implications for local and national approaches to the conservation of banded rail and their habitats, as well as other fauna found in saltmarsh-mangrove environments.

At an estuary scale, this study highlights the need for invasive predator control in mangrove-saltmarsh complexes in Mangawhai (and likely elsewhere). It is of note that cameras captured mustelids and rodents along the mangrove-saltmarsh interface (MSI) in multiple study sites, areas that correspond to breeding, roosting, and foraging habitats for banded rails (Elliott 1987; Marchant & Higgins 1993; Beauchamp 2015, 2022) and numerous other avifauna (Cox 1977). Invasive predators have dramatically reduced New Zealand bird populations (Russell *et al.* 2015), and although intertidal areas present a challenge to trapping efforts, these habitats are likely the last stronghold for banded rail populations in New Zealand (Elliott 1983; Marchant & Higgins 1993; Bellingham 2013). As such, predator control and exclusion within saltmarsh-mangrove complexes is a much needed management intervention, particularly as predation of banded rail nests within saltmarsh habitats is a known phenomenon (Elliott 1983; Parker & Brunton 2004).

At a national scale, the findings of this study have implications for the management of saltmarsh and mangrove habitats in New Zealand. Banded rails are commonly associated with mangrove habitats in New Zealand; an estimated 80-90% of New Zealand's banded rail population occurs in saltmarsh-mangrove complexes on the North Island (Bellingham 2013). While mangrove expansion in New Zealand may provide additional habitat to banded rails, contemporary removal of mangroves in many harbours may displace banded rails. However, the effects of removal on banded rails are likely site specific (Chapter 3) and the broader ecological effects of removal in New Zealand remain poorly understood (Lundquist *et al.* 2014). In addition, saltmarsh and other saline habitats in the upper North Island have been progressively replaced by farmland and coastal infrastructure in recent decades (Walker *et al.* 2008; Beauchamp 2015), which has reduced the availability of banded rail breeding grounds. Results from this study suggest that both saltmarsh and mangrove habitats play an important role in the daily habitat use patterns of banded rails, affirming the need to conserve both habitats for banded rails.

5.5.3 Cameras and drift fences – a novel use case

Monitoring the habits and habitats of the banded rail *Gallirallus philippensis* in New Zealand presents a compelling but challenging use case for camera traps. Banded rails are difficult to monitor using established survey types for avifauna – such as point counts, auditory surveys, line transects, rope dragging or camera trap arrays – given their cryptic behaviour and their use of densely vegetated habitats. This challenge extends to multiple species of Rallidae and other ground-foraging birds in a variety of contexts (Colyn *et al.* 2020). Camera traps have often provided an effective monitoring solution for such species (e.g., Murphy et al. 2017, Znidersic 2017, Colyn et al. 2019, Znidersic et al. 2019), although their efficacy can be limited by dense vegetation and small-bodied, fast-moving target species (Marcus Rowcliffe *et al.* 2011; Hobbs & Brehme 2017).

5.5.3.1 Improving detectability

As the use of camera traps in ecological study has grown, researchers have developed an array of study designs to optimise the ability of cameras to detect wildlife (Rovero *et al.* 2013; Meek *et al.* 2014a). For example, numerous studies make use of linear features in the landscape – such as fence lines, roads, clearings, or wildlife trails – to improve the chances of detecting target species (Cusack *et al.* 2015; de Satgé *et al.* 2017; Kolowski & Forrester 2017; Wysong *et al.* 2020; Hofmeester *et al.* 2021; Tanwar *et al.* 2021), while other studies have used baits or lures at cameras to attract elusive species (du Preez *et al.* 2014; McLean *et al.* 2017; Mills *et al.* 2019;

Holinda *et al.* 2020). Where these methods fail to sufficiently improve detection rates – as is often the case for small, ectothermic, or bait-averse animals (Wellington *et al.* 2014; Meek *et al.* 2015) – researchers have used drift fences to funnel animals into a camera's field of view (Welbourne 2013, 2014; Hobbs & Brehme 2017; Martin *et al.* 2017; Neuharth *et al.* 2020).

Drift fences have long been used in animal trapping as a component of live-capture traps (Low 1935; Bub 1991; Meissner 1998; Sutherland *et al.* 2004; Perkins *et al.* 2010) but have only recently been used in camera trap studies, primarily in the study of reptiles (Hobbs & Brehme 2017; Martin *et al.* 2017; Welbourne *et al.* 2017; Neuharth *et al.* 2020). Using drift fences in conjunction with camera traps improves detectability relative to standalone cameras in two ways. First, the effective trapping area covered by a camera is increased by its adjacent drift fences, as this fencing serves to funnel target species towards the camera's field of view (a 'concentration method' – Welbourne *et al.* 2017). Second, the known locations of gaps in the drift fencing allows for premeditated camera positioning that optimises for picture clarity and framing (Neuharth *et al.* 2020). This is particularly useful in densely vegetated environments such as mangrove forests or rush-saltmarsh, where plant structures can obscure the camera's field of view and result in many false triggers. The assertion that cameras flanked by drift nets outperform standalone cameras in detecting banded rails is supported by anecdotal evidence from camera testing preceding this study; a trial of standalone camera traps in study sites in 2018 yielded markedly fewer successful photos per trap day (of all observed species) than the rates observed in this study.

In the case of banded rails, there is a clear need to improve the rate of their detection in wildlife surveys. For example, Hill *et al.* (2015) used ten-minute playback counts to detect the presence of banded rails in 8 coastal wetland sites on the Okahukura Peninsula, detecting banded rails in 7 of 8 sites, but only in 11 of the 48 counts conducted over a month. Using a CDF approach to banded rail monitoring may reduce need for such labour-intensive surveys, while potentially improving detection rates (Welbourne *et al.* 2017; Neuharth *et al.* 2020). In addition, trials of the CDF setup in other habitats, including freshwater wetlands and coastal saltmarshes without mangroves, have proven effective in detecting banded rails (Section 5.7, Supplementary material). However, further study is needed to compare banded rail detectability among different survey types.

5.5.3.2 Delineating areas of interest in the landscape

In camera trap studies to date, drift fences have been used exclusively as funnelling infrastructure to concentrate animals (Welbourne *et al.* 2017) and improve detection rates (e.g., Martin et al. 2017, Hobbs and Brehme 2017, Neuharth et al. 2020). However, fence positioning in a landscape presents an additional opportunity to delineate and monitor boundaries of research interest. For example, Dupuis-Désormeaux et al. (2016, 2018) monitored gaps in established fence lines surrounding a conservancy in Kenya to determine animal migration patterns in and out of protected areas. While this study uses fence lines to similar effect, the *a priori* design of drift fences – including fence positioning, size, and length – could be optimised for banded rails, the target species, and allowed for targeted hypothesis testing.

The application of drift fences presents an opportunity to delineate the landscape and observe how target species move between areas of interest. As demonstrated by this study, where nets delineate different habitats, ecologists can study patterns of species movement as they move between different habitats. Future possible applications of drift fences in camera trap studies could include delineations along urban-rural boundaries, animal territorial boundaries, or protected area perimeters, where fencing and camera designs can be tailored to a wide range of taxa. For practical purposes, the CDF method is best used to target animals with smaller home ranges, and/or animals that evade detection of standalone camera traps and other survey techniques.

5.5.3.3 Drawbacks

Although drift fences can improve camera detection rates and delineate boundaries of interest in the landscape, their use has drawbacks. Logistically, drift fences can be costly and time-consuming to construct, potentially limiting the scale of their use. To date, drift fences have seldom extended more than a few metres from camera traps in studies of small-bodied reptiles, arthropods, amphibians, and rodents (Welbourne 2013, 2014; Hobbs & Brehme 2017; Martin *et al.* 2017; Neuharth *et al.* 2020). Larger animals require taller, more robust fences, which extend for longer distances to intercept animals with big home ranges. While the use of existing fence lines can enable studies at larger scales (e.g., Dupuis-Désormeaux et al. 2016, 2018), this restricts research questions to the location and configuration of existing infrastructure.

Beyond the practical costs of implementing drift fences, the use of drift fences has the potential to alter the behaviour of target species, rendering observations as artefacts of study design rather than reflecting natural behaviour. The effects of study design and camera equipment are well discussed in camera trap studies, and a number of authors note that camera traps, baits, and lures are likely to influence species behaviour to varying degrees (Meek *et al.* 2014b, 2015, 2016; Rocha *et al.* 2016; Mills *et al.* 2019; Holinda *et al.* 2020; Iannarilli *et al.* 2021). Drift fences represent an additional piece of infrastructure in camera trapping and affect species' behaviours intentionally, given that they are designed to redirect animal movement. However, this effect can be minimised by allowing for adequate gaps in fence lines, ensuring that redirected movement still largely reflects natural movement patterns. This study ensured that >2 netting gaps were placed within the estimated foraging range of banded rails, thereby redirecting banded rail movement along the MSI (past camera traps) without impeding their natural movement between saltmarsh and mangrove habitats. Nevertheless, it is possible that banded rail movement patterns in this study reflect fence design rather than natural behaviour (but results of Chapter 6 suggest this is not the case).

5.5.3.4 Wider applications

The potential for drift fencing to improve species detectability can benefit other camera trapping applications, including species inventories and occupancy studies. Camera-based species inventories rely on high species detection rates to determine the maximum number of species in an area (Rovero *et al.* 2013) and should use a mix of survey design strategies to maximise encounter frequencies (Iannarilli *et al.* 2021). Similarly, camera-based studies of species occupancy – defined as the proportion of an area, patches, or sites occupied by a species (Mackenzie *et al.* 2002; MacKenzie 2006) – rely on sufficient detection probabilities to determine reliable presence-absence data (Rovero *et al.* 2013). In both species inventories and occupancy studies, drift fences present a viable option to improve detection rates of target species, particularly for species that are not easily detected by standalone cameras or other survey methods.

5.6 References

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5.7 Supplementary material

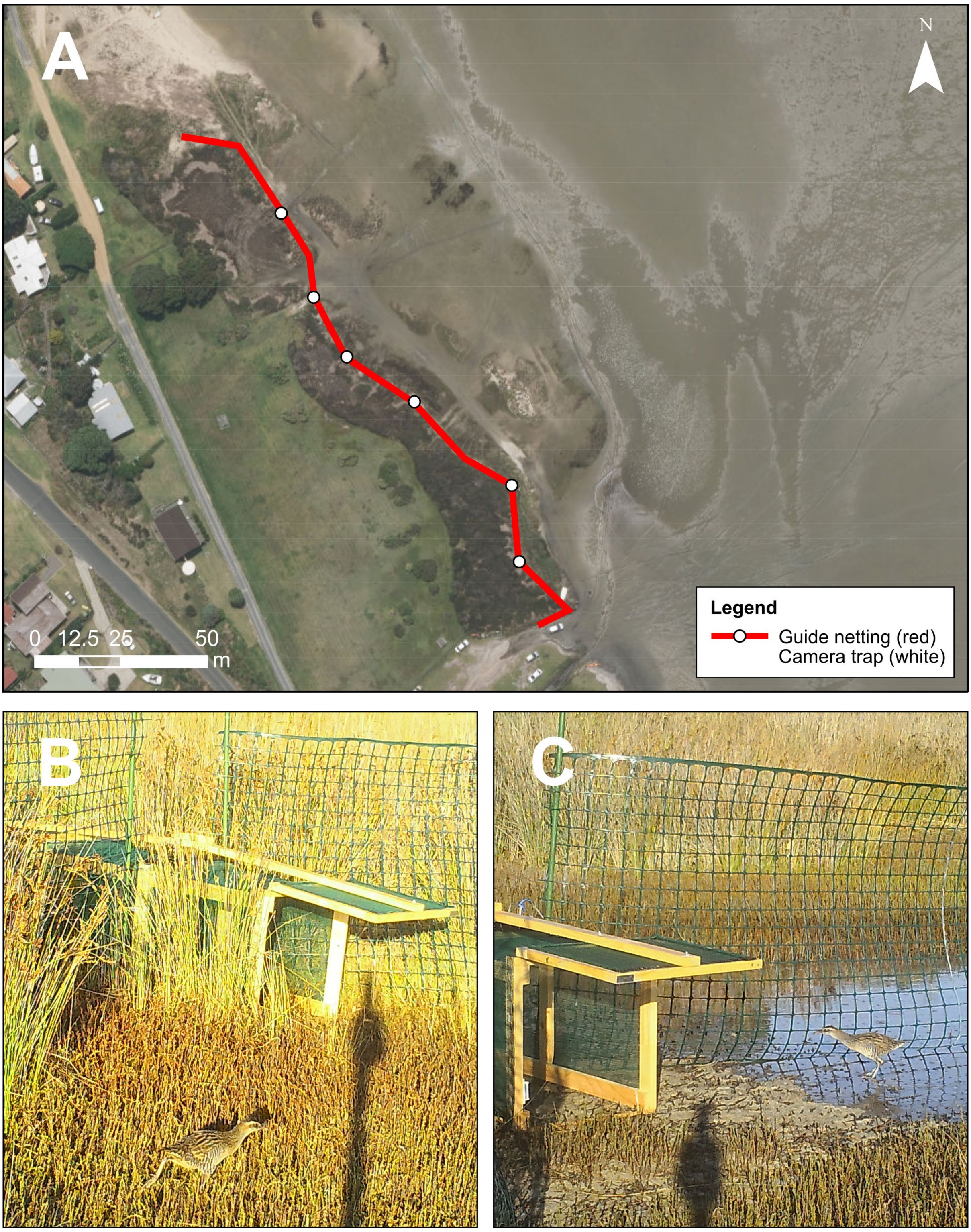

Figure S5.1 A trial of the CDF method for monitoring banded rails in Lincoln Reserve, Mangawhai (Panel A). Drift fences (red lines, Panel A) were built along the interface of saltmarsh habitat and sandflats of Mangawhai estuary. Six camera traps (white circles, Panel A) were installed at 20–40-meter intervals along fence lines to monitor cage traps (or fence gaps where cage traps were not installed). Panels B and C provide examples of resulting images of banded rails captured by camera traps at Lincoln Reserve.

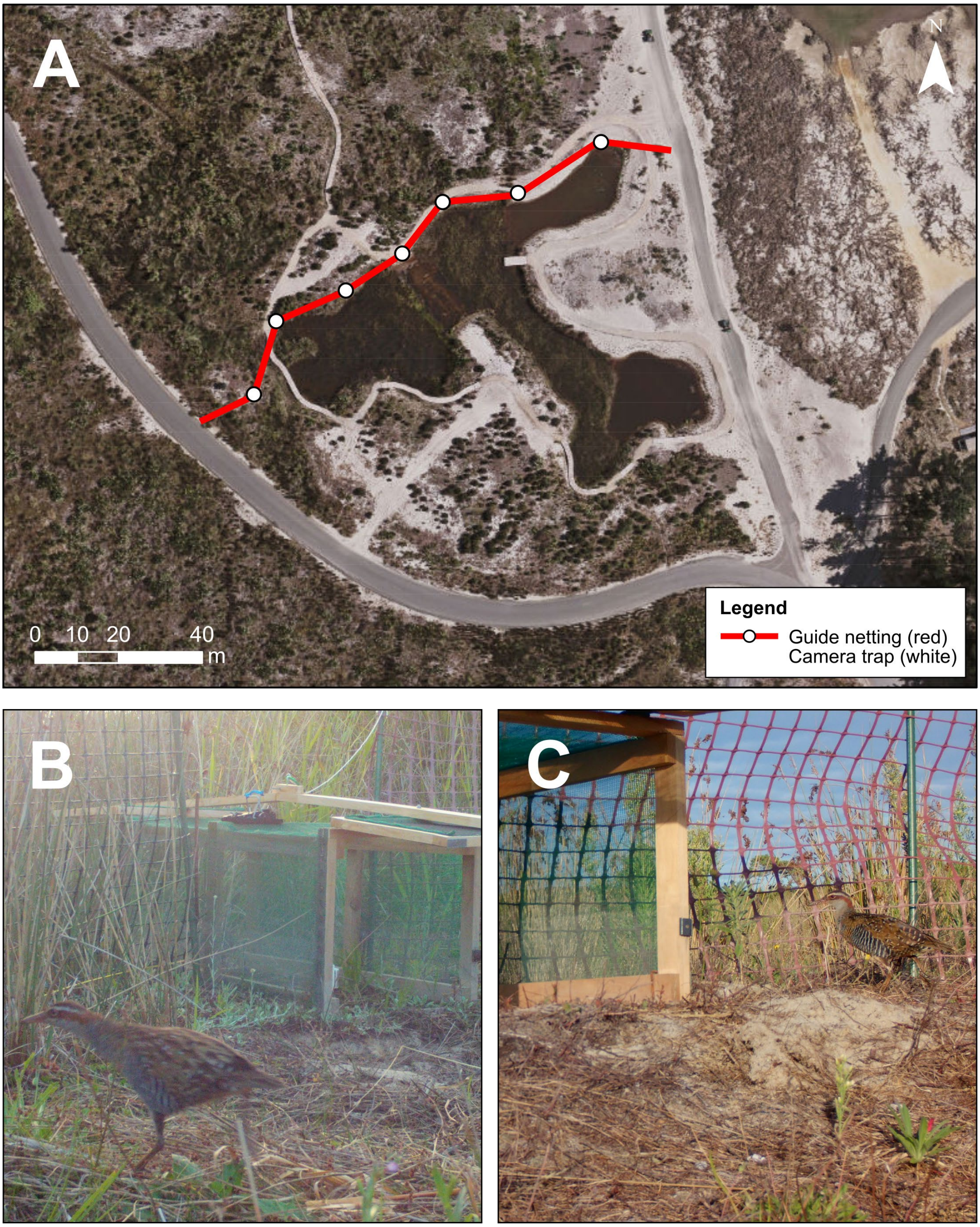

Figure S5.2 A trial of the CDF method for monitoring banded rails in a freshwater wetland at Tara Iti Golf Club, Mangawhai (Panel A). The small wetland (the T-shaped darker area in Panel A) lies within 1.5km of the Mangawhai estuary. Drift fences (red lines, Panel A) were built along the northern edge of the wetland, separating wetland vegetation and terrestrial scrub habitat. Seven camera traps (white circles, Panel A) were installed at 20–30-meter intervals along the fence line to monitor cage traps (or fence gaps where cage traps were not installed). Panels B and C provide examples of resulting images of banded rails captured by camera traps at Tara Iti.

Chapter 5, Statement of Contribution:

MASSEY UNIVERSITY
TE KUNENGA KI PŪREHUROA
UNIVERSITY OF NEW ZEALAND

GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.

Student name:	Jacques de Satge
Name and title of main supervisor:	Associate Professor Weihong Ji
In which chapter is the manuscript/published work?	Chapter 5
What percentage of the manuscript/published work was contributed by the student?	95%

Describe the contribution that the student has made to the manuscript/published work:
Jacques developed the manuscript's design and research questions, sourced the data, analysed the data, and wrote the manuscript in its entirety. Weihong provided guidance in establishing the manuscript's research design and editorial input on the final draft of the manuscript.

Please select one of the following three options:

- ○ The manuscript/published work is published or in press
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- ○ The manuscript is currently under review for publication
  Please provide the name of the journal:
- ◉ It is intended that the manuscript will be published, but it has not yet been submitted to a journal

Student's signature:	Jacques de Satge Digitally signed by Jacques de Satge Date: 2023.03.09 10:39:39 +13'00'	Main supervisor's signature:	Weihong Ji Digitally signed by Weihong Ji Date: 2023.03.08 14:59:08 +13'00'

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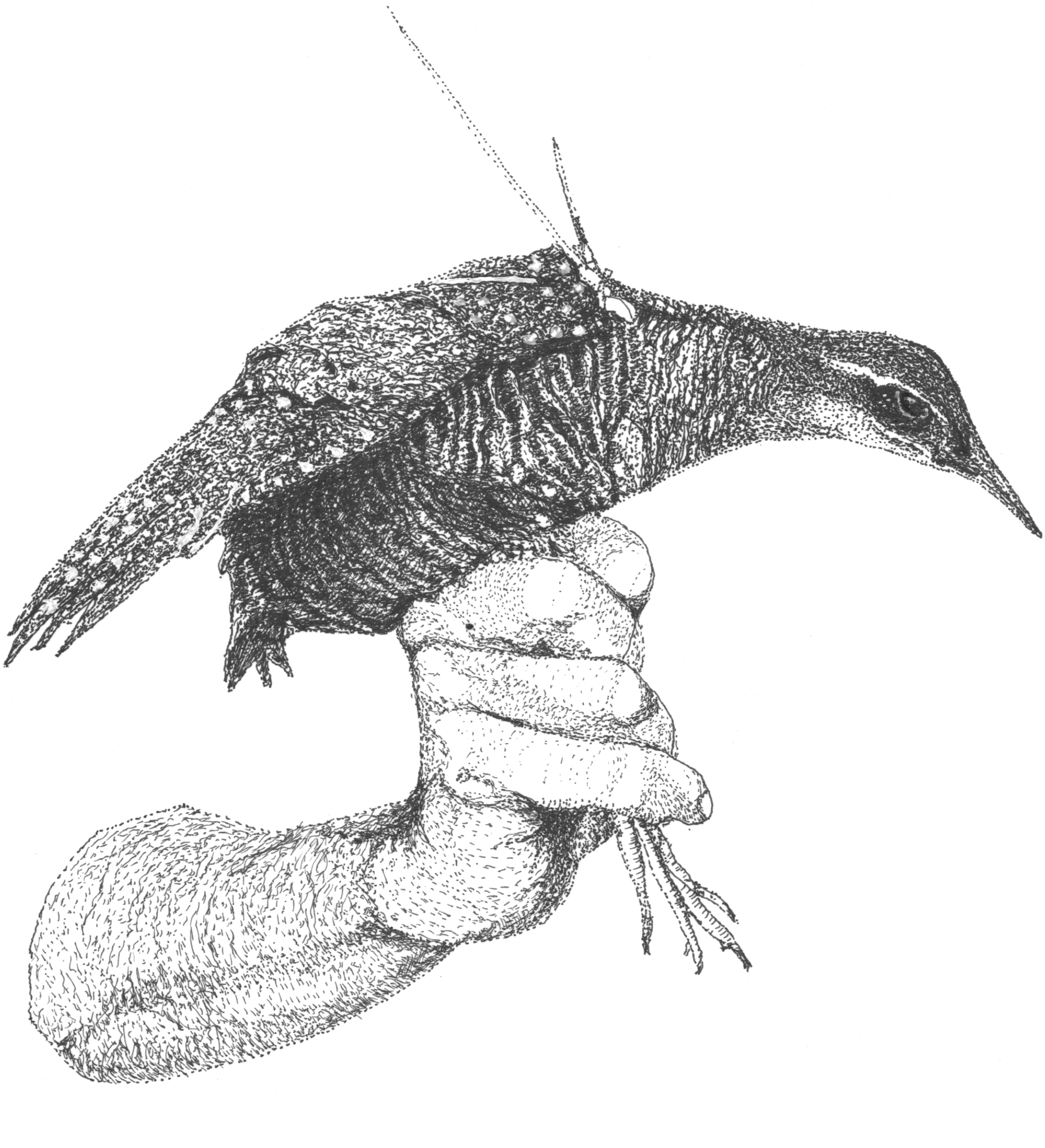
Chapter 6

Habitat selection and use by banded rails: implications for conservation



In this chapter, I assess the home range size, habitat selection, and habitat use patterns of banded rails in saltmarsh-mangrove complexes in northern New Zealand. To inform this assessment, I analyse movement data from six banded rail individuals tagged with GPS transmitters. In so doing, I address the fourth research objective of this thesis:

Objective 4: Quantify banded rail habitat selection and habitat use in saltmarsh-mangrove complexes

Chapter 6 cover image: A banded rail in the hand is worth two in the bush, three if it has a GPS tag attached. Artwork by Rick de Satgé.

6.1 Abstract

Understanding how birds use and select habitats is critical for their effective conservation. The rapid uptake and advancement of biotelemetry technologies in recent decades has transformed scientific understanding of habitat selection and use by birds, enabling the studies of spatial ecology for new species in areas which are poorly accessible to researchers. As is the case for many members of the *Rallidae* family, little is known about the ecology of New Zealand's banded rail *Gallirallus philippensis assimilis*, a concern given its ongoing population decline. The banded rail's distribution in New Zealand overlaps significantly with mangrove forests – a habitat type which is expanding but also subject to removal by regional authorities – yet the role mangroves play in supporting banded rails remains poorly quantified. Addressing this knowledge gap, this study tagged six banded rail individuals with GPS transmitters to evaluate their home ranges, habitat selection, and habitat use in saltmarsh-mangrove complexes in Mangawhai, northern New Zealand. Banded rail home ranges were largely restricted to saltmarsh and mangrove habitats and ranged in size from 2.4 – 5.9 hectares. As informed by Manly selection rations, banded rails generally selected for mangrove and saltmarsh habitats, and avoided mudflats, terrestrial scrub, and residential gardens. Rails' use of mangroves and saltmarsh was correlated with time of day and tide state finding that banded rails primarily used mangroves diurnally to support foraging behaviours, whereas saltmarshes were used nocturnally (as roosting sites) and during high tides. However, individual variation in habitat selection was observed, including observations of two banded rail individuals using mangroves as roosting habitats – a novel observation for this species. Additionally, banded rail habitat use was strongly correlated with temporal and tidal cycles. These findings have serious implications for conservationists, policymakers, and coastal managers in New Zealand – especially given the context of mangrove removals in New Zealand – as they show that banded rails use mangroves more than had been previously understood.

6.2 Introduction

A habitat is, in its simplest form, the place where an organism lives (Odum 1971). Viewed from a 'functional' perspective (Gaillard *et al.* 2010), habitats provide a set of resources – the fundamentals being food, water, and cover (Leopold 1933) – which determine the distribution, density, and productivity of wildlife populations (Pulliam 2000; Morrison *et al.* 2006). Complementing this view, habitats can be understood as 'structural' (Gaillard *et al.* 2010), whereby sets of resources correspond with dominant plant species and community types (Hutto 1985), resulting in the "common-sense resource-based" definition of a habitats as spatially contiguous, homogenous, and physiognomically distinct categories of vegetation communities (Gaillard *et al.* 2010, p. 2256).

The ways animals use and select habitats and the resources they contain are critical to their survival and reproduction (Cody 1981; Block & Brennan 1993; Fischer *et al.* 2018). Importantly, habitat use and selection are distinct concepts within ecological theory (Jones 2001); habitat use is the manner in which a species uses environmental components to meet life requisites (Block & Brennan 1993) whereas habitat selection refers to the innate and learned behaviours which enable an animal to distinguish and select for environmental components to influence survival and fitness (Block & Brennan 1993; Jones 2001; Manly *et al.* 2002). Although habitat use and selection are conceptually distinct, in practice habitat-use patterns are the product of habitat-selection processes (Krausman 1999; Jones 2001).

Habitat selection can be viewed hierarchically, partitioned into four levels by the scale of selection (Johnson 1980): first-order selection takes place at a geographic scale, second-order selection determines the location of home ranges within a landscape, third-order selection is the non-proportional uses of habitat components within the home-range, and fourth order selection is for resources within habitat components (Hall *et al.* 1997; Gaillard *et al.* 2010). Different ecological processes may influence habitat selection by animals at different scales of selection (Cunningham *et al.* 2022). For example, animals may select habitats for the locations of home ranges to optimise resource availability and acquisition (Mitchell & Powell 2004), while habitat structure may influence third- or fourth-order habitat selection (Plumb *et al.* 2019; Cunningham *et al.* 2022; Nugent *et al.* 2022).

In recent decades, scientific understanding of animal habitat selection and use has been transformed and expanded by the uptake of biotelemetry technologies like radiotracking and

Global Positioning Systems (GPS) transmitters in biological research (White & Garrott 1990; Ropert-Coudert & Wilson 2005; Hebblewhite & Haydon 2010; Recio *et al.* 2011; Wilmers *et al.* 2015). These tracking technologies have enabled the study of animals at a variety of spatial and temporal scales (Börger *et al.* 2008; Burger & Shaffer 2008; Laver & Kelly 2008; Li *et al.* 2022), providing researchers with previously unprecedented access to animal movement data (Cooke *et al.* 2004; Rutz & Hays 2009), and allowing animal tracking in remote and poorly accessible areas, irrespective of time or weather conditions, and at high spatial resolutions (Recio *et al.* 2011). Moreover, biotelemetry has enabled the study of a variety of cryptic (i.e., difficult to observe or detect) species (Rutz & Hays 2009; Cagnacci *et al.* 2010), and increasingly lightweight tracker units are expanding this field of study to ever smaller species (Recio *et al.* 2011; Hallworth & Marra 2015; Fijn *et al.* 2017; Pedersen *et al.* 2019). Data derived from animal tracking efforts help inform conservation efforts and wildlife management (Kays *et al.* 2015; Wilmers *et al.* 2015) as data from biotelemetry-based methods can provide detailed ecological information relating to animal behaviour, survivorship, spatial ecology (i.e., the distribution of animals in space and time), energetics, and physiology (Cooke 2008).

As is the case for numerous rallids, New Zealand's banded rail *Gallirallus philippensis assimilis* – a cryptic marsh bird – represents a challenging species to study given its secretive nature and preference for dense and logistically challenging environments (Marchant & Higgins 1993; Taylor & van Perlo 1998; Conway & Gibbs 2005; Heather & Robertson 2005; Colyn *et al.* 2017; Kolts & McRae 2017; Znidersic 2017). However, these hindrances can be overcome using a biotelemetry-based approach to ecological study (Warnock & Takekawa 2003; Cagnacci *et al.* 2010; Recio *et al.* 2011), as demonstrated by several studies that elucidate the spatiotemporal ecology of rallids using data derived from radio-telemetry (e.g., Fox *et al.* 2013; Jedlikowski *et al.* 2016; Seifert *et al.* 2018; Haverland *et al.* 2021). In the case of New Zealand's banded rails, such data are sorely needed to inform effective conservation strategies, given that *G. p. assimilis* populations are declining, they are range restricted, and predicted to be adversely impacted by long-term climate trends (Robertson *et al.* 2021).

Once widely distributed throughout the country in freshwater and coastal wetlands, New Zealand's banded rail population has been dramatically reduced by habitat loss and invasive predators in the early 20th century (Elliott 1983). Recent surveys suggest banded rails are seldom found in freshwater wetlands (Robertson *et al.* 2004; eBird 2022), with an estimate a decade ago suggesting that the saltmarsh-mangrove complexes (SMCs) of northern New Zealand support

80-90% of the remaining banded rail population, while a small population of ca. 200 birds inhabits saltmarshes at the top of the South Island (Bellingham 2013). Given the overlapping distributions of banded rails and saltmarsh-mangrove complexes in the North Island, limited study has sought to determine the role of these estuarine habitats in supporting banded rails. Observations of banded rail behaviour are largely anecdotal as no studies to date have quantified banded rail habitat selection among habitat types in saltmarsh-mangrove complexes, nor delineated home ranges in these environments. Prior to this study, banded rails have never been tracked using biotelemetry-based methods to elucidate their habitat selection or use.

From existing observations of banded rail habitat use (Elliott 1987; Botha 2011; Beauchamp 2022), rush-saltmarsh – typically comprising *Juncus kraussi* and *Apodasmia similis* – is considered to be nesting, roosting, and foraging habitats for banded rails, whereas monotypic mangrove forests, *Avicennia marina*, are considered to be primarily foraging habitats. Although intertidal mudflats frequently abut saltmarsh-mangrove complexes (SMCs) in northern New Zealand, banded rails are thought to avoid open habitats given the threat of aerial predation (Botha 2011; Beauchamp 2015). Existing studies of habitat use have relied on proxy measures of banded rail presence, including calls (Beauchamp 2015) and footprints (Elliott 1983, 1987; Botha 2011), or limited visual observations (Beauchamp 2022).

Ongoing changes to estuaries and coastal regions in northern New Zealand have shone a spotlight on the ecological relationship between banded rails and SMCs and the repercussions for conservation management. Over the 20th century, saltmarsh habitats have become progressively reduced through land reclamations (Beauchamp 2015), whereas mangrove forests have rapidly expanded seawards across intertidal flats in recent decades, fuelled by anthropogenically driven increases in terrigenous sediment in estuaries and along coastlines (Morrisey et al. 2010, Horstman et al. 2018). The increase in mangrove area, and resulting coastal management practices, have driven socio-political debate and policymaker deliberation around the ecological value of intertidal flats and mangrove forests (Morrisey *et al.* 2007; Harty 2009; Lundquist *et al.* 2014) and sparked a rise in legal and illegal mangrove removal in many coastal areas. Mangrove removal is typically considered a restoration tool, used create open habitats and restore cultural, aesthetic, and recreational values associated with these habitats (Harty 2009; Lundquist *et al.* 2014). However, the ecological consequences of this mangrove removal are poorly understood (Stokes *et al.* 2016), particularly for cryptic bird species such as the banded rail.

Knowledge of a species' habitat and space requirements is a prerequisite for informed conservation management, particularly where habitat changes may influence species' decline (Luck 2002; Botero-Delgadillo et al. 2015; Seifert et al. 2018; Li et al. 2022). Thus, in the face of declining saltmarsh habitats, expanding mangrove forests, and ongoing mangrove removal, it is necessary to understand how banded rails make use of saltmarsh-mangrove complexes in New Zealand. Accordingly, the aims of this study were to (1) determine the spatial extent of banded rail home ranges in saltmarsh-mangrove complexes, (2) quantify habitat selection a by banded rails within these complexes, and (3) analyse the influence of local environmental conditions on banded rail habitat use in coastal environments. To realise these aims, I obtained and analysed spatio-temporal data from six GPS-tagged banded rail individuals in two saltmarsh-mangrove sites in Mangawhai, New Zealand.

6.3 Methods

6.3.1 Site selection

I selected four study sites in Mangawhai Harbour, New Zealand (Figure 6.1) with the aim of capturing and GPS-tagging banded rails to evaluate their home ranges and concomitant selection and use of estuarine habitats. Study sites were selected for their accessibility, the existence of established populations of banded rail, and for their habitat composition. Here, habitat was defined structurally, i.e., as distinct categories of vegetation communities (Gaillard *et al.* 2010). Three of the four study sites (Sites A, B, and C) were 'saltmarsh-mangrove sites' comprising both rush-saltmarsh (dominated by *Juncus kraussi* and *Apodasmia similis*) and mangrove forest (*Avicennia marina*), while Site D was a 'saltmarsh-only site' containing rush-saltmarsh but lacking mangroves (Table 6.1). Site D had previously contained a small area (4,500m^2) of mangrove forest, but this was manually removed from the site in 2014 soon before this study began in 2020. In Mangawhai, Site D is the only saltmarsh-only site where banded rails persistently occur year-round and where they have been observed successfully breeding (de Satge, unpublished data).

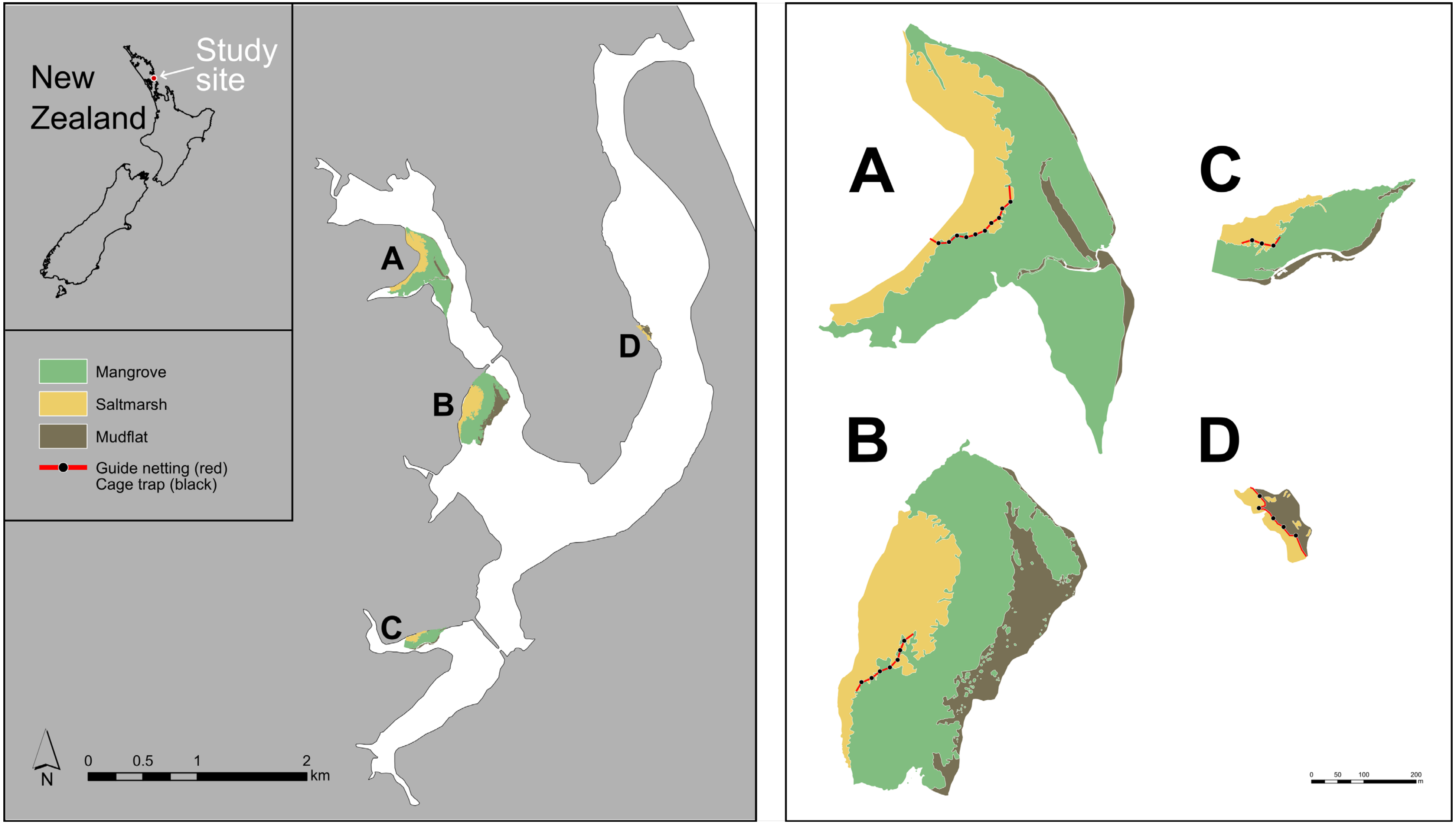


Figure 6.1 *Left panel* - The location of study sites in Mangawhai estuary (shown in white) in northern New Zealand (inset). *Right panel* - Enlargements of each site (A-D) show the position of trap lines (red) and cage traps (black dots) along the mangrove-saltmarsh interface in sites A, B, and C and the saltmarsh-mudflat interface in site D.

Table 6.1 Selected habitat features of study sites in Mangawhai Harbour as well as information on the trapping infrastructure used at each site for banded rail capture

	Site A	Site B		Site C	Site D	*Total*
Habitat features						
Saltmarsh area (m^2)	46,960	46,200		7,870	4,300	*105,330*
Mangrove area (m^2)	133,290	105,230		27,480	0	*266,000*
MSI[1] length (m)	860	510		240	180	*1,790*
Trapping infrastructure						
Year	2021	2020	2021	2020	2021	
Dates in place	19.01-05.02	29.01-21.02	19.03 -04.04	30.01-21.02	19.01-05.02	
Netting length (m)	240	160	240	80	180	*900*
Cage traps	10	7	10	3	5	*35*
Netting : MSI	0.28	0.31	0.47	0.33	1.00	*n/a*
Trap-acclimatisation days[2]	13	20	12	19	13	*77*
Active trapping days[3]	4	3	4	3	4	*18*

[1]The full length of the mangrove-saltmarsh interface (MSI) within a given study site. In site D, this was the mudflat-saltmarsh interface as mangroves were absent
[2]Days where cage traps were locked open (i.e., unset), allowing banded rails to walk through traps without being captured
[3]Days where cage traps were set (i.e., capable of trapping banded rails) and not locked open

6.3.2 Cage trapping and telemetry

To catch banded rails for GPS tagging in 2020 and 2021, I installed drift fences and cage traps along the mangrove-saltmarsh interface in sites A, B, and C, and the saltmarsh-mudflat interface in site D (Figure 6.1; Table 6.1). Drift fences of up to 240 meters were installed in 20–30-meter lengths at each site (Table 6.1), with 0.5-meter gaps left between consecutive lengths of fencing for cage traps. Drift fences were 0.9 meters tall and secured in place with metal poles and weed pins. The mesh size of fences (5 x 5 cm) was small enough to prevent banded rail from passing through the fences, but big enough to allow smaller animals such as fish, crabs, eels, and small birds to pass through. Double-door tripwire cage traps (adapted from Elliott 1983) were installed in each netting gap. The spacing of netting gaps along the fence lines ensured that ≥2 cage traps fell within the anticipated foraging range of a banded rail, as per conservative estimates of banded rail density in intertidal saltmarshes (Elliott 1983). The timing of cage trap installation varied over the two years of the study; in 2020, cage traps were installed ten days after drift fences were erected, whereas in 2021, cage traps and camera traps were installed simultaneously. In both years, cage traps remained open and unset for ≥12 days prior to trapping to acclimatise banded rails to their presence (see Table 6.1: trap acclimatisation period).

Following the trap acclimatisation period, I undertook 3 – 4 days of consecutive trapping at each site, resulting in a total of eighteen days of trapping across all sites (Table 6.1). Traps were set an hour before sunrise until two hours after sunset, but deactivated (i.e., locked open) during a two-hour window around high tide to avoid trapping birds in water. Where logistics allowed, trapping sessions were timed such that high tides fell at or near midday to enable active traps during crepuscular hours when banded rails typically move between saltmarsh and mangrove habitats (Chapter 5). Trap doors were wired to MinkPolice trap monitors to provide real-time alerts of trap triggers, including via SMS, email, and mobile app updates. I responded to alerts within ten minutes of being notified of a trap trigger. When banded rails were trapped, individuals were carefully extracted from cages by guiding them into bird bags. Birds were then carried in their bags to a processing station established on the landward edge of the saltmarsh habitat.

At the processing station, I took morphological measurements – including body weight, tarsus length, bill length, and wing length – and fitted each bird with an E-sized steel leg-band for identification. Blood samples were not taken, in line with animal ethics considerations. I adopted a cautious approach to bird handling to minimise stress, particularly given how little is known about the stress response of banded rails. As a result, birds were not formally sexed. Male and female banded rails cannot be sexed visually, although males are typically larger than females (Elliott 1983; Marchant & Higgins 1993). After being banded, birds were fitted with a Lotek PinPoint VHF 75 SWIFT GPS tag attached with a backpack-style polypropylene harness designed with a cotton weak link (as per Collen *et al.* 2016). Combined, the GPS tag and the harness weighed 7.5 grams and was only fitted to birds where it did not exceed 5% of the individual's body weight (Table 6.2) to avoid artefacts through abnormal behaviour, increased energy demands or reduced manoeuvrability (Fiedler 2009). After being fitted with a GPS tag, birds were placed in a portable aviary and monitored for fifteen minutes to ensure harnesses were fitted correctly. Following a final inspection to check for harness fit, tagged birds were released back into saltmarsh within twenty metres of their capture location.

GPS tags were programmed to start recording location data (i.e., to become 'active' tags) three days after the last day of each trapping session (each session was 3 – 4 days long, Table 6.1), allowing for time to remove trapping infrastructure from field sites and for birds to adjust to harnesses, thereby excluding movement data reflecting fence line locations or initial behavioural changes. This provided birds with a minimum tag adjustment period of 4 – 6 days (Table 6.3), two to four times longer than adjustment periods in comparable tracking studies of other rallids (e.g., Tsao *et al.* 2009; Fox *et al.* 2013; Pickens & King 2013; Kolts & McRae 2017). Birds carried GPS tags for 16 – 30 days between capture and recapture, of which tags were active for 11 days on average (Table 6.3). In both 2020 and 2021, GPS tags were programmed to take SWIFT fixes (see Forrest *et al.* 2022) at twenty-minute intervals from 05:00 – 21:00 daily until tags ran out of battery. In 2021, an additional fix was scheduled for 00:00 to confirm that birds' roosting positions remained consistent overnight. While tags were active, their data were wirelessly downloaded daily using a Lotek Pinpoint VHF Commander linked to a Yagi antenna, a set-up allowing remote download in a range of two-hundred meters. Within two weeks of the last tag running out of battery – battery life of individual tags ranged from 5-14 days (Table 6.3) – I reinstalled the trapping infrastructure to recapture tagged individuals and remove GPS tags and harnesses. Untagged birds captured during recapture sessions were measured and fitted with E-sized steel leg-bands for identification for potential future trapping sessions (Table 6.2) but were not fitted with GPS tags.

Table 6.2 Morphometric data and GPS tagging information of banded rail individuals captured at all study sites in 2020 and 2021.

Bird ID	Date	Site	Age	Weight (g)	Tarsus length (mm)	Wing length (mm)	Bill length (mm)	GPS tagged	Backpack weight (% bodyweight)
E238801	18-Feb-20	B	Adult	164	40.2	wing moult	32.1	Yes	4.7
E238802	18-Feb-20	B	Adult	214	43.6	144	36.4	Yes	3.5
E238803	18-Feb-20	B	Adult	181	41.4	134	35.3	Yes	4.1
E238804	19-Feb-20	B	Adult	209	48.9	149	39.5	No; equipment shortage	n/a
E238805	3-Feb-21	D	Subadult	122	35.0	134	28.0	No; weight limit	n/a
E238806	4-Feb-21	A	Adult	186	40.0	134	32.0	Yes	4.1
E238807	1-Apr-21	B	Adult	160	38.0	109	31.0	Yes	4.6
E238808	1-Apr-21	B	Adult	228	45.0	144	38.0	Yes	3.3
E238809	2-Apr-21	B	Adult	188	43.5	139	34.5	Yes	4.0
E238810	2-Apr-21	B	Adult	143	40.5	130	32.5	No; recapture phase	n/a
E238811	1-May-21	B	Adult	232	43.0	145	39.0	No; recapture phase	n/a
E238812	1-May-21	B	Adult	223	43.0	141	38.2	No; recapture phase	n/a
E238813	1-May-21	B	Adult	175	41.5	139	33.5	No; recapture phase	n/a
			Average±SE	*186.5±9.4*	*41.8±0.9*	*136.8±3.0*	*34.6±1.0*	-	*4.03±0.20*

Table 6.3 A summary of the GPS-tracking information for banded rails which were fitted with a GPS transmitter, including GPS performance (active tag days, total fixes secured, and fix success rate [FSR]), data filtering (based on Vmax and HDOP values), and estimates of home range size, including minimum convex polygon (MCP) and kernel density utilisation distribution (UD) estimates.

					GPS performance			Data filtering				Home range size (ha)			
Bird ID	Site	Date tagged	Total days tagged	Tag adjustment days	Tag active days	Fixes (n)	FSR (%)	Vmax (km/h)	Fixes HDOP>20	Fixes >Vmax	Fixes filtered (%)	MCP (100)	MCP (95)	UD (95)	UD (50)
E238801	B	18-Feb-20	30	6	12	589	97.8	0.188	14	15	4.9	3.01	1.99	2.51	0.46
E238802	B	18-Feb-20	NA[2]	6	11	518	96.1	0.219	14	1	2.9	5.35	4.84	5.82	1.39
E238806	A	4-Feb-21	16	4	12	595	99.2	0.183	8	8	2.7	5.48	4.49	5.90	1.57
E238807	B	1-Apr-21	30	5	14	695	99.3	0.184	7	9	2.3	4.31	2.78	3.05	0.76
E238808	B	1-Apr-21	29	5	5	250	98.0	0.149	5	6	4.4	3.11	1.88	2.78	0.67
E238809	B	2-Apr-21	30	5	14	698	99.7	0.167	4	2	0.9	4.72	2.88	3.47	0.87
E238803[1]	B	18-Feb-20	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Total or *average±SE*			135	32	67	3345	*98.4 ±0.5*	*0.182 ±0.009*	52	41	*3.0 ±0.6*	*4.33 ±0.44*	*3.14 ±0.51*	*3.92 ±0.63*	*0.95 ±0.18*

[1]The GPS tag deployed for bird E239903 suffered a technical failure and did not yield data
[2]Bird E238802 was not recaptured, hence the total days tagged is unknown

Fieldwork in Mangawhai, including banded rail capture, banding, and GPS tagging, was undertaken in accordance with permits granted by the New Zealand Department of Conservation (74169-RES) and the Massey University Animal Ethics Committee (19/04).

6.3.3 Analyses

6.3.3.1 Data filtering

To generate reliable home-range estimates for each individual, I used empirically derived estimates of banded rail movement to filter out unrealistic outlier GPS locations, as per analyses by Forrest (2021) and Shimada *et al.* (2012, 2016). I created a subset of high-accuracy GPS locations by restricting fixes to those obtained by ≥6 satellites and with Horizontal Dilution of Precision (HDOP) values of <20. The average number of satellites is a determinant of fix accuracy (Forrest *et al.* 2022); the more satellites that are used to derive a GPS location, the smaller the average linear errors of that location (Recio *et al.* 2011; Forrest 2021). Although HDOP values correlate poorly with location accuracy (Recio *et al.* 2011; Adams *et al.* 2013; Ironside *et al.* 2017; Forrest *et al.* 2022), high HDOP values (>20) typically indicate low-resolution fixes with high location error (Lewis *et al.* 2007; Fischer *et al.* 2018). Using R package *SDLfilter*, I calculated the maximum speed (Vmax) between successive locations for each individual bird using its respective subset of high-accuracy locations (Table 6.3). The Vmax value for each bird was then used as a filter for locations from any number of satellites; locations with a speed that exceeded Vmax before *and* after the location were excluded (Table 6.3).

6.3.3.2 Home range calculations

A home range is defined as “the area traversed by the individual in its normal activities of food gathering, mating, and caring for young” (Burt 1943). Using the R package *adehabitatHR* (Calenge 2006), I determined the utilisation distribution for each banded rail with a fixed kernel estimator using the ‘href’ smoothing parameter, reporting the 95% kernel density (home range) and the 50% kernel density (core use area) (Tsao *et al.* 2009; Haverland *et al.* 2021). Fixed kernel density is an empirically-informed statistical estimator of home range that accounts for the intensity of use of areas within the home range but excludes areas used minimally (White & Garrott 1990; Haverland *et al.* 2021). In addition, I calculated home ranges for each bird using a 100% and a 95% Minimum Convex Polygon (MCP, Mohr 1947) to aid comparisons with home ranges of other species.

6.3.3.3 Home range comparisons: systematic literature review

For comparative purposes, I conducted a systematic literature review to ascertain the home range sizes of Rallidae species which primarily occur in freshwater and/or coastal wetlands (Ripley 1977; Taylor & van Perlo 1998), including 91 species belonging to genera such as *Hypotaenidia*, *Rallus, Laterallus*, *Aramides*, and *Zapornia* (Table S6.1, Supplementary material). For each species in scope, I searched Web of Science, Google Scholar, and Scopus databases with several search-term combinations, including: ('common name' AND "home range"), ('latin name' AND "home range"), ('common name' AND "habitat use"), ('latin name' AND "habitat use"), ('common name'), and ('latin name'). Literature searches limited to 'common name' or 'latin name' (name-only searches) were only undertaken where other search terms did not yield relevant search results. These name-only searches were manually screened for references to home range or habitat use. In studies that determined home range size, I recorded the home range size in hectares and error in the estimate (where available), the field method used to determine the home range (e.g., radiotelemetry), the statistical estimator of home range (e.g., kernel density), the season the home range was estimated for (breeding season, non-breeding season, or an annual average), and the habitat type occupied by the study species (Table S6.1, Supplementary material).

6.3.3.4 Habitat selection

To analyse habitat selection in banded rails, I determined the habitat availability and use for all individuals GPS-tagged in site B (n=5). Using R package *adehabitatHS* (Calenge 2006), I determined resource selection ratios for banded rails, comparing designs that did not account for variation among individual birds (design I – population level) with a design which did (design II – individual level) (Thomas & Taylor 1990). Both designs assessed 'second-order' habitat selection (Johnson 1980), i.e., selection of the home-range within a landscape, in this instance defined as the boundaries of the study site (as per Seifert *et al.* 2018, see Figure S6.1, Supplementary material).

The resource selection ratio, or Manly selection ratio w_j, was calculated by comparing the use and availability of each habitat class, as defined by:

$$w_j = \frac{u_j}{a_j}$$

where u_j is the proportion of use of the habitat class j and a_j is the proportion of availability of this habitat class (Manly *et al.* 2002; Seifert *et al.* 2018). Habitat selection ratios were significant if their 95% confidence intervals did not include 1; values >1 indicated selection for a given habitat, while values <1 indicated avoidance of a given habitat (Manly *et al.* 2002). To minimise location errors (Forrest *et al.* 2022), habitat use data were subset from the Vmax-filtered data to contain fixes from ≥6 satellites (n = 1,903). For both designs (design I and design II), habitat use data were divided into diurnal (n = 1,427) and nocturnal (n = 476) locations to assess habitat selection for roosting habitats (nocturnal data) and foraging habitat (diurnal data) separately. For diurnal data, I determined six habitat classes of available habitat in study site B – residential areas, terrestrial scrub, saltmarsh, mangrove, mangrove-mudflat interface (MMFI), and mudflat (Figure S6.1, Supplementary material). For nocturnal data, residential areas and mudflats were excluded from the habitat class set as birds were not observed in these habitats at night.

6.3.3.5 Habitat use modelling

To determine whether banded rail habitat use was correlated with temporal and tidal changes within sites A and B, I built a generalised linear mixed effects model (GLMM) using the *lme4* package ver.1.1-29 (Bates *et al.* 2015) in RStudio (RStudio Team 2020). The GLMM used a subset of the Vmax-filtered dataset whereby data were limited to locations with ≥6 satellites (n = 2,341) to minimise location errors (Recio *et al.* 2011; Adams *et al.* 2013; Forrest *et al.* 2022). For reference, a study by Forrest *et al.* (2022) that tested the same Lotek GPS transmitters as used in this study, reported that when six or more satellites were used as a threshold, half of GPS locations were within 5 metres of the true location, and ninety-five percent of GPS locations were within 19 metres.

I defined the GLMM's response variable 'habitat' as a binomial term reflecting the habitat location of each GPS location, defined as either 'terrestrial' or 'mangrove'. To spatially assign GPS locations to their corresponding habitats, I mapped habitat polygons to temporally matched satellite imagery of study sites in ArcGIS, manually delineating polygons corresponding to residential gardens, terrestrial scrub vegetation, rush-saltmarsh, mangroves, the mangrove-mudflat interface (MMFI) and mudflats (see Figure S6.2, Supplementary material, for habitat definitions). Using R-package *sf* (version 1.0-8), GPS locations in mangroves and MMFI habitat polygons were classed as 'mangrove' locations, while locations in terrestrial scrub and rush-saltmarsh polygons were classed as 'terrestrial' locations. Among all GPS locations in the GLMM dataset, no locations were observed in mudflat habitats or residential gardens.

In the GLMM, the binomial response variable ‘habitat’ was regressed against explanatory variables ‘time of day’ (TD), ‘relative tide’ (RT), ‘tide height’ (TH), the interaction between TD and TH, the interaction between RT and TH, and a random effect ‘Bird ID’ (the band number of each GPS-tagged bird). Time of day (TD) was defined as a factor variable with two levels: ‘day’ and ‘night’. Day was defined as the time from thirty minutes before sunrise to thirty minutes after sunset (i.e., the period when solar irradiance is clearly visible [Spitschan *et al.* 2016]), and night as the inverse period of time. Relative tide (RT) was a temporal measure of the tidal cycle, defined as the absolute time, in hours, to the closest high tide. Tide height (TD) was defined as a continuous variable comprising the average daily height of high tide in meters, reflecting a range of tidal heights (2.2 – 2.7 meters) over the course of the study.

The GLMM did not control for inter-annual variation; GPS data were captured within the same temporal window (post breeding season) in consecutive years, and I did not expect differences in habitat use behaviour among years. The GLMM was fitted by restricted maximum likelihood estimation and specified with a binomial distribution. I tested for model misspecification by examining scaled residuals in quantile–quantile plots and histograms (Zuur *et al.* 2009) using package DHARMa ver. 0.3.3.0 (Hartig 2020).

6.4 Results

6.4.1 Banded rail trapping

In total, I caught, measured, and ringed thirteen banded rails across three of the four study sites during trapping efforts in Mangawhai in early 2020 and 2021 (Table 6.2). On average, banded rails weighed 186.5 ± 9.4 grams, with a tarsus length of 41.8 ± 0.9 millimetres, wing length of 136.8 ± 3.0 millimetres, and bill length of 34.6 ± 1.0 millimetres (Table 6.2).

Of the thirteen banded rails caught, seven were fitted with a GPS tag, but only six of the seven tags successfully captured location data (Table 6.3). The remaining six untagged individuals were either captured during the recapture phase of fieldwork when tags were not being fitted, exceeded the 5% ratio for bodyweight to tag weight, or were not tagged due to equipment shortages. For birds fitted with GPS tags, tag weight ranged from 3.3% to 4.7% of banded rail body weight (Table 6.2). Of the six tagged birds, five were caught (and subsequently tracked) in Site B and one was caught and tracked in Site A, both saltmarsh-mangrove sites. Although a bird was captured and measured in Site D, the sole saltmarsh-only site in the study area, the bird did not meet the bodyweight threshold to be fitted with a GPS tag (Table 6.2). Thus, I could unfortunately not compare banded rail habitat use in saltmarsh-mangrove and saltmarsh-only sites.

6.4.2 GPS collection and filtering

Data collection from GPS tags ranged from 5 to 14 days (mean = 11 ± 1.33 SE), excluding a GPS tag that failed to record any locations (Table 6.3). On average, each GPS tag collected 558 fixes with fix success rates remaining consistently high for all tags (range: 96.1 - 99.7%). This resulted in a total of 3,345 successful location fixes for all tagged banded rails (Table 6.3). From nocturnal fix data, roosting locations for all birds remained consistent each night, with 21:00, 00:00, and 05:00 fixes falling within the expected linear error range (0-19 meters) for consecutive static fixes (Forrest 2021).

The Vmax from 6 or more satellites ranged from 0.149 to 0.219 km/h among individual banded rail, with an average speed of 0.182 ± 0.01 km/h. Using Vmax as a filter removed 41 fixes (1.2%) from the dataset, in addition to the 52 fixes (1.6%) excluded because they exceeded the threshold HDOP value of 20 (Table 6.3).

6.4.3 Home range estimates and comparisons

Individual home range sizes among banded rails (n = 6) ranged from 2.51 hectares to 5.90 hectares, as calculated by the 95% kernel density (Table 6.3). Core use areas – as calculated by the 50% kernel density – largely comprised areas of mangrove and/or saltmarsh habitat for all tagged birds (Figure 6.2a-c) and ranged in size from 0.46 – 1.57 hectares. Banded rail home range size was positively correlated with body weight (Figure S6.2, Supplementary material).

When reviewing the literature pertaining to home range sizes of 91 species of Rallidae, I identified research articles that quantified home range sizes for 14 species (Table S6.1, Supplementary material). Most home range estimates for rallids were derived from radiotelemetry data using a 95% kernel density method (Table S6.1, Supplementary material). Estimates were primarily determined during the breeding season (n=11), while just two species were observed during both the breeding season and the non-breeding season. This study was the only study among those identified to use GPS tags rather than radio transmitters to track birds. Among rail species for which home range estimates were available, home range size appears to be positively correlated with body weight (Figure 6.3). Relative to other species of

Rallidae, banded rails have slightly larger home ranges relative to their own bodyweight than expected (Figure 6.3), although banded rail home range size is comparable to estimates of similarly sized rails such as *Pardirallus sanguinolentus*.

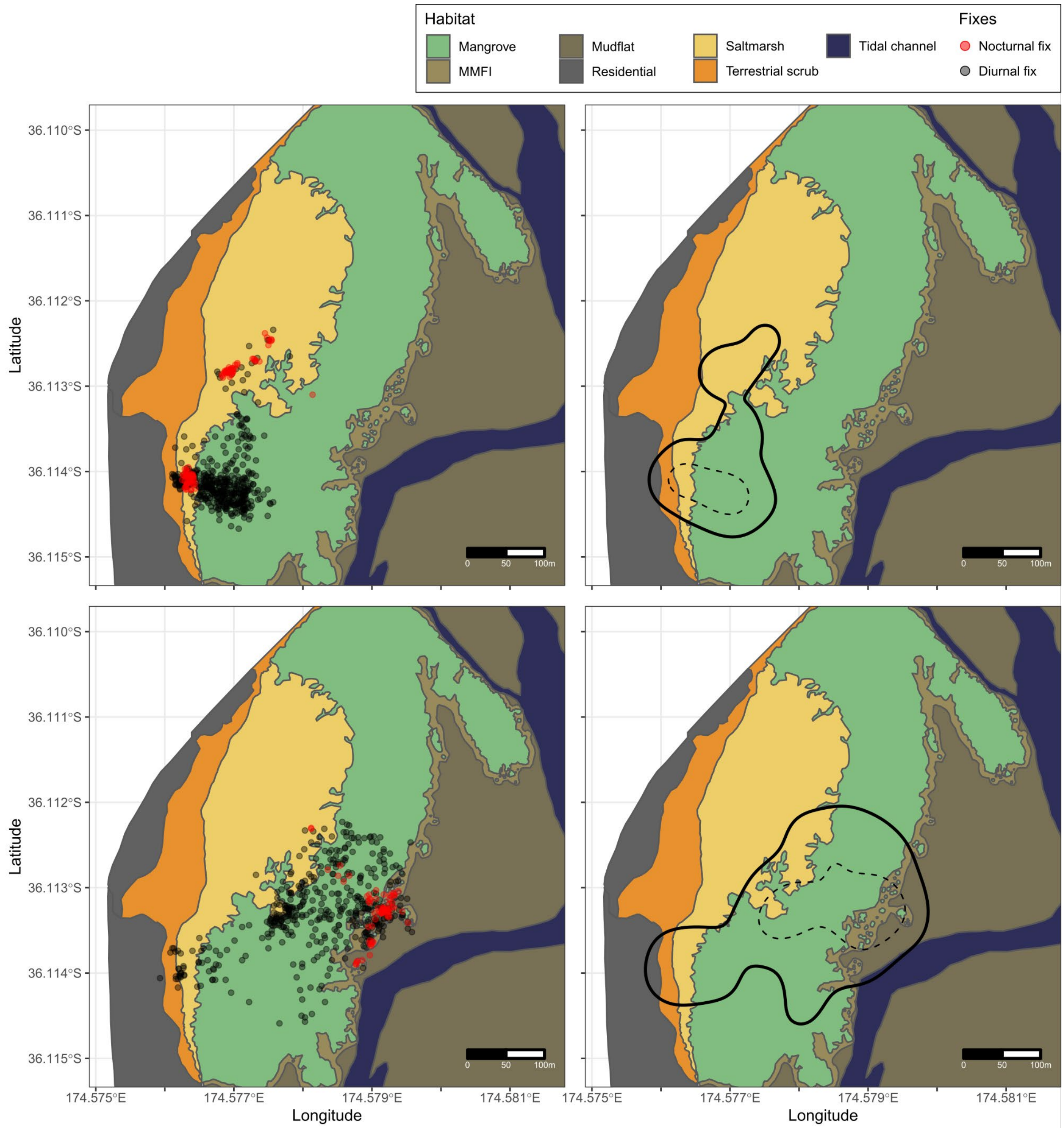


Figure 6.2a GPS fix locations (left column) and concomitant utilisation distributions (right column) for two banded rails (E238801 – top row; E238802 – bottom row) tracked using GPS transmitters in February 2020 in study site B, Mangawhai estuary. Utilisation distributions (right column) were calculated by kernel density estimated and are illustrated by the 50th (dashed line) and 95th (solid line) isopleths, corresponding to birds' core and home ranges. GPS fixes are coloured by temporal period; red dots are nocturnal fixes, while black dots are diurnal fixes.

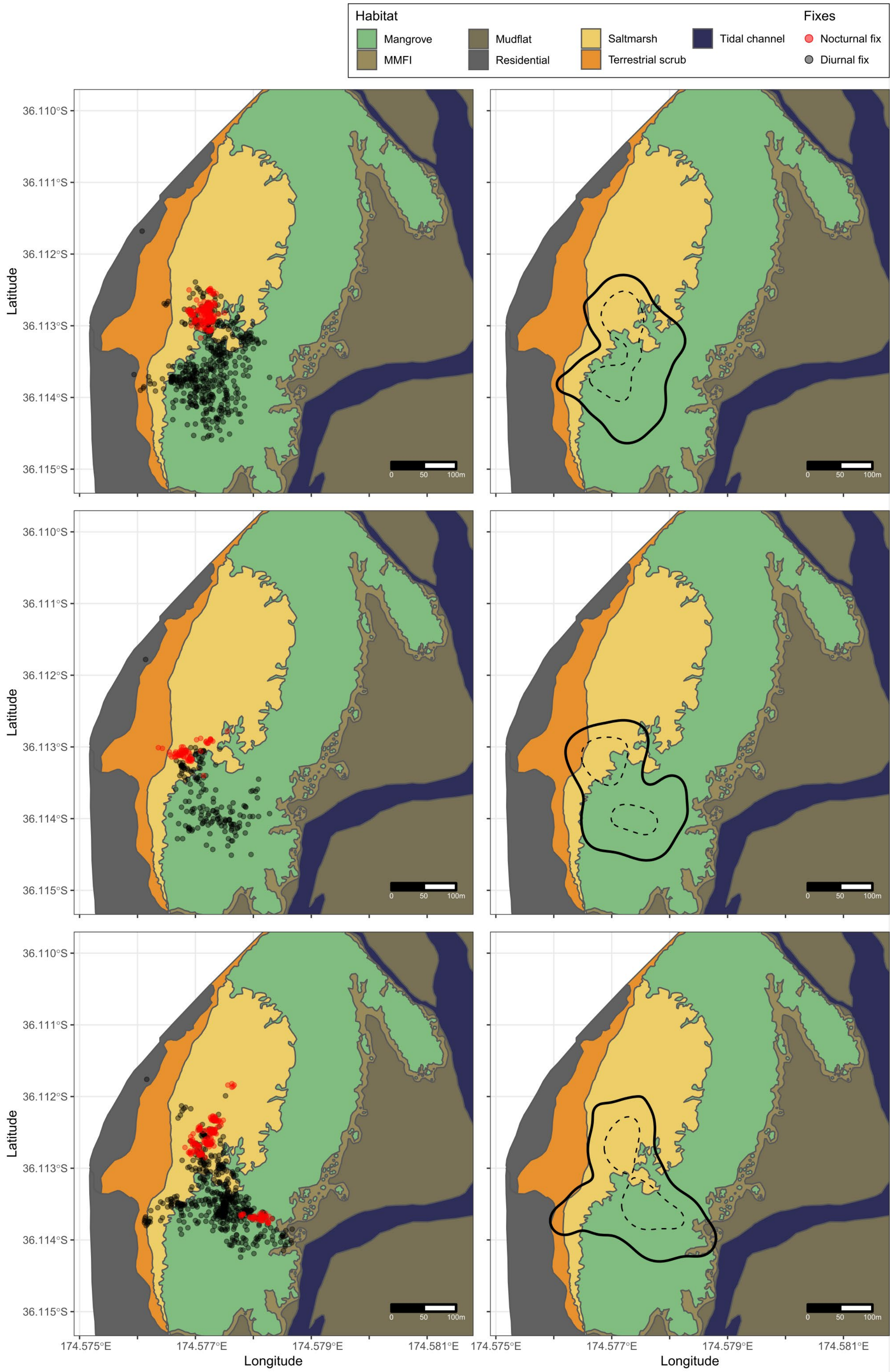


Figure 6.2b GPS fix locations (left column) and concomitant utilisation distributions (right column) for three banded rails (E238807 – top row; E238808 – middle row; E238809 – bottom row) tracked using GPS transmitters in April 2021 in study site B, Mangawhai estuary.

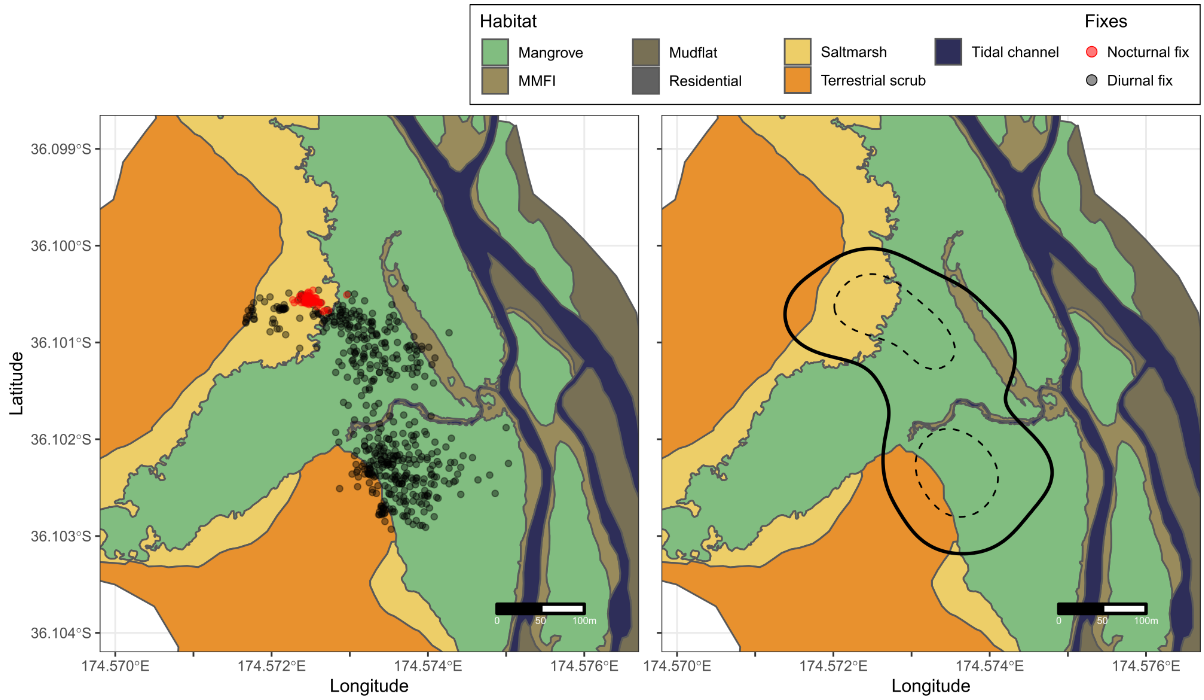


Figure 2c GPS fix locations (left panel) and concomitant utilisation distributions (right panel) for banded rail E238806 tracked using a GPS transmitter in April 2021 in study site A, Mangawhai estuary.

6.4.4 Habitat selection

I observed strong evidence of resource selection by banded rails for both design I (χ^2 = 1,306.3, df = 5, $p < 0.001$) and design II ($\chi^2 = 204.9$, df = 20, $p < 0.001$) analyses of resource selection during diurnal hours. During the day, banded rails in Site B used mangroves significantly more than expected based on their availability, while avoiding terrestrial scrub, mudflat, and residential habitats (Figure 6.4). In design I analysis, where individual variation was not considered, banded rails used saltmarsh significantly more than expected based on availability (Figure 6.4a) and avoided selection of MMFI habitats. The direction of the selection ratios from design II is the same as that from design I, but variation among individuals increases the confidence intervals in design II making some selection ratios non-significant (Figure 6.4b).

In addition, I observed strong evidence of resource selection for both design I (χ^2 = 692.6, df = 3, $p <$ 000.1) and design II (χ^2 = 299.5, df = 12, $p <$ 000.1) analyses of selection during nocturnal hours. At night, banded rails used saltmarsh significantly more than expected based on availability, while mangroves and terrestrial scrub were avoided – a set of observations consistent to both design I and design II analyses (Figure 6.5). MMFI habitats were generally avoided at night (Figure 6.5a), although the positive selection of this habitat by bird E238802 resulted in substantial variation in global selection ratios (Figure 6.5b).

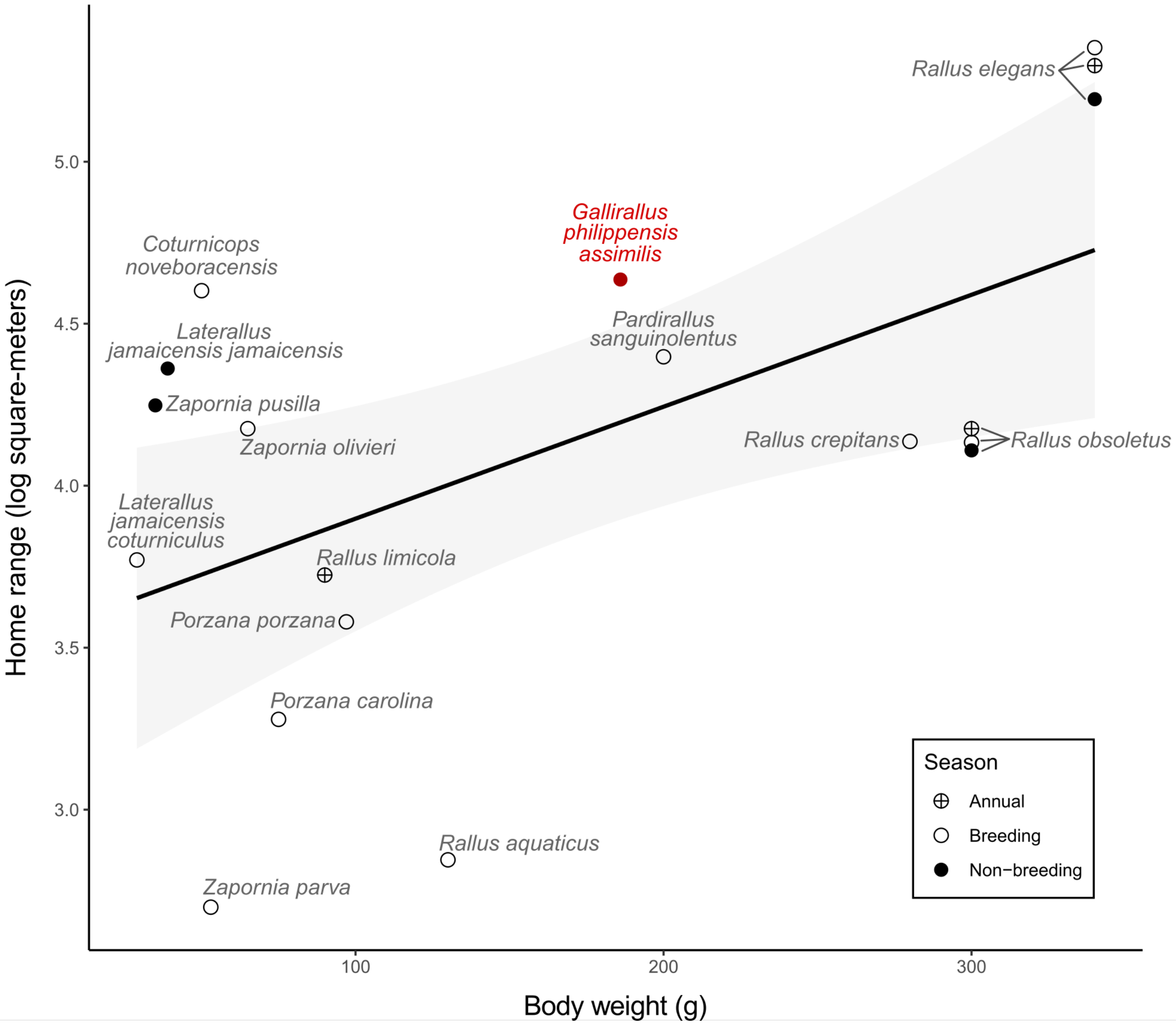


Figure 6.3 The relationship between log-transformed home range sizes and the average body weight of various species of Rallidae. Home range estimates (circles) also indicate seasonality; filled circles are estimates derived during the non-breeding season, empty circles during the breeding season, and crossed circles represent the annual home range of species. The subject of this study, *G. p. assimilis*, is indicated in red

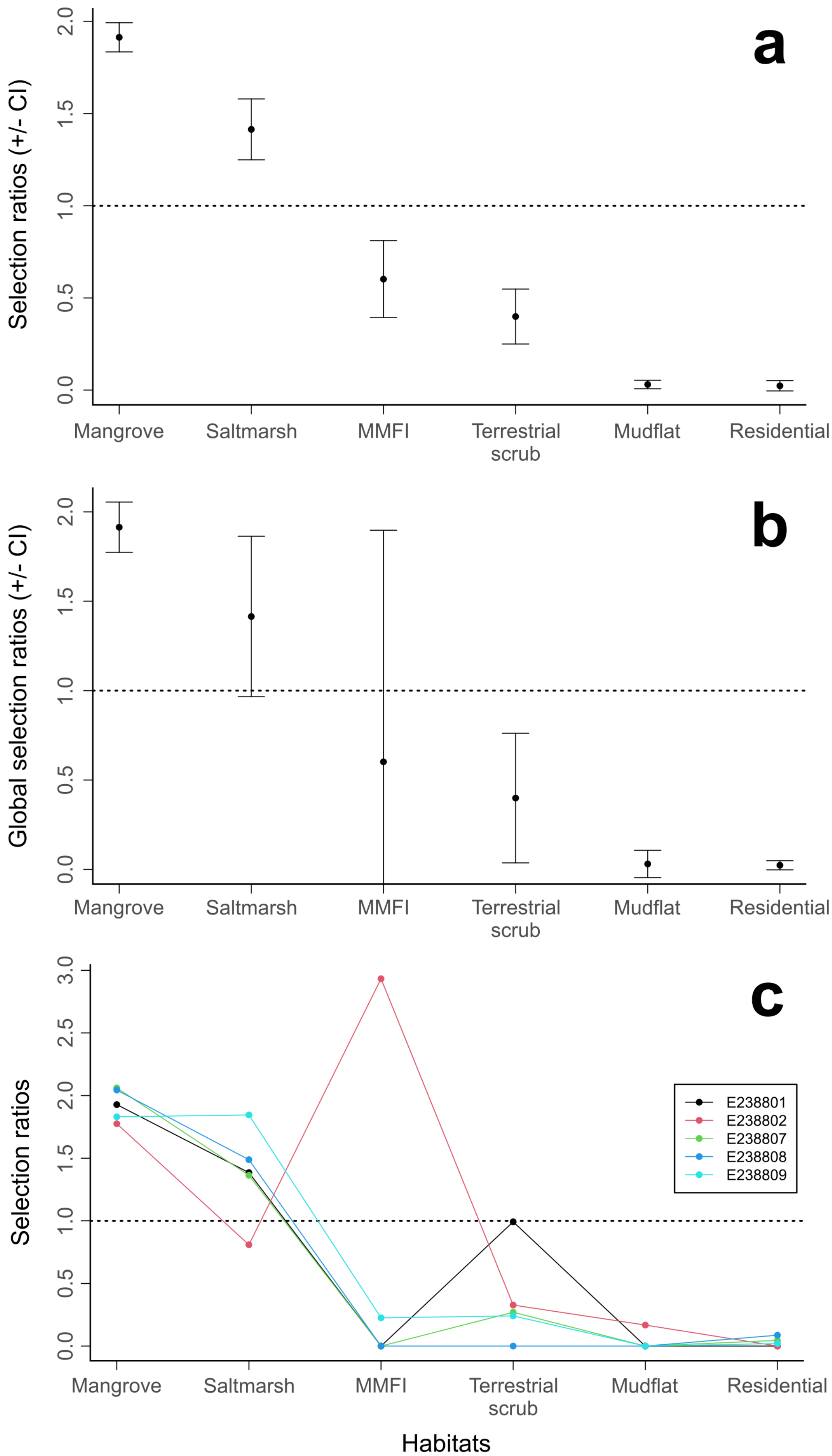


Figure 6.4 Manly selection ratios (+- SE) for design I (a) and design II (b, c) for five banded rails tracked via GPS transmitters in study site B, limited to GPS locations captured during the day (i.e., during daily activities, such as foraging). Ratios are significant if their 95% confidence intervals do not include 1 (indicate by bold dashed line); values >1 indicate selection, value <1 indicate avoidance. Panel C indicates selection ratios for each bird, as indicated by band ID numbers.

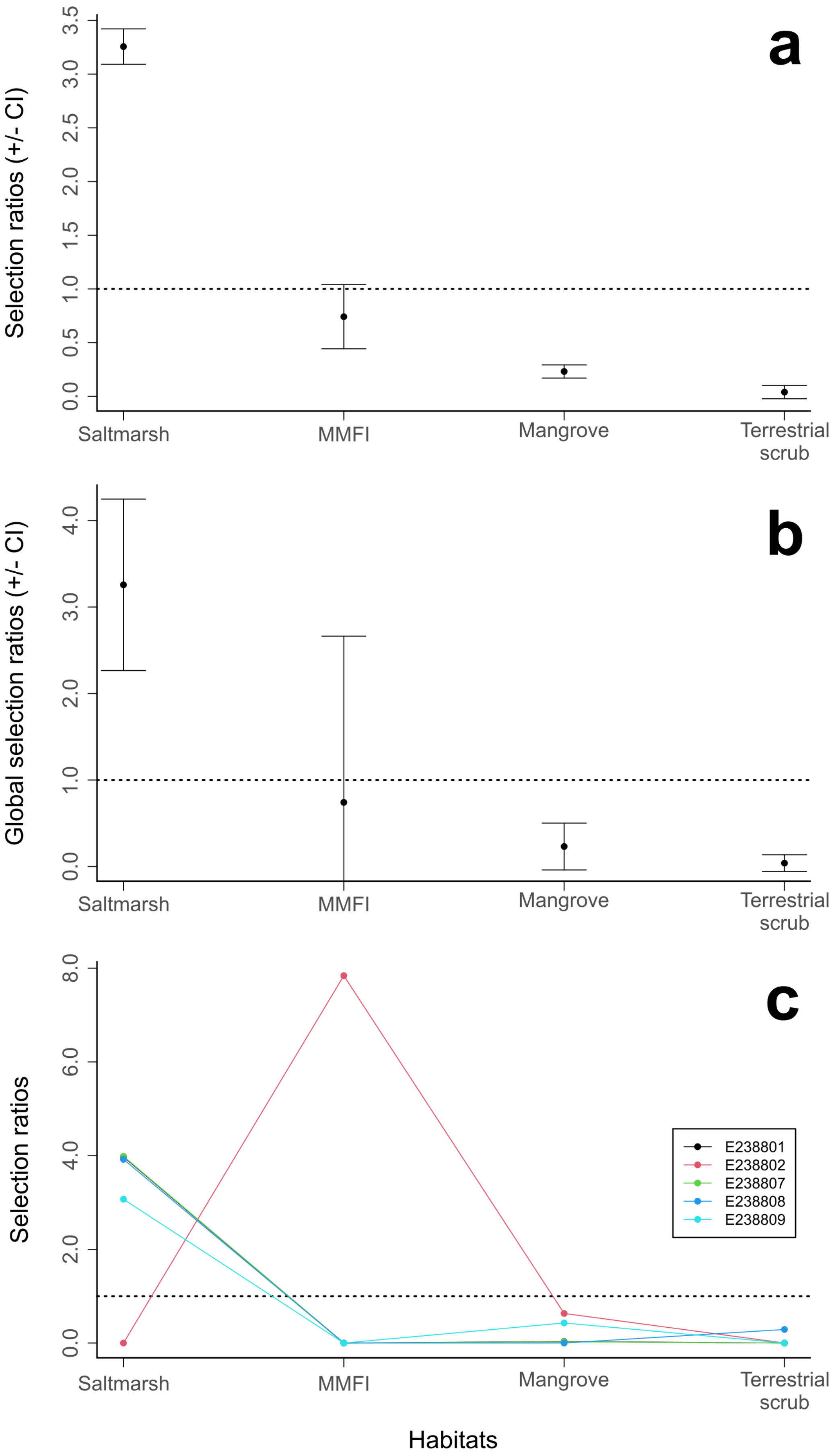


Figure 6.5 Manly selection ratios (+- SE) for Design I (a) and Design II (b, c) for five banded rails tracked via GPS transmitters at study site B, limited to GPS locations captured at night (i.e., during nightly roosting). Ratios are significant if their 95% confidence intervals do not include 1 (indicate by bold dashed line); values >1 indicate selection, value <1 indicate avoidance. Panel C indicates selection ratios for each bird, as indicated by band ID numbers.

6.4.5 Habitat use

Changes in banded rail habitat use were strongly correlated with temporal and tidal changes (Table 6.4). Time of day – a binomial coefficient expressing times ‘day’ or ‘night’ – explained significant variation in habitat use, as did the interaction between time of day and the relative tide (Table 6.4). During the day, the likelihood of banded rails using terrestrial habitats (saltmarsh and scrub) increased significantly with decreasing time to high tide (Figure 6.6). By contrast, habitat use remained consistent at night; banded rails typically remained in saltmarsh habitats overnight, irrespective of the relative tide time (Figure 6.6). However, patterns of habitat use varied among individuals (Figure 6.7). For example, Bird E238802 roosted exclusively in mangroves, in contrast with other tagged birds who either exclusively or primarily roosted in rush-saltmarsh (Figure 6.7). During the day, tagged banded rails behaved consistently in spending most of their time in mangrove habitats (Figure 6.7). Again, Bird E238802 was slightly different from its counterparts, spending notable amounts of time along the seaward edge of mangroves forests.

The relative tide – expressed as an absolute measure of the time to high tide – explained significant variation in habitat use (Table 6.4), and its relationship with habitat use was mediated by tide height. During larger high tides (defined by tide height), banded rails were significantly more likely to be in saltmarsh habitats than in mangrove forests, whereas the inverse was true during smaller tides.

Table 6.4 Model estimates and analysis of variance (Type II Wald) for fixed effects time of day, relative tide, tide height, and interaction terms for GLMM model of habitat use.

Explanatory variables	Estimate ± SE	Analysis of variance		
		df	χ^2	p
Intercept	-18.44 ± 2.20	-	-	-
Time of day (night)	1.47 ± 0.26	1	401.48	**<0.001**
Relative tide	4.93 ± 0.60	1	81.00	**<0.001**
Tide height	7.40 ± 0.87	1	3.07	0.080
Relative tide × Tide height	-2.16 ± 0.24	1	77.40	**<0.001**
Time of day × Relative tide	0.43 ± 0.08	1	30.91	**<0.001**

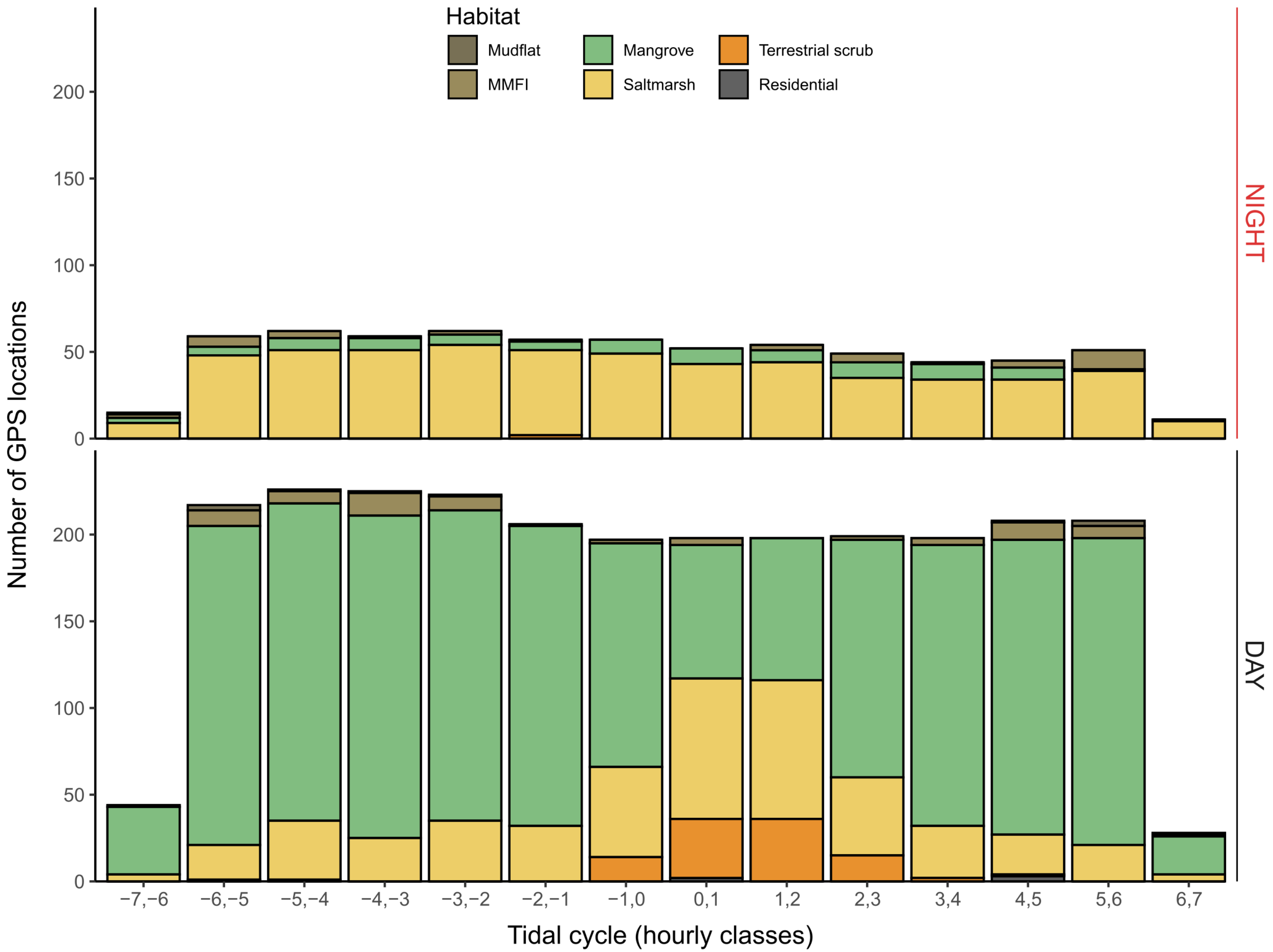


Figure 6.6 Banded rail habitat locations during the day (bottom panel) and at night (top panel) relative to the tidal cycle, expressed as hour-long intervals between consecutive low tides (-6.3 hours to +6.3 hours). Accordingly, high tide is represented by zero along the x-axis. Bars for each temporal interval show the habitat types used by all banded rails during that hour, expressed proportionately.

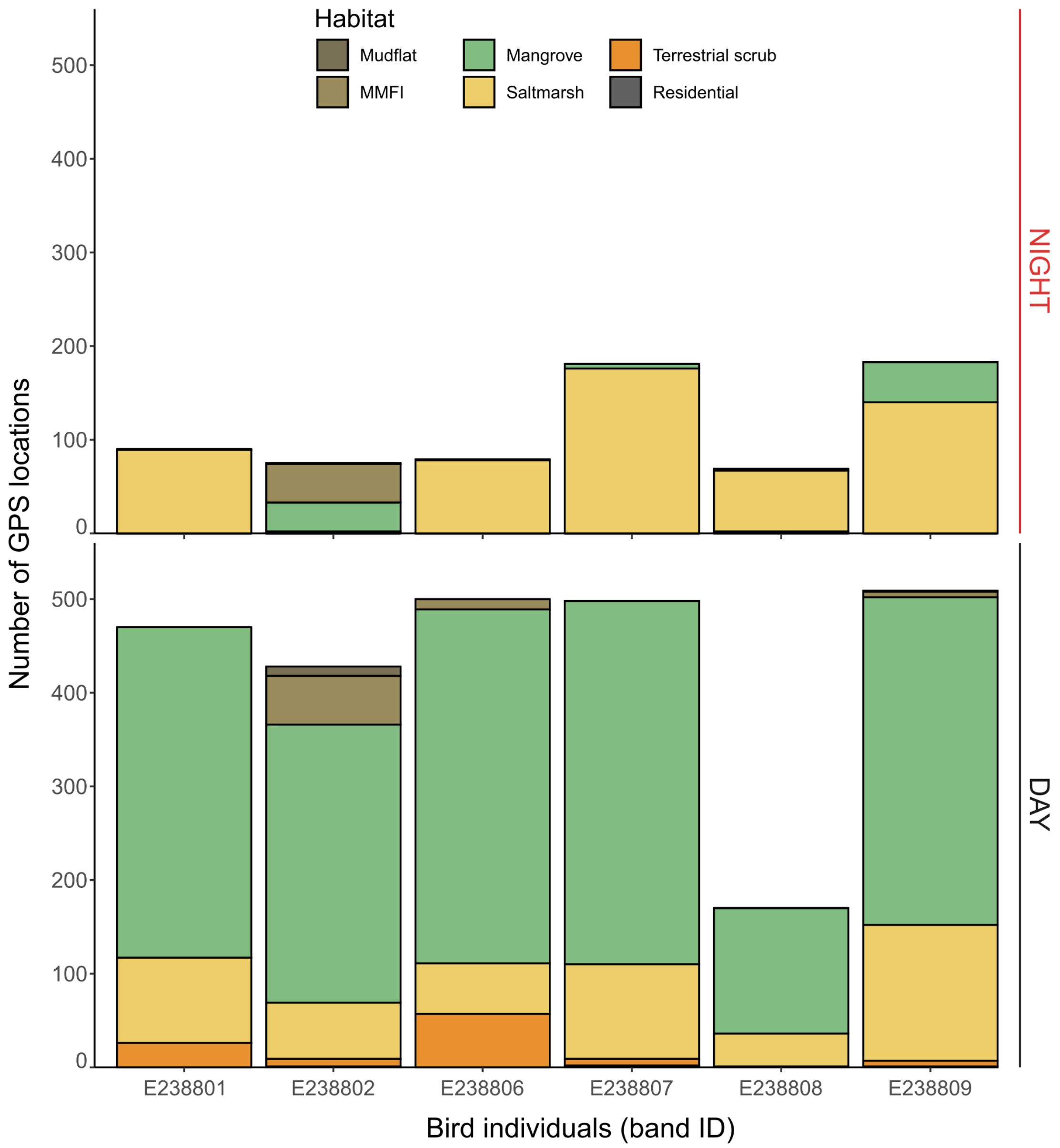


Figure 6.7 Proportional habitat use by six GPS-tagged banded rail individuals in Mangawhai estuary, as determined by habitat-matched fix locations during the day (bottom panel) and at night (top panel).

6.5 Discussion

To better understand the ecology of banded rails in mangrove ecosystems, I used data from GPS-tagged banded rails to quantify their home range sizes and habitat selection and use in saltmarsh-mangrove complexes in northern New Zealand. Within an estuary in Mangawhai Harbour, banded rails were largely confined to saltmarsh and mangrove habitats, with home ranges ranging in size from 2.41 – 5.90 hectares among individuals. Within a single saltmarsh-mangrove complex, banded rails selected for mangrove and saltmarsh habitats and generally avoided mudflats, terrestrial scrub, and residential areas. Habitat use of mangrove and saltmarsh was correlated with time of day and tide state; banded rails primarily used mangroves diurnally, whereas saltmarshes were used nocturnally and during high tides. However, individual variation in habitat use was also observed.

6.5.1 Home range

This study is the first to provide estimates of *G. philippensis* home range sizes, both in New Zealand as well as throughout the species' distribution in Oceania and the Indo-Pacific. In saltmarsh-mangrove complexes, banded rail home ranges were 3.92 ± 0.63 hectares on average and varied in size among individuals, with the largest home range more than double the area of the smallest (range: 2.51 – 5.9 ha; Table 6.3). Existing research suggests that variation in animal home range sizes can be attributed to several factors (Seifert *et al.* 2018), both internal and external (Rühmann *et al.* 2019). Internal factors include age, sex, and body condition (Seifert *et al.* 2018; Rühmann *et al.* 2019), while external factors include resource availability, seasonality, latitude (climate), local weather, competition, predation risk, social organisation, population density, habitat structure and quality, and human disturbance (Mcloughlin & Ferguson 2000; Haskell *et al.* 2002; Rolando 2002; Morellet *et al.* 2013; Kolts & McRae 2017).

In this study interpretation of banded rail home range estimates is constrained by limited knowledge and study of the internal and external factors that affect home range size. With respect to internal factors, this study observed banded rail home range size to be positively correlated with body weight (Figure S6.2, Supplementary material) but did not determine the age or sex of tagged individuals. Similarly, external factors were not explicitly measured, although seasonality, latitude, or habitat structure are not expected to drive inter-individual variation as these factors were kept consistent within the study design. Contrarily, variation in home range sizes among tagged individuals might be explained by the effects of weather, predation, competition, population density, and inter-annual variation in resource availability; however, these factors were not measured as they were beyond the scope of this study. Moreover, the short timeframe used to determine home ranges may have emphasised the influence of short-term effects on home range (e.g., heavy rainfall or seasonal food availability) and concurrently excluded longer-term effects such as seasonality or reproductive behaviours that may influence home range shape and size (Kolts & McRae 2017).

The home range areas estimated by this study can be contrasted with range size estimates for banded rails in saltmarsh environments of the South Island (Elliott 1983). In this study, situated in the saltmarsh-mangrove complexes of Mangawhai Harbour, I estimated banded rail home ranges to be 3.92 ± 0.63 hectares on average. By comparison, in the Nelson Bays region of New Zealand, Elliott (1983) observed banded rails using patches saltmarsh which seldom exceeded two hectares. Although Elliott did not measure home range size explicitly (in fact, he measured density, estimating 1.29 breeding pairs per 1.29 hectare of saltmarsh), his observations suggest that banded rail home ranges sizes in Mangawhai SMCs (this study) are notably larger than those of banded rails in Nelson saltmarshes. The apparent discrepancy in these estimates may be driven by the density of animals or the make-up of available resources in respective study sites (Pickens & King 2013). For example, Elliott's (1983) study sites in the South Island lack mangroves; thus, smaller banded rail home range sizes may reflect the limited availability of suitable intertidal vegetation (Tsao *et al.* 2009). Alternately, saltmarsh sites in the South Island may be more resource rich than the saltmarsh-mangrove complexes of this study, given home range size often negatively correlates with resource abundance (Kolts & McRae 2017; Seifert *et al.* 2018).

Notably, there is significant variation in home range size estimates of different species of Rallidae. Although home range size generally increases with body weight among rallids (Figure 6.3), several species buck this trend. For example, *Zapornia parva* and *Coturnicops noveboracensis*, are similarly sized rails weighing <50 grams, yet are estimated to have average home range sizes of 1.8 and 4.0 hectares respectively. Similarly inconsistent, this study's estimates of banded rail home range size were some 1.5 hectares larger than estimates for *Rallus obsoletus*, despite banded rails being more than 100 grams lighter than *R. obsoletus*. While much of this variation may be explained by internal and external factors that affect home range size (Rühmann *et al.* 2019), differences in the statistical estimators used to calculate home range size may explain further variation (Table S6.1, Supplementary material). In the context of other

Rallidae home range estimates (Figure 6.3), estimates from this study suggest banded rails have a larger home range size than expected for their body weight, although this may simply reflect the method and timing of home range estimation. Alternately, this finding could indicate that the density of food resources within mangrove habitats of Mangawhai is relatively low, meaning banded rails must maintain larger home ranges to ensure adequate resources. However, without comparing banded rail home ranges among multiple sites and over different temporal periods, these assertions remain hypothetical.

6.5.2 Habitat selection

While studies have documented banded rails in mangrove and saltmarsh habitats in estuarine environments (Elliott 1983, 1987; Parker & Brunton 2004; Botha 2011; Beauchamp 2015, 2022), this study is the first to determine how banded rails select for these different habitats. Additionally, this study partitions this selection into diurnal and nocturnal periods. Analyses of habitat selection at a population level (design I) established that banded rails select for both mangrove and saltmarsh habitats during diurnal hours and for saltmarsh habitat only during nocturnal hours, but avoid mudflats, terrestrial scrub, and residential gardens during both periods. During nocturnal hours, banded rails typically avoided mangroves and the mangrove-mudflat interface (MMFI).

Notably, habitat selection ratios that accounted for differences among individuals (design II) showed a similar pattern of banded rail habitat choice, both diurnally and nocturnally, to habitat selection ratios at the population level (design I). However, the variation in design II selection ratios was notably wider than in design I ratios, reflecting varied habitat selection choices among individuals. For example, banded rails generally avoided the mangrove-mudflat interface (MMFI) both diurnally and nocturnally (Figure 6.4, Figure 6.5), yet one individual (E238802) spent large periods of the day foraging along the mangrove-mudflat interface and roosting in this habitat overnight (Figure 6.2a). Similarly, two individuals (E238802 and E238809) spent multiple nights roosting in mangroves despite other banded rails generally avoiding this habitat at night. This latter observation contradicts the common assumption that banded rails in coastal regions roost exclusively in saltmarsh or terrestrial scrub (Marchant & Higgins 1993; Botha 2011; Bell & Blayney 2017). In short, the findings of this study largely support existing hypotheses of banded rail habitat selection (Botha 2011; Beauchamp 2022) but also shows that banded rails select habitats more widely than had been previously recognised.

At the home range scale, animals optimise habitat selection for resource availability and acquisition (Mitchell & Powell 2004). In this study, mangrove habitats comprised a substantial proportion of all banded rail home ranges (Figures 6.2a-c), and were selected by rails during diurnal hours, presumably to support foraging efforts (Beauchamp 2022). While the abundance of food in mangroves may vary by site and forest age (Morrisey et al. 2003; Ellis et al. 2004; Alfaro 2006; Chapter 4), the selection behaviour of banded rails in this study indicates that mangroves provide readily available food resources. While saltmarsh and mangrove habitats can provide similar levels of food resources to banded rails (Botha 2011; Chapter 4), the structural profile of mangrove vegetation may facilitate easier access to these resources than saltmarsh vegetation. The understory in mangrove forests in New Zealand is typically less dense than the understory in adjacent rush-saltmarsh, a difference that may mean banded rail prey species such as mud crabs (*Austrohelice crassa*) are easier to observe and pursue in mangrove habitats. This hypothesis aligns with observations made by Elliott (1987) in saltmarsh habitats of the South Island, where banded rail used sea rush *Juncus kraussii* subsp. *australiensis* more frequently than other rush species such as *Apodasmia similis*. Elliott attributed this discrepancy to the clumped structure of *Juncus* that provides aerial cover while leaving much of the ground bare (with prey easy to spot), whereas *Apodasmia* is much denser at ground level.

In addition to potentially providing accessible food resources, the structure of mangrove forests is hypothesised to reduce the threat of aerial predation for banded rails. In Ohiwa Harbour, Botha (2011) observed more banded rail activity in mangrove habitats than adjacent rush saltmarsh. Given food was not limited among estuarine habitats (saltmarsh, mangrove, and mudflat), Botha suggested that the dense canopy of mangrove forests provide banded rails with better cover from aerial predators than saltmarsh habitats. While predation events of banded rails are seldom observed, aerial predators are a known threat to banded rails; for example, Cox (1977) observed kahū (Australasian harrier *Circus approximans*) successfully capturing a banded rail in the Kaipara Harbour, while banded rails have been observed to run for cover in Pahuhure Inlet when kahū pass overhead (Ian Southey, pers. comm.). Although this study did not correlate the movement patterns of banded rails with the presence of aerial predators, GPS data from tagged banded rails are consistent with the premise that banded rails remain under cover during diurnal hours, when aerial predators such as kahū are active.

Arguably, mammalian predators pose a larger threat to banded rail populations than aerial predators in New Zealand (Elliott 1983; Parker & Brunton 2004), although it is unclear how pressure from mammalian predators varies among estuarine habitats such as saltmarsh and mangrove habitats. Limited evidence suggests that rats and mice frequent both saltmarsh and mangrove habitats (Dencer-Brown et al. 2020; Chapter 5), while mustelids and cats have been observed in rush saltmarsh and along mangrove fringes (Parker & Brunton 2004; Chapter 5). However, further study is needed to quantify the threat these predators pose to banded rails and how this may influence habitat selection.

6.5.2.1 Limitations of habitat selection analysis

Importantly, there are notable caveats in interpreting habitat selection ratios presented by this study. First, the scope of this study is limited to second-order habitat selection (Johnson 1980) and a narrow time window directly following the breeding season. Logistical and financial constraints – including wildlife permit stipulations, Covid-19 lockdowns, and the high cost of GPS transmitters – restricted site selection to an individual estuary and fieldwork within short time frames, resulting in a small sample size of six tagged individuals. Second, the estimation of available habitat used to inform Manly selection ratios describes habitat spatially and does not account for temporal variation in availability, namely brief daily periods when intertidal habitats are submerged (the role of tidal action is further discussed in Section 6.4.3 below). Third, the habitat composition of study sites is not representative of all habitats used by New Zealand's population of banded rails, particularly for populations inhabiting offshore islands or saltmarsh-dominated sites on the South Island (Elliott 1983; Marchant & Higgins 1993; Heather & Robertson 2005; Bellingham 2013). Consequently, the results of this study should be interpreted with caution; the habitat preferences of banded rails presented here do not capture the multivariate processes that influence habitat selection, including season or spatial scale (Block & Brennan 1993; Jedlikowski et al. 2016).

Although the habitat composition of SMCs in Mangawhai is not representative of all habitats used by banded rails, it is typical of many estuaries and harbours in the northern North Island home to the vast majority of New Zealand's banded rail population (Bellingham 2013). Several regions, including, but not limited to, Tauranga, Whangamata, Whangārei, the Coromandel, the Bay of Islands, and the Firth of Thames contain numerous SMCs, which are structured by the same tidal gradients governing those in Mangawhai. Given similarities in habitat structure between SMCs in Mangawhai (this study) and other SMCs in northern New Zealand, it is plausible that the habitat use patterns observed by this study hold true for numerous other populations of banded rails which occupy other SMCs. However, further study is required to determine whether microscale- and site-specific habitat features (e.g., mangrove height, food availability, or the ratio of saltmarsh to mangrove habitat) affect the banded rail habitat selection within SMCs.

6.5.3 Habitat use

GPS data from six GPS-tagged banded rails showed that banded rails make use of both mangrove and saltmarsh habitats, confirming limited previous observations of banded rails in these habitats (Botha 2011; Beauchamp 2015, 2022). Moreover, analyses of GPS locations suggest banded rail habitat use may be mediated by tidal and temporal cycles; model results indicated banded rails were significantly more likely to use 'swamp' habitats (mangrove and MMFI) during daylight and low tide hours relative to 'terrestrial' habitats (saltmarsh and adjacent scrub) (Figure 6.7). In the context of other diurnal observations of banded rail in mangrove forests (Botha 2011; Beauchamp 2022), banded rails' use of mangrove habitats in Mangawhai estuary is likely to represent foraging behaviours. Here, I show that this foraging behaviour is affected by incoming tides; diurnal location data suggests that banded rails retreat to saltmarsh rushes as the incoming tide pushes into the mangroves, likely because ground-based foraging is impeded by increasing water depth. While tide may alter foraging behaviour, it does not appear to influence roosting behaviours; banded rails roosted in saltmarsh habitat overnight irrespective of tidal cycles, while individuals roosting in mangrove trees also maintained their position overnight.

A limited number of studies have appraised banded rail habitat use in saltmarsh or mangrove habitats (Elliott 1987; Botha 2011; Beauchamp 2015, 2022), but not in both habitats concurrently. Elliott (1987), who studied banded rail footprints in coastal bays in the Nelson region (where mangroves are naturally absent), suggested that banded rail activity was limited to saltmarsh rushes and varied in intensity over the day, peaking in the morning, slowing in the middle of the day, and increased again in the evening. In mangrove forests of Ohiwa Harbour, Botha (2011) observed banded rail footprints spread widely throughout mangrove forests, including around large, isolated mangroves trees beyond the seaward edge of the contiguous mangrove forest. This use of mangroves is described as foraging behaviour in Beauchamp's (2022) visual observations of banded rails in Whangarei Harbour, where he regularly recorded banded rails and their chicks foraging in mangrove forests and their pneumatophores. While these studies provide a baseline understanding of banded rail habitat use in estuarine habitats, their insights are limited to proxy observations of presence (i.e., footprints) and fleeting visuals observations among tall, sparse mangrove trees. Although banded rail footprints are easily recognisable (Elliott 1983) and are occasionally used in marsh bird surveys in New Zealand (Chapter 3), their use as a proxy for presence is limited by substrate quality and tidal action (Elliott 1983; Beauchamp 2015), do not allow differentiation among individuals. Similarly, banded rail individuals are not easily visually distinguishable, particularly where they inhabit dense environments.

6.5.4 Conservation implications

The findings of this study have serious implications for conservationists, policymakers, and coastal managers in New Zealand as they show that banded rails use mangroves more than had been previously understood. Not only do mangroves make up a substantial part of banded rail home ranges in saltmarsh-mangrove complexes, but banded rail foraging was almost exclusively restricted to mangroves in sites of this habitat structure. Moreover, individual banded rails were observed to roost within mangrove forests – a previously undocumented behaviour. These findings highlight the important role of mangroves as habitats to banded rails, in a context where there is historical and current socio-political pressure to remove mangroves (Harty 2009, Chapter 3) and a conservation directive to counteract the ongoing decline of banded rail populations in New Zealand (Robertson *et al.* 2021).

Knowledge of species' ecological requirements is fundamental to informed conservation management decisions, particularly where habitat changes can influence species decline (Luck 2002; Zeale et al. 2012; Botero-Delgadillo et al. 2015; Seifert et al. 2018; Li et al. 2022). In a context where an estimated 80-90% of New Zealand's banded rail population is found in saltmarsh-mangrove complexes (Bellingham 2013), this study illustrates how these habitats are used and selected for by banded rails. Mangrove habitats play a key role in supporting foraging activities, a function complemented by saltmarsh habitats that support roosting and breeding activities (Marchant & Higgins 1993; Heather & Robertson 2005) and provide refuge during high tides.

The availability of saltmarsh habitats plays an important role in supporting New Zealand's mainland population of banded rails, given these habitats are used by *G. p. assimilis* as nesting grounds (Elliott 1987; Botha 2011; Beauchamp 2015). Critically, saltmarshes are declining in New Zealand (Walker *et al.* 2008; Saintilan *et al.* 2014), reflecting patterns of saltmarsh loss globally (Campbell *et al.* 2022). Contrarily, mangrove habitats are expanding rapidly in New Zealand (Horstman *et al.* 2018), thereby increasing areas of foraging and roosting habitat available to banded rails. Notably, the presence of mangrove habitats may make small patches of adjacent saltmarsh viable breeding grounds; banded rails have been observed in tiny pockets of saltmarsh (<0.001 ha) where they are surrounded by extensive areas of mangrove forest (Beauchamp 2015). However, it is unclear whether banded rails persist in areas comprising exclusively mangroves, as such sites lack nesting habitat. Field observations suggests banded rail could use dense grass and scrub vegetation as nesting habitat (Fagan 1954; Elliott 1983; Marchant & Higgins 1993; Botha 2011) should this be available adjacent to mangrove forests – however, further investigation of banded rail breeding habitat is needed to assess the suitability of these habitats. In addition, invasive predators and the continued loss of alternate habitat, such as freshwater wetlands, remain fundamental threats to banded rail persistence (Elliott 1983; Robertson *et al.* 2017). Thus, protection of saltmarsh habitats should be considered a conservation priority, particularly where these saltmarshes make up part of a sequence of coastal vegetation that includes mangroves (e.g., intact intertidal vegetation sequence including sandflats, mangrove, saltmarsh, and terrestrial coastal vegetation).

The future pathway for mangrove management in New Zealand will depend on how mangrove management is framed by decision-makers. In other words, it matters which theoretical lens is applied to mangrove habitats (elaborated in Chapter 1), as well as the extent to which banded rail conservation is weighted and prioritised in decision-making. The more common framing for estuary management in New Zealand is a ‘structural’ one (Gaillard *et al.* 2010), as has been shown in Chapter 3, which reviewed mangrove management in New Zealand. Viewed through the lens of structural habitat – the characterisation of habitats as distinct categories of vegetation (Hutto 1985) – the spread of mangroves can be considered beneficial to banded rail populations, as it increases the total amount of habitat potentially available to banded rails. However, in its simplicity, the structural habitat concept fails to account for spatial and temporal variation, while habitat is not species-specific and its quality to a given animal is difficult to measure (Gaillard et al. 2010). Given that a structural view of estuarine habitats is commonly taken by policymakers and communities in New Zealand (Harty 2009; Stokes *et al.* 2016), management interventions such as mangrove removal are likely to ignore variation within and among habitats. As a result, interventions framed this way may well overlook the functional role habitats play in supporting species. For example, increases in mangrove area may quantifiably benefit banded rails, but this will depend on whether mangrove increases are ‘functionally’ linked to banded rail persistence and performance (Pulliam 2000; Morrison *et al.*

2006; Gaillard *et al.* 2010). Thus, it is important for coastal managers to assess the quality of mangrove habitat in proving resources for survival, reproduction and population persistence (Block & Brennan 1993) for species like the banded rail.

While an overall increase in mangrove forests in New Zealand has increased structural habitat for banded rails, several factors may limit the ability of these habitats to functionally support banded rail populations. First, mangroves are subject to intensive management practices in many New Zealand harbours; more than 330 hectares of mangrove forest have been removed in New Zealand legally, almost a quarter of which has been cleared in large, contiguous patches (> 1,000 square meters) (Chapter 3). While the effects of this removal on banded rail populations or individuals have not been formally studied, removal is likely to reduce habitat availability by removing cover vegetation and creating significant disturbance. The resulting reduction in available habitat is likely to reduce the carrying capacity of local saltmarsh-mangrove complexes (Chapter 3). Second, habitat quality may vary among mangrove forests. For example, prey abundance in new-growth mangroves may not match abundance in old-growth forests (Chapter 4), although this pattern may be site specific (Morrisey *et al.* 2003). Third, factors operating at catchment-level spatial scales may influence the quality of local mangrove habitats. For example, new-growth mangroves are likely subject to higher rates of sedimentation than old-growth forests, and in turn have lower benthic macrofaunal diversity and/or abundance (Ellis *et al.* 2004), potentially reducing prey availability to banded rails.

As evidenced by this study, mangrove and saltmarsh habitats comprise much of the banded rail's home range within in a coastal environment typical of those which hold the vast majority of New Zealand's banded rail population. Given their use as breeding habitats, saltmarshes are likely critical to the persistence of New Zealand's mainland banded rail population. While mangrove habitats are not a pre-requisite for banded rail survival at an individual level (Elliott 1983; Marchant & Higgins 1993), they likely facilitate the presence of banded rails across much of their distribution in New Zealand by providing foraging habitat. Although mangrove removal has increased within the last two decades and may threaten local banded rail populations, the pace of mangrove expansion has dramatically outstripped removal efforts (Suyadi *et al.* 2019). Nevertheless, mangrove removal should not be undertaken in the absence of ecological understanding, particularly as mangroves may vary functionally in their ability to support banded rail populations. Thus, it is important that coastal managers assess habitat quality of mangroves, quantify the presence and persistence of native avifauna, recognise the value of coastal vegetation sequences include both saltmarsh and mangrove habitats, understand the potential ramifications of their interventions (see Lundquist *et al.* 2014), and undertake long-term monitoring of a variety of biotic and abiotic factors to assess the outcomes of management strategies (Stokes *et al.* 2016).

6.6 References

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6.7 Supplementary material

Table S6.1 A summary of home range estimates for species of *Rallidae* as available from a systematic review of relevant scientific literature. Home range estimates are contextualised by season, habitat, and bird weight, while statistical estimators (minimum convex polygon [MCP], kernel density utilisation distribution [UD], and concave polygon) and tracking methodology are also recorded.

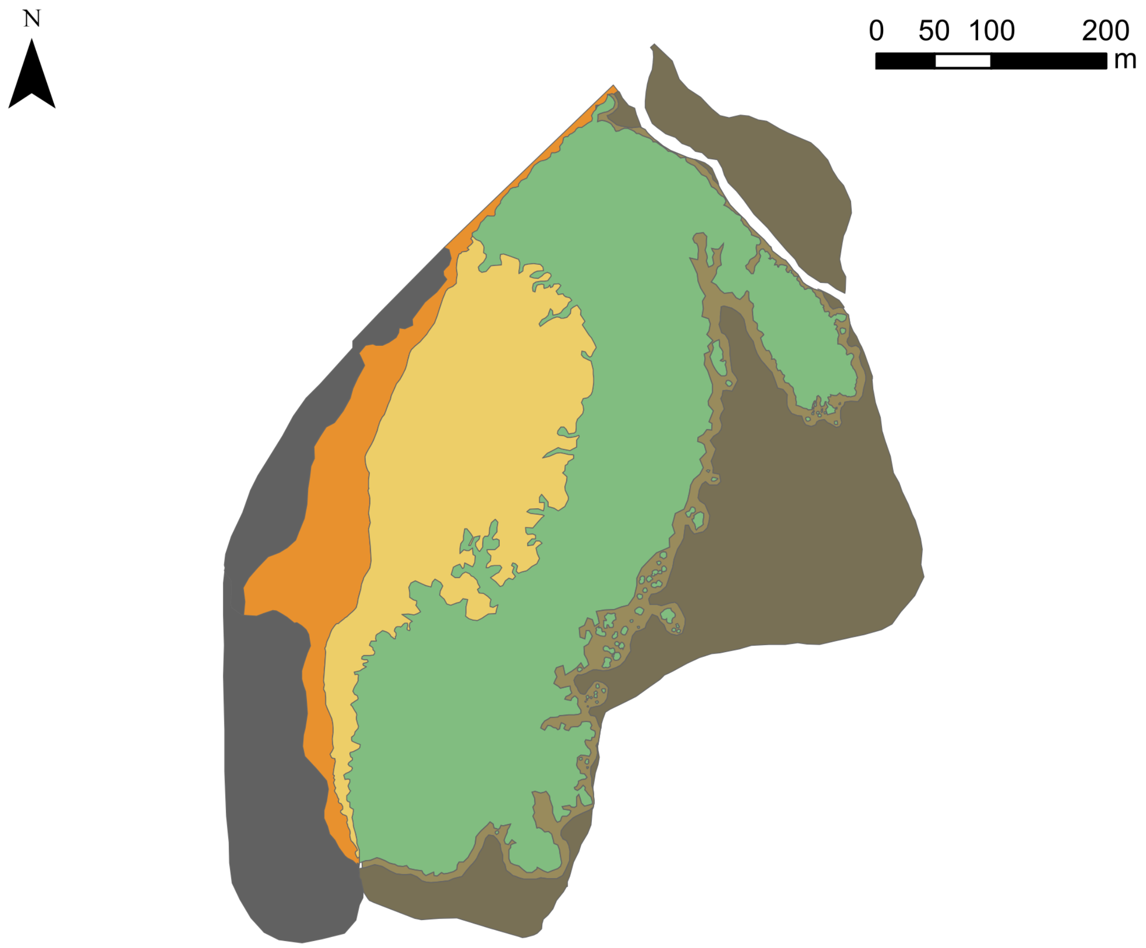
Common name	Species	Season	Habitat	Average body weight (g)	Home range ha±SE (n)	Statistical estimate	Method	Publication
Yellow rail	*Coturnicops noveboracensis*	Breeding	Freshwater wetland	50	4 (8)	MCP100	Radiotelemetry	Bookhout & Stenzel 1987
Buff-banded rail	*Gallirallus philippensis assimilis*	Non-breeding	Tidal marsh	186	4.33±0.63 (6)	UD95	GPS	This study
California black rail	*Laterallus jamaicensis coturniculus*	Breeding	Tidal marsh	29	0.59±0.05 (48)	UD95	Radiotelemetry	Tsao *et al.* 2009
Eastern black rail	*Laterallus jamaicensis jamaicensis*	Non-breeding	Tidal marsh	39	2.3±0.49 (13)	UD95	Radiotelemetry	Haverland *et al.* 2021
Plumbeous rail	*Pardirallus sanguinolentus*	Breeding	Tidal marsh	200	2.5 (2)	UD95	Visual observations	Chávez-Villavicencio & Contreras-Hernández 2017
Sora	*Porzana carolina*	Breeding	Freshwater wetland	75	0.19 (10)	MCP100	Radiotelemetry	Johnson & Dinsmore 1986
Spotted crake	*Porzana porzana*	Breeding	Freshwater wetland	97	0.38±0.064 (4)	MCP100	Radiotelemetry	Fox *et al.* 2013

Table continues

Water rail	*Rallus aquaticus*	Breeding	Freshwater wetland	130	0.07±0.01 (10)	Concave polygon100	Radiotelemetry	Jedlikowski & Brambilla 2017
Clapper rail	*Rallus crepitans*	Breeding	Tidal marsh	280	1.37±0.27 (10)	UD95	Radiotelemetry	Rush *et al.* 2010
King rail	*Rallus elegans*	Annual	Freshwater wetland	340	19.8±5.0 (15)	UD95	Radiotelemetry	Kolts & McRae 2017
		Breeding	Freshwater wetland	340	22.5±6.9 (13)	UD95	Radiotelemetry	Kolts & McRae 2017
		Non-breeding	Freshwater wetland	340	15.6±3.5 (10)	UD95	Radiotelemetry	Kolts & McRae 2017
Virginia rail	*Rallus limicola*	Annual	Freshwater wetland	90	0.53±0.11 (6)	UD95	Radiotelemetry	Gamboa 2011
Ridgway's rail	*Rallus obsoletus*	Annual	Tidal marsh	300	1.5 (41)	UD95	Radiotelemetry	Rohmer 2010
		Breeding	Tidal marsh	300	1.36 (26)	UD95	Radiotelemetry	Rohmer 2010
		Non-breeding	Tidal marsh	300	1.32 (25)	UD95	Radiotelemetry	Rohmer 2010
Sakalava rail	*Zapornia olivieri*	Breeding	Freshwater wetland	65	1.5 (2)	MCP100	Radiotelemetry	Pruvot *et al.* 2018
Little crake	*Zapornia parva*	Breeding	Freshwater wetland	53	0.05±0.005 (17)	Concave polygon100	Radiotelemetry	Jedlikowski & Brambilla 2017
Baillon's crake	*Zapornia pusilla*	Non-breeding	Freshwater wetland	35	1.77±0.86 (18)	UD95	Radiotelemetry	Seifert *et al.* 2018

Table continues

Species included in the literature review where no home range data was available: *Aenigmatolimnas marginalis*, *Amaurolimnas concolor*, *Aramides albiventris*, *Aramides axillaris*, *Aramides cajaneus*, *Aramides mangle*, *Aramides ypecaha*, *Aramidopsis plateni*, *Cabalus lafresnayanus*, *Canirallus oculeus*, *Coturnicops exquisitus*, *Coturnicops notatus*, *Crecopsis egregia*, *Cyanolimnas cerverai*, *Dryolimnas cuvieri*, *Eulabeornis castaneoventris*, *Gallirallus calayanensis*, *Gymnocrex plumbeiventris*, *Gymnocrex rosenbergii*, *Gymnocrex talaudensis*, *Habroptila wallacii*, *Himantornis haematopus*, *Hypotaenidia insignis*, *Hypotaenidia okinawae*, *Hypotaenidia owstoni*, *Hypotaenidia rovianae*, *Hypotaenidia sylvestris*, *Hypotaenidia torquata*, *Hypotaenidia woodfordi*, *Laterallus albigularis*, *Laterallus exilis*, *Laterallus fasciatus*, *Laterallus flaviventer*, *Laterallus leucopyrrhus*, *Laterallus levraudi*, *Laterallus melanophaius*, *Laterallus ruber*, *Laterallus spilonota*, *Laterallus spiloptera*, *Laterallus xenopterus*, *Lewinia mirifica*, *Lewinia muelleri*, *Lewinia pectoralis*, *Lewinia striata*, *Megacrex inepta*, *Micropygia schomburgkii*, *Mustelirallus albicollis*, *Neocrex colombiana*, *Neocrex erythrops*, *Pardirallus maculatus*, *Pardirallus nigricans*, *Poliolimnas cinereus*, *Porzana fluminea*, *Rallina canningi*, *Rallina eurizonoides*, *Rallina fasciata*, *Rallina tricolor*, *Rallus aequatorialis*, *Rallus antarcticus*, *Rallus caerulescens*, *Rallus indicus*, *Rallus longirostris*, *Rallus madagascariensis*, *Rallus semiplumbeus*, *Rallus tenuirostris*, *Rallus wetmorei*, *Rougetius rougetii*, *Rufirallus castaneiceps*, *Rufirallus viridis*, *Zapornia akool*, *Zapornia atra*, *Zapornia bicolor*, *Zapornia flavirostra*, *Zapornia fusca*, *Zapornia paykullii*, and *Zapornia tabuensis*.



Habitat	Description
Residential	Houses, driveways, and surrounding lawns
Terrestrial scrub	A mix of low-growing vegetation, including oi oi (*Apodasmia similis*), ribbon wood (*Plagianthus divaricus*), pampas (*Cortaderia selloana*), swamp flax (*Phormium tenax*), scrub pohuehue (*Muehlenbeckia complexa*), interspersed with kanuka (*Kunzea ericoides*), manuka (*Leptospermum scoparium*), and cabbage trees (*Cordyline australis*)
Saltmarsh	Rushes dominated by two species: *Juncus kruassii* and *Apodasmia similis*
Mangrove	Monotypic low-growing forest of *Avicennia marina*
MMFI	A ten-meter-wide strip/ecotone between the seaward edge of the mangrove forest and the adjoining mudflat. The MMFI also contains outlying mangrove trees
Mudflat	Open habitat dominated by muddy sediment

Figure S6.1 Habitat map of study site B used to define the area of habitat available to banded rails in determining Manly selection ratios. Habitat descriptions provided within the figure.

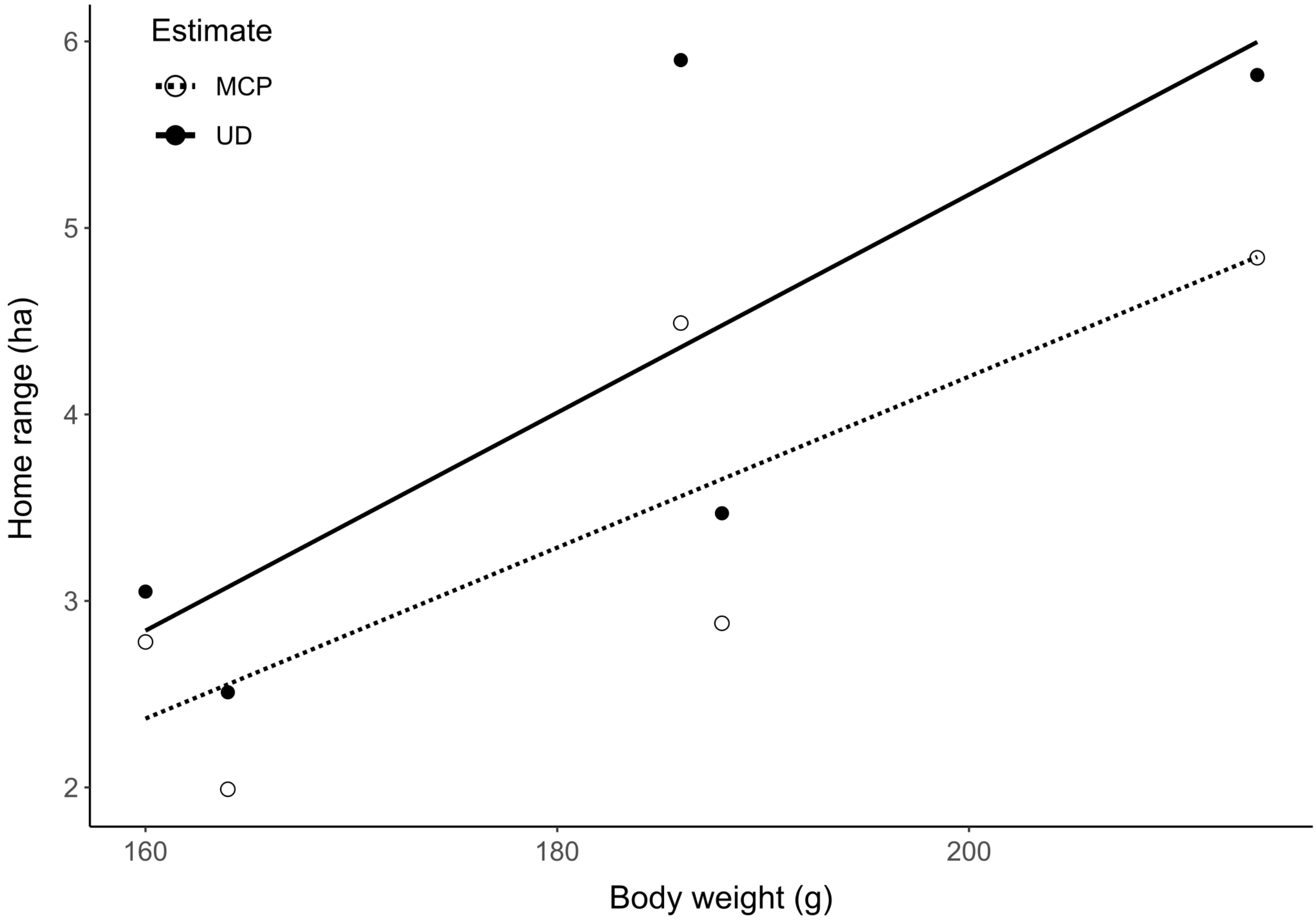


Figure S6.2 Home range estimates relative to body weight for five banded rail individuals. For each individual, two estimates were calculated: the 95% Minimum Convex Polygon (MCP – hollow circles and dashed trendline) and 95th isopleth Utilisation Distribution (UD – filled circles and solid trendline) estimated by kernel density.

Figure S6.3 *Top* - A Lotek Pinpoint VHF75 GPS tag is fitted to a banded rail using a polypropylene backpack harness by Jacques, under the supervision of DOC's Graeme Elliott. *Bottom* - Weihong holds the GPS-tagged banded rail for a quick photo after helping to check the fit of the backpack harness.

Chapter 6, Statement of Contribution:

MASSEY UNIVERSITY
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STATEMENT OF CONTRIBUTION
DOCTORATE WITH PUBLICATIONS/MANUSCRIPTS

We, the student and the student's main supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the student's contribution as indicated below in the Statement of Originality.

Student name:	Jacques de Satge
Name and title of main supervisor:	Associate Professor Weihong Ji
In which chapter is the manuscript/published work?	Chapter 6
What percentage of the manuscript/published work was contributed by the student?	95%

Describe the contribution that the student has made to the manuscript/published work:

Jacques developed the manuscript's design and research questions, sourced the data, analysed the data, and wrote the manuscript in its entirety. Weihong provided guidance in establishing the manuscript's research design and editorial input on the final draft of the manuscript.

Please select one of the following three options:

- ○ The manuscript/published work is published or in press
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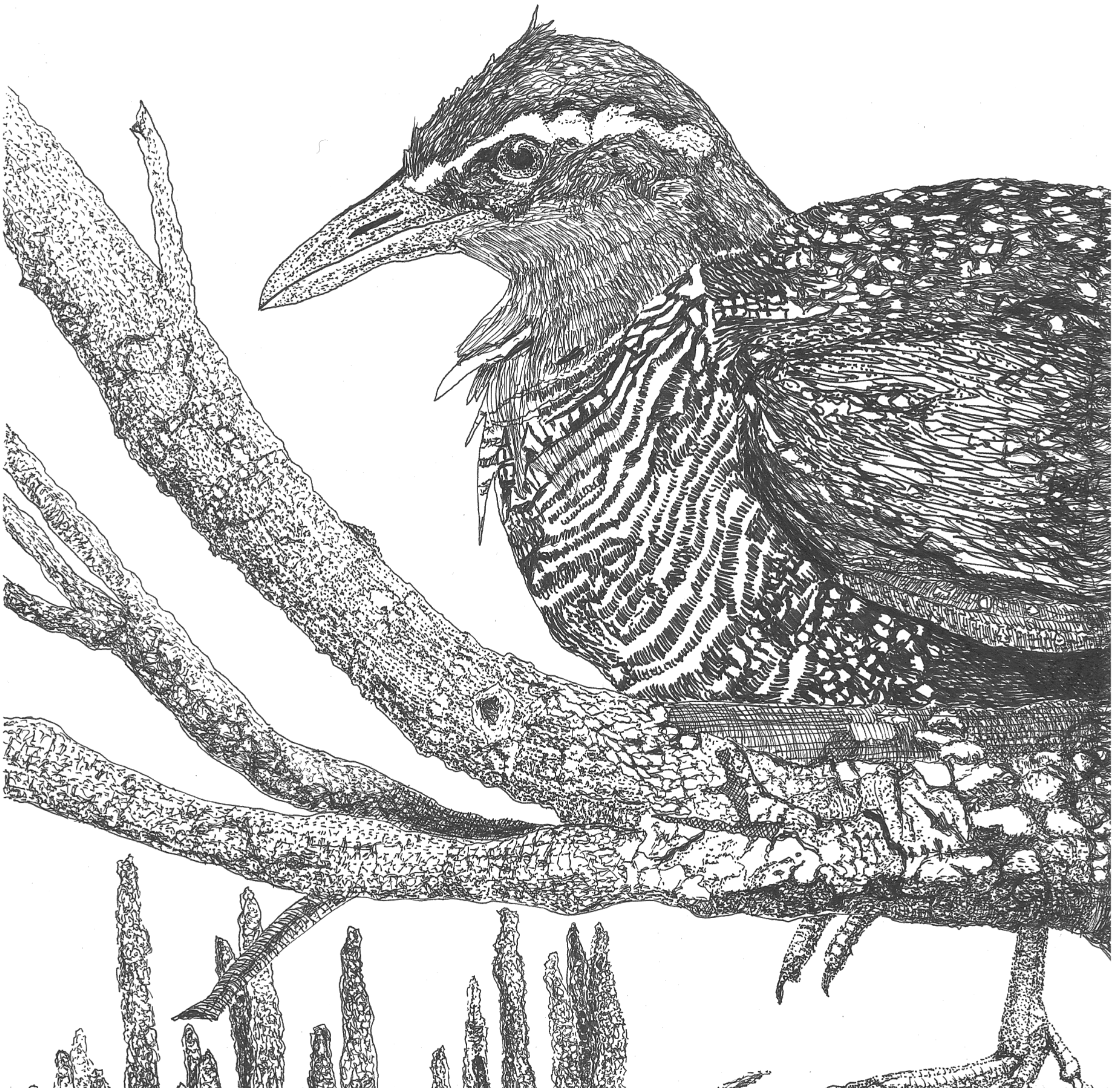
  Please provide the name of the journal:
- ● It is intended that the manuscript will be published, but it has not yet been submitted to a journal

Student's signature:	Jacques de Satge Digitally signed by Jacques de Satge Date: 2023.03.09 10:40:00 +13'00'	Main supervisor's signature:	Weihong Ji Digitally signed by Weihong Ji Date: 2023.03.08 15:01:47 +13'00'

This form should be placed at the beginning of each relevant thesis chapter.

CHAPTER 7
CONCLUSIONS AND FUTURE DIRECTIONS



Chapter 7 cover image: A banded rail lurks among the pneumatophores and low-hanging branches of a mangrove tree. Artwork by Rick de Satgé.

7.1 Overview

The principle aim of this thesis is to improve the ecological understanding of the relationships between banded rails *Gallirallus philippensis assimilis* and mangrove forests in New Zealand. This aim was informed by the overarching research question of this thesis:

"In the context of mangrove removal practices in New Zealand, what is the importance of mangrove forests as habitats for the banded rail *Gallirallus philippensis assimilis*?"

This broad question pushes the boundaries and practical scope of a PhD thesis, and requires sub questions, in the form of narrower and specific research objectives for the study. Determining how important a habitat is to a species can be measured in myriad ways and the importance of this relationship is dependent on the social, political, and ecological context of both a species and its habitat (Giles 1978). To shape my investigation of this question, I developed a theoretical framework (Chapter 1) which situates the ecological importance of mangroves to banded rails within habitat theory and contextualises this species-habitat relationship in wildlife and habitat management. Using this framework as a guide, I clarified four research objectives – which correspond to four thesis chapters – to investigate the relationships between banded rails and mangrove forests in New Zealand:

1. (i) Determine the extent and configuration of mangrove removal in New Zealand, and (ii) its potential effects on banded rail populations (Chapter 3)
2. Determine the relative quality of mangrove habitats for banded rails in saltmarsh-mangrove complexes (Chapter 4)
3. Establish and implement a reliable method for monitoring banded rails in intertidal environments (Chapter 5)
4. Quantify banded rail habitat selection and habitat use in saltmarsh-mangrove complexes (Chapter 6)

In this concluding chapter, I discuss the main findings of Chapters 3 - 6, highlighting their contributions to scientific knowledge as well as their implications for ecological study and/or conservation management. I also identify the limitations and areas for future exploration for each research component. Thereafter, I explore how findings among chapters interlink to provide novel insights into banded rail ecology and to answer the overarching research question.

7.2 Mangrove removal and its effects on banded rail populations

Mangrove removal is a common and contentious mechanism used by regional authorities to tackle the spread of the mangrove plant *Avicennia marina* var. *australasica* within its distribution in northern New Zealand. Understanding how mangrove removal may affect mangrove-using birds such as the banded rail, was, in-part, a key motivation of this PhD thesis. However, as is typical of PhD theses, the scope of this question quickly widened as I recognised how little is known about mangrove removals themselves in New Zealand. As a result, Chapter 3 determined the scale and configurations of mangrove removal in New Zealand and provided an overview of the underlying motivations for this management intervention, to contextualise banded rail-mangrove relationships (explored in Chapters 4–6) within contemporary management practices and community perspectives.

7.2.1 Significance and limitations

In Chapter 3, I used data derived from mangrove removal resource consents to show that (1) more than 330 hectares of mangrove forest have been legally removed in New Zealand since 1994, (2) removal events occur at a variety of scales and spatial configurations, the most common of which are large, contiguous removals of >1,000 m^2 of mature mangrove forest, (3) large-scale removals are commonly motivated by desires for improved amenity and recreation and not by ecological restoration or avian conservation, (4) monitoring of avifauna in association with mangrove removals is infrequent and typically of a poor standard, and (5) in monitored removal sites, banded rail populations persisted after removal events although potentially at lower densities.

The findings of Chapter 3 make several useful contributions to the study of mangroves and their management in New Zealand. Firstly, this thesis is the first to provide an estimate of the area of mangrove removed legally (i.e., by regional councils). This estimate likely significantly underestimates the total area of mangrove removal in New Zealand as it excludes illegal mangrove removals – an activity which by some estimates could account for a further 300 hectares (or more) of mangrove removal. Nevertheless, mangrove growth in New Zealand has significantly outpaced its removal, be it legal, illegal, or the combination thereof (Lundquist *et al.* 2014; Swales *et al.* 2015; Suyadi *et al.* 2019). Secondly, findings pertaining to the configuration of mangrove clearances highlight that mangrove removal seldom follows best-practice guidelines (Lundquist *et al.* 2017), typically removing areas of mangrove in large, contiguous patches rather than seaward strips. Thirdly, Chapter 3 shows that mangrove removal projects focus on vegetation clearance and seldom address the underlying cause of mangrove expansion by targeting excess sediment, entrenching a symptom-oriented management style instead of a driver-oriented approach.

Unfortunately, the effect of mangrove removals on banded rail populations remains largely unclear; the poor standard and infrequent nature of monitoring efforts in association with resource consents limited my ability to make robust conclusions on the effects of mangrove removal on avifauna. Based on limited monitoring data from resource consents, I suggest that mangrove removal projects may lead to a reduced density of banded rails in affected estuaries, and that this effect may be more obvious where removal is a large-contiguous clearance rather than seaward-strip clearance. Notably, Chapter 3 makes clear that, despite mangrove removals, the area of mangroves available to banded rail populations has increased over time, although it is uncertain whether new-growth mangrove forests represent high-quality habitat (see Chapter 4 discussion).

7.2.2 Future directions: keeping track of mangroves and their avifauna

My study of mangrove management in New Zealand was temporally bounded, starting with consents issued in 1994 –when mangrove removal became regulated by regional councils – and ending in 2020 with my data collection. Under current legislation among regional councils, mangrove removal remains a legal, consented activity in New Zealand (Environment Waikato 2012; Auckland Council 2019; Bay of Plenty Regional Council 2019; Northland Regional Council 2020). To better inform scholarly understanding of mangrove environments and improve mangrove management going forward, I propose two areas of research on mangroves and their avifauna in New Zealand:

7.2.2.1 Mapping and tracking changes in coastal environments

New Zealand's mangroves have garnered much research attention in recent years, with a large section of this work examining mangrove expansion (e.g., Lundquist *et al.* 2014; Swales *et al.* 2015; Horstman *et al.* 2018; Suyadi *et al.* 2019). Despite this comprehensive body of research, no one that I am aware of has attempted to track changes in mangroves or other coastal habitats (e.g., saltmarsh, seagrass, or sandflats) throughout their New Zealand distribution – although excellent examples exist at more localised scales (e.g., (Swales *et al.* 2007; Suyadi *et al.* 2019). While intertidal habitats can be difficult to map accurately, improvements in satellite imagery, remote sensing and image analysis have made this work feasible (Suyadi *et al.* 2018; Campbell *et al.* 2022). As such, I propose four-part research which (i) maps and continuously tracks the expansion and loss of mangrove forests in New Zealand, as well as other intertidal habitats such as saltmarshes or seagrasses, (ii) tracks changes in mangrove distribution in relation to sea-level rises (McBride *et al.* 2016) and warming temperatures (Friess *et al.* 2022), (iii) compares contemporary rates of mangrove expansion with both historical and current rates of sedimentation throughout New Zealand on a per-estuary basis, and (iv) explicitly assesses potential invasion of saltmarsh habitats by mangroves (Saintilan *et al.* 2014), given observations of this phenomenon in other temperate saltmarsh-mangrove ecosystems (Saintilan & Rogers 2013; Kelleway *et al.* 2017).

7.2.2.2 Understanding New Zealand's mangrove avifauna communities

Remarkably little is known about the community structure and diversity of avifauna in New Zealand's mangrove environments, with existing research limited to just two locations over short timeframes (Cox 1977; Dencer-Brown *et al.* 2020). Understanding the effects of mangrove expansion or mangrove removal on avifauna requires a baseline level of assessment of mangrove avifauna – an area of research currently missing in New Zealand literature. In light of this, I propose that future research mangrove avifauna communities determines (i) the diversity of avifauna throughout New Zealand's mangrove distribution, (ii) the variation in this diversity with latitude and habitat structure, reflecting the trend of taller mangroves in the north of New Zealand which gradually become low scrub at their southern limit (Morrisey *et al.* 2007), (iii) the influence of adjacent habitat types on avifauna diversity in mangroves, and (iv) the effects of mangrove removal – including different spatial configurations – on avifauna diversity and community composition. I also suggest researchers develop a standardised approach to monitoring avifauna in mangrove environments which captures the full complement of species present.

7.3 Habitat quality in mangrove environments

In Chapter 4, I assessed habitat quality in saltmarsh-mangrove complexes (SMCs) by quantifying the diversity and abundance of macrofauna along a tidal habitat gradient. Although not the first study to study macrofauna communities in mangrove environments of New Zealand (see Morrisey *et al.* 2003; Alfaro 2006, 2010; Ellison 2007), this study makes a unique contribution to this field of research by using macrofauna for a resource-based assessment of habitat quality – in this case contextualising macrofauna diversity, abundance, and biomass in relation to the habitat requirements of the banded rail. Given benthic macrofauna comprise the majority of a banded rail's diet (Elliott 1983), the distribution and availability of these resources likely plays a key role in defining habitat quality for banded rail populations.

7.3.1 Significance and limitations

Analyses of macrofauna communities in Mangawhai's saltmarsh-mangrove complexes provide several novel insights: (1) mangroves, in particular old-growth forests, represent high quality foraging habitats to banded rails, relative to other habitats in SMCs; (2) contrary to expectations, mangrove forests show the highest species richness among measured intertidal habitats, (3) the age of mangrove forests may determine the abundance of their macrofauna as new-growth forests hold significantly fewer macrofauna than old-growth forests (both by abundance of all species and by biomass of key prey species), (4) mangrove habitats do not contain a unique set of macrofauna species – inter-habitat differences in macrofauna community composition were driven by relative abundance and not species identity, and (5) based on literature and in-field observations, mangroves are hypothesised to have the highest availability of resources among SMC habitats for banded rails

In part, these insights reflect existing research on macrofauna in mangrove environments. Both in Australia and New Zealand, mangroves are not considered to have their own distinctive set of macrofauna, only showing small differences from neighbouring intertidal flats dictated by the relative abundance of species (Butler *et al.* 1977 and Morrisey *et al.* 2007). Additionally, higher abundances of key prey species in old-growth forests relative to new-growth forests has been observed in another New Zealand estuary (Morrisey *et al.* 2003), although patterns of macrofauna abundance and diversity are likely site-specific and difficult to generalise (Morrisey *et al.* 2003; Ellis *et al.* 2004; Alfaro 2006; Ellison 2007). Contrary to existing research (Alfaro 2006, 2010), Chapter 4 has shown that mangroves can hold macrofauna communities which are more diverse than neighbouring saltmarshes. However, it should be noted that I did not observe large differences in macrofauna diversity among SMC habitats and that measures of species diversity are highly dependent on sampling method.

Notably, this piece of research is the first to quantify habitat quality for banded rails. In so doing, this study has highlighted a conundrum in assessing habitat quality for cryptic species like the banded rail: a resource-based approach requires simple measures of habitat features but is constrained by the limited ecological understanding of the study species, whereas a species-based approach requires demographic information which is often unfeasible or highly impractical to obtain. For Chapter 4, I adopted a resource-based approach as this was a guaranteed method of assessing habitat quality for banded rails (macrofauna are significantly easier to catch and survey than banded rails) but acknowledge that this approach has two notable limitations. Firstly, this approach relies on the assumption that I, the researcher, understand which resources and ecological constraints govern banded rail fitness. Here, I have used limited research and field-based observations to build an understanding of these constraints (see Table 4.4, Chapter 4). Secondly, a resource-based approach provides a *relative* assessment of habitat quality rather than an absolute one, as findings are not directly linked with demographic parameters. As such, concluding that new-growth mangroves are lower quality habitat relative to old-growth mangroves may be true, but this does not preclude new-growth mangroves from being high quality habitat in absolute terms. This is evidenced by study site A2 (Figure 4.1, Chapter 4) which contained mangroves which had established more recently than other sites but is also home to an established and sizeable banded rail population.

The comparison of 'new' and 'old' mangroves by this study provides valuable perspective but also highlights a limitation of this study. By establishing that new- and old-growth mangroves hold different abundances of macrofauna, this study has shown that mangrove forests should not be viewed as uniform environments with identical resources. A range of factors – including mangrove forest age, sedimentation rates, and vegetation sequences – are likely to influence macrofauna communities and the concomitant quality of mangrove habitats; a fact which would not be lost on coastal managers or policymakers. However, a limitation of this research chapter lies in simplified comparison of 'new' and 'old' growth mangroves. Based on satellite imagery, 'new' mangrove forests established and have been expanding since ca. 1980, whereas old mangroves have been established since prior to 1946. While this presents an interesting contrast, it does not capture a gradient of mangrove ages. Moreover, my definition of 'new' mangroves does not capture variation associated with mangrove saplings, nor the vast areas of mangroves which have spread within the last 10 – 20 years. Given that recent mangrove growth has substantially expanded the structural habitat available to banded rails, it would be interesting, and of conservation relevance, to establish their habitat quality.

7.3.2 Future directions: macrofauna and species-based habitat quality

This study has provided a platform for future research into the habitat quality of mangrove environments. Here, I propose two areas of study to improve biologists' understanding of mangrove environments and their value to avifauna like the banded rail:

7.3.2.1 Linking macrofauna communities with mangrove development

Given the historical and ongoing expansion of mangrove forests in New Zealand, understanding how macrofauna communities change as mangroves establish, grow, and spread, represents an important area of research, both for the study of macrofauna as well as research on the quality of mangrove habitats to mangrove avifauna. Further study of macrofauna in the context of mangrove expansion has the potential to address several research questions, including: (1) Do macrofauna communities become more species rich and complex with mangrove development? (2) How does mangrove growth rate and/or sediment deposition rate affect macrofauna community structure in New Zealand? (3) Are macrofauna communities a reliable indicator of sediment properties (e.g., mud content, grain size, oxygen content) (4) How do changes to below-ground organic matter and habitat structure driven by mangrove growth affect macrofauna community structure and abundance? (5) How much do macrofauna communities vary among different mangrove forests – at different latitudes, of different patch sizes, of different heights (e.g., tall vs dwarf mangroves; Suyadi *et al.* 2019) – and at different times of year? Establishing variation in macrofauna abundance and diversity among a diversity of mangrove sites in New Zealand would be a useful measure of habitat quality for banded rails (and other ground-foraging birds), particularly if it can be linked to demographic parameters of these species (see below).

7.3.2.2 Species-based assessments of mangrove habitat quality

Undertaking a species-based assessment of habitat quality (Johnson 2007) presents a logical next step in determining the habitat quality of mangrove forests. However, this is likely to be a challenging undertaking as this approach typically requires measuring demographic parameters such as breeding success, survival rates, or population abundance of banded rails – parameters which are notoriously difficult to quantify for cryptic species (Williams 2016; Colyn *et al.* 2019). Moreover, quantifying multiple indicators of habitat quality is advisable, as habitat conditions which favour density, survival, and reproduction may not be the same (Franklin *et al.* 2000). Alternately, future research could assess habitat quality by determining patterns of the banded rail's spatial distribution. In New Zealand, Beauchamp (2015) has determined banded rail occupancy across multiple sites in Whangarei Harbour, a good starting point which could be expanded to cover multiple sites across New Zealand. This work lends itself to citizen science and publicly available data; for example, the ongoing NZ Bird Atlas Scheme is collecting data on the distribution of all of New Zealand's bird species from June 2019 to May 2024. This data could be used to inform modelling of banded rail habitat selection at several spatial scales, an approach which is commonly used to inform species-based assessments of habitat quality (Johnson 2007).

7.4 A novel approach to banded rail monitoring

Monitoring banded rails has long presented a challenge to researchers and conservationists alike (Dunlop 1970; Elliott 1983), a challenge common to cryptic species and exemplified by the *Rallidae* family globally (Taylor & van Perlo 1998). In Chapter 5, I implemented monitoring infrastructure novel to the study of banded rails (or any marsh bird), using a combination of camera traps and drift fences to capture patterns of banded rail movement between saltmarsh and mangrove habitats. While this method was designed and used for banded rails, it can also be used more broadly. Having a reliable method of surveying species is fundamental to both ecological study and effective conservation (Nichols & Williams 2006; Dowding 2012; Burton *et al.* 2015; Robertson *et al.* 2021). In this regard, the camera-drift fence (CDF) setup trialled in Chapter 5 provides another string to the bow of monitoring methods for banded rails, as well as multiple other cryptic ground-dwelling species, and has shown the potential to provide valuable information beyond simple presence-absence data.

7.4.1 Significance and limitations

In Chapter 5, I showed that (1) CDF infrastructure presents a viable method of monitoring banded rails in intertidal habitats, providing presence-absence data as well as time-stamped movement data, and data on 'by-catch' species, (2) banded rail movements between saltmarsh and mangrove habitats (inter-habitat movement) are non-random and correlated with temporal and tidal cycles, (3) banded rail activity is likely restricted to diurnal and crepuscular hours, (4) inter-habitat movement peaks during crepuscular hours as banded rails move from saltmarsh into mangrove habitats during dawn hours and return to saltmarsh habitats during dusk hours, and (5) banded rails are more likely to move into saltmarsh habitats (than into mangroves) on incoming tides during diurnal and crepuscular hours.

The combination of camera traps and purpose-built drift fences is uncommon in ecological study; to date; studies implementing CDF infrastructure have typically targeted reptiles (e.g., Welbourne *et al.* 2017; Neuharth *et al.* 2020). The use of cameras to study birds is long established (Cutler & Swann 1999), yet Chapter 5 is the first piece of research – to the best of my knowledge – to combine camera traps with drift fences to monitor a species of bird. The success of this method has implications for monitoring other cryptic species, as well as camera trap studies more broadly. Firstly, CDF-based monitoring provides a viable alternative to traditional avifauna survey methods, many of which are ill-suited to monitoring cryptic birds like banded rails. Secondly, the incorporation of drift fences provides a 'concentration method' to improve species detectability (Welbourne *et al.* 2017), a particularly useful characteristic for targeting cryptic species, especially those which live in dense and inaccessible habitats, and/or species which occur at low densities. In addition, drift fences enable the study of animal movement across natural (e.g., ecotones or territories) and unnatural (e.g., urban-rural delineations) boundaries in the landscape. Although cameras have been used along existing fence lines to study animal movement patterns (albeit for large mammals; Dupuis-Désormeaux *et al.* 2016, 2018), designing and installing fences *a priori* allows for hypothesis testing tailored to species of interest.

Although banded rails have been observed in both mangrove and saltmarsh habitats (Elliott 1983; Botha 2011; Beauchamp 2015, 2022), until this study researchers in New Zealand had not established the patterns of movement between these habitats. Given an estimated 80-90% of New Zealand's remaining banded rail population occurs in or adjacent to saltmarsh-mangrove complexes, an understanding of habitat use in these environments is of conservation significance. Inferring habitat use from of camera trap data in Chapter 5, saltmarshes represent important roosting habitats to banded rails, while mangrove habitats are primarily used for foraging (a pattern later confirmed in Chapter 6). Although this pattern of habitat use has long been assumed (Botha 2011), this study is the first to provide quantitative evidence which supports this assumption.

The CDF survey method has two notable limitations. Firstly, drift fences can be costly and time-consuming to construct, and secondly, fences may influence the behaviour of the target species. To counteract the latter constraint, it is advisable to install drift fences in a manner likely to capture natural moment patterns, rather than artificially induce new behaviours, requiring some prior knowledge of species' habitat use. A simple mechanism to reduce the need to redirect (or concentrate) animals as they move is to increase the frequency of netting gaps along fence lines. The trade-off here is that this requires a greater number of cameras to monitor netting gaps.

With respect to broader limitations of this study, I only present data derived from CDF monitoring from a limited number of study sites (n = 3) within Mangawhai estuary, all of which were similar in their habitat composition. However, I did trial the CDF method in two other sites in Mangawhai which were not saltmarsh-mangrove complexes (a saltmarsh-only site and a freshwater wetland, see Chapter 5 Supplementary Material) and successfully detected banded rails in both areas. This suggests that the CDF method may be suitable for a variety of sites and habitat configurations. A further limitation of this study is that I did not formally compare survey methods for banded rails and measure changes in detectability. Thus, while I have shown that CDF presents a novel and feasible method of monitoring banded rails, I cannot definitively conclude that this method performs better at detecting banded rails than alternate approaches such as footprint monitoring (e.g., Elliott 1987; Botha 2011; Martin 2017), auditory surveys (e.g., Beauchamp 2015) or visual observations (e.g., Beauchamp 2022).

7.4.2 Future directions: advancing and applying monitoring

The study of birds with camera traps is long-established (Cutler & Swann 1999) with methods diversifying to meet evolving research goals (O'Brien & Kinnaird 2008; Delisle *et al.* 2021). Chapter 5 illustrates the wide-ranging potential of monitoring banded rail populations with a combination of camera traps and drift fences, an original use-case for this monitoring infrastructure. Here, I propose two areas of research which can advance and apply the use of this camera trapping methodology in the study of ground-dwelling and cryptic birds like the banded rail:

7.4.2.1 Comparing monitoring methodologies for banded rail

Following an experimental approach to compare the effectiveness of different monitoring methodologies in detecting banded rail is a logical next step in developing a standardised monitoring approach for banded rails. During 2022, MSc student Indiana Miller began to test the effectiveness of different monitoring methods (cameras, acoustic counts, and footprint surveys) for banded rails, under the guidance of supervisor Associate Professor Weihong Ji and with input from this PhD. The potential for such study is wide-ranging; future research could measure survey effectiveness by assessing changes in species detectability, their practicality and time-cost (e.g., Williams *et al.* 2018), could explore opportunities for the automation of monitoring methods(Kalan *et al.* 2015; Priyadarshani *et al.* 2018; Schroeder & McRae 2019), and could trial the implementation by citizen scientists or public-interest groups (e.g., Beauchamp 2015). With regard to camera traps specifically, when detecting banded rails (or other target species), it would be useful to compare the effectiveness of the CDF design with cameras deployed in grids or stratified random arrays, as well as to determine the effects of camera number/density, deployment length, and time of year (Meek *et al.* 2014; Kays *et al.* 2020).

7.4.2.2 Assessing sites of different habitat composition

Highly relevant to contemporary mangrove management practices, future research could apply CDF infrastructure to a variety of sites containing banded rail populations in order to contrast detection rates and movement patterns among saltmarsh-mangrove complexes, saltmarshes where adjacent mangrove has been removed, and saltmarshes in sites where mangroves are naturally absent. Additionally, camera traps could be an effective monitoring tool for avifauna in freshwater wetlands (e.g., Colyn *et al.* 2017); applying CDF infrastructure in wetland environments may present a useful way of monitoring other wetland species such as the spotless crake (*Zapornia tabuensis*) or the marsh crake (*Zapornia pusilla*) in New Zealand.

7.4.2.3 Determining abundance from camera trap data

Reliable estimates of species abundance or density are important to informed conservation decision-making (Nichols 2014). Many traditional methods of abundance estimation require marked individuals, although camera traps are emerging as a means to estimate the abundance of unmarked populations (Gilbert *et al.* 2021). Determining whether the CDF method is suited to abundance estimation techniques is a sensible next step in developing this survey method further. If data captured by a CDF setup could reliably estimate banded rail population abundance (or that of other target species), it would diversify the utility of this method and provide valuable information to conservationists and coastal managers. Specifically, future research could explore the applicability of site-structured models (Kéry & Royle 2015; Gilbert *et al.* 2021), or a variation thereof, to data collected by camera traps flanked by drift fences.

7.5 Banded rail habitat selection and use

Although banded rails are considered widely distributed in mangrove habitats of northern New Zealand (Robertson *et al.* 2004; Bellingham 2013; Beauchamp 2015), studies of banded rail habitat use in these environments are highly limited and often qualitative in nature. In Chapter 6, I quantified banded rail habitat selection and using biotelemetry – a first for this species throughout its distribution – and shed new light on the ecology of banded rails in saltmarsh-mangrove complexes in northern New Zealand.

7.5.1 Significance and limitations

In Chapter 6, I showed that (1) mangrove and saltmarsh habitats constitute the majority of banded rail home range areas in saltmarsh-mangrove complexes; (2) banded rails select for mangrove habitats diurnally, likely in order to support foraging efforts; (3) mangroves are also used by some banded rail individuals nocturnally as roosting habitat – an novel observation for this species; (4) banded rail habitat use is mediated by the tidal cycle during diurnal hours; during high tide banded rails move into saltmarsh and terrestrial scrub habitats but otherwise remain in mangroves; (5) banded rails avoid (selected against) open habitats such as mudflats or residential gardens but do use the seaward edge of mangrove forests (<10m from the outer edge), especially around isolated mangrove trees; and (5) a majority of banded rails select for saltmarshes nocturnally as roosting habitats.

This study yielded several scientific firsts in the study of banded rails: prior to this research, banded rails had not been captured and morphometrically measured in mangrove environments, nor had they been fitted with GPS-tracking devices, nor had their home range size been measured or their habitat selection quantified. The importance of this novelty lies in its relevance to conservation because banded rails are considered a threatened and declining native species in New Zealand (Robertson *et al.* 2021), a status designated, in part, by a lack of data about their ecology. Thus, providing detailed information on banded rail home-range sizes, habitat selection, and habitat use is a first step to remedying this data deficiency.

Throughout their New Zealand distribution, some 80 – 90% of banded rails are thought to occur in and around saltmarsh-mangrove complexes on the North Island (Bellingham 2013). This estimate is derived from early 2000's Atlas distribution data (Robertson *et al.* 2004) and echoed by renewed and ongoing Atlas mapping efforts for New Zealand avifauna (eBird 2022). However, observations in the original Atlas data were sourced from ten-kilometre grid square field surveys, meaning that inferences about the banded rail's reliance on mangroves is derived from data set at a spatial scale far larger than the boundaries of banded rail habitat use. The observations are also drawn from anecdotal evidence and limited study (Botha 2011; Beauchamp 2015, 2022). In this context, this study provides key evidence to support the assumption that mangroves play a valuable role in supporting banded rail populations. By narrowing the focus of this study to a home range scale, I have linked banded rail movement patterns with their surrounding habitats, showing that mangroves provide foraging and roosting habitats to banded rails, functions complemented by adjacent saltmarshes which provide roosting habitats and nesting sites (Elliott 1987; Marchant & Higgins 1993; Parker & Brunton 2004; Beauchamp 2015). These findings highlight the potential importance of intertidal vegetation sequences to banded rails in northern New Zealand, with different habitats along an intertidal gradient in saltmarsh-mangrove complexes providing different sets of resources to banded rails. The importance of these sequences is of conservation relevance, with repercussions for the way coastal managers and policymakers view the ecological value of intertidal habitats. Intact ecological sequences containing terrestrial coastal vegetation, saltmarsh, mangrove, and seagrass are currently protected as Significant Ecological Areas within the Auckland region (Auckland Council 2019), a stance which is supported by the findings of this study and could be applied to mangroves in other political jurisdictions.

Several constraints temper the interpretation of the banded rail home range size, habitat selection, and habitat use data presented in Chapter 6. GPS observations were taken over a short period of time for each bird (<2 weeks) in one estuary, a consequence of logistical constraints and the trade-off between fix frequency and battery life of GPS tags. Resultant home-range estimates thus provide a temporally and spatially limited snapshot of space use, omitting variation associated with different seasons, behaviours, locations, or habitat structures (Kolts & McRae 2017; Rühmann *et al.* 2019). Similarly, the habitat preferences presented in Chapter 6 do not capture the multivariate processes which influence habitat selection, including season, spatial scale, competition, predation risk, and local habitat conditions (Block & Brennan 1993; Jedlikowski et al. 2016). Clearly, there is scope for further research into the factors affecting banded rail home range sizes, as well as variation habitat selection preferences (see section 7.5.2). Thus, although the results of this study provide novel insights into the habitat use by banded rails, they should be viewed as a reference point for comparative study rather than a complete picture of banded rail ecology.

7.5.2 Future directions: exploring variation in habitat use

7.5.2.1 Habitat selection at multiple scales

Different ecological processes can govern habitat selection by animals at different spatial scales (Johnson 1980; Seifert *et al.* 2018; Cunningham *et al.* 2022). While this PhD has examined banded rail habitat selection at the home-range scale – Johnson's (1980) second order of selection – it is useful to determine how other spatial scales influence selection, both for advancing ecological understanding of banded rails and to inform their conservation. For example, habitat heterogeneity or predation avoidance may drive selection at localised or micro scales (third- or fourth-order selection), whereas resource availability may dictate selection at wider or macro scales (Mitchell & Powell 2004; Plumb *et al.* 2019; Cunningham *et al.* 2022; Nugent *et al.* 2022). For banded rails, there are two clear opportunities to study habitat selection at macro- and microscales. At a macroscale, the citizen-science dataset being gathered by the NZ Birds Atlas Scheme presents an opportunity to model the banded rail's distribution (Herrando *et al.* 2019), linking bird sightings to surrounding landscape and habitat features (e.g., Botero-Delgadillo *et al.* 2015; Glisson *et al.* 2017; Regos *et al.* 2018). This type of research could yield answers to questions such as 'does adjacent terrestrial vegetation influence banded rail presence in mangrove habitats?', 'do banded rails require a freshwater source within their home range?' (as suggested by Elliott 1983), or 'what is the minimum viable area of mangroves or saltmarsh required by a breeding pair of banded rails?'. At a microscale, banded rail footprint surveys – a commonly used approach for monitoring (Don 2015; Bell & Blayney 2017; Martin 2017) – provide a unique opportunity to link the precise location of banded rails with surrounding habitat, at scales ranging from centimetres (e.g., prey abundance in the immediate vicinity of footprints) to meters (e.g., density of trees surrounding prints). Research at this scale could help answer questions such as 'do banded rails show a preference for mangroves of a certain height?', or 'does the abundance of surface macrofauna correlate with the density of banded rail footprints?', or 'how does canopy cover influence banded rail habitat use?'.

7.5.2.2 Drivers of home-range variation

Several factors, both internal (e.g., body weight or sex) and external factors (e.g., resource availability or habitat composition) have been found to influence the home range size of animals (Rühmann *et al.* 2019). In the context of mangrove removal in New Zealand, a relevant future area of research could be to determine how banded rail home range sizes vary in sites comprising different habitat configurations. These could include, for example, sites where mangroves have been removed but saltmarsh remains, sites containing intact sequences of estuarine vegetation, sites which exclusively contain saltmarshes, or inland wetland sites (areas where banded rails used to occur with far higher frequency). In addition, banded rails are considered territorial (Marchant & Higgins 1993; Lachish & Goldizen 2004), yet we have little understanding of how territory maintenance affects home ranges. Here, examination of home ranges could yield interesting insights into territorial behaviours, addressing questions such as 'are banded rail home ranges more constrained during periods of higher territoriality (e.g., during nesting and chick rearing)?', 'how do territory sizes differ between males and females?', or 'when do banded rails start showing territorial behaviour'?

7.6 Interlinking insights and overarching observations

This thesis has been written 'by-publication' style, allowing each research chapter to stand alone on its own terms and as individual publishable pieces of scientific work. However, these research chapters have also been designed to create intersectional insights into banded rail ecology and conservation. Here, I summarise notable links between research chapters, their significance, and their implications for future research.

7.6.1.1 Banded rails may prefer mangroves even when they contain fewer resources than alternate habitats

The mangroves of study site B (Backbay, Mangawhai) contained the fewest prey species (macrofauna, by abundance and biomass) among all study sites and habitat types (Chapter 4). Contrary to expectations, this site was well used by banded rails; trapping rates (both from cameras and live capture traps) were highest in site B, while telemetry data showed banded rails made extensive use of the area's mangrove forest for foraging (Chapters 5 and 6). This discrepancy may be explained by inter-annual variation in macrofauna populations; data collection for the macrofauna study was undertaken in 2017, while the camera and biotelemetry studies were undertaken 3 and 4 years later. However, these studies took place at a similar time of year (mid- to late-summer) across years, and existing, albeit limited, research suggests that inter-habitat patterns of macrofauna abundance may be seasonally stable (Alfaro 2006). If the abundance of prey species was indeed lower in mangroves relative to other habitats during biotelemetry data collection, this would suggest that banded rails make use of mangroves *despite* these habitats containing relatively fewer food resources. This phenomenon may be explained by the relative availability of these resources – as I argued in Chapter 4 (see Table 4.4). Mangroves may have the highest availability resources relative to other estuarine habitats by minimising predation threat and/or competition and enabling easy access to resources. To test these predictions, future research could concurrently evaluate banded rail movement patterns and the availability of habitat resources.

7.6.1.2 Biotelemetry data validates camera trap modelling

In Chapter 5, I used data from camera trap photos to show that banded rails' movement between saltmarsh and mangrove habitats was correlated with the time of day and tidal cycles. These findings, derived from photos of the body position of banded rails as they crossed drift fences, were mirrored by biotelemetry data for individual banded rails located at 20-minute intervals by satellites (Chapter 6). In other words, I observed the same movement patterns using two different methods. As predicted by camera trap modelling, GPS tracks for banded rails showed most individuals moving between saltmarsh and mangrove habitat during crepuscular hours and during high tides. Although camera trap models took a 'broad brushstroke' approach, modelling banded rail movement as simple binomial data, the underlying signal of banded rail movement in this data was validated by biotelemetry – an approach considered one of the most reliable in determining movement patterns of cryptic species (Cagnacci *et al.* 2010; Recio *et al.* 2011). This speaks to the utility and value of the CDF monitoring approach, capable of providing ecologically informative data beyond the remit typically expected of camera trapping studies.

7.6.1.3 Mangrove removal may reduce home range sizes for banded rails

Monitoring data from mangrove removal areas (summarised in Chapter 3), suggested that banded rails persist in mangrove removal sites but do not seem to use areas where mangroves have been cleared. During live-capture trapping (Chapter 6), I observed a family of banded rails in study site D (Lincoln Reserve, Mangawhai), an area containing small patches of sea rush, oi-oi grass, and ribbonwood but no mangroves as a 4,500 square-metre area of forest was removed in 2014. Unfortunately, I was unable to tag a banded rail with a GPS unit in this site. However, I did spend numerous afternoons observing the movements of the three individuals at this site (two parents and their fledgling). During these observation periods, the family of rails would forage exclusively between and within grass patches and their fringes. While often in the open, birds were never further than 10 – 15 meters beyond the seaward edge of this habitat, despite the vast areas of mudflat available beyond this point. Although I don't know the historical patterns of habitat use in this site, based on biotelemetry data (Chapter 6) I would assume banded rails would have made use of the mangroves in this site prior to their removal. Contrasting this assumption with my observations, I would hypothesise that banded rail home ranges have contracted at this site following mangrove removal. Testing this hypothesis experimentally would be useful (and was an early hope for this PhD thesis) but requires mangrove removal in a site with a known banded rail population – a logistically difficult and ethically ambiguous undertaking. However, given that mangrove removal remains the primary strategy for managing mangroves by regional authorities, there may be opportunities in future to determine how banded rails adjust their home ranges and movement patterns to mangrove removal in sites which they already inhabit.

7.6.1.4 Cameras could fill a monitoring gap

In Chapter 3, I show there is a need to improve both the frequency and quality of avifauna monitoring in association with mangrove removal, particularly for banded rails. While I make recommendations for the improvement of banded rail footprint surveys (see Chapter 3 Supplementary Material), I also suggest that the financial cost and accuracy of these surveys limit their application. In this context, the CDF method (trialled in Chapter 5) could provide a workable and adaptable solution to banded rail monitoring in removal sites, overcoming issues of non-standardised monitoring and potentially reducing the need for numerous, lengthy in-person site visits for footprint surveys. Arguably, there is a need to develop a standardised monitoring framework for mangrove removals (Stokes *et al.* 2016). Novel techniques for banded rail monitoring could be relatively easily integrated into such a framework.

7.7 So, what is the importance of mangroves for banded rails?

Prior to this thesis, the relationships between banded rails and mangroves have received little academic attention, despite the spatial overlap between banded rail populations and the distribution of mangrove forests in New Zealand. Combining the findings of this PhD with existing research provides an opportunity to comment on the importance of mangroves to banded rails, viewed both at an individual and population level.

Viewed from an individual banded rail's perspective, mangroves are *not* a prerequisite for survival and persistence. Banded rails are well established on New Zealand's offshore islands (e.g., Great Barrier Aotea and Stewart Island Rakiura) and a sizeable population of some 200 individuals occupies saltmarshes of the Nelson-Marlborough region (Elliott 1987; Bellingham 2013) while banded rails have historically occurred in numerous inland wetland sites (e.g., Whangamarino and Waitakere wetlands). Indeed, the Department of Conservation attempted to reintroduce banded rails to Whangamarino wetland within the last decade (New Zealand Department of Conservation 2017), although officials have been unable to ascertain whether this was successful or not. Moreover, banded rails are known to persist in sites and estuaries where mangroves have been partially or entirely removed, although potentially at lower densities than prior to mangrove removal (Chapter 3).

While mangroves may not be a prerequisite for banded rail survival, they may be a preferred habitat choice for individual birds, even when alternate estuarine habitats are available. As shown in Chapter 6, banded rails select for mangroves over saltmarsh (or other open habitats) to support foraging efforts, potentially even doing so when the abundance of food resources in mangroves is lower than in adjacent habitats. Arguably, this selection is underpinned by the high availability of resources to banded rails in mangrove environments, as these habitats may minimise predation risk and competition relative to other habitats. Moreover, mangroves can act as roost sites for banded rails, increasing the likelihood that mangroves forests can cover the functional needs of banded rail individuals outside of the breeding season. In addition, the presence of mangroves may make small patches of breeding habitat viable for banded rails; Beauchamp (2015) has observed banded rails to consistently occupy tiny patches of saltmarsh (< 0.001 ha) where these breeding habitats are surrounded by extensive areas of mangroves. There is also a chance that mangroves bordered by dense vegetation such as grasses or ribbonwood, rather than saltmarsh, provide a habitat composition which can support both breeding and foraging efforts (Botha 2011). More research is needed into the effects of habitat composition on banded rail persistence and breeding success.

Viewed from a population perspective, mangroves likely play an important role in supporting New Zealand's banded rail population – an estimated 80-90% of banded rails occur in the saltmarsh-mangrove complexes lining the northern shores of New Zealand's (Bellingham 2013). However, in a fictional scenario where New Zealand authorities removed all its mangroves (but not its saltmarshes), the banded rail metapopulation of northern New Zealand are likely to persist, given that the species inhabits similar saltmarsh ecosystems on the South Island. But this fictional outcome has a notable caveat: removing mangroves would almost certainly lead to a substantial decline in the banded rail metapopulation and the disappearance of local sub-populations (Huang *et al.* 2020). While this seems a logical statement based on existing research, this thesis provides evidence for this assertion, showing that mangroves are preferred over saltmarsh by banded rails for foraging and that mangroves comprise a substantial proportion of a banded rail's home range area (Chapter 6). Moreover, limited monitoring data from mangrove removals suggests that banded rail populations may decline following mangrove removal, and in some instances disappear altogether from patches of previously suitable habitat (Chapter 3). Additionally, the assumption that a loss of mangroves would lead to banded rail decline aligns with historical data for the banded rail's population and distribution in New Zealand. The loss of suitable inland wetland habitat during the 20th century, combined with introduced predators (Elliott 1983), has all but wiped out the population of inland banded rails. Thus, while breeding habitats like saltmarsh may remain the ultimate limiting factor for banded rail populations in New Zealand, their ability to provide functional habitat would likely be significantly reduced by the loss of adjacent mangroves. Moreover, the effects of habitat loss would be exacerbated by fragmentation and the small population paradigm, dramatically increasing the risk of extinction in a species of 5,000-20,000 individuals classified as declining and range-restricted and predicted to decline 10-30% in the next 10 years (Caughley 1994; Robertson *et al.* 2017, 2021). Consequently, the fictional removal of all mangroves in New Zealand makes for a bleak outlook from a conservation perspective.

Thankfully, the chances of losing all New Zealand's mangrove forests in the foreseeable future are slim to none. As shown in Chapter 3, mangrove expansion in New Zealand has significantly outpaced mangrove removal efforts. Moreover, mangrove forests are predicted to continue expanding unless rates of sedimentation decline substantially (McBride *et al.* 2016), a calculation which accounts for the effects of sea-level rise. While mangrove removal remains a threat to banded rail populations, this threat is currently contained to localised areas and affects a small minority of the total mangrove area in New Zealand (Chapter 3). Nevertheless, coastal managers need to ensure they are discerning in their interventions, being careful not to remove high-quality areas of mangrove forests which support persistent populations of banded rails. To complement this approach, future research should focus on the habitat quality of new-growth mangroves to determine if they compensate for mangroves lost to removal.

In summary, this study has shed light on the importance of mangrove habitats to banded rails. Within the context of habitat theory, this PhD thesis has shown that banded rails select for and extensively use mangrove habitats in saltmarsh-mangrove complexes. Contextualising these findings within conservation and habitat management practices, this thesis suggests that mangroves play an important role in preserving New Zealand's banded rail population and preventing the further decline of this species. Three observations from this thesis are particularly relevant to conservationists and coastal managers in New Zealand: (1) mangroves are not uniform habitats; mangrove forests may appear structurally similar, but can be functionally different in their ability to support avifauna populations, (2) mangroves are more important to banded rails than previously understood or quantified; mangroves are preferred as foraging habitat to banded rails, can support roosting behaviours, and may make small patches of adjacent saltmarsh or terrestrial scrub viable breeding habitats, and (3) mangrove removal is likely to adversely affect local populations of banded rail, but more research is required to understand the nuances of these effects.

7.8 References

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