

# **Resources to Aid Decision-Making in Conservation Translocations**

***Developing and Evaluating Ecological Models for Takahē (Porphyrio hochstetteri)  
Applied to a Reintroduction to Kahurangi National Park***

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The candidate confirms that the work submitted is their own, except where work which has formed part of jointly-authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

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## Abstract

Species translocations, including reintroductions, are an increasingly important tool for the management of many threatened species. However, globally the success rate of reintroductions has been low. This is due in large part to gaps between ecological theory and conservation practice inhibiting effective planning and execution of reintroductions. Better integration between ecological theory and practice can be achieved through the application of clear strategic frameworks. Predictive ecological models are also increasingly being used to inform conservation practice, and these models have potential to bridge gaps between theory and practice in translocation management.

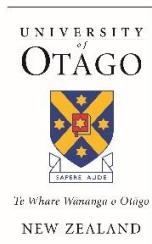
South Island takahē (*Porphyrio hochstetteri*), like many species subject to reintroduction efforts, persist in relict and small, restored, populations in often marginally suitable environments. Generating useful models and predictions of habitat suitability in reintroduction landscapes based on data collected within a relict range is therefore difficult, requiring careful treatment and interpretation. I illustrate this for the takahē by modelling habitat suitability in a reintroduction landscape based on location records from a relict distribution. Through careful interpretation of relict-population data potentially useful predictions are generated for informing management of the translocated population, including supporting the view that there is suitable habitat around release sites in the Gouland Downs. However, these predictions are sensitive to model settings relating to the interpretation of input data, as there was an 84% greater area of suitable habitat predicted by models that were fitted to allow more extrapolation, when compared with conservatively fitted models.

Post-release monitoring is crucial for the adaptive management of translocated populations. Satellite and radio-tag tracking methods were used to monitor the reintroduced takahē population. I first use data collected from this monitoring to provide an early evaluation of reintroduction success, finding that following initial breeding success and high survival, high rates of post-release dispersal appeared to be associated with mortality events two years after initial releases. Following a preliminary evaluation of reintroduction success, I develop models of space use based on the radio-tracking dataset, and models of resource selection based on the satellite tracking dataset. Integration of these two models in a hybrid model framework enabled me to combine insights from these individually limited, but

complementary, datasets, producing a high-resolution estimated distribution for the reintroduced population.

Model validation is a crucial step in the development of ecological models, as this can highlight the strengths and limitations of predictive models and ensure that they are applied to management with a suitable weight and confidence. I use independently observed and modelled post-release data to evaluate the habitat predictions based on observations from the takahē's relict distribution. These evaluations suggest that predictive models are reasonably effective, with the best performing models of post-release movements, resource selection, and population distribution having an estimated accuracy of 74.6%, 59.4%, and 72.2%. Routes for further refinement of the predictive models as well as estimating their overall predictive accuracy are also indicated by these evaluations.

I expect that the developments made in this thesis will be of value, providing a strong evidence-base that enables a rigorous application of ecological data and theory to drive improvements in conservation practice. These benefits should apply both to takahē and to other species management programmes to which the developed ideas and methods can be readily applied.



## Co-Authorship Form

This form is to accompany the submission of any thesis that contains research reported in co-authored work that has been published, accepted for publication, or submitted for publication. A copy of this form should be at the front (after the thesis abstract) of the thesis submitted for examination and library deposit.

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Chapter/ Append.	Paper title	Authors	Contribution of candidate and co- authors – please detail the nature and extent (%)	Journal	Status (e.g. under review, forthcoming, published)
Chapter 2 (with parts of Chapter 4 and Appendix A in Suppleme ntary Informati on)	Novel conditions in conservation translocations: a conservative- extrapolative strategic framework	Hunter-Ayad, James Jarvie, Scott Greaves, Glen Digby, Andrew Ohlemüller, Ralf Recio, Mariano R Seddon, Philip J	JH-A (candidate)- Conceived the idea and scope of the work; reviewed the literature and led the writing of the manuscript. (70%)  SJ- Synthesised the literature and led the writing of the tuatara case-study; critical review of the whole	<i>Frontiers in Conservatio n Science</i>	Published

			<p>work (10%).</p> <p>GG+AD- Significant input and feedback on the Takahē case-study and critical review of the whole work (7%).</p> <p>RO+MRR- Contributed to development of the subject/scope of the work; critical review of all drafts (5%).</p> <p>PS- Idea for submission to special topic; contributed to development of the subject/scope of the work; critical review of all drafts; oversaw development/submission of work (8%).</p>		
3	Reintroduction modelling: A guide to choosing and combining models for species reintroductions	Hunter-Ayad, James Ohlemüller, Ralf Recio, Mariano R. Seddon, Philip J.	<p>JH-A (candidate)- Conceived the idea and scope of the work; reviewed the literature and led the writing of the manuscript. (80%)</p> <p>RO+MRR- Contributed to development of the subject, scope and content of the work; Critical review of all drafts (8%).</p> <p>PS- Impetus for development of review paper; contributed to development of the subject, scope and content of the work; critical review of all</p>	<i>Journal of Applied Ecology</i>	Published

			<p style="text-align: center;">drafts; oversaw development/submiss ion of work (12%).</p>		
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**Certification by Primary Supervisor:**

The undersigned certifies that the above Table correctly reflects the nature and extent of the candidate's contribution to this co-authored work

Name: *Professor Philp J Seddon*

Signature:



Date: 25 Nov 2021



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## **Chapter 1**

### **General Introduction**

Reintroductions are a key component of conservation management for many species and should be informed by the most robust ecological understanding possible; ecological models are often employed to provide this. In this thesis I develop and evaluate resources to support the reintroduction and conservation management of South Island takahē (*Porphyrio hochstetteri*). This chapter provides an overview of the conceptual backbones of this study: 1) reintroduction biology, 2) New Zealand conservation, 3) the study species-takahē and 4) reintroduction modelling. I conclude by stating the scope, aims and objectives of my PhD and providing an overview of the chapter structure.

#### **1.1 Reintroduction Biology**

In recent decades there has been a progressive shift from “fortress-style” conservation towards more active ecological manipulations aimed at restoring lost biodiversity (D’Amico, 2015; Pettorelli *et al.*, 2018). Conservation translocations, or the human-mediated movement of living organisms from one area, with release in another where the primary objective is conservation benefit (IUCN/SSC, 2013), are an example of this new wave of more intensive manipulations. Reintroductions are an important subset of conservation translocations, defined as the deliberate movement of organisms from one site for release into parts of its indigenous range from which they have disappeared (IUCN/SSC, 2013). Reintroductions and other conservation translocations are an increasingly important component of conservation strategies aiming to restore and enhance ecosystems and preserve endangered species. Reintroduction has been proposed as a potentially effective method to mitigate declines in biodiversity and ecosystem health brought about by anthropogenic damage and degradation (Seddon *et al.*, 2014; Taylor *et al.*, 2017).

Although reintroductions can potentially have drastic and significant positive impacts by bringing iconic species back from the brink of extinction (Seddon *et al.*, 2014), they are fraught with ecological, societal, and financial risk. Ecological risks include the outright failure of a reintroduction, resulting in increased mortality and population declines for the focal species (White *et al.*, 2015). Also of concern is the potential introduction of pathogens, parasites, or pests to a new area, through inadvertent co-introduction with focal species

(Smith, Werner and Kelcey, 2012; Carter, Foster and Lock, 2017; Doherty and Ritchie, 2017). Further, there is also a risk of unforeseen trophic disruption, resulting from the reintroduction of a species into a food web that has shifted since their extirpation, inherent in many reintroductions (Hunter *et al.*, 2015; Svenning *et al.*, 2016).

Societal risks that may be encountered include pushback (and potential sabotage and/or retaliatory killing of released animals) resulting from local human communities having their land-use and freedoms restricted as a result of an area acting as a reintroduction site (Fernández, Kramer-Schadt and Thulke, 2006). This is particularly likely when controversial or potentially dangerous animals are reintroduced, e.g., large carnivores (Schadt *et al.*, 2002; Phillips, 2017).

Financial risks are inherent in activities necessary to conduct a reintroduction, e.g., capture of wild animals and/or captive breeding and rearing of reintroduction cohorts, transport to release sites, release site management and post-release monitoring and management, not to mention public consultation and planning. These are costly endeavours and there is always a risk that this investment will be lost if a reintroduction is unsuccessful (Kramer-Schadt, Revilla and Wiegand, 2005).

In light of these risks it becomes important that reintroductions are carefully planned so that as many of these risks as possible can be managed and mitigated (Ovenden *et al.*, 2019). Reintroduction plans are often complex due to the necessity to account for the highlighted ecological, social and financial impacts of any reintroduction attempt. Ecological modelling has increasingly been recognised as a key tool to aid reintroduction planning and increase the chances of success (Seddon, Armstrong and Maloney, 2007; IUCN/SSC, 2013). In this thesis I develop resources, including ecological models, to inform and support the management and planning of conservation translocations.

## 1.2 New Zealand Conservation

New Zealand (also known as Aotearoa New Zealand, hereafter NZ) is an iconic setting for ecological conservation. As an isolated archipelago NZ has a unique biota considered to have developed in the absence of terrestrial mammalian lineages (excepting Microchiropteran bats; Greaves, Mathieu and Seddon, 2006; but see Worthy *et al.*, 2006), until the discovery of the landmass by humans ~1280 A.D. (Wilmshurst *et al.*, 2008) and the consequent introduction of numerous mammal species (O'Donnell, Weston and Monks,

2017). The unique biodiversity of NZ has been degraded as a result of increasing anthropogenic ecosystem modification over several waves of human colonisation, including from direct harvest, land modification, and the introduction of mammalian predator, pest and competitor species (Jamieson, Wallis and Briskie, 2006). This has resulted in the extinction of many ecologically unique species that were found nowhere else on the planet, notably all nine known moa species (order *Dinornithiformes*), Haast's eagle (*Heiraasetuts moorei*), laughing owl (*Ninox albifacies*), and adzebills (*Aptornis* sp.; Worthy and Holdaway, 2002). Many other of the iconic avian, reptilian, and insect species characteristic of the pre-human NZ ecosystem, although avoiding extinction, nevertheless experienced severe population and range declines (Saunders and Norton, 2001; Garcia-R and Di Marco, 2020).

Although declines in NZ's native biota cannot easily be reversed, there has long been awareness and concern over the decimation of the country's biodiversity. As such, NZ became a pioneering nation in the field of ecological conservation in the 20<sup>th</sup> century (Lloyd and Powlesland, 1994; Lee and Jamieson, 2001; Saunders and Norton, 2001; Jamieson, Wallis and Briskie, 2006). Conservation management strategies developed in NZ include the use of offshore islands as natural reserves, where populations of invasive species are absent and/or can be effectively eradicated. The use of translocations has allowed the establishment of "safe" populations of highly threatened species via their establishment on predator-free islands. For example, the persistence and/or recovery of species such as kākāpō (*Strigops habroptillus*), black robin (*Petroica traversi*), North Island tīke (*Philesturnus rufasater*) and hihi (*Notiomystis cincta*) is largely thanks to the successful establishment of populations on predator-free islands (Cassey et al., 2007; Panfyllova et al., 2016; Lentini et al., 2017; Massaro et al., 2018). Through pioneering, increasingly intensive and high-impact management strategies, biodiversity managers in NZ provide hope that what remains of the unique ecological heritage of the islands might yet be conserved and to some degree restored (Saunders and Norton, 2001; Nelson et al., 2002; Panfyllova et al., 2016).

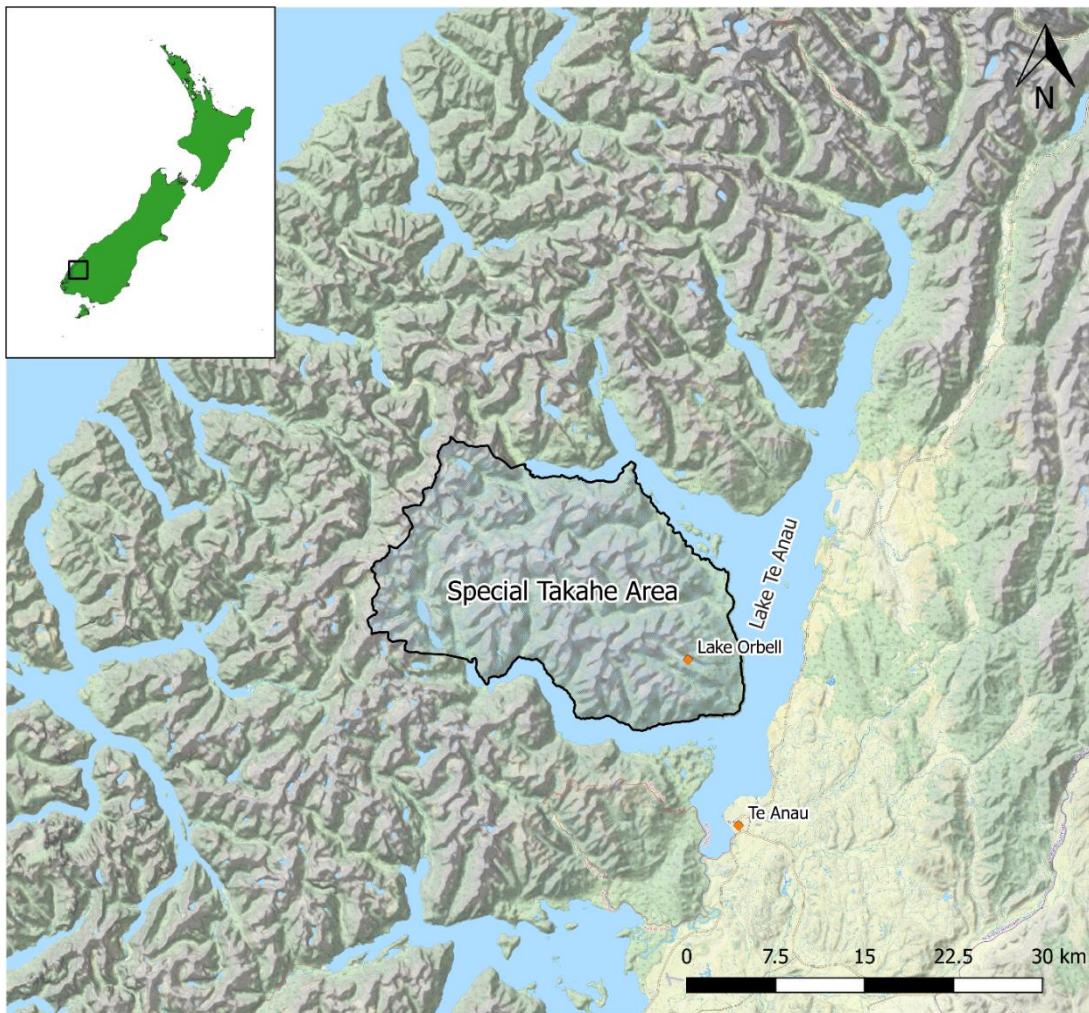
### 1.3 South Island Takahē

To provide a detailed case-study highlighting the application of concepts and modelling methods to reintroductions I use evidence from the nationally significant (given the taonga status of takahe, plus media and public attention given to the Kahurangi reintroduction as a flagship initiative) reintroduction programme for South Island takahē (*Porphyrio hochstetteri*,

hereafter takahē). Takahē are a globally endangered (Birdlife International, 2016b) and nationally vulnerable (Robertson *et al.*, 2016) flightless rail species endemic to New Zealand (Lee and Jamieson, 2001). At the time of human settlement in NZ, takahē were fairly common and widespread, with distinct species on the South and North Islands (*P. hochstetteri* and *P. mantelli*, respectively: Beauchamp and Worthy, 1988). However, these large flightless birds were a valuable food source for early human settlers and were likely easy prey for an array of introduced mammalian predators (O'Donnell, Weston and Monks, 2017). As a result takahē were likely near extinction by the time of European description of the species in the mid nineteenth century (Greuber and Jamieson, 2011). Between 1849 and 1898 only four contemporary encounters with takahē were recorded by Europeans (although subfossil, or partially fossilised, remains were found throughout NZ), all in the Fiordland region, meaning that by the start of the twentieth century the takahē was considered to be yet another NZ endemic lost forever (the status of *P. mantelli* and *P. hochstetteri* as separate species was not clear at that time; Lee and Jamieson, 2001).

However, the South Island species, *P. hochstetteri*, persisted, although as a relict population, largely restricted to the remote Murchison Mountains of Fiordland. This isolated population was rediscovered by an expedition led by Dr Geoffrey Orbell in 1948 (Lee and Jamieson, 2001). This dramatic rediscovery of a species previously presumed extinct triggered one of the earliest (both nationally and globally) large-scale species conservation initiatives, leading to the designation of a Special Takahē Area covering the whole of the Murchison Mountains (Figure 1.1; Hegg *et al.*, 2012).

The designation of the Special Takahē Area protected the only known population of takahē from ambitious hunters and would-be explorers and adventurers. However, the remote isolation of the Murchison Mountains (considered to be the major factor allowing this population to avoid eradication by humans and associated introduced species) was not enough to protect the population indefinitely, and severe population declines were observed in the 1970s (Lee and Jamieson, 2001). These declines were eventually put down to a combination of predation by invasive stoats (*Mustela erminea*) and competition from the introduced red deer (*Cervus elaphus*) which graze the tussock grasses on which takahē in the Murchison Mountains predominantly feed (Mills *et al.*, 1991).



**Figure 1.1-** Map of the Te Anau-Fiordland area showing the extent of the Special Takahē Area (border indicated by the black line) and the location of Lake Orbell, where South Island takahē (*Porphyrio hochstetteri*) were rediscovered in 1948. Basemap shown is the “outdoors” layer sourced from thunderforest.com.

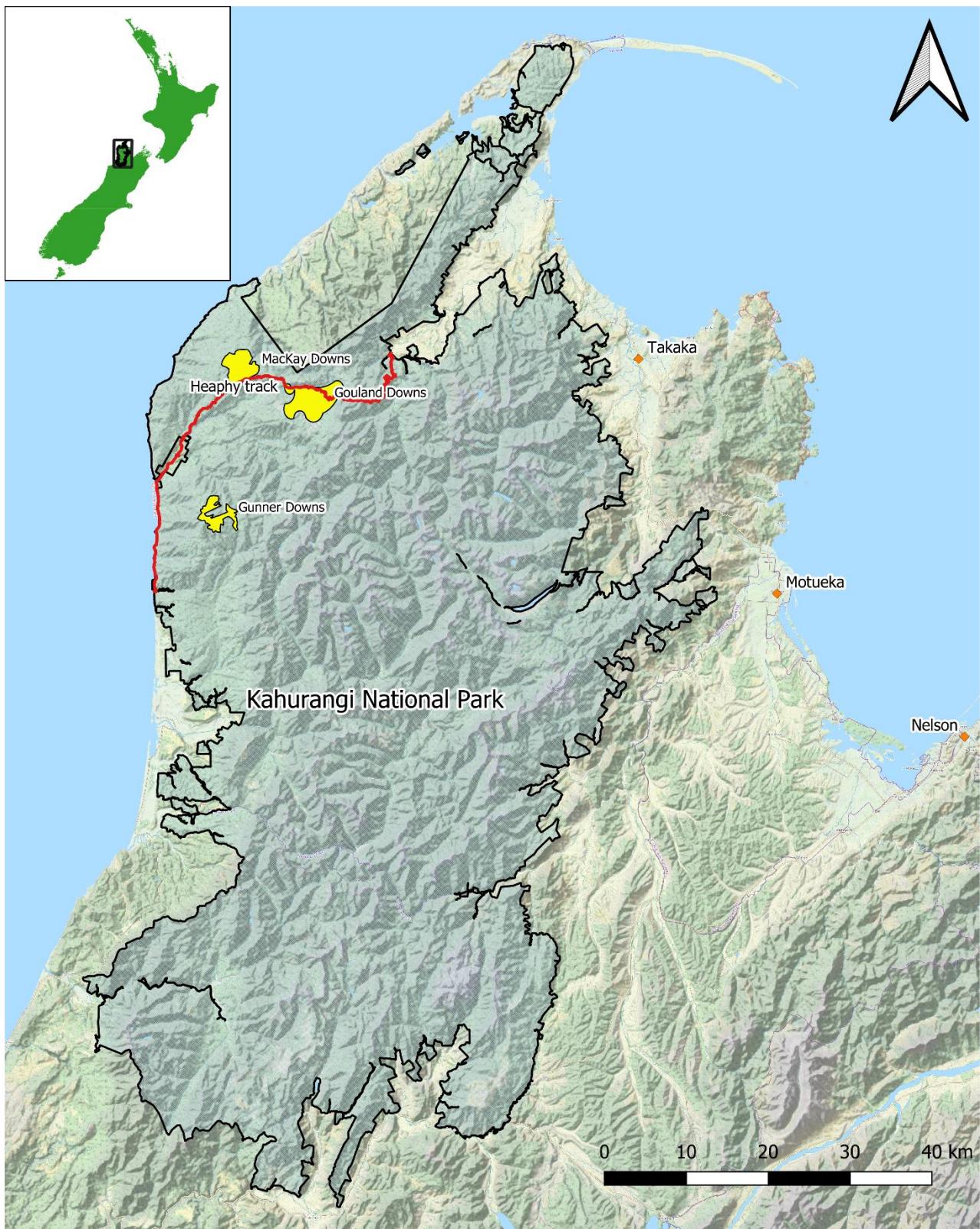
Although the emergence of these threats from introduced species was much delayed in the Murchison Mountains, compared with more readily invadable regions of NZ, they could not now be ignored if the species was to persist. The discovery of threats from invasive mammals in the 1970s triggered a review of conservation strategies and initiated a new phase of active management of takahē (Lee and Jamieson, 2001). Within the borders of the Special Takahē Area population control for deer and stoats was initiated, and has since continued to be a key aspect of takahē conservation (Mills *et al.*, 1991; Hegg *et al.*, 2012). Efforts also began in the 1970s to breed takahē in captivity and to establish captive populations to serve as a backup in case of a catastrophe in the one remaining, and increasingly vulnerable, wild population (Maxwell and Jamieson, 1997; for further review of

takahē conservation, focusing on translocation and reintroduction management, see section 2.7).

After almost forty years of active conservation management there is no longer any immediate threat of extinction for takahē. The wild population in the Murchison Mountains is growing every year (although it is assumed that this growth depends on reinforcements via releases of captive-bred birds, as the long-term average natural mortality rate outstrips breeding recruitment in the Murchison Mountains) and there are multiple small managed populations established in secure sites (a variety of offshore islands and nature reserves where invasive species are absent; Figure 2.3) across NZ (Greuber, Maxwell and Jamieson, 2012).

Although there now exists a secure national metapopulation of takahē, this is also highly managed, with regular translocations required to maintain demographic and genetic diversity. This intensive management entails high upkeep costs in terms of the financial, time and logistic resources required to maintain the structured metapopulation (Lees *et al.*, 2014). Moving from this high-cost, highly-managed metapopulation towards establishing independent, self-sustaining takahē populations is a goal of the current phase of takahē management, which began in the mid-2010s with the first large-scale mainland reintroduction of the species (Takahē Recovery Program, 2016).

Having a secure and growing national population meant that by 2016 all existing sites maintaining takahē populations were reaching capacity. This meant that not only was a mainland reintroduction now possible, but it was required with some urgency (as further investment in alternative measures, e.g., conservation in the Murchison Mountains or establishment of further secure sites was considered to likely be inefficient and ineffective Takahē Recovery Program, 2016). A release site was eventually identified in the Gouland Downs, Kahurangi National Park (hereafter NP), in the north-western corner of the South Island (Figure 1.2). This site was selected due to the availability of large areas of apparently suitable habitat and either an absence or low density of invasive mammalian predators and competitors. It was further considered that Kahurangi NP was climatically and topographically more benign than the Murchison Mountains, which was expected to be beneficial for reintroduced takahē. The initial release of 30 birds sourced from the takahē breeding program took place in Gouland Downs in early 2018, with releases on the 20<sup>th</sup> March and the 1<sup>st</sup> May.



**Figure 1.2** - Map of Kahurangi National Park (border indicated by the black line), showing the location of the Gouland Downs release site and other Downs expected to provide suitable habitat (yellow) and the Heaphy Track (red), which provides access to the release area for recreation and conservation work, including post-release monitoring. Basemap shown is the “outdoors” layer sourced from [thunderforest.com](http://thunderforest.com).

### 1.3.1 Ecology and Behaviour of Takahē

It is difficult to provide definitive information regarding the fundamental aspects of takahē behaviour and ecology. This is in part due to the highly managed nature of the species, meaning that many patterns and observations are dependent on conditions modified by management interventions (e.g., translocations, captive breeding and resource supplementation). While additionally, and in some part due to these constraints, there is also limited information available in the peer-reviewed literature regarding the species as, particularly in recent years it has been difficult to conduct robust studies and when these have been conducted the impacts of various modified conditions must be taken into account. However, despite these constraints, there is much relevant and important knowledge of takahē of a species that is relevant to relay here, although it is often synthesised from a variety of unpublished sources, e.g., from unpublished and anecdotal observations combined with expert experience and inference. While more weight is perhaps given to observations in the takahē's relict distribution (as this is the closest to 'natural' conditions), I also incorporate knowledge and insight from captive breeding and secure sites to contextualise and supplement this information. In light of this pragmatic need to infer ecological information from a synthesis of non-ideal sources, I take care to highlight sources of ecological inference throughout the thesis. I also highlight where even the best available understanding presented must be considered potentially inaccurate and should be interpreted with caution.

Takahē are a moderately long-lived species, with a lifespan of approximately 20 years in secure sites (although this is rarely reached in the Murchison Mountains where this is reduced to  $\approx$  15 years: TRG, unpublished demographic data). Takahe form territorial breeding groups that are maintained over several years, these are most commonly monogamous but can include polygamous groups of up to 5 individuals (this is perhaps encouraged and over-represented in the small, closed populations at secure sites). Takahē breed annually, nesting between September and January, with offspring usually remaining with their parental group as nest helpers until their second year, when they leave their parental group and attempt to breed independently (both in secure sites and in the Murchison Mountains).

The primary food source of takahē in the Murchison Mountains is of the leaf bases of three species of snow tussock grasses (*Chionochloa pallens*, *C. flavescens*, *C. crassiuscula*). However, in winter, when tussock grasses are inaccessible due to snow cover, takahē

instead feed on rhizomes of summer-green fern, *Hypolepis millefolium* (Mills *et al.*, 1991). Food resources at secure sites are generally more variable, and at some sites are supplemented with cereal-based pellets. This has led to some local behavioural adaptations as takahe at secure-sites expand their use of resources that have limited availability in the Murchison Mountains such as fallen fruits, exotic grasses, small reptiles, and the chicks of other bird species (particularly ducks). This has demonstrated that takahē are a more adaptable and generalist species than is evident from their behaviour and ecology within their relict population, though the degree of their generalist nature remains unclear (Beauchamp and Worthy, 1988).

### **1.3.2 National Population Management**

Prior to the Kahurangi reintroduction the global takahē population was managed as an artificially established and maintained meta-population (Lees *et al.*, 2014; Greaves *et al.*, 2020). This management entails continual translocations between and within the relict population and secure site network to promote population stability and growth as well as to maintain current levels of genetic diversity within the species (although genetic diversity in the species is expected to be much reduced from levels prior to population and range declines; Greuber and Jamieson, 2011). In the future there is potential for the Kahurangi population to be incorporated into this program as for the relict site, though this cannot, and should not, occur unless or until a stable population becomes established in the NP. The long-term goal for the takahē management is to establish sustainable wild populations of takahē within their historic natural range. Maintaining the national meta-population plays a critical role for genetic insurance and population growth purposes, though the structure of this meta-population (particularly the use and extent of secure sites) continues to be reviewed and adapted as species recovery progresses and circumstances change (Lees *et al.*, 2014; Greaves *et al.*, 2020).

A key goal of species management has been to remove gender biases across both global and local takahe populations (as recruitment potential is maximised with a 50:50 gender split; Greaves *et al.*, 2020). Historically, a male bias was observed in the Murchison Mountain population, which led to attempts to restore balance through release of female-biased groups when conducting reinforcements. This has been possible due to an abundance of females in the Sanctuary Site population (Lees *et al.*, 2014; Greaves *et al.*, 2020). Although balanced populations are the target, this has been hampered by several years of strong female bias in recruitment, and high rates of male mortality. Although these

gender balance issues have largely been resolved, some unexpected male mortalities prior to the Kahurangi NP reintroduction meant that the cohort was female biased (19 females:11 males). While compromises in terms of sex ratio are acknowledged, this was an informed decision based on observations from other populations and bird fitness was not compromised. It was hoped that a female gender bias would not present an issue as observations from secure sites indicated that gender biases generally lead to a higher incidence of polygamous breeding groups (i.e., trios and quads; TRG, unpublished data), though this assumed that experience from secure site management would apply to the wild release. However, it remains a key aim to have a 50:50 gender split for future site establishments (Greaves *et al.*, 2020).

Although there is now a long history and established practices for takahē translocations, with regards to expectations for the Kahurangi reintroduction, this is the first release of its type so historical inferences have limited applicability. The majority of takahē releases occur in sites with an established population (i.e., relict distribution and secure sites). Releases in the Murchison Mountains are very successful in terms of survivorship and establishing pairings and territories, although dispersal can be high (Hegg *et al.*, 2012). New island and sanctuary sites are not particularly relevant as dispersal is strictly limited by water or fenced boundaries (Greuber, Maxwell and Jamieson, 2012).

The only other wild reintroduction attempt for takahē was to the Stuart Mountains, Fiordland, which saw releases between 1987-92, but ultimately failed. Due to technology available in the 1980 and early 1990's, plus funding and site accessibility limitations, inferences gleaned from post release monitoring are limited. Only 22% of released birds were known to be alive by 1994, with the majority of the rest having an unknown fate. However, a few suggested lessons did help inform the Gouland release – particularly releasing adults and family groups, and increasing the size of release cohorts (Maxwell, 1995).

### **1.3.3 Release Procedures**

#### *Pre-release*

Before being transported to the release site, all birds in the reintroduction cohort were appropriately trained for the conditions in the release area (i.e., alpine tussock environments) at Burwood Takahē Centre, Te Anau (Department of Conservation, 2021). This protocol followed the same process that has proven successful in bolstering the post-

release survival and establishment of birds translocated to tussock environment in the Murchison Mountains (Hegg, Mackenzie and Jamieson, 2013). The only major change specifically for the Kahurangi reintroduction is that family groups were released together, rather than groups of sub-adult unpaired birds. This was an effort to release birds that may be exhibit more stable social dynamics, potentially allowing them to establish and provide useful data more rapidly (Haydon *et al.*, 2008; Panfyllova *et al.*, 2016).

#### *Post-release*

Birds were transported from Te Anau to their release sites in Kahurangi NP via air travel (by aeroplane from Queenstown to Nelson and then by helicopter into the NP; Department of Conservation, 2021). The reintroduction followed a hard-release procedure, where birds were allowed to roam freely immediately following transport to the release-site (Attum and Cutshall, 2015). Soft-release, involving the use of penning or another method of temporary containment at the release sites, was not considered to be either practical (given the lack of appropriate infrastructure at the remote sites) or particularly beneficial (as previous experience has shown limited value in soft-releases; Greuber, Maxwell and Jamieson, 2012). Additionally, no supplementary food was provided following releases as this was considered untenable given the scale of releases that were being undertaken into the wild (Elliott, Merton and Jansen, 2001; Chauvenet *et al.*, 2013).

A pest-control programme covering Kahurangi NP was in place long before the reintroduction was conceived and has continued throughout the reintroduction. This pest-control involves a combination of static trap-lines (using approximately 170 ‘DOC 200’ box-traps, which were being supplemented with a novel deployment of approximately 700 Goodnature A24 self-resetting traps in the period following the release of takahē) and periodic aerial drops of poison baits (using sodium fluoroacetate, or 1080; Eason *et al.*, 2011). This scenario constitutes a feasibility test, given the many unknowns prior to release, though it was nevertheless informed by successful ‘hard’ releases elsewhere (Greuber, Maxwell and Jamieson, 2012).

## **1.4 Predictive vs. Descriptive Reintroduction Models**

The takahē reintroduction project is reliant on stretched and limited resources, as is the case for many conservation-management programmes. It is imperative that such programmes are based on the best possible ecological understanding so that management

can be as effective and efficient as possible (White *et al.*, 2015). However, for relict species such as takahē, that are known to inhabit only a fraction of a prior range, developing this ecological understanding is complex, as records are typically fragmented and relate to small numbers of individuals in atypical settings. Developing an ecological understanding and making quantitative predictions based on such data must necessarily involve some level of inference and extrapolation (Elith, Kearney and Phillips, 2010; Keeley *et al.*, 2017).

Such inference or extrapolation can be formalised when an ecological model is created. These models provide managers with quantitative, and often spatially explicit, predictions of a system or process and how these might respond to various management actions. These predictions will be based on inferences around empirical data made by applying statistical and ecological knowledge. These ecological models can be a valuable management tool as they allow management policies and actions to be tailored to maximise likely success prior to resources being invested on the ground. It is of key importance that these models be robust and able to accurately reflect ecological patterns and requirements for focal species. The current takahē distribution is strongly influenced by both historic and recent interactions with humans and human-introduced biota (see sections 1.3 and 2.7). This introduces bias into ecological records for takahē, which must be taken into account when inferring patterns from these data in order to ensure that ecologically meaningful relationships are identified (Breiner *et al.*, 2015; Britnell *et al.*, 2021).

In this thesis I differentiate two conceptually distinct applications of ecological modelling to conservation management; pre-management prediction and post-management analysis, hereafter termed predictive and descriptive models, respectively (following Arntzen, 2006). Under this framework, predictive models are those developed in order to advise and direct management actions through pre-emptive identification of patterns and responses to putative threats and/or management actions (Heikkinen *et al.*, 2015; Stone and Guy, 2017). Descriptive models, on the other hand, are models directed towards post-hoc analysis of observed data with the aim of evaluating current approaches to inform future decisions, for example, via adaptive management frameworks (Yott *et al.*, 2011; Peters *et al.*, 2015; Massaro *et al.*, 2018).

As this distinction is application-focused rather than structure focused, there are several modelling approaches that could be applied both predictively and descriptively. However, the structure, data requirements, and assumptions inherent in different model methodologies will make some more suited to predictive or descriptive applications, while

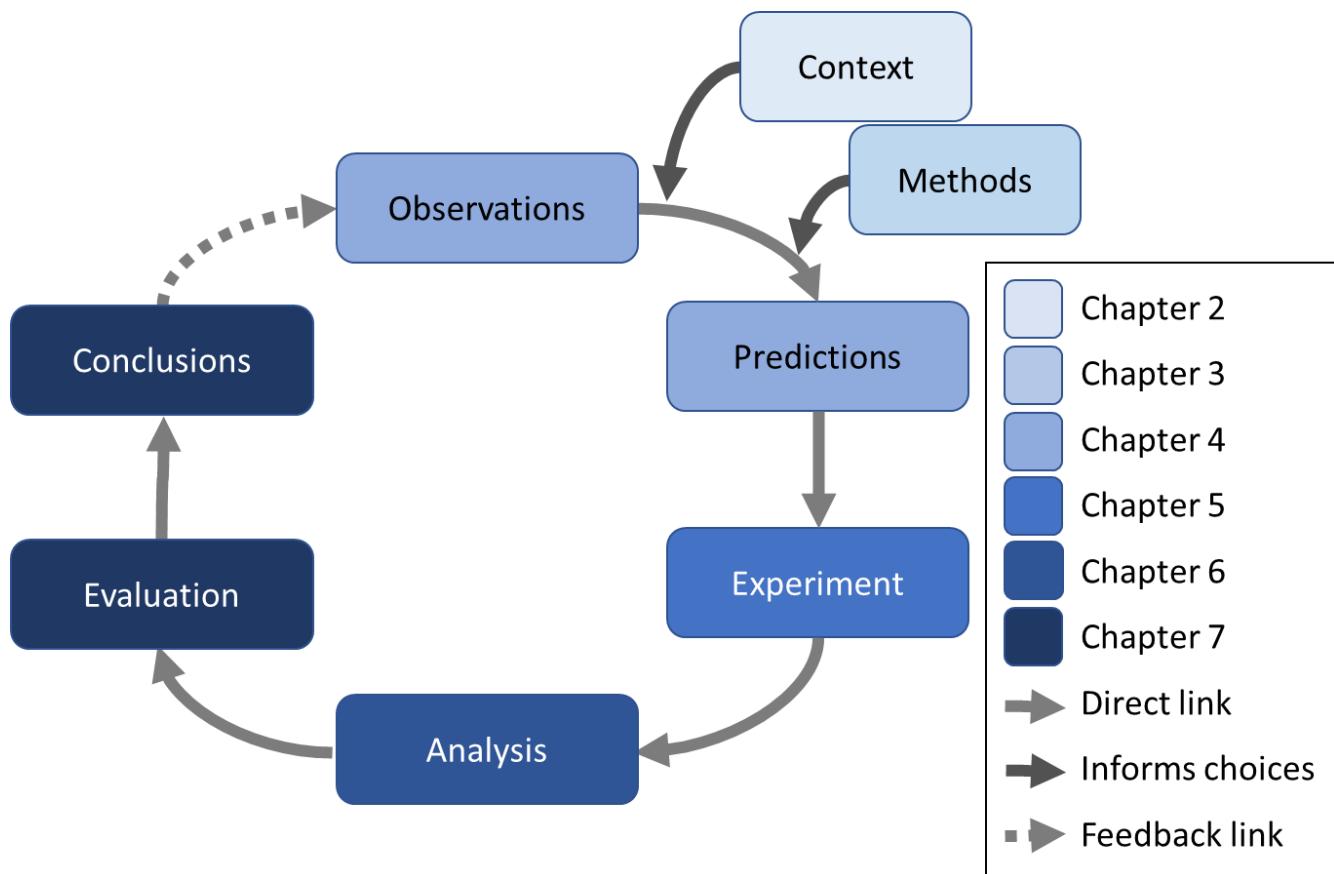
others can, and often are, applied in both predictive and descriptive contexts (Ehrlén and Morris, 2015; Araújo *et al.*, 2019).

## 1.5 Broad Scope- Applied Ecology Research

Beyond specific applications to takahē conservation, this thesis can be considered as a case-study for the application of ecological concepts and analytical methods to support the management of conservation translocations. I hope that the outputs and methods within the thesis will be useful for informing the management of conservation translocations for a range of species. Therefore, I will briefly consider the broader context of integrating conservation science and practice and describe how this has influenced my approach to the takahē study.

Conservation science and practice are often poorly linked (Bormpoudakis and Tzanopoulos, 2019), including in reintroduction biology (Taylor *et al.*, 2017). While there are many complex factors inhibiting science-led management (e.g., time lags in producing research outputs, a lack of clear communication between researchers and managers and compromises to meet the needs of multiple stakeholders; McGregor *et al.*, 2014; Weng, 2015), one contributing factor is the often opportunistic and correlational nature of applied conservation research. In most ecological systems of conservation interest there are limited opportunities to apply experimental treatments (along with appropriate control treatments), reducing the rigour with which scientific standards can be maintained. This has the follow-on effect that ecology is often perceived as a ‘soft-science’, as the reduced capacity to control and manipulate focal systems means that there is often less clarity and confidence in the attribution of causal mechanisms when compared to standards in the ‘hard-sciences’, e.g., physics, chemistry and mathematics (Seddon, Armstrong and Maloney, 2007). While this paradigm will likely never be fully overcome, one feature that at least may be improved in some cases is the increased and transparent application of the scientific method (following the formalised steps whereby observations lead to hypotheses, which generate predictions to be tested, leading to the evaluation and appropriate revision of the posited hypotheses; Kovačić-Popović, 2021; Figure 1.3) within ecological studies aiming to inform conservation management (Armstrong and Seddon, 2008). Application of this more formal study design may help to increase the confidence and clarity with which research outputs can be communicated to conservation practitioners, potentially increasing the integration of these outputs into management plans (Zurell *et al.*, 2021).

The work within this thesis was conceived and structured in order to follow the principles of the scientific method (Kovačić-Popović, 2021; Figure 1.3). First, observations were gathered from the records kept by the Takahē Recovery Group (TRG). These were then used to develop predictive models representing hypotheses regarding takahē habitat requirements and dispersal patterns. The application of these models to the Kahurangi reintroduction allowed these hypotheses to be translated into predictions. Following this, to test predictions, the post-release dynamics in the reintroduced population were observed. Following the application of descriptive models to post-release datasets (to interpret these data and provide outputs comparable in format to those in which predictions were presented) these independently gathered observations were compared with predictions to evaluate the accuracy of these predictions and thus the validity of underlying hypotheses. This process means that the outputs of this thesis should be able to be applied to takahē management and presented with an appropriate level of confidence/weight given specific strengths and limitations observed during the evaluation process. Application of similar research frameworks also have the potential to strengthen evidence-led adaptive management for translocations of other species.



**Figure 1.3-** Conceptual workflow showing the broad strategy employed throughout this thesis. Box colours indicate the chapter in which each aspect is of the workflow is covered. Arrow colour indicates what type of link is illustrated, a direct methodological connection (light grey), an interpretive/decision informative link (dark grey) or a potential feedback link (dashed light grey). Note that while the feedback links are set up within the thesis, recommendations from evaluations and conclusions have not yet been implemented.

## 1.6 Thesis Aims and Objectives

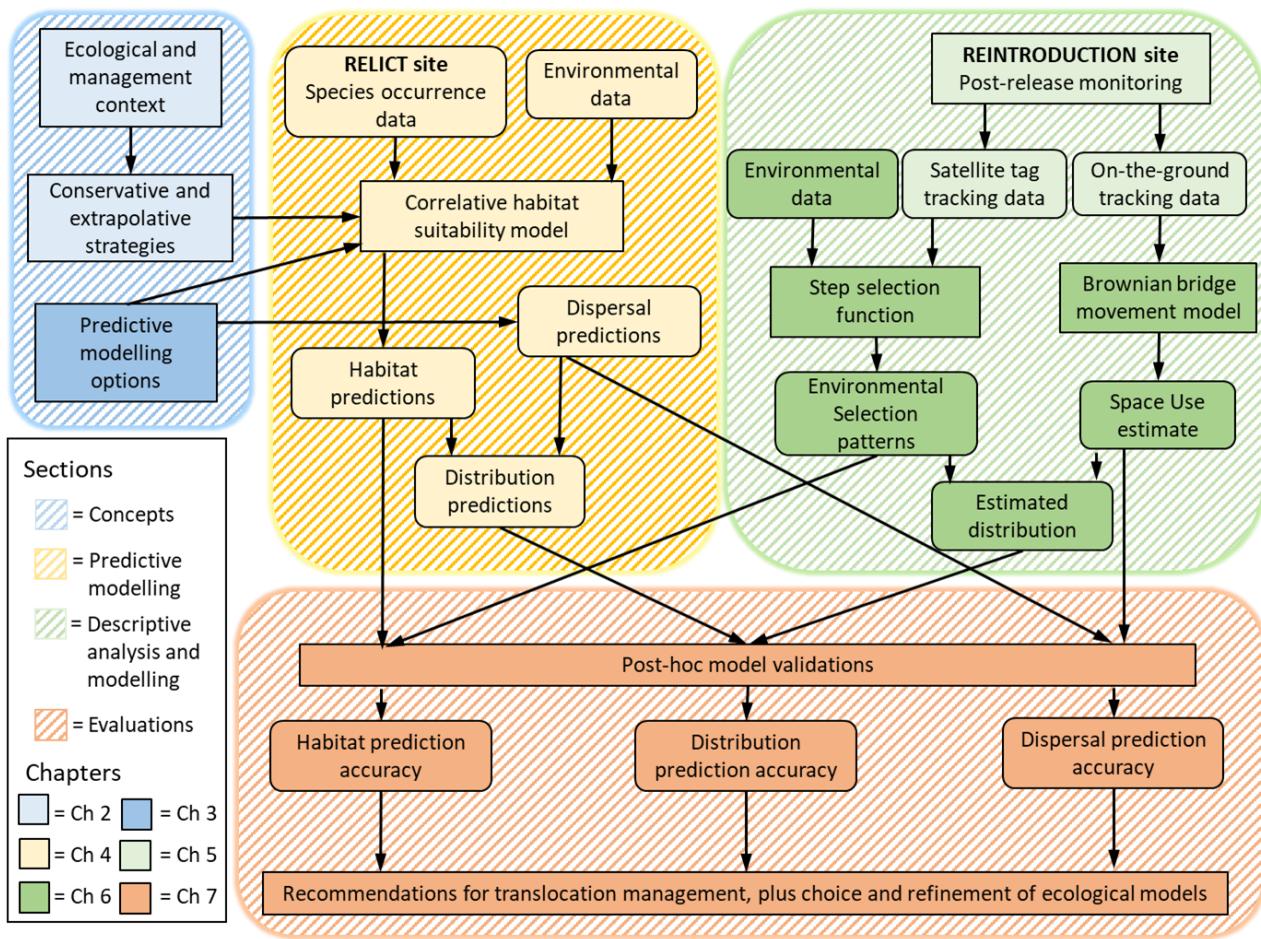
My PhD project has been developed as a collaboration between the Department of Conservation's (DOC) Takahē Recovery Group (TRG) and the University of Otago Department of Zoology. The main aim of this thesis is to develop resources to inform the conservation management of takahē into the future. While a secondary, broader, objective is to use the case-study of takahē to illustrate concepts, strategies, and methods for enhancing linkages between conservation practice and ecological theory applicable across many species.

## 1.7 Thesis Outline

In this thesis I explore how conservation practice might be better linked with ecological data and theory to better plan, execute, and evaluate conservation translocations. To this end I have developed literature-based chapters developing both strategies and methods that may be applied to reintroduction management. The following data chapters are then focused on the case-study of the reintroduction of takahē to Kahurangi NP, NZ, in 2018.

This thesis is written as a series of stand-alone but inter-related papers (see Figure 1.4) intended for publication, plus a General Introduction and General Discussion. As a result, some overlap and repetition between chapters was inevitable; I tried to minimise this by avoiding repeated descriptions of the taxonomic status of takahē and sampling sites used in multiple chapters (Chapters 4, 5, and 6) and combining field methodology into one chapter (Chapter 5). Two chapters (Chapters 2 and 3) have already published and, in such cases, a note at the beginning of each chapter makes this clear. To improve the flow of the thesis, I employ a standard format, use the first person singular and cross-reference by chapter number, including a publication reference when referencing chapters 2 and 3.

Chapter 2, published in *Frontiers in Conservation Science*, develops the practical context of the thesis. Here, with my co-authors, I developed a strategic framework, suggesting approaches that can be taken towards the exposure of translocated species to novel conditions. The development and presentation of this framework incorporates the review of a wide range of ecological studies, considering the numerous important practical and ecological dimensions of planning conservation translocations. This framework is also applied to reviewing the history and development of translocation management for tuatara (*Sphenodon punctatus*) and takahē to illustrate the application of the developed strategies. Author Contributions for this work: J.H.-A., P.J.S., M.R.R. and R.O. conceived the idea and scope of the work; J.H.-A. reviewed the literature and led the writing of the manuscript. S.J. led the writing of the tuatara case-study, while A.D. and G.G. provided crucial comments towards the takahē case study, as well as the manuscript as a whole. All authors contributed critically to the drafts and gave final approval for publication.



**Figure 1.4-** Methodological workflow showing the process followed throughout the thesis and indicating key links between chapters and sections. Colours are used to group the thesis into sections and identify which chapters contain specific outputs/processes. See main text for definitions and further details.

Chapter 3, published in the *Journal of Applied Ecology*, synthesises the current literature on ecological modelling to provide a broad overview of the types of predictive models available to support reintroduction decision making. The chapter considers many model types in terms of their potential utility and limitations when applied to conservation reintroductions, and further provides a framework for combining models of different aspects of species ecology in order to maximise their utility to practitioners. Author Contributions for this work: JH-A, PS and RO conceived the idea and scope of the work; JH-A reviewed the literature and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Chapter 4 uses data from the relict distribution of takahē in the Murchison Mountains to develop correlative habitat suitability models, which are applied to the reintroduction area

for takahē in Kahurangi NP. These models, using data from the only free-ranging takahē population (prior to the Kahurangi NP reintroduction), are useful for identifying home-range level habitat availability for takahē. The models predict the extent, structure, and quality of habitat available to the reintroduced population. To account for limited dispersal and exploration opportunities since the time of takahē release in the Gouland Downs, habitat predictions were coupled with simple dispersal models in order to predict the population distribution 30 months after release.

Chapter 5 explores the data that have been collected in the first 30 months since the initial release of takahē in the Kahurangi NP reintroduction. This exploration describes patterns of dispersal, survival, and productivity following initial releases, providing the basis of a preliminary evaluation of the relative success of the reintroduction.

Chapter 6 develops descriptive models based on the tracking data described in chapter 5. Long-term movement models are based on the low-resolution, high-coverage dataset produced by on-the-ground monitoring. While environmental selection models are based on the high-resolution, low-coverage dataset produced by satellite tag monitoring. Recognising a synergy and complementarity between the previous models, I combined them to produce a detailed estimated distribution of the reintroduced takahē in Kahurangi NP over the 30-month study period.

Chapter 7 evaluates of the predictive accuracy of models developed in chapter 4 via comparisons with outputs of descriptive models developed in chapter 6 (Figure 1.4). This evaluation allows the relative performance of different model options to be compared and confidence placed on the associated predictions. This is valuable in highlighting the relative strengths and weaknesses of predictive models, providing valuable feedback suggesting the extent to which such models can be relied on to guide future management of takahē, while also suggesting directions for their further development.

Finally, Chapter 8 is a general discussion discussing the practical applications and future directions for work developed in the thesis.

## Chapter 2

### Practical Context: Novel Conditions in Conservation Translocations

This chapter presents a strategic framework for approaching novel conditions in conservation translocations. This conservative-extrapolative framework is discussed with regard to relevant applications in conservation management and ecological research, with two case studies: tuatara (*Sphenodon punctatus*) and takahē (*Porphyrio hochstetteri*) included.

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#### 2.1 Introduction

Anthropogenic ecosystem degradation has occurred throughout human history (Waters *et al.*, 2016), resulting in species declines and extinctions. There has been an estimated 68% decrease in population sizes of mammals, birds, amphibians, reptiles, and fish between 1970 and 2016 alone (WWF, 2020). These population declines often go hand in hand with dramatic range contractions for many species (Faurby and Araújo, 2018). Conceptually this can be viewed as shrinkage of a species' realised niche as human activity reduces the portion of their fundamental niche space that is accessible (Scheele *et al.*, 2017). Species are often excluded from core niche spaces and restricted to a peripheral realised niche representing marginally tolerable conditions for the species (Crooks *et al.*, 2017). Such species typically persist in a relict distribution, representing areas of low habitat quality, but often with little human activity (Kerley, Kowalczyk and Crome, 2012; Kerley *et al.*, 2020).

Species that occupy only a fraction of their former geographical distribution are often conservation priorities, as without the factors driving their range contractions being halted and/or reversed, they remain at high risk of extinction (White *et al.*, 2014; Hunter *et al.*, 2016). The restoration of such range-reduced species increasingly includes conservation translocations, or the human-mediated movement of living organisms from one area, with release in another where the primary objective is conservation benefit. Reintroductions, to re-establish populations in areas of the species' indigenous range from which they had

previously been extirpated, and reinforcements, the release of individuals into an existing population of conspecifics to increase population viability, are important forms of conservation translocations (IUCN/SSC, 2013; Seddon *et al.*, 2014). There is inherent uncertainty in translocating range-reduced species, as most direct information of species' behaviour and environmental preferences will come from observations in their relict distribution (Mihoub *et al.*, 2014). While reintroductions will typically aim to release animals into areas of their indigenous range, such areas will rarely be directly analogous to the relict distribution (Osborne and Seddon, 2012; White *et al.*, 2014; Taylor *et al.*, 2017). As such, there will always be a degree of novelty inherent in conservation translocations.

I suggest that strategies for dealing with novelty, and resulting uncertainty, can be conceptually classified into "conservative" and "extrapolative" at the two ends of a continuous spectrum of approaches. For translocations following a conservative strategy, novel conditions would be avoided as much as possible, with release sites selected to be as similar as possible to areas within the current (relict) distribution of the translocated species. In contrast, under an extrapolative strategy, more exploratory or experimental translocations would be considered, allowing species to encounter novel conditions. Here choices would be based on predicting species' behaviour through extrapolation from observed patterns. While I primarily propose these strategies for species restricted to a relict distribution, I note that they might also have relevance for other species and translocation objectives. For example, in translocations where individuals are relocated due to displacement by infrastructure, animal welfare concerns could promote a conservative strategy, as this could minimise stress for relocated animals (Teixeira *et al.*, 2007). Alternatively, extrapolative strategies in such translocations could be used as an opportunity to pursue more active ecosystem engineering objectives (Perring *et al.*, 2015).

Multiple options for species conservation management could also be compared using a similar classification system. For example, threat management within a species relict distribution could be considered a conservative option compared with the alternatives of either translocating individuals or taking them into captivity (Snyder *et al.*, 1996). However, here I am specifically referring to management following the decision to translocate animals, rather than considering translocations relative to alternative actions.

I identify the challenges posed by the novelty inherent in conservation translocations in relation to release-site selection and post-release habitat use and provide a conceptual framework to explore how this novelty can be approached following either a conservative or

an extrapolative strategy. I illustrate this framework using case studies of the translocation management of two endemic NZ species that have suffered dramatic anthropogenic range contractions; a reptile, the tuatara (*Sphenodon punctatus*), and a flightless bird, the South Island takahē (*Porphyrio hochstetteri*).

## 2.2 Novelty

I define novelty at two levels: the individual level due to a founder animal's initial unfamiliarity with the specific features of the release area, and the species level when a release area differs considerably from the extant range of a species (Thatcher, Manen and Clark, 2006; Yott *et al.*, 2011; Attum and Cutshall, 2015). These sources of novelty create uncertainty that can undermine the decision-making process for conservation translocations (Seddon, Armstrong and Maloney, 2007). This uncertainty is manifest in two key areas:

- Reintroduction site selection, where choices based on relict distributions should identify areas where a translocated cohort is able to persist, but might potentially miss sites with conditions best able to support population growth and persistence (Kerley, Kowalczyk and Crome, 2012; Osborne and Seddon, 2012).
- Post-release resource use, where expectations based only on relict populations are unlikely to anticipate the full range of potential responses of the reintroduced population under novel conditions (Mihoub *et al.*, 2014; Massaro *et al.*, 2018).

These sources of novelty and consequent uncertainty are represented in two of the consequences for reintroductions listed in Osborne and Seddon (2012): “present day locations might not indicate currently suitable habitat,” and “present day locations where a species is absent might not indicate unsuitable habitat.” Here I provide a framework for how each of these uncertainties can be approached, through making either relatively conservative or extrapolative inferences.

## 2.3 Conservative Strategy

Adopting a conservative strategy, candidate release sites are given priority based on their similarity to conditions within the current distribution of the species, regardless of past population declines and range contractions. As such, selected translocation sites will have conditions similar to those in which the species is known to survive, which should reduce the number of novel or unknown factors. Reinforcements may be considered a conservative

translocation strategy, as the presence or proximity of conspecifics provides clear evidence that the species can survive in a release area. A conservative approach can increase confidence that an introduced population will be able to survive in selected release areas. However, this conservatism will inevitably reduce the number of potential release sites to be considered, and is likely to miss suitable, or even preferred, release sites with conditions that are not represented within a species relict distribution (Kerley, Kowalczyk and Cromsigt, 2012; Kerley *et al.*, 2020).

Similarly, following a conservative strategy, predictions of resource selection and population growth for conservation translocations would be made and evaluated based on patterns observed within the focal species' current range. This would have the advantage of limiting novelty, and thus uncertainty, as the founding cohort would be expected to require the same resources as are available in their relict range. Where not all resources are available, management could focus on providing these. This could be through the provision of supplementary feed and/or breeding shelter, such as nest boxes (Panfyllova *et al.*, 2016), removal of pests and predators (Hegg *et al.*, 2012; Taylor, Nelson and Ramstad, 2018), vegetation management (Lloyd and Powlesland, 1994) and/or controlling human activity to reduce harvest or persecution (Chapron *et al.*, 2014). This has the advantage of reducing uncertainty in post-release outcomes as the environment is managed to provide conditions known to be at least minimally adequate for species persistence (Seddon *et al.*, 2014). Similarly, and particularly in the case of reinforcements, decisions relating to population carrying capacities and appropriate social and demographic structures would be based on and evaluated with reference to observed patterns in relict populations.

In addition to potential additional management costs associated with release site modifications, there are potential missed opportunities associated with a conservative post-release strategy. Reducing novel conditions in a reintroduction area will remove opportunities for adaptation, whether through behavioural plasticity or genetic mechanisms, which could benefit the survival and management of the species in the long term (Zeisset and Beebee, 2013). There will likely be cases where removing or reducing resource provision such as feeding or nest sites, while reducing population growth in the immediate term, could provide the impetus for animals to explore previously unexploited resources and might eventually lead to greater population growth and stability over subsequent generations (Mertes *et al.*, 2019). Furthermore, conditions in a species' relict range might lie on the fringes of a species' niche if the relict range represents refugia from anthropogenic

threats (Kerley, Kowalczyk and Crome, 2012). If these are used as a benchmark for identifying population growth and persistence potential, then it will be difficult to identify sub-optimal performance in reintroduced populations (Beauchamp and Worthy, 1988).

Management practises could also inadvertently reinforce or perpetuate these sub-optimal conditions, thus limiting population growth. For example, a population growth rate at least as strong as that observed within the relict range might be considered satisfactory by managers, despite this potentially being well below the maximum biological rate for the species (Morris and Doak, 2002; Kerley, Kowalczyk and Crome, 2012; Kerley *et al.*, 2020).

## 2.4 Extrapolative Strategy

In order to make predictions beyond currently observable conditions, extrapolative translocation management could consider additional data sources from outside the relict population. This could include indigenous distributions prior to range contractions (Lentini *et al.*, 2017) or biophysical and behavioural information from captive animals (Mitchell *et al.*, 2012). Alternatively, evidence could be sought from other species, e.g., from sister-species (Hunter-Ayad and Hassall, 2020), or trophically analogous species (Andelman and Fagan, 2000). However, while additional data sources can inform extrapolative translocations, they are not always available, or might not be considered reliable due to temporal, spatial, environmental, ecological, and/or taxonomic distance from the relevant management conditions (Osborne and Seddon, 2012; Svenning *et al.*, 2016). Additional data are not always necessary to enable extrapolation, as trends within a species' relict distribution can be extended beyond observed conditions by expert inference (Beauchamp and Worthy, 1988; Kerley, Kowalczyk and Crome, 2012; Kerley *et al.*, 2020) or through statistical or biophysical models (Elith, Kearney and Phillips, 2010; Gallien *et al.*, 2012). Regardless of the methods of extrapolation, confidence in predictions regarding translocation outcomes will be proportional to the differences between conditions at release sites relative to those in the input data, as more separation will necessitate a higher degree of extrapolation to generate predictions. As such, post-release establishment and persistence will tend to be less assured than under more conservative strategies.

Tolerating a higher degree of novelty when selecting release sites would mean that candidate sites would not be rejected simply because conditions differ from those in a species' relict distribution. This has the advantage of expanding the number and type of

release sites that can be considered by conservation managers (Kerley *et al.*, 2020). For reinforcements, while site selection is clearly based on the presence of conspecifics, extrapolative choices could be those that are considered more experimental with regards to the populations chosen for reinforcement. For example, rather than reinforcements being used as a tool to “save” struggling or declining populations, a common use (Hegg *et al.*, 2012), they could be used to promote rapid growth in stable or increasing populations under extrapolative strategies. However, a key challenge under extrapolative strategies is determining what novelty is acceptable. Many novel conditions will render a release site clearly unsuitable, whereas other types of novelty could be suitable for a species.

Ecological habitat models (e.g., correlative and mechanistic niche models) are a valuable tool in addressing this challenge as they can be used to estimate potential release site suitability even under novel conditions (Mitchell *et al.*, 2012; Chauvenet *et al.*, 2013; Lentini *et al.*, 2017; Chapter 3; Hunter-Ayad *et al.*, 2020).

When predicting and evaluating post-release resource selection, extrapolative management would consider a broad array of resources as potentially usable in a release area. However, there might be considerable uncertainty in the degree to which any or all novel resources will be exploited, and when this might be. There might be temporal latency arising from the necessity for animals to explore novel resources and to adapt their behaviour appropriately (Osborne and Seddon, 2012). For example ‘Alalā, or Hawaiian crow (*Corvus hawaiiensis*) reintroduced to the island of Hawai‘i steadily transitioned from reliance on familiar areas and supplementary feed, towards exploring novel areas and natural food sources over a 200 day post-release tracking period (Smetzer *et al.*, 2021). Such adaptions to make use of novel resources could be useful in distinguishing whether certain resource uses observed in refugee populations are facultative or obligate in nature. For instance, apparent dietary specialisation in giant pandas (*Ailuropoda melanoleuca*) is potentially a consequence of a restricted breadth of suitable food in their relict distribution and, speculatively, they could adapt to make use of novel food sources were they translocated outside of this distribution (Kerley *et al.*, 2020).

However, the risk with such conservation translocations is that the species is unable to adapt and exploit novel resources, and consequent high post-release mortality might increase the likelihood of the extinction of the founder cohort (White *et al.*, 2014).

Additionally, population, social, and demographic structures are likely to vary upon exposure to novel environments, or be altered via reinforcements, and should not be judged

directly against patterns in extant populations. As such, reintroductions conducted following an extrapolative strategy will tend to have more open-ended predictions of post-release performance. This will also change the nature of any evaluation of the translocation; as expected goals and outcomes are less certain, post-release monitoring could be an opportunity to reveal new data regarding the species and to inform their conservation into the future, rather than checking whether focused goals are being met *per se*. The greater underlying uncertainty arising from the translocated species reaction to novel conditions will mean that such reintroductions carry a higher risk of failure and unintended or unforeseen outcomes.

## 2.5 Applying the Strategies

Both conservative and extrapolative strategies have specific strengths and limitations, and thus will be suitable in different contexts (Table 2.1). For instance, the inflexibility of conservative strategies, basing management on observations only from a relict population, can hamper adaptive management and reduce the ability for species management to respond to emerging threats (Corlett, 2016). However, this is a long-term concern and there are many instances where maximising confidence in rapid actions is required to save a species from immediate extinction (Lloyd and Powlesland, 1994; Massaro *et al.*, 2018; Mukhlisi *et al.*, 2020). In contrast, extrapolative strategies can often fail to provide certainty or concrete recommendations, making them a less palatable option to inform high stakes conservation decisions. It would be more appropriate to consider extrapolative predictions of release site suitability as hypotheses which can be tested via a translocation and subsequent monitoring (Armstrong and Seddon, 2008). As such, extrapolative translocations can be useful in an adaptive management setting as effective monitoring of post-release performance can provide evidence and information for the long-term conservation management of the reintroduced species (Seddon *et al.*, 2014). However, the scope to experiment with extrapolative translocations is often not a luxury afforded in conservation plans for many threatened species.

**Table 2.1-** Summary of conditions lending themselves to conservative and extrapolative translocation management.

Features	More suitable for <b>conservative</b> translocation approaches	More suitable for <b>extrapolative</b> translocation approaches
Traits	<ul style="list-style-type: none"> <li>- Ecological specialists</li> <li>- Obligate rigid behaviours</li> <li>- Poor genetic diversity</li> <li>- Low fecundity</li> <li>- Long generation times</li> </ul>	<ul style="list-style-type: none"> <li>- Ecological generalists</li> <li>- Behaviourally plastic</li> <li>- High genetic diversity</li> <li>- High fecundity</li> <li>- Short generations</li> </ul>
History	<ul style="list-style-type: none"> <li>- Recent range contraction</li> <li>- Causes known and remedied</li> </ul>	<ul style="list-style-type: none"> <li>- Extirpation in the distant past</li> <li>- Uncertain drivers</li> <li>- Ecosystem changes since contraction</li> </ul>
Population size/trend	<ul style="list-style-type: none"> <li>- Low global population</li> <li>- Declining global population</li> <li>- High extinction risk</li> </ul>	<ul style="list-style-type: none"> <li>- Multiple protected populations</li> <li>- Positive population trend</li> <li>- Supported by captive breeding programmes</li> </ul>
Current threats	<ul style="list-style-type: none"> <li>- Direct anthropogenic actions (e.g., harvest, persecution or land-use change)</li> <li>- Predation (e.g., introduced mammalian predators in NZ)</li> <li>- Available release sites where these threats are controlled, e.g., national parks or protected areas</li> </ul>	<ul style="list-style-type: none"> <li>- Novel/emerging threats</li> <li>- Climate change</li> <li>- Threats cannot be controlled in release areas</li> </ul>
Timeframe	<ul style="list-style-type: none"> <li>- One-off action</li> <li>- No chance of “second try”</li> <li>- No adaptive management for species</li> <li>- Required as a proof-of-concept for further funding and support</li> </ul>	<ul style="list-style-type: none"> <li>- Long-term management prioritisation and funding</li> <li>- Plans entailing several translocations with successive monitoring</li> <li>- Can feed into adaptive management</li> </ul>

*Choices should be considered across features (i.e., most features make a species suitable for one translocation strategy), as different features will likely be split between conservative and extrapolative suitability for most species.*

In addition to the conservation context of species’ being translocated, consideration should be given to the life-history traits of that species, as some species will be inherently more suited to conservative or extrapolative translocations, respectively. For instance, species

with generally low adaptive potential (i.e., behavioural rigidity and/or low genetic diversity) are likely to have little tolerance for novel stresses (Gillies and St. Clair, 2008; Heikkinen *et al.*, 2015). Therefore, these less adaptable species are inherently suited to more conservative translocation strategies. Whereas, species with high adaptive potential (i.e., behavioural plasticity and/or genetic diversity) are much more likely to be able to adapt to novel stresses encountered following a translocation (Gillies and St. Clair, 2010), so are inherently better candidates for extrapolative translocations. I note, however, that the inherent suitability of a translocated species must still be balanced with other factors that influence the suitability of a given strategy for each specific setting. The strategic challenge for conservation managers then becomes determining how to balance several considerations, which might produce conflicting views over which strategy should be pursued.

My framework can also be considered at multiple levels (i.e., community, clade, genus, species, population, individual, and life-stage), as these considerations are relevant to developing both broad strategies (ecosystem management) as well as for detailed decision making (make-up of release cohorts). In this way, these rules-of-thumb can guide practitioners in considering from the widest scope, ecosystem function and services (Hale and Koprowski, 2018), to the finest detail, individual personality and traits (Koolhaas *et al.*, 2007; Boyer *et al.*, 2010).

For species facing a high risk of extinction in the short-term due to a combination of species' traits and sustained or increasing threats within their relict range, a conservative approach is likely to be most suitable. This would focus on securing stable populations to save the species in the short-term, which must be a management priority, albeit while perhaps limiting long-term population growth potential. However, species not under immediate risk of extinction, with stable or growing populations might be better served by an extrapolative strategy where novelty need not be avoided. Although this might seem counter intuitive, this situation does occur. For instance, species might maintain stable or growing populations over a large, but still reduced, range. Eurasian cranes (*Grus grus*) are an example of this, as they were reintroduced to South-West England in 2010 in order to restore and enhance ecosystems in this region. Cranes were extirpated from the British Isles in the sixteenth century, though large populations persist on the Eurasian mainland, so the species has never been threatened and is listed as least-concern on the International Union for Conservation of Nature (IUCN) Red List for threatened species (Birdlife

International, 2016a; Soriano-Redondo *et al.*, 2019). Alternatively, species could have stable or growing populations due to active management in captivity and/or in the wild (such as the tuatara and takahē case studies given below). In this case, growing populations provide opportunities for extrapolative translocations to be considered, even though species survival remains dependent on ongoing conservation efforts.

In cases where extinction is not an imminent concern there is scope to view conservation translocations as ecological experiments, enabling researchers and conservationists to learn more about the niche-breadth of the species, as well as aspects of species ecology such as dietary and behavioural plasticity (Sarrazin and Barbault, 1996). In such cases even a failed translocation attempt can provide valuable information for the conservation of the species (Taylor *et al.*, 2017). For example, a “failed” translocation could perhaps confirm that at least one condition in the release area was outside of the species niche, or that the release procedure was unsuitable, without jeopardising species’ survival. I expect the conservative and extrapolative strategies laid out above to be useful in clarifying decision making processes for conservation managers and scientists. For instance, the choice of a conservative vs. extrapolative strategy can inform several key decisions in the building of ecological models (i.e., how models are set up, including what data used as model input and the kinds of relationships fitted to those data), a key tool in supporting conservation management (Hunter-Ayad *et al.*, 2020).

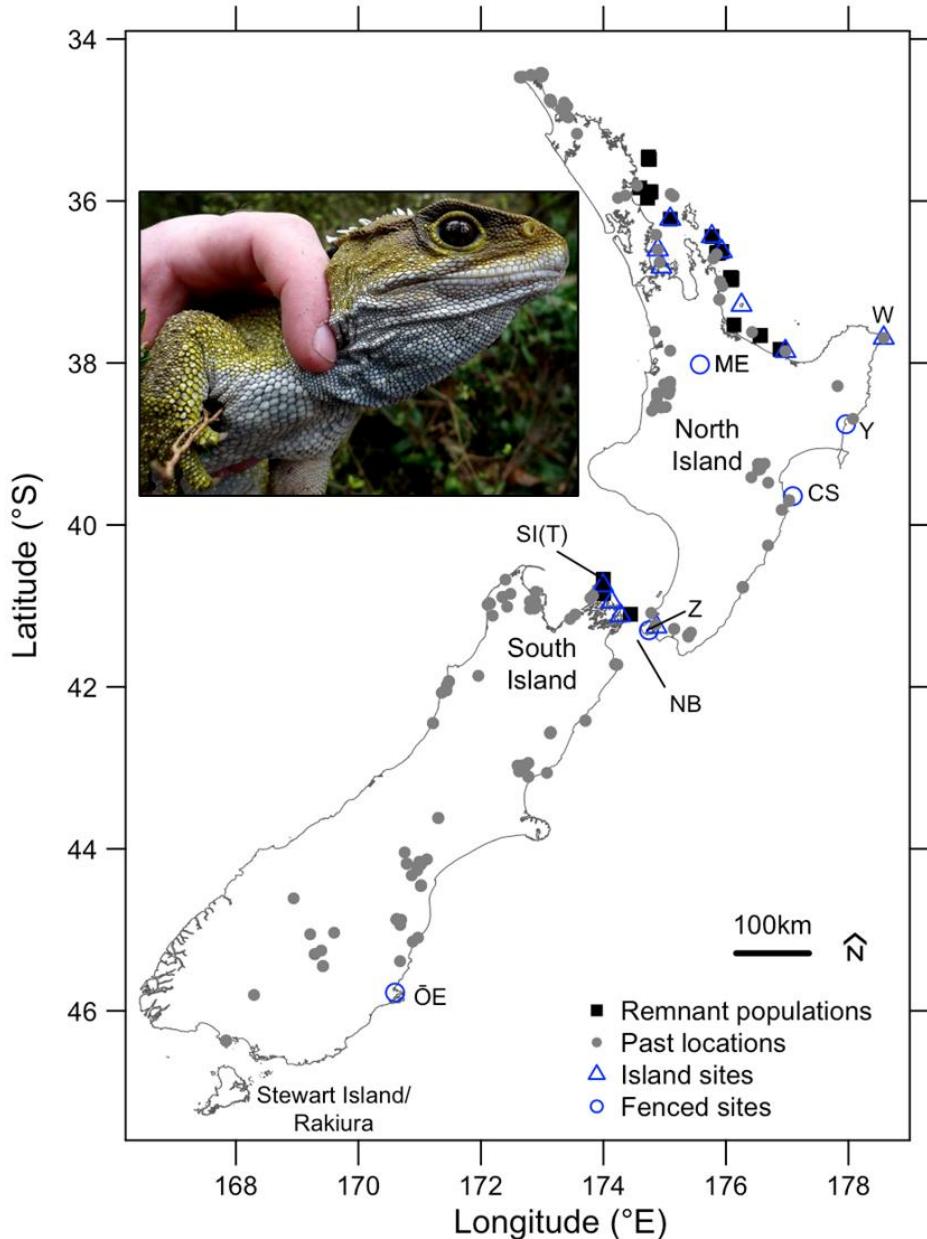
To examine my conservative-extrapolative translocation framework, I use two case studies for species where conservation translocations have formed an integral part of their rehabilitation: the tuatara and the takahē. Both of these species are endemic to NZ, which was discovered by humans in ~AD 1280 (Wilmshurst *et al.*, 2008). Tuatara and takahē were extirpated from the majority of their indigenous range following the arrival of humans to NZ (Figures 2.1 and 2.3), with this largely attributed to predation by introduced mammals and habitat loss (Beauchamp and Worthy, 1988; Cree, 2014). Both species are of cultural significance in NZ to the indigenous Māori people as *taonga* (treasures), as well as to European communities (Lee and Jamieson, 2001; Cree, 2014). For several decades, conservation management of tuatara and takahē has included conservation translocations, making them suitable candidate species to examine my conservative-extrapolative framework. Tuatara management has been extensively documented in the published literature, whereas for takahē, recent developments are largely unpublished outside of the

grey literature. Ongoing takahē research will draw from and emulate the work to date with tuatara, developing quantitative models to identify potential impacts of climate change.

## 2.6 Tuatara Case Study

Tuatara (*Sphenodon punctatus*) are a lizard-like reptile endemic to NZ and of evolutionary significance as the sole living representative of Rhynchocephalia, the sister group to Squamata (Cree, 2014). Tuatara are diurno-nocturnal and adapted to cooler climates, being active at body temperatures from ~5 to 30°C (Barwick, 1982; Thompson and Daugherty, 1998). Compared to most other reptiles tuatara have a long maturation time (~13–20 years), lengthy inter-clutch intervals (~2–9 years), a small clutch size (~8 eggs; range 1–17), and a long life span of at least 100 years (Cree, 2014). Once widespread across NZ's North and South Islands, as well as many offshore islands (Figure 2.1), tuatara became restricted to a relict distribution, being only found naturally on 32 offshore islands. Although taxonomy remained uncertain for living tuatara until recently (Hay *et al.*, 2010), all living populations of tuatara are currently considered to be *S. punctatus* (Hay *et al.*, 2010; Gemmell *et al.*, 2020).

Conservation translocations to islands from which introduced mammals have been eradicated (Gaze, 2001), and to mainland predator-fenced sanctuaries have been used to create insurance populations and to restore ecosystem function (Miller *et al.*, 2012; Jarvie *et al.*, 2021). Beginning in 1995, tuatara have now been translocated to 14 islands and 5 mainland fenced sanctuaries, increasing the number of populations to 47 (Figure 2.1; see Jarvie *et al.*, 2021). Most conservation translocations of tuatara arose out of well-documented recovery planning during the 1990s and early 2000s (Cree and Butler, 1993; Gaze, 2001), although these recovery plans are now out of date. The long-term goal for tuatara from the most recent Recovery Plan is to preserve genetic diversity of all existing populations and to restore new populations throughout their pre-human range, including locations with increased accessibility to the general public (Gaze, 2001).

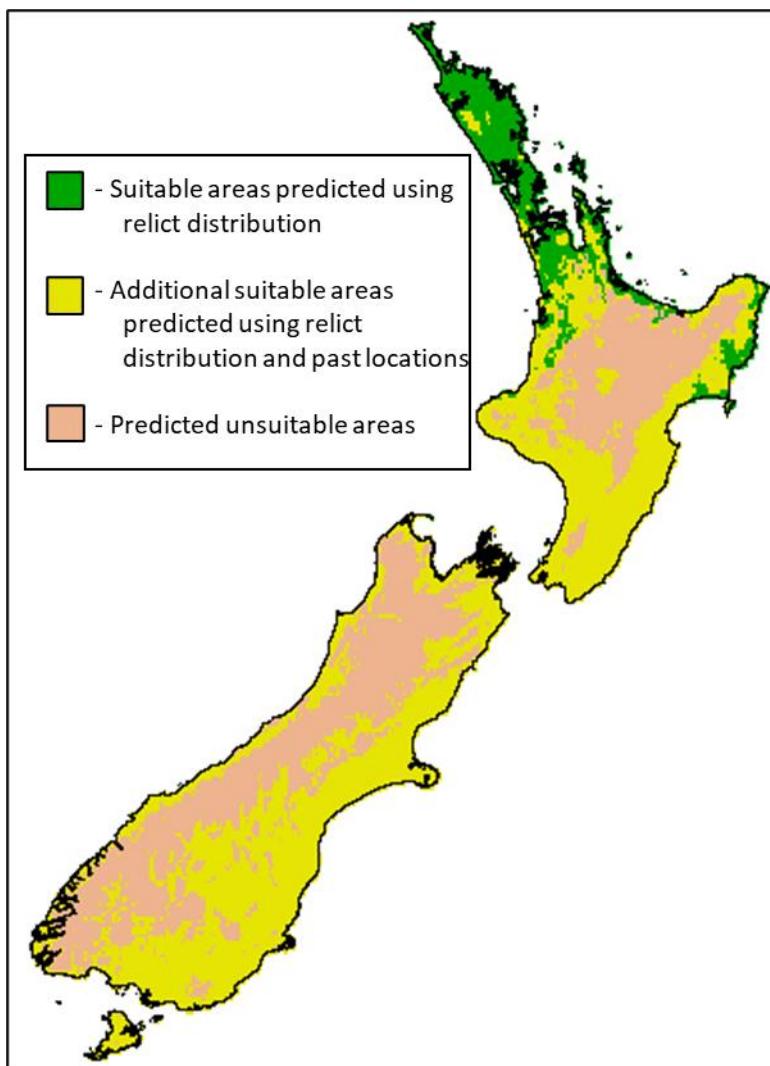


**Figure 2.1** - Map: Tuatara remnant and past locations as well as translocation release sites. Past locations (grey circles) from Holocene-aged fossil deposits (last 11,650 cal years BP, as determined by biochronological reasoning, namely the dominance of the moa *Anomalopteryx didiformis*; Worthy and Holdaway, 2002) and other known or probable extinctions from offshore islands (Cree, 2014). The remnant populations (black squares) and translocation sites (blue outlines) are split into groups of island and fenced sites, as these entail more conservative and extrapolative translocations, respectively. Locations of key places mentioned in the text are listed from north to south: W, East Island/Whangaokeno; ME, Maungatautiri Ecological Island; Y, Young Nick's Head; CS, Te Matau a Maui—Cape Sanctuary; SI(T), Stephen Island (Takapourewa); Z, ZEALANDIA; NB, North Brother Island; OE, Orokonui Ecosanctuary. Inset: An adult male tuatara about to be reintroduced to OE; photo by SJ. Adapted from Cree (2014) and Jarvie *et al.* (2021).

Following a conservative strategy, earlier conservation translocations of tuatara focused mainly on restoring populations within the same ecological region as the source population (Jarvie *et al.*, no date; Cree, 2014). These population restorations included both reintroductions and reinforcements. Initial reintroductions included establishing new populations with at-risk genetic stocks (Cree and Butler, 1993), such as the release of tuatara previously identified as a separate species (*S. guntheri* from North Brothers Island, which is now considered to also be *S. punctatus*; Hay *et al.*, 2010). With encouraging provisional results, a more extrapolative strategy was adopted for the reintroduction of tuatara to the predator-fenced mainland sanctuary of ZEALANDIA (formerly known as Karori Wildlife Sanctuary) in 2005 (Figure 2.1; McKenzie, 2007). The tuatara were released in the sanctuary, which was mostly free of introduced mammals, except for the house mouse (*Mus musculus*). Because of the possible impacts of mice, most of the translocated tuatara (60 of the 70) were released within a small (1 ha) mouse-proof enclosure within the larger sanctuary. The remaining 10 tuatara were released into the outer sanctuary (225 ha) and were monitored using radio-transmitters to assess the possible impacts of mice before further releases (McKenzie, 2007). Following high rates of survival of the released tuatara in both the mouse-proof enclosure and outer sanctuary, the population was reinforced in 2007 (Cree, 2014; Jarvie *et al.*, 2021). In 2012, tuatara were translocated following an extrapolative strategy to considerably outside of the ecological region of the source population, to four predator-fenced mainland sanctuaries and an island (Figure 2.1; Cree, 2014; Jarvie *et al.*, 2021). While mice are periodically detected at some mainland sites, their effects on tuatara remain uncertain. Several mainland locations have also had occasional incursions of larger introduced mammals such as Norway rats (*Rattus norvegicus*), ship rats (*R. rattus*), and stoats (*Mustela erminea*), but control of these predators has been needed to minimise the threat to tuatara. Preliminary survivorship of tuatara at monitored mainland locations is encouraging (McKenzie, 2007; Cree, 2014; Jarvie *et al.*, 2015, 2016, 2021; Price *et al.*, 2020), although continued vigilance and monitoring for introduced mammals remains necessary.

Prior to previous conservation translocations for tuatara, climatic suitability of release sites was considered on the basis of laboratory studies, field studies, and expert inference, and have been informed by knowledge of the Holocene fossil record (Cree, 2014; Jarvie *et al.*, 2014, 2021). A recent study built correlative species distribution models (SDMs) using occurrence records from remnant populations and past locations from the Holocene (Figure

2.1) as well as paleoclimates, to estimate climatically suitable areas (Figure 2.2; Jarvie et al., 2021). By incorporating locations of Holocene deposits and/or knowledge of past locations in SDMs, larger areas of suitable climate were identified compared to SDMs derived from remnant populations only. These results highlight the need to consider data from outside relict distributions when assessing climate suitability for future conservation translocations for tuatara, and other relict species.



**Figure 2.2-** Map of current climatic suitability from a maximum entropy model (Phillips, Anderson and Schapire, 2006) trained with remnant populations and past locations for tuatara (*Sphenodon punctatus*) across New Zealand. Green areas were identified as suitable by models using only data from remnant populations of tuatara (Figure 2.1), whereas the yellow areas show the additional space predicted to be suitable when remnant populations and past locations (Figure 2.1; radio-carbon dated deposits, Holocene-age deposits, and known or probable extinctions) were also used as model inputs. For full methodological details see Jarvie et al. (2021), including with Figures showing projections under climate change and with model uncertainty.

To support future conservation management of tuatara, research should be undertaken to inform translocations. Comparisons of remnant populations with translocated populations are useful to understand changes in demography (e.g., sex ratios, mating systems, and populations trends), phenotypic plasticity and phenology (e.g., Mitchell *et al.*, 2008; Miller *et al.*, 2012; Rout *et al.*, 2013). Further development of mechanistic models for tuatara should be undertaken to explore responses of populations to climate change in existing and novel environments (e.g., Carter *et al.*, 2018). The resulting mechanistic models could also be compared to results from correlative SDMs, potentially providing key insights into processes shaping the species' range limits (Tingley *et al.*, 2014; Briscoe *et al.*, 2016). Because the evolutionary consequences of translocations in long-lived species might not be apparent for centuries, confirming the accuracy of predictions based on correlative SDMs and mechanistic models could take decades. The continued measurement of responses of extant populations to climate change will be key for model validation.

Population viability analyses and gene retention modelling could be used to inform management of source and translocated populations, including investigating demographic responses to ambient temperature and population density. In some instances, the choice of founders from more than one source population might also be considered to maximise genetic diversity (Weeks *et al.*, 2011; Miller *et al.*, 2012). For example, where release sites are between remnant populations, founder populations could comprise individuals from adjacent genetic groups (Hay *et al.*, 2010) to increase the adaptive potential of any new population.

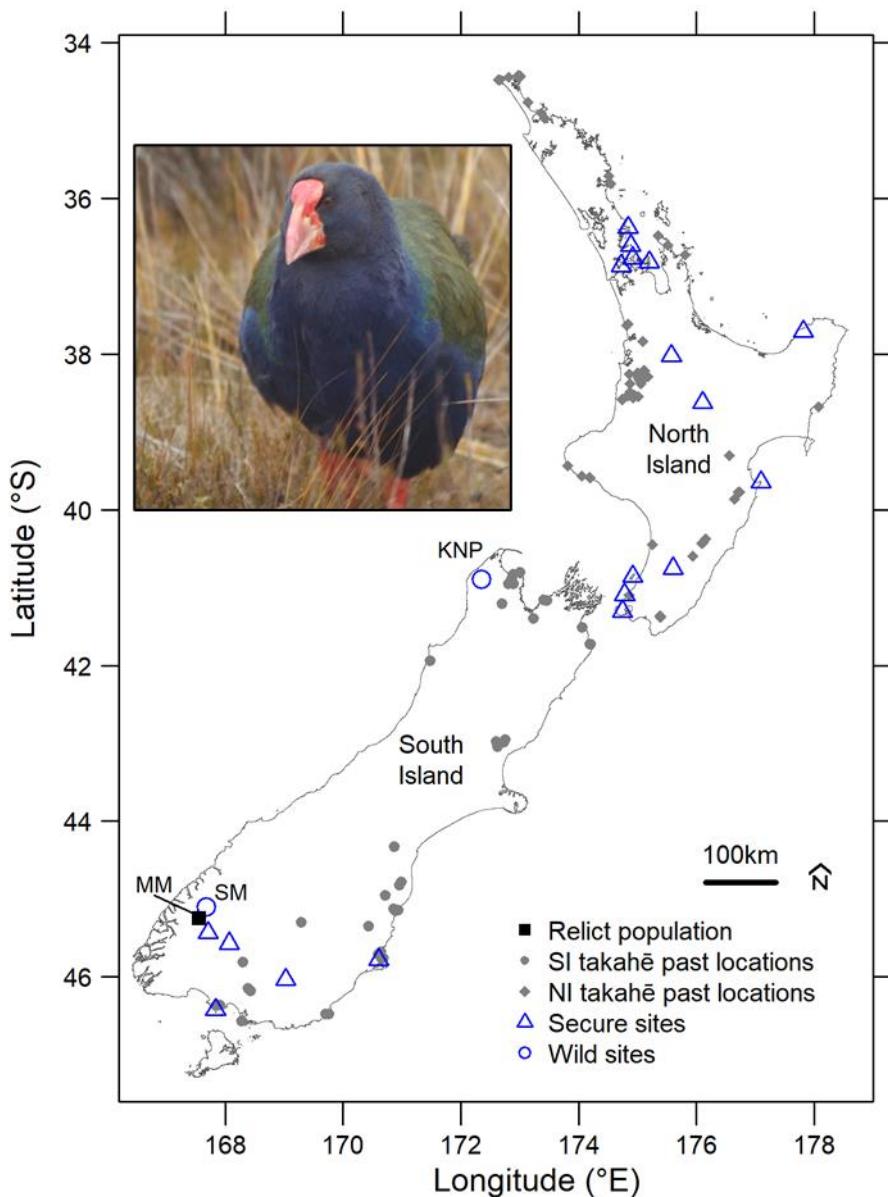
However, more extrapolative translocations might have benefits and unintended drawbacks (Miller *et al.*, 2012). On one hand, there might be an increase in fitness due to greater genetic variation and hybrid vigour, and there could be microevolutionary responses because of adaptation to new local conditions (Jamieson, Wallis and Briskie, 2006). On the other, the resulting hybridisation could cause outbreeding depression or maladapted phenotypes, and expose founders from different populations to novel diseases (Miller *et al.*, 2012). A mixed-stock approach to future translocations of tuatara would require careful monitoring, for example, of short-term survival and growth of founders, recruitment, and performance of hybrids relative to founder stock (Weeks *et al.*, 2011). Intensive consultation with stakeholders and iwi (Māori tribes) partners prior to translocations would also be necessary (Miller *et al.*, 2012).

For selection of future release sites, an increasingly extrapolative approach could be considered if remnant populations remain secure and translocated populations become established within the indigenous range. While reintroductions and reinforcements should still be used for future translocations to establish populations within the indigenous range, consideration could also be given to introductions of tuatara to islands or mainland sites where habitat is predicted to be suitable under climate change. The combined use of correlative SDMs and mechanistic models could inform such translocations. Proposed release sites could include assisted colonisation (Brodie *et al.*, 2021) of tuatara to locations such as Stewart Island/Rakiura, which is outside the indigenous range of the species.

## 2.7 South Island Takahē Case Study

The South Island takahē (*Porphyrio hochstetteri*) is the world's largest extant rail species, characterised by their size and flightlessness. Takahē, along with the kākāpō (*Strigops habroptila*), represent the last vestige of NZ's unique pre-human guild of flightless herbivorous birds. They were presumed extinct in the early twentieth century and a high-profile rediscovery in 1948 instigated over half a century of conservation effort to preserve and restore the species (Lee and Jamieson, 2001). Prior to the arrival of humans, the takahē's indigenous range was widespread across the South Island, with a distinct species, the North Island takahē (*Porphyrio mantelli*), on the North Island. However, following the arrival of humans and the associated introduction of mammalian predators, the North Island species was driven to extinction. While the South Island takahē was largely restricted to a single mountain range (the Murchison Mountains, Fiordland) by the early 1940s (Hegg *et al.*, 2012; Hegg, Mackenzie and Jamieson, 2013; Figure 2.3).

The location of the relict population of takahē has been designated a special protected area since the 1950s. Despite this, the species remained vulnerable to extinction as it persisted only as a single population (Hegg *et al.*, 2012). Consequently, conservation translocations began in the 1970s to create secondary, secure populations in predator-free reserves and small islands (hereafter "secure sites") in case of extirpation of the single relict population (Hegg, Mackenzie and Jamieson, 2013). The primary recovery goal for the takahē is to establish sustainable wild populations of takahē within their pre-human distribution. The secure site populations play a critical role for genetic insurance and population growth purposes, though the use and extent of secure sites continues to be reviewed as wild population security grows (DOC Unpublished Strategies).



**Figure 2.3** - Map: Takahē remnant and past locations and translocation release sites. Past locations (grey circles) from Holocene-aged fossil deposits (last 11,650 cal years BP, as determined by biochronological reasoning, namely the dominance of the moa *Anomalopteryx didiformis*; Worthy and Holdaway, 2002) are used to indicate of the pre/early human distribution of both North Island (NI) takahē (*Porphyrio mantelli*) and South Island (SI) takahē (*P. hochstetteri*). The relict population (Murchison Mountains, MM), wild sites (blue-outlined circles, SM, Stuart Mountains; KNP, Kahurangi National Park), and secure sites (blue-outlined triangles) are also shown. Inset: A South Island takahē following reintroduction to KNP; photo by JH.

Between 1987 and 1992 a reintroduction of takahē was attempted to an open mainland site (hereafter “wild site”). This was to establish a population in the Stuart Mountains, neighbouring the relict population in the Murchison Mountains (Hegg, Mackenzie and Jamieson, 2013). However, this reintroduction was ultimately unsuccessful, despite conservative site selection, as high mortality and dispersal prevented establishment of a population. This failure was attributed to the small size of annual release cohorts, unusually harsh winters in the early 1990s and high densities of mammalian predators (Lee and Jamieson, 2001; DOC Unpublished Records).

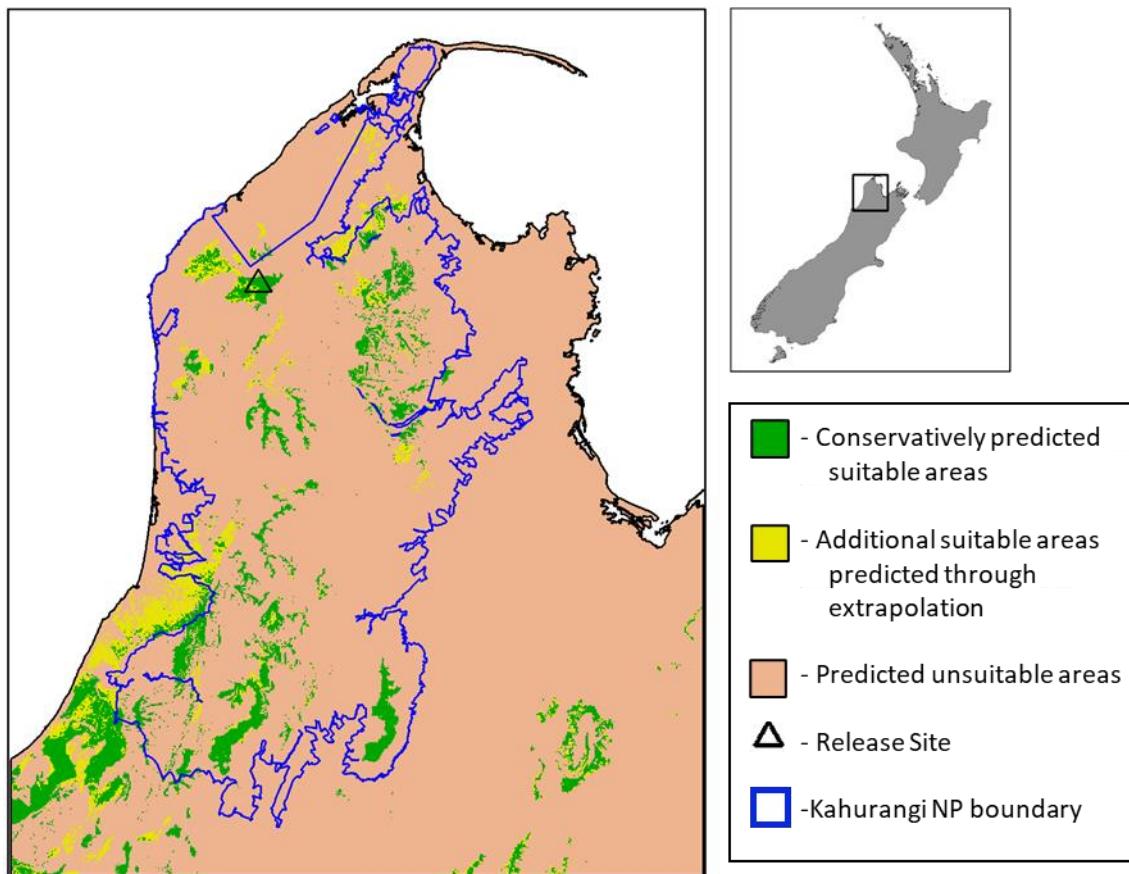
Following the failure of the Stuart Mountains reintroduction, focus shifted to conservation efforts within the Murchison Mountains relict population, as well as a continued establishment and management of small populations at secure sites. The most important criteria for selecting a secure site were the absence of introduced mammalian predators and operational access (as the remoteness of the Stuart Mountains hampered monitoring and management actions there). All secure sites represent novel conditions outside of the relict distribution in the Murchison Mountains, as they are different in terms of climate, ecological community and human activity. As a result, this site selection can be viewed as extrapolative. However, rather than being a preference of management this was due to the necessary focus on the major threat to takahē persistence, invasive predators, and the lack of conservative sites in which these predators could be effectively controlled. Takahē have now been established in 18 secure sites, removing immediate risks of extinction and beginning to reverse the decline of the species, such that today there are ~500 living takahē, up from a low of 124 birds in 1981 (Hegg *et al.*, 2012; Department of Conservation, 2019; DOC Unpublished Data). This resulted in a downgrading of the NZ species threat level, from Nationally Critical to Nationally Vulnerable, in 2016 (Robertson *et al.*, 2016).

While selection of secure sites has been necessarily extrapolative, management of post-release resource selection has followed a more conservative approach. Habitat management for takahē has been employed, when necessary, at secure sites, particularly to prevent vegetation succession. Prior eradication and on-going exclusion of invasive mammalian predators has been essential, while supplementary food is also provided at some sites. Genetic resources and population densities are also strictly managed, with breeding pairs established to maintain current levels and patterns of genetic diversity (Greaves *et al.*, 2020). This population admixture serves the purpose of avoiding inbreeding and genetic bottlenecks. However this might also limit the ability of takahē to adapt to

conditions in any one secure site, as continual translocations between secure, relict and wild sites may inhibit the emergence of novel adaptations (Lees *et al.*, 2014; Zavodna *et al.*, 2015; Greaves *et al.*, 2020). However, despite this control, some local behavioural adaptations have been observed, for instance takahē at secure sites exploit food resources that have limited or no availability in the Murchison Mountains. Examples of novel food resources exploited by takahē at secure sites include fallen fruits, exotic grasses, small reptiles, and the chicks of other bird species (particularly ducks). This has demonstrated that takahe are a more adaptable generalist species than is evident from their behaviour and ecology within the relict population, though the degree of their generalist nature remains unclear (Beauchamp and Worthy, 1988; Mills *et al.*, 1991).

From the mid-late 2010s mainland reintroductions of takahē were again planned to establish new wild sites, able to support larger populations with less intensive management than at secure sites. This followed population growth across multiple secure sites and increased ecological understanding and refinement of management methods, enabling policy to become more ambitious in scope (DOC, Unpublished Data). The first reintroduction has been to Kahurangi National Park in 2018, in the north-west of the South Island. This site was chosen relatively conservatively as it bears similarities to takahē-inhabited areas in the Murchison Mountains. However, post-release management (particularly a lack of fencing/containment) allowed takahē to establish and roam as they pleased (except into farmland), making this aspect of the reintroduction more extrapolative than at secure sites. Ongoing research is building SDMs using occurrence records from the Murchison Mountain takahē population, to estimate environmentally suitable areas in Kahurangi for the species (Figure 2.4; Chapter 4).

Although mammalian predators are controlled to low densities within Kahurangi, eradication was not considered essential for the release of birds. Thus far, no supplementary feed has been provided as the extensive tussock grasslands at the release site are intended to provide sufficient food for released takahē, though post-release monitoring will be crucial to confirming if this is the case. Additionally, having a relatively large release cohort of 30 individuals allowed greater complexity in social structures and interactions to arise post-release than in previous translocations.



**Figure 2.4** - Map of current environmental suitability from a maximum entropy model (Phillips, Anderson and Schapire, 2006) trained with records from South Island takahē (*Porphyrio hochstetteri*) relict population (Figure 2.3). Green areas were identified as suitable by a conservatively fitted model, whereas the yellow areas show the additional space predicted to be suitable when the model fitting was relaxed to allow a greater degree of extrapolation. The conservative model only identifies habitat in environments analogous to those occupied in the models' input data, whereas the extrapolative model focuses on excluding areas only because they are analogous to unused areas in the species training data. For full details of the methods used to generate these predictions see Chapter 4.

Early post-release monitoring of this population seems to indicate similar patterns of resource-use, population growth, and social structure to that of the relict population (DOC Unpublished Data). However, this was initially disrupted, possibly in part due to a female gender bias in the release cohort. Excess females were observed to disturb established breeding groups, causing them to disband prior to and during the first post-release breeding season, potentially contributing to low overall breeding efforts. Dispersal away from the release site was also observed predominantly in unpaired birds, rather than in stable pairs (Chapter 5). Further investigation of post-release resource use in Kahurangi is planned,

using methods such as faecal analyses, stable isotope analysis, and eDNA to provide more information on dietary composition and changes over time (DOC Unpublished Proposals).

The conservation management plan for takahē considers that future reintroductions will be essential to maintain and restore the species, with an increasingly extrapolative attitude being adopted as the species becomes more secure from historic threats while encountering new threats from climate change. The Takahē Recovery Programme is continuing to use existing sites to improve in-situ population performance and to predict likelihood of success at new sites. Future reintroduction management will likely be more extrapolative as takahē appear to prefer low-mid elevation and benign topography and climate. The primary focus is on likely predation pressure from introduced mammals and the feasibility of mitigation, ease of access and minimising excessive dispersal through natural barriers.

## **2.8 Discussion**

In this chapter I have sought to develop a strategic framework to inform translocation strategies in terms of environmental novelty, highlighting the risks and rewards of opposing attitudes. I separate strategies into two broad categories based on defining novel conditions as those not represented within a species relict distribution. I define these as conservative (novelty avoidance) and extrapolative (novelty exposure) strategies, suggesting that each strategy has specific advantages and drawbacks, so will be suited to different species and conservation contexts. Case studies demonstrate how previous translocation decisions can be viewed through the lens of this conservative-extrapolative framework. Management of both tuatara and takahē has shown a general trend of moving from initial conservative, cautious translocations, and towards generally more extrapolative, experimental manipulations. For tuatara this progress has followed this trend relatively clearly, with more recent translocations establishing populations further outside of their relict distribution than ever before. Whereas, for takahē, specific setbacks and practical restrictions meant that earlier site-selection decisions were extrapolative by necessity while population management was conservative, and more recent translocations have become more conservative in terms of site-selection while post-release management has become more extrapolative. I hope that these case-studies will demonstrate how the proposed framework can provide a lens through which both historic and future translocations decisions can be viewed.

As each of the proposed strategies create specific opportunities and risks, they are intrinsically better suited to certain species, situations, and management objectives. It will remain a challenge to assess and balance numerous factors that will suggest a more conservative or a more extrapolative approach is suitable (Table 2.1). These factors are likely to counteract one another in many instances. For example, a species that has been through a population bottleneck, such as the alpine ibex (*Capra ibex ibex*), might have low genetic diversity and adaptive potential, suggesting suitability for conservative translocations, despite having a large and growing population, suggesting they could be candidates for extrapolative reintroductions (Stüwe and Nievergelt, 1991). Balancing such conflicting conditions will remain a significant challenge for translocation management, and I emphasise two key aspects to bear in mind: firstly, these strategies can be considered as “rules-of-thumb” or guiding principles, and secondly that, although I have defined the strategies categorically for convenience, they in fact characterise the ends of a continuum of attitudes to novelty exposure. Based on these considerations I propose that these strategies are best applied at the discretion of management when opportunities and conditions allow. Furthermore, application of the strategies in the face of conflicting factors can be flexible. Choices here would be based either on a judgement call from conservation practitioners based on their priorities or be a compromise where applied strategies are somewhat intermediate, conservative in some respects but more extrapolative in others. This ability to be flexibly applied should make the framework potentially useful in many settings and given many constraints.

Historically, reintroduction has mostly been the limit of ambition for ecosystem management and restoration by managers and scientists, although there have been key exceptions (Lloyd and Powlesland, 1994; Greuber, Maxwell and Jamieson, 2012; Carter, Foster and Lock, 2017). I expect that strategies for dealing with novelty in translocations will become much more extrapolative in the future, as the scope and ambition of emerging management goals will allow less room for the strict control of resources and conditions that conservative strategies require. Thus, my framework provides a structure for the development of adaptive management strategies for conservation translocations (Osborne and Seddon, 2012; Smith, Werner and Kelcey, 2012). I expect this to facilitate the development of strategies where the exposure to risk from novel conditions is explicitly considered in terms of species traits, and population conservation status (Kennedy *et al.*, 2013). However, a cautious, conservative approach will likely be most appropriate for the early stages in the

restoration of highly threatened species, as securing a stable population and removing the imminent threat of extinction must be a priority in such cases. Conservative translocations will also often be viewed more favourably by the public, indigenous peoples, and other stakeholders, whereas extrapolative translocations are likely to be more controversial (e.g., Ricciardi and Simberloff, 2009).

Extrapolative strategies have particular importance in the context of ongoing anthropogenic climate and land-use change. To combat emerging threats, increasingly more extensive ecosystem manipulations are suggested, including assisted colonisation (Brodie *et al.*, 2021), the translocation of individuals outside of their established range as a response to threats such as climate change (IUCN/SSC, 2013). These sorts of translocations, moving organisms outside of both their current and indigenous ranges are inherently extrapolative, as managers are knowingly creating unprecedented conditions and ecological interactions (Rendall, Coetsee and Sutherland, 2018; Bouma *et al.*, 2020).

However, caution is warranted in the application of extrapolative translocation strategies, particularly with regard to assisted colonisation and rewilding projects that seek to create novel ecosystem conditions (Corlett, 2016). In these cases, where there is so much inherent uncertainty, decisions should always be informed by what data are available, and even the most experimental translocations should require evidence-based support regarding the potential success and risks of the translocation (Armstrong and Seddon, 2008; Bouma *et al.*, 2020). This is due to the cautionary tales from the field of invasive species management, in which many species that have been introduced outside of their native range, whether accidentally or intentionally, are a major driver of ecosystem degradation and biodiversity decline, costing conservation management vast resources to reduce and reverse the resulting damage (Brook, Sodhi and Bradshaw, 2008; O'Donnell, Weston and Monks, 2017). I strongly suggest that a minimum requirement for conservation introductions be that there is evidence that the focal species will not only survive but will also have (at least) no negative impact on the overall biodiversity and ecosystem functioning of the release area (for instance using the methodology demonstrated in Peterson and Bode, 2021).

The principles developed in the conservative-extrapolative framework can also be applied to other areas of conservation practise, beyond translocations. For example, distinguishing a similar continuum of conservative to extrapolative measures could usefully refine and clarify decision making for predator/pest control (Recio, Seddon and Moore, 2015; Roy *et*

*al.*, 2016; O'Donnell, Weston and Monks, 2017), resource extraction (Peres *et al.*, 2016) and tourism volume (Daily *et al.*, 2009), relating these choices to specific ecological evidence and considerations. These strategies can be framed generally as an application of a non-monetary cost-benefit analysis to conservation management (Chee, 2004; Fletcher *et al.*, 2011) and could usefully enhance the clarity and transparency of risk management in decision making processes (Sutherland *et al.*, 2004).

Inherent risks and uncertainties emphasise the need for caution in planning conservation translocations. I add to previous calls to view translocations as ecological experiments, following a mindset whereby explicit *a priori* predictions are made and then tested, even in cases where scientific enquiry is not the primary objective of management (Seddon, Armstrong and Maloney, 2007; Taylor *et al.*, 2017). I believe the conservative-extrapolative framework presented here will help with the application of this concept. Following this framework can help to ensure that predictions are appropriately framed in terms of the confidence that should be placed on them and that “tests” from post-release monitoring are also viewed and incorporated into adaptive management plans in a suitable way. I expect a conservative-extrapolative framework will have increasing relevance as conservation practise is developing away from traditional, preservationist approaches, so called “fortress” conservation, towards goals with increasing ambition and scope to include ecosystem services, ecological restoration, and rewilding as key objectives (Seddon *et al.*, 2014; Corlett, 2016).

## **Chapter 3**

### **Methods Review: Predictive Models for Reintroductions**

In this chapter I provide a synthesis of published literature around paradigms and methodologies in ecological modelling. Model options are discussed with specific regard to reintroduction applications.

A version of this chapter has been published as; Hunter-Ayad, J. *et al.*, (2020)

Reintroduction modelling: A guide to choosing and combining models for species reintroductions', *Journal of Applied Ecology*, 57(7), pp.1233–1243. doi: 10.1111/1365-2664.13629.

#### **3.1 Introduction**

Conservation reintroductions are the deliberate movement of organisms from one site, for release into its indigenous range from which it has disappeared (IUCN/SSC, 2013). They are a key component of biodiversity conservation (Seddon *et al.*, 2014). Decisions as to when, where and how to reintroduce are frequently based on limited empirical data.

Reintroductions create novel conditions with unexpected dynamics and reintroduced populations out of equilibrium (Roy *et al.*, 2016). Some of these dynamics might be predicted before investing in a reintroduction by applying ecological models using knowledge of species' ecology and conditions in the reintroduction area (Sun *et al.*, 2016). However, as new ecological models are constantly under development, there is an expanding, even bewildering, diversity of approaches available to practitioners.

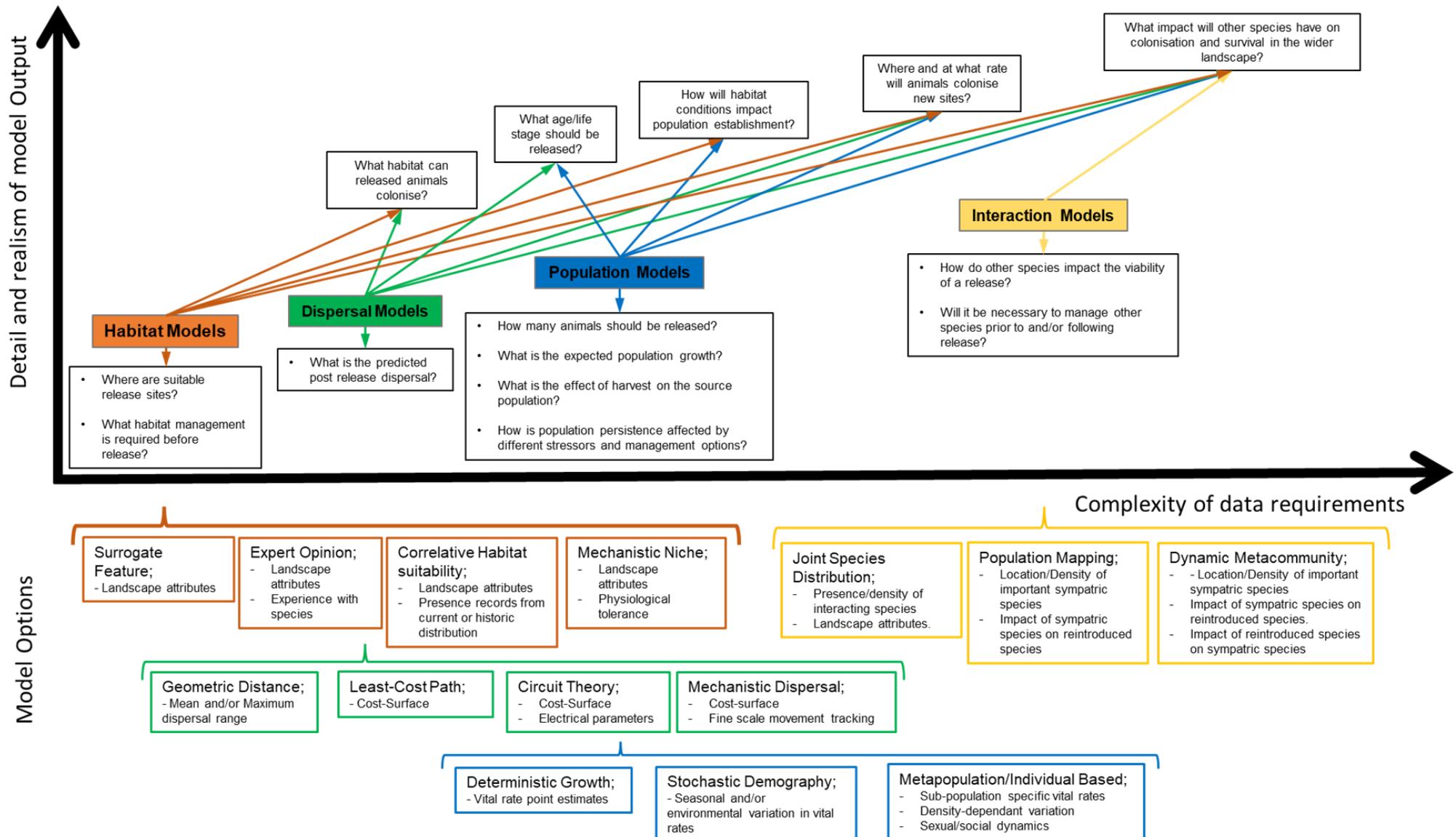
Effective reintroduction planning often requires more than empirical field data. It is usually impractical to collect the data required to predict accurately how reintroduced species will react to alternative management actions (Duffy *et al.*, 2007) and experimental manipulation can be applied rigorously only in controlled and simplified systems (Altermatt *et al.*, 2015). This has resulted in the widespread use of ecological models which combine the best available data with an understanding of ecological mechanisms and a degree of pragmatism to provide useful predictions (Aben *et al.*, 2014). Here, I present a 'shoppers guide' for practitioners interested in applying ecological models to reintroductions, providing a conceptual comparison of models. I review the types of models that might be applied to reintroductions, compare strengths and weaknesses, and discuss how models of different

aspects of species ecology can be combined to answer focused management questions. This overview provides a starting point for practitioners to enable them to ‘get their bearings’ in the deep, and somewhat murky waters of the ecological modelling literature. There are four key components to be considered when modelling reintroductions (Figure 3.1; Guisan and Thuiller, 2005):

1. Habitat suitability: to predict the ability of an area to support reintroduced populations (Gutt *et al.*, 2017).
2. Dispersal processes: to predict the spread of founders from release sites (Aben *et al.*, 2016).
3. Population dynamics: to predict population growth in reintroduction areas (Sewell, Baker and Griffiths, 2015).
4. Interspecies interactions: to predict impacts of other species, for example, predators, prey and competitors, on reintroduced populations (Laperriere, Brugger and Rubel, 2016).

Here I cover these four main components, but acknowledge other factors to consider when modelling reintroductions. For example, disease commonly causes reintroduction failure and models of disease mechanics can help to identify disease mitigation strategies (Sharkey, 2011). However, here I focus on the core ecological factors important across all reintroduction programmes. Factors such as disease dynamics, inbreeding risk and other genetic considerations can be examined as elaborations of these core elements (especially of population and interspecies interaction models).

Advances in computation, data processing and simulations allow the combination of components as nested, interacting aspects of a species' ecology (Aben *et al.*, 2016). Complex feedbacks between components can thus be represented (Zurell, 2017), although some management questions can be addressed without the need for all areas to be fully nested (see Figure 3.1)



**Figure 3.1 (previous page)-** Groups of ecological models and key questions for the management of reintroductions they can inform. Arrows indicate which kind of model, or combinations of models are required for each question. Boxes below the axis identify specific models and their data inputs.

### 3.2 Habitat Models

In many reintroductions, a typical first step is to identify the quality and spatial attributes of candidate release sites, such as the size and location of habitat patches (Stone and Guy, 2017). Overall habitat quality is often not the primary reason a site is selected (other criteria might include absence of human disturbance or competition from invasive species), but the release site must be able to support an establishing population. Habitat modelling can also provide parameter estimates for other models (e.g., carrying capacity for population models) based on resource availability. Data requirements vary between habitat models, but all require spatially explicit data for the attributes determining habitat suitability such as land cover, altitude, rainfall and/or temperature.

The term ‘habitat’ is applied vaguely and inconsistently in ecological studies (Stadtman and Seddon, 2018). For simplicity, I use the term to denote the geographical area providing abiotic and biotic conditions for species persistence but omit trophic interactions such as predation. This definition is a geographical projection of a species’ fundamental niche, the entire set of conditions under which an animal can survive and reproduce, as factors limiting access to this fundamental niche are best considered in models interacting with the habitat model (Figure 3.1; Pulliam, 2000).

The simplest method for estimating habitat structure (location and extent of habitat patches) uses a single landscape attribute as a surrogate, such as the extent of dominant vegetation. For example, grassland extent can be used as a habitat surrogate for grazers, and forest cover for browsers (Zanin *et al.*, 2017). While surrogates are computationally straightforward, they are also ecologically simplistic and exclude many factors that determine habitat suitability (Stadtman and Seddon, 2018). Surrogates are unlikely to provide enough detail to predict landscape use beyond coarse classifications.

Correlative habitat suitability models provide a more nuanced prediction of habitat structure (Sun *et al.*, 2016). These consider multiple landscape attributes and species location records (e.g., presence–absence data or presence-only data from surveys or observations) to identify habitat based on correlations between local conditions and species occurrence

(Austin, 2007). Correlative models are commonly used to estimate habitat distribution at large spatial scales and to predict shifts in distribution under climate change (Phillips, Anderson and Schapire, 2006; Keith *et al.*, 2008). These models assume that the populations from which presence records are drawn are in equilibrium, limited from spreading only by climatic and landscape factors. As this assumption is not upheld for reintroduced populations at establishment and growth stages, care must be taken in selecting species records and explanatory environmental attributes. Correlative models might otherwise mis-identify the dynamic range boundaries of expanding populations as niche limits (Jiménez-Valverde *et al.*, 2011).

Alternatively, expert opinion can be used to map the occurrence of suitable conditions (Larson *et al.*, 2004). Although lacking statistical rigour, expert-based models may potentially outperform statistical models for some reintroductions as datasets for focal species commonly lack records from locations analogous to release areas. Landscape change since species extirpation often means the release area is a novel environment for the reintroduced species (Chapter 2; Hunter-Ayad *et al.*, 2021). Thus, correlative models will likely underestimate habitat availability in proposed release locations if the habitat is good quality but outside the range of training data (Jiménez-Valverde *et al.*, 2011). Experts in the ecology of the reintroduced species can provide the knowledge lacking in formalized datasets to make appropriate inferences when quality data are limited. However, the subjectivity of models based on ‘opinion’ means that comparison between species and landscapes, as well as defining appropriate scaling and thresholds, becomes problematic.

Mechanistic niche models can be used in reintroduction planning to estimate niche requirements from first principles. They infer environmental tolerances from the physiological and biophysical attributes of a species to map their fundamental niche (Peterson, Papeş and Soberón, 2015). Although these models can overcome the subjectivity of expert opinion, and errors associated with correlative models, their required data are rarely available. Where physiological and biophysical data are available, it is usually only for a few specimens, meaning individual-level variability is overlooked when inferring population-wide patterns (Peterson, Papeş and Soberón, 2015).

Current habitat modelling methods provide insight into the spatial properties of habitat for a reintroduced species but assume that landscape and climate attributes are static. Temporal dynamics, including seasonality, succession and climate change, alter the size, location and quality of habitat. This variability has been addressed in some studies by modifying

habitat model outputs, mostly with reference to anthropogenic climate change predictions (Dullinger *et al.*, 2012). Creating more realistic, dynamic habitat models remains a challenge because data to detect temporal changes are limited. Metrics such as rainfall and temperature are commonly calculated as long-term averages (Fick and Hijmans, 2017), whereas surveys of attributes such as vegetation and land cover are conducted too infrequently to detect short-term dynamics (Leathwick *et al.*, 2002).

For habitat models to be useful, the spatial resolution of habitat data must be relevant to the scale at which the modelled species exhibits habitat preferences. Ecologically relevant scales often do not overlap with the scale of landscape data recording, or the scale of human modifications. Animals can also respond to separate landscape attributes at different scales, so considering a single scale can introduce bias (McGarigal *et al.*, 2016). To address this issue, models often choose a spatial resolution by compromising between an estimated functional scale for the species and pragmatic use of available data (Austin, 2007). The development of multi-scale niche models is at the cutting edge of this issue (DeCesare *et al.*, 2012).

Habitat models can identify potential reintroduction sites when applied at national or international scales. Subsequently, they can be used at local scales to identify release sites and lower quality habitat within release areas that might require active management, such as supplementary feeding. Nüchel *et al.* (2018) apply a correlative habitat suitability model using contemporary and historical records to estimate the distribution of suitable conditions for snub-nosed monkeys (*Rhinopithicus*), a first step in screening for reintroduction sites.

### **3.3 Dispersal Models**

Dispersal is the process of individuals or propagules (e.g., seeds, spores or larvae) moving between patches of habitat. Dispersal mode is a key determinant of habitat use following reintroduction (Ziółkowska *et al.*, 2016). In order to map accessible resources for re-introduced populations, dispersal must be considered (Holloway, Miller and Gillings, 2016). For example, a ‘habitat map’ might identify high-quality reintroduction areas based on large areas of habitat (Corlett, 2016) but, if dispersal barriers exist, the site could be a poor choice, as founders would be unable to colonize the wider landscape (Moraes *et al.*, 2018).

In the long term, dispersal also determines how reintroduced species establish metapopulation dynamics, influencing population viability and determining gene flow across

the landscape (Hanski, 1999). Thus, reintroduction programmes should consider both long-term and short-term dispersal patterns as these impact both population establishment and persistence (IUCN/SSC, 2013).

In the simplest approach, geometric distance models, only the straight-line distance between habitat patches limits dispersal. These distances are easily calculated (Raines, 2002) but do not consider the way animals move through landscapes. Dispersing animals will choose relatively hospitable areas and avoid dangerous ones; they might use small habitat patches as ‘stepping-stones’, or follow linear connecting elements (e.g., riverbanks, hedgerows). Failure to account for these processes leads to inaccurate predictions, though there will likely be broad correlation as nearby habitat patches are generally easier for dispersing animals to find and colonize. Population-scale dispersal patterns can be incorporated into spatial distance models using dispersal kernels, distributions describing the range of distances potentially travelled by any individual, where levels of dispersal decline more rapidly with increasing distance between patches (Slone, 2011). As these do not consider structure in the inter-habitat matrix, the areas that are not habitat for the focal species, they are likely to produce poor estimates of dispersal in landscapes with significant inter-habitat heterogeneity (Keller, Van Strien and Holderegger, 2012).

Cost-distance models have been developed to account for the structure of the landscape matrix and how this affects the movement of animals (Graves *et al.*, 2014). To calculate cost-paths between habitat patches, the landscape is modelled as a cost-surface, where features are scored according to their resistance to movement. The least-cost path is then the route between two habitat patches with the lowest resistance, with dispersal frequency being inversely proportional to this least-cost path. However, least-cost models are structural models and have been criticized for not taking into account the cognitive processes of dispersing animals (Simpkins *et al.*, 2018). Their main drawback is that cost-distance models assume dispersers have perfect knowledge of the landscape and take detours or pass through bottlenecks to reach certain patches. This can be reasonable, for example where animals use paths marked by conspecifics or follow established migration routes, but often it is not (Mateo-Sánchez *et al.*, 2015). Other methods take more account of the cognitive processes involved in dispersal, but still rely on a cost-surface to quantify the impacts of matrix structure in directing movements. A variety of methods are used to estimate cost-surfaces, including expert opinion (Graves *et al.*, 2014), animal tracking (Cushman, Lewis and Landguth, 2014), genetic distances (Zeller *et al.*, 2018) and inverting

habitat suitability estimates (Keeley, Beier and Gagnon, 2016). The cost-surface should capture the resistance of matrix elements to species movements to ensure models generate useful predictions (Keeley *et al.*, 2017). Creating a cost-surface for a reintroduction is likely to face data-limitation issues, like those of habitat models. Landscape resistance must be often inferred from data collected outside of the release area (from currently occupied areas) and novel landscape features will cause issues.

Circuit theory models use the analogy of electrons moving in an electrical system to represent the movement of animals across the landscape (Hanks and Hooten, 2013). Habitat patches are represented as nodes, connected by a resistance surface. When a voltage is placed across the model landscape, this stimulates movement from a point of origin, a power source in the analogy, to a destination, an earth (Cowley, Johnson and Pocock, 2015). The advantage of circuit theory models over cost-distance models is that rather than modelling dispersal via a single pathway, all routes between two nodes are considered. Use of pathways is weighted according to conductivity (inverse resistance), predicting relative use of all available pathways during dispersal and population radiation (Mateo-Sánchez *et al.*, 2015). The electronics analogy can hamper parameterization and interpretation of the dispersal model, possibly leading to inappropriate model set-up and reduced impact of outputs due to confusion over the meaning of input parameters and output metrics (Hanks and Hooten, 2013).

Another group of advanced models are mechanistic dispersal models, which simulate how individuals make dispersal decisions and interact with landscape features (Bocedi, Zurell, *et al.*, 2014). These models incorporate knowledge of the landscape by considering dispersal as semi-random diffusion based on erratic motion (Codling, Plank and Benhamou, 2008). Refinements recognize that animals do not move entirely randomly, with correlated random walk models incorporating a tendency to maintain a consistent heading (Byers, 2001). The most cutting-edge mechanistic models explicitly model movement decisions as having random elements, but influenced by directional consistency, sensory range and a cost-surface (Coulon *et al.*, 2015). However, such models require difficult factors such as directional persistence and perceptual range to be estimated (Bocedi, Palmer, *et al.*, 2014). As these models are process-based with predictions emerging from species' fundamental traits, rather than population-level inferences, mechanistic models might better predict dispersal patterns in a novel landscape than alternatives.

Considered in isolation, dispersal models can predict release site-fidelity, aiding managers in determining an appropriate release cohort size for establishment. This utility can be enhanced by incorporating demographic and life-history factors, such as seasons when animals disperse (Hinderer, Litt and McCaffery, 2017), and incorporating information from habitat models. Combining habitat and dispersal models can provide specific predictions of how much habitat is available via dispersal. For example, (Peters *et al.*, 2015) use coupled habitat and dispersal models for brown bears (*Ursos arctos*) to estimate post-release habitat use.

### **3.4 Population Models**

Habitat and dispersal models predict the habitat accessible to a founder population, and how they might colonize the wider landscape. But colonization depends on the founder population providing new dispersers through population growth (Adams *et al.*, 2015). Modelling population dynamics can improve predictions of post-release establishment and spread (Larson *et al.*, 2004; Schurr *et al.*, 2012). Through population modelling, complex processes can be represented, such as metapopulation source–sink dynamics (Hanski, 1999; Lee and Bolger, 2017). These models can predict where stable populations might establish, estimate population growth in different patches and identify where dispersal might establish a subpopulation or inter-breeding in a metapopulation (Walker, Marzluff and Cimprich, 2016).

Population models must be capable of predicting the realized population growth rate in a given setting. The main challenge is identifying factors determining survival and breeding success (Akçakaya, 2000). The simplest population model for most species would use observed population rates for mortality and fecundity in a deterministic linear population growth equation, ignoring variation in landscape and environmental conditions.

Incorporating factors such as carrying capacity and density-dependent feedbacks requires making inferences from census data (Stubben and Milligan, 2007). Further, mortality and fecundity data from a relict range might not reflect post-release responses, as factors constraining population growth might differ between areas. For example, if the relict population persists in suboptimal conditions, the reintroduced population might be freed from environmental constraints (Kerley, Kowalczyk and Crooks, 2012; Panfyllova *et al.*, 2016).

More complex population models express vital rates, that is, birth, death and dispersal, as random (stochastic) responses to local environmental conditions and population density, with the parameters for response functions inferred from census data (Bocedi, Palmer, *et al.*, 2014). These models can also incorporate individual (age, sex, phenotype, personality) and local population effects on vital rates and predict demographics of establishing populations. For a reintroduced population, density is likely to be lower than in the current range, so a response function from that range could yield inaccurate predictions, for example, due to Allee effects (Xia *et al.*, 2013).

Complex population models include metapopulation models and individual-based models (MacPherson and Gras, 2016; Mestre *et al.*, 2016). Both can incorporate the effects of local conditions, population density and individual traits when predicting population growth and structure. They differ in the scale at which equations are applied; metapopulation models apply functions at the level of subpopulations, whereas individual-based models simulate every animal within a metapopulation. While metapopulation models are computationally less intensive, the abstraction of patterns to a population scale can make them less intuitive than individual-based models where such patterns arise from individual interactions (Akçakaya, 2000). Both groups of models can be used to predict population growth, so long as factors determining survival, fecundity and dispersal are appropriately represented. Individual-based models are an intuitive choice for reintroductions, as these will typically involve small populations.

Population models can determine the size of release cohort required for population establishment, with more detailed models also indicating the ideal age/gender balance of this release cohort. Incorporating effects of stressors and management options such as supplementary feeding can give insight into the best management options. When founder animals come from wild sites population models can also identify the maximum sustainable harvests for source populations (Dimond and Armstrong, 2007). Combining population models with predictions of habitat quality in the release area allows estimation of the impacts of local conditions on population growth; adding dispersal then allows predictions of the rate and pattern of population expansion. For example, Ovenden *et al.* (2019) use an individual-based population model and a mechanistic dispersal model for Eurasian lynx (*Lynx lynx*) to simulate reintroductions with different founding populations (Also see Box 1 for an example of these models in practice).

### Modelling the reintroduction of the Meadow Brown butterfly (*Maniola jurtina*) in South West Finland (Heikkinen et al. 2015)

The Meadow Brown butterfly (*Maniola jurtina*) is a dry grassland specialist in its northern range margin in Southwest Finland. Dispersal limitation has prevented the species from tracking changing climate conditions, making it a candidate for assisted colonisation northwards.

#### Habitat Model

The authors determined habitat suitability using corelative niche models (generalized linear models, generalized additive models and generalized boosting method). They refined this climatic suitability to habitat cover using grassland landcover classes. Twelve sites were chosen as release sites for simulations (shown in Figure 3.2).

#### Dispersal Model

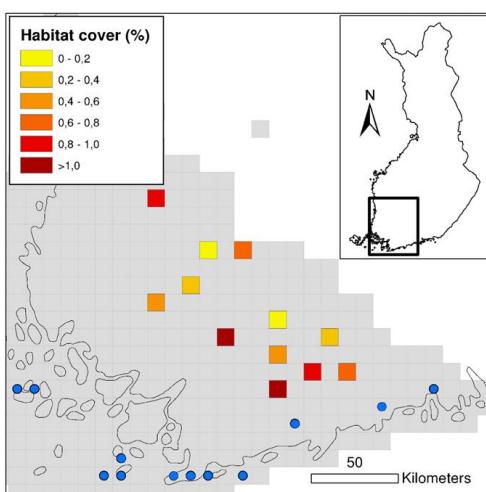
A dispersal kernel was used with a density-independent dispersal rate to simulate radiation from the release sites.

#### Population Model

A female-only individual based model with non-overlapping generations was used to simulate stochastic growth dynamics. Using growth rate ( $r_{max}$ ) and carrying capacity (K) estimates from a literature search, surveys and expert opinion.

#### Integration

Habitat, dispersal and population simulations were combined using the RangeShifter v1.0 software (Bocedi et al. 2014), to create a spatially-explicit, dynamic metapopulation model to simulate post-release dynamics following the release of 40 females to each of the 12 reintroduction sites.



**Figure 3.2-** From Heikkinen et al. (2015). Distribution of the selected twelve 10 × 10 km (“10 × 10 km landscapes”) used in the modelling of translocation potential of *M. jurtina* in SW Finland. Cover of suitable habitat in the selected 10 × 10 km cells is shown using a 6-level scale. Grey shading indicates climatically suitable area for the species and blue dots (midpoints of 10 × 10 km grid cells) known occurrences in 2001–2010.

#### Results

Simulations highlighted the importance of population growth rate and use of multiple release sites for successful establishment, providing recommendations for management of the proposed reintroduction. Authors highlighted the need for long-term population dynamic data to validate model outputs and for further development of models considering individual variation and genetic effects.

### 3.5 Interspecific Interactions

By combining models of habitat, dispersal and population dynamics, temporally and spatially explicit predictions can be made (Adams *et al.*, 2015). While these incorporate details of reintroduced species attributes, they ignore interactions with other species (Dormann, Bobrowski, *et al.*, 2018). In reintroductions, interactions with introduced species, parasites and humans are often significant and negative (Adams *et al.*, 2015; Corlett, 2016). Combining spatially dynamic models for multiple species is rarely considered due to technical challenges and data requirements as these models remain at the forefront of computational capacity. Nevertheless, they represent the next major development for ecological simulations, and warrant some consideration here.

One developing method that might enable identification of species interaction effects is joint species distribution modelling. These models use presence or abundance data for multiple species and landscape data to identify patterns of co-occurrence not explainable by differences in habitat requirements (Tikhonov *et al.*, 2017). However, such patterns are correlational, so these models do not identify causal mechanisms with many processes able to produce similar patterns in outputs (Dormann, Bobrowski, *et al.*, 2018). Additionally, correlations in species co-occurrence may also be explained by responses to an unmeasured variable (Ovaskainen, Rybicki and Abrego, 2019). Joint species distribution models also assume species interactions are consistent across all areas, which is often not the case, especially since reintroductions might create novel species interactions (Ovaskainen *et al.*, 2016). Consequently, joint species distribution models should be interpreted with care, and perhaps be used for hypothesis generation rather than directly predicting interactions in release areas (Pollock *et al.*, 2014).

The simplest species interaction models require a population map of interacting species and an estimate of interaction impacts (e.g., on mortality, fecundity and dispersal). Estimates are often uncertain and might not be generalizable (Ovaskainen *et al.*, 2019), or may be based on theoretical assumptions (Thompson, Rayfield and Gonzalez, 2017). These responses can be binary (based on presence/ absence) or continuous (based on the population density of interacting species). Numerous interactions can be modelled, including predation, parasitism and competition. This method has the drawback of being one-directional and non-dynamic, as interacting species are mapped according to survey or habitat data and would not be influenced by the introduced species (Hale and Koprowski, 2018). However, going beyond one-way impact requires much greater modelling effort.

Mechanistic models with two-way species interactions need separate models for each interacting species considered. Prey, competitors, predators and parasites require modelling to the same level as the reintroduced species, and spatial and temporal aspects of interactions then need to be incorporated (Viljugrein *et al.*, 2001). This requires the formulation of complex interaction terms between each model constructed. Data availability and computational power will likely limit such spatially explicit metacommunity modelling. Nevertheless, they could provide the most accurate, explicit, and useful predictions.

Interspecific models identify how other species will affect the viability of a reintroduction, with more detailed models providing specific predictions of tolerable population sizes for coexistence which can indicate the intensity of control required for species expected to have a negative impact on the reintroduced species. When combined with other models to form spatially explicit metacommunity models, the predictions from these models have a great capacity to contribute detailed and specific information to inform reintroduction management plans (Thompson, Rayfield and Gonzalez, 2017).

### **3.6 Practical Recommendations**

The components of a holistic model to manage species reintroductions have been discussed. I have reviewed the methods available for each sub-model (Summarized in Table 3.1) and described how these could be combined to predict reintroduction dynamics (Figure 3.1; Guisan and Thuiller, 2005). In many cases, it will not be necessary to combine all sub-models, as a single model (e.g., a habitat model) can address key management questions. Depending on the question and the data available, using simpler model structures might be the best option. While integrating more data and considering more parameters and processes adds to the potential realism of models, it also adds to the uncertainty of model outputs. As each parameter measurement has associated error, the more parameters included in a model, the greater the cumulative uncertainty of model outputs (Conlisk *et al.*, 2013).

**Table 3.1-** Summary of predictive models applied to reintroductions. Cited references are published examples of each model type applied in a reintroduction context.

Model Group	Model	Strengths	Weaknesses	References
<b>Habitat Models</b>	Surrogate feature	Can be applied with limited data (e.g., one land cover class). Analytically simple. Suitable for specialised species.	Often ecologically simplistic. Unsuitable for species with complex or flexible habitat requirements.	Rendall, Coetsee, & Sutherland (2018)
	Correlative Habitat Suitability	Statistically rigorous. Based on niche theory and empirical data.	Requires data from stable populations to reliably identify niche boundaries. To niche boundaries for reintroductions.	Stone & Guy (2017)
	Expert opinion	Can make inferences beyond limited datasets.	Difficulty comparing species and landscapes. Inferring beyond broad categorisation dubious.	Dolný, Šigutová, Ožana, & Choleva (2018)
	Mechanistic niche	Predicts the species niche from first principles. Potentially accurate in novel settings.	High and specific data requirements. Impractical in most cases.	
<b>Dispersal Models</b>	Geometric Distance	Easy to calculate Identifies fragmentation of habitat	Does not consider matrix structure	Howell, Muths, Hossack, Sigafus & Chandler (2018)
	Least-Cost Paths	Considers effects of matrix directing species movement.	Does not consider dispersal behaviours Calculation of costs is critical.	Alexander, Olimb, Bly, & Restani (2016)
	Circuit Theory	Enables simultaneous consideration of available dispersal pathways.	Parameterisation and outputs can be obscure.	Hinderer, Litt, & McCaffery (2017)
	Mechanistic Dispersal	Detailed consideration of species behaviour during dispersal.	Requires knowledge of perceptual range and turning frequency.	Haydon et al. (2008)
<b>Population Models</b>	Deterministic Linear Growth	Computationally simple. Direct extrapolation from census data.	Does not consider feedbacks e.g., habitat quality and density-dependence.	Lalas & Bradshaw (2003)
	Stochastic Demography	Can incorporate numerous feedback mechanisms affecting vital rates.	Requires detailed understanding of demography.	Panfyllova, Bemelmans, Devine, Frost & Armstrong (2016)
	Metapopulation	Computationally efficient at large population sizes.	Population level equations less intuitive than individual level.	Howell et al. (2018)
	Individual Based	Simulates individual interactions leading to metapopulation patterns. Sound analogue for ecological processes.	Computationally intensive, especially with large populations. High data requirements.	Sun et al. (2016)
<b>Interspecific Interaction Models</b>	Joint Species Distribution	Relatively simple inputs required. Identifies patterns in species co-occurrence.	Correlational, no mechanistic understanding. Assumes interactions are consistent.	Magory Cohen & Dor (2019)*
	Population Mapping	Incorporates impact of sympatric species on reintroduction. Impact could be mediated via effects on habitat quality.	Assumes that interacting species do not respond to the reintroduced species.	Berger & Gese (2007)**
	Dynamic Metacommunity	Enables consideration of dynamic interactions between multiple species.	Extremely high levels of data required for multiple species and their interactions. Computationally intensive.	Hale & Koprowski (2018)***

\* Species invasion, ecologically analogous to a reintroduction.

\*\* Pattern based, non-dynamic, empirical study that could be the basis of a model.

\*\*\* Review highlighting the lack of metacommunity considerations in species reintroductions.

Simpler models often hide statistical uncertainty behind unrealistic assumptions and so just because the uncertainty stated in their outputs is low, this will not always indicate that these models will yield accurate predictions. To avoid constructing advanced models of little practical benefit, or models that are inaccurate due to poor input data, both the research question and the quality of available data must be considered. In most cases, it is recommended that the simplest accurate model be used to aid in the understanding of the model and to increase the transparency of recommendations. However, identifying this ‘simplest accurate model’ is not straightforward, as tests of predictive accuracy cannot be performed until independent data are available after the reintroduction has commenced.

Choosing between model options is complicated as methods are rarely compared directly, and when they are they tend to produce conflicting outputs (Simpkins *et al.*, 2018; Zeller *et al.*, 2018). Model choice is often based on personal preference and ease of application, rather than evaluations of accuracy (Mateo-Sánchez *et al.*, 2015). Model validation is therefore a crucial, but often neglected, stage in the modelling process, necessary to enable model selection based on measures of performance accuracy (McClure, Hansen and Inman, 2016). Reintroductions provide a unique opportunity for model validation. As reintroduced populations are small and localized compared with most naturally occurring populations, less effort is required for surveys (Mihoub *et al.*, 2014). Standard monitoring methods should provide sufficient data to validate predictions made by each sub-model, and the overall predictions of combined models (Cagnacci *et al.*, 2010).

I recommend the following: (a) reintroduced populations should be appropriately monitored to provide a dataset against which model predictions can be evaluated; (b) predictions of sub models and combined models should each be validated to identify effects of cumulative uncertainty and (c) model validation is used to improve models and parameter estimates, rather than as a requirement to ‘finish’ a study. Effective validation can then allow the most accurate model to be identified and refined, to inform if, where and how reintroductions should occur.

### **3.7 Conclusions**

This chapter provides a digestible overview of the options available for predictive modelling of reintroductions and indicates how different models can be combined to create nuanced predictions of post-release patterns. This will enable non-modellers to get their bearings in the vast literature on ecological models. However, further research into specific models will

be necessary to enable the effective application of the models covered in this review. The following rules of thumb should be considered throughout the modelling process; from conception to evaluation of reintroduction modelling projects attention should be paid to:

- The overall aims of the reintroduction.
- Specific management questions that the models seek to address.
- The attributes of the focal species.
- Major threats/stressors to the species within its native range and whether these are different in the reintroduced area.
- Quality and type of data available for use in fitting predictive models.

These factors determine which modelling options are preferable and will guide choices between options. I recommend that effort is invested in model validation so that models can be applied with confidence based on their predictive accuracy and can be refined or developed further as necessary.

## **Chapter 4**

### **Predictive Modelling: Relict Distribution Habitat Models**

In this chapter I use species and environmental information from the takahē' relict distribution in the Murchison Mountains to predict post-release space and resource use by reintroduced takahē in Kahurangi National Park. To do this I use takahē presence data collected through systematic monitoring of the relict wild takahē population in the Murchison Mountains between 2012 and 2020 as the basis for correlative habitat suitability models. These models identify the environmental characteristics of areas most exploited by takahē in their relict distribution and use this to infer habitat suitability. I project this model to the reintroduction landscape of Kahurangi National Park to predict the distribution and relative quality of takahē habitat in this area. I then couple these with predictions of post-release dispersal to account for the limited opportunity released birds have to explore and colonise the landscape in the first years following their reintroduction, providing a final output predicting the distribution of the reintroduced population a short time following release.

#### **4.1 Introduction**

In order for conservation translocations to have a chance of success, it is essential that there are sufficient resources available in the translocation area to enable species survival and propagation, i.e., that at least portions of the translocation area can be defined as 'habitat' (as defined in the previous chapter; Stadtmann and Seddon, 2018; Chapter 3; Hunter-Ayad *et al.*, 2020). However, defining what resources and areas constitute habitat for a given species and translocation area can be difficult, especially in the case of reintroductions and assisted colonisations for range-reduced species that are often the focus of conservation translocation initiatives (Kerley, Kowalczyk and Crome, 2012; IUCN/SSC, 2013). There are many alternative methods to help identify habitat in translocation areas with correlative habitat suitability models (described in Chapter 3) being a popular choice (Guisan *et al.*, 2013; Lentini *et al.*, 2017; Massaro *et al.*, 2018; Chapter 3; Hunter-Ayad *et al.*, 2020; Jarvie *et al.*, 2021; Zurell *et al.*, 2021).

Predictions from habitat suitability models can be used in the planning and post-release management of conservation translocations. Insights into the suitability and spatial structure of habitat in a translocation area can inform expectations of where populations are likely to

establish and concentrate (Osborne and Seddon, 2012). Additionally, habitat predictions can give insight into potential colonisation patterns in case of dispersal away from release sites (Cornelius *et al.*, 2017). Such predictions can guide management focus in terms of identifying key areas for population monitoring and/or threat mitigation, such as where translocated animals are likely to encounter humans (Recio, Sand and Virgós, 2020; Recio *et al.*, 2021), livestock (Fernández, Kramer-Schadt and Thulke, 2006), and/or predators (Warren *et al.*, 2017). Additionally, some areas for habitat restoration may be highlighted, e.g., where predicted habitat suitability is low but it would be desirable to increase carrying capacity (Roberts, Cooper and Luther, 2021) and/or to encourage connectivity between extant habitat patches (Gillies and St. Clair, 2008).

Predictions generated by correlative habitat suitability models are most commonly presented on a scale relative to the probability of presence of the focal species, where outputs are often assumed to be equivalent to an estimate a species' distribution (an alternate term for these models is "Species Distribution Model"; Guisan and Thuiller, 2005; Anderson, 2017). However, in cases where models trained only with data from a relict population are applied to reintroduced populations (and other contexts where populations are in disequilibrium) predictions should only be interpreted as an index of habitat suitability. While this does not mean that habitat predictions for translocated species are useless, it does perhaps mean that they need to be interpreted more carefully than in some other contexts (Guillera-Arroita *et al.*, 2015). Instead of estimating the current distribution of a species, when habitat models are applied to translocation landscapes, they can be better understood to predict the potential future distribution of a reintroduced population (at the point that the population reaches carrying capacity and is in equilibrium with its environment). Therefore, when research aims to predict distribution and resource use in translocated populations during early stages of establishment it may be necessary to combine predictions of habitat suitability with additional predictions of focal animals' post-release movements. In this way the expected distribution of the establishing population can be predicted based on habitat structure and suitability while accounting for the limited opportunities for dispersal and population expansion in the translocated population (Sun *et al.*, 2016; Mertes *et al.*, 2019; Soriano-Redondo *et al.*, 2019).

In order for habitat suitability predictions to be useful, they must be reasonably accurate, and at least able to differentiate habitat from inter-habitat matrix with a reasonably low error rate (Fletcher *et al.*, 2019). A key consideration in this regard are the location data used as

input for correlative habitat suitability models, what assumptions are made regarding these data, and methodological choices based on these data and assumptions (Chapter 3; Hunter-Ayad *et al.*, 2020; Chapter 2; Hunter-Ayad *et al.*, 2021). While these choices should always be informed by ecological understanding (both general ecological theory and current best knowledge of the species and scenarios being considered), such knowledge is often incomplete and fragmented (van der Vaart, Johnston and Sibly, 2016; Yates *et al.*, 2018). This means that there is often, implicitly or explicitly, a choice made with regard to the interpretation of incomplete knowledge. In chapter 2 (Hunter-Ayad *et al.*, 2021) I presented two explicit strategies for approaching knowledge gaps which are encountered when translocated animals are expected to encounter novel conditions, defined as conservative and extrapolative strategies. Here I apply my proposed strategies to develop habitat and post-release space-use models for takahē (*Porphyrio hochstetteri*) reintroduced to the Gouland Downs, Kahurangi National Park in 2018. These predictions are based on data from the only extant wild population of takahē in the Murchison Mountains, Fiordland (Chapter 1; Mills, Lavers and Lee, 1984). When developing correlative habitat models, I considered the ecological context of input data and performance metrics relating to a large set of potential model settings (Muscarella *et al.*, 2014).

This chapter has three objectives:

1. Use location records from the relict population of takahē in the Murchison Mountains to generate a habitat suitability model for takahē under conservative and extrapolative assumptions.
2. Project habitat models to the reintroduction landscape of Kahurangi National Park to predict habitat suitability and structure across this landscape.
3. Combine habitat suitability predictions with simple dispersal models to provide specific predictions of post-release takahē distribution considering both habitat suitability and post-release dispersal processes for the reintroduced takahē population.

## 4.2 Methods

### 4.2.1 Species Data - Murchison Mountains Population

The relict takahē population in the Murchison Mountains has been the focus of research and conservation efforts for over 70 years, with records from the monitoring of this population, e.g., location, population, demographic, and breeding data, collected more

frequently and more accurately as technology and methodology has advanced throughout the decades. Takahē monitoring in the Murchison Mountains now takes advantage of leg banding, VHF radio tracking, and aerial support. The current monitoring program includes a complete population census every three years and nesting/breeding monitoring to track demographic patterns within the population (Hegg *et al.*, 2012). This ongoing monitoring effort provides a valuable resource in the form of spatially and temporally explicit individual observation records collected over multiple years. These data can be a far superior input for correlative habitat suitability models than other commonly used sources (online databases, casual records, etc.; Yates *et al.*, 2018). However, this dataset is appropriate only for presence-only or presence-background modelling methods, as unrecorded movements of takahē between surveys mean it is not possible to confirm consistent absence locations within the Murchison Mountains (Guillera-Arroita *et al.*, 2015).

Although continuous, structured monitoring of the Murchison takahē population has provided long-term, accurate, and largely unbiased (in terms of spatially even survey effort) presence records for habitat modelling, these are not without limitations. The historic and ecological context of the relict population must be considered when constructing correlative habitat suitability models. The relict range is restricted both latitudinally and altitudinally, and from this models could infer a narrow, specialised niche with regard to latitudinally and/or altitudinally correlated factors (Fitzpatrick *et al.*, 2007). However the current range limitation is understood to be a result of human activity and historic extirpation from the wider landscape, rather than reflecting specialisation to the specific latitude or altitude of the Murchison Mountains (Beauchamp and Worthy, 1988). It is therefore inappropriate to infer that latitudinal and/or altitudinal gradients are drivers of takahē resource use and therefore such predictors should not be included in correlative models using the Murchison Mountains records (based on the principles established in Guillera-Arroita *et al.*, 2015).

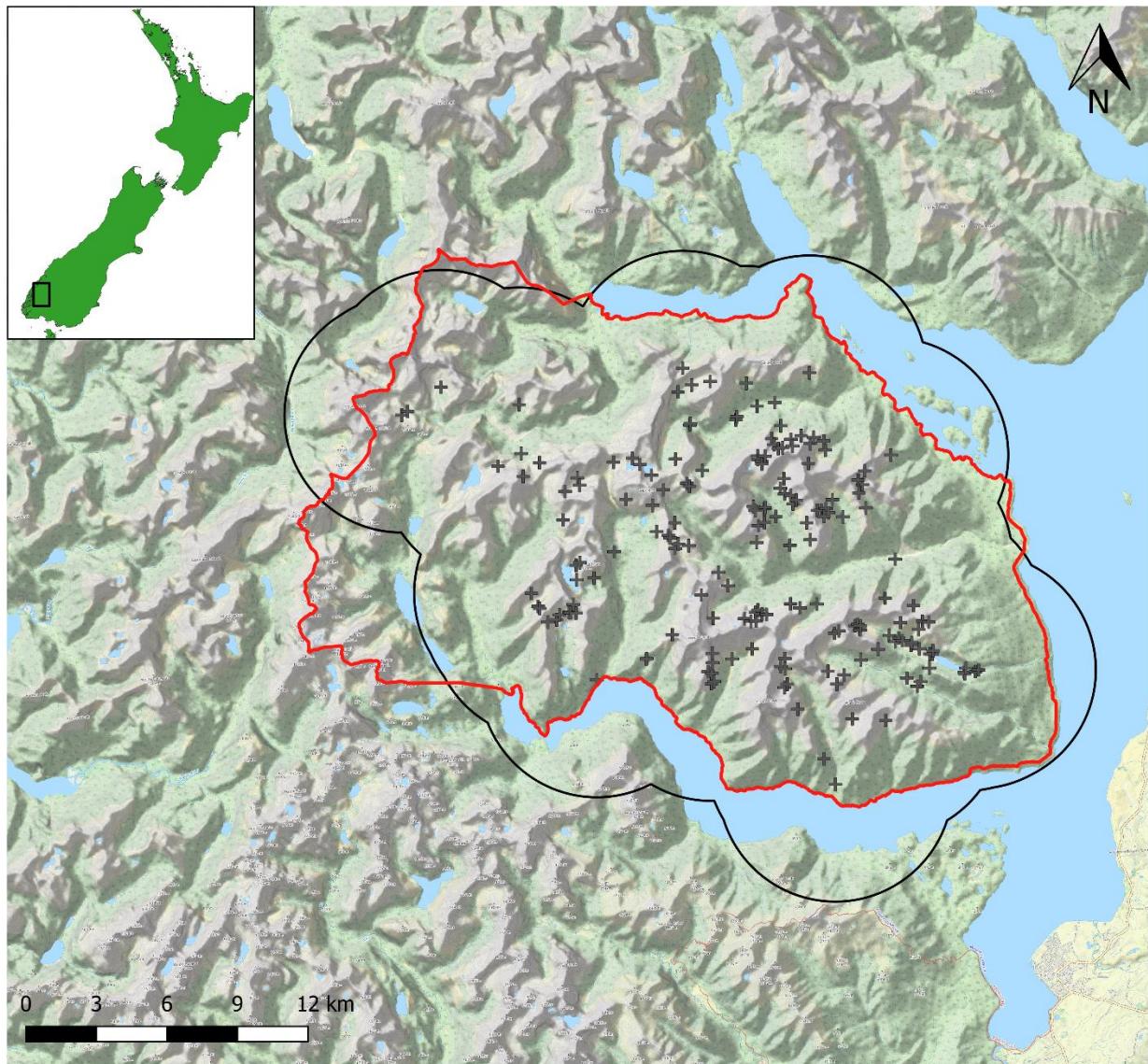
In addition to the careful selection of environmental predictors, the selection of background, or pseudo-absence, data for use with presences from the relict population must be considered carefully (Liu, Newell and White, 2019). Following historic range and population contractions, the Murchison Mountains takahē population has been significantly below stable equilibrium numbers for several decades, approaching the expected carrying capacity of the Special Takahē Area only in the last few years (Hegg, Mackenzie and Jamieson, 2013; Greaves *et al.*, 2020). This means that while recent records from the Murchison Mountains can reasonably be assumed to come from a population in dynamic

equilibrium, absence from the wider geographical area cannot be attributed confidently to niche limitations. As the effect of historic extirpation and dispersal limitation (as the fluctuating population has likely been a poor source of emigrants) cannot be disentangled in the areas surrounding the relict population, taking pseudoabsence points from outside the general range of the Murchison Mountains population will likely produce misleading inferences regarding takahē niche tolerance (Anderson and Raza, 2010; Barve *et al.*, 2011). However, the effect of environmental factors in determining resource use at local scales can be investigated by selecting background samples from within the local area of observations records. In this way the models will identify takahē niche preferences at the scale of home range selection (second-order selection; Johnson, 1980).

A set of location records for takahē was extracted from the South Island takahē database maintained by the Takahē Recovery Group (TRG) in September 2020. Records were filtered by site (Murchison Mountains), locational data (coordinates recorded), observation method (physical, telemetry or visual, meaning that locations were considered accurate to within 5–25m; Neill and Jansen, 2014) and date (1<sup>st</sup> October 2012–10<sup>th</sup> September 2020). From this a dataset of 276 presence records relating to 135 individual birds was extracted. This dataset was then resampled so that no landscape cell (200m resolution, an approximate minimum home-range size for takahē; for more information see section 4.2.3) contained more than one occurrence point using the *gridSample* function from the *dismo* package in R version 3.5.1 (Hijmans *et al.*, 2017; R Core Team, 2020), providing a finalised set of 179 records from 113 birds (shown in Figure 4.1).

#### **4.2.2 Background Points**

Background points for use in the correlative models were drawn from a 5km buffer area around the full set of occurrence records (Figure 4.1). This restriction limits the area of model inference to an area within which it was assumed the takahē population has had the chance to explore and to select home ranges (Anderson and Raza, 2010). However, infrequent, and historic observations of takahē outside of the Murchison Mountains are known in Fiordland (Lee and Jamieson, 2001; TRG, unpublished records). Thus, while the boundary seems appropriate for the records retrieved, it should not be taken as a firm spatial limit to the Fiordland/Murchison Mountain takahē population. All background points were randomly sampled from within this area.



**Figure 4.1-** Takahē records used as input for correlative habitat suitability models, extracted from the Takahē Recovery Group database in the Murchison Mountains. Crosses indicate cleaned presence records, while the red line shows the boundary of the Special Takahe Area. The black line indicates the area from which background samples were drawn, a 5km buffer around all presence data.

While it has been shown that using smaller numbers of background points can reduce model overfitting (Jiménez-Valverde *et al.*, 2011), reduced background samples also introduce stochasticity into model runs. As background sample sizes increase they approach a complete sample of the landscape, meaning that any two large “random” background samples will be more similar than any two small background samples. For example, theoretically multiple random samples taken with 50 % landscape coverage will, on average, have 25 % overlap in landscape cells included, whereas when only 25 % of the landscape is sampled, there will be an average overlap of 6.25 % between repeated

random samples. As the background sample makes up at least half of data input for most correlative niche models, variation in the selected background sample will lead to variation in fitted models and output predictions (Qiao, Soberón and Peterson, 2015). Based on trials using different background samples I determined it would be beneficial to run multiple model iterations, each taking a different, random background sample as input with final output being taken as an average of serial model runs. This was especially important when the background sample used was relatively small.

To investigate the impact of varying background sample sizes on model predictions and variance I tested models using several sizes of background sample (500, 1000, 2000, 5000 and 10,000 points) and the model optimisation and replication procedure outlined in section 4.2.4. Models with  $\geq 5000$  background points were deemed to be conservative as they consistently predicted low habitat suitability in areas representing novel conditions relative to model building region (the area from which presence and background points were drawn). I therefore used a sample of 5000 background points for constructing conservative models. For extrapolative models 1000 background points were used as the appropriate number as this was the largest tested background sample where models did not strictly exclude novel areas from habitat estimations, but rather the standard deviation of extrapolative predictions was seen to scale with environmental novelty (Figure 4.10). The only difference in conservative and extrapolative models constructed was background sample size, all following settings and processes were identical for both model options presented.

#### **4.2.3 Environmental Predictors**

I considered an initial set of 31 potential candidate environmental predictors for the relict correlative distribution models, covering a wide range of climatic and structural (vegetation and topographical) variables that could potentially influence takahē habitat suitability. These predictors were derived from national database sources (see Appendix A.1 for details of data sources and formatting). To explore the suitability of potential predictors I first cropped all data to the extent of the focal study areas (the Te Anau Ecoregion for model fitting and Kahurangi National Park for model projection). Next, I converted the cropped layers into consistent 200m (4ha) resolution raster layers, so that cell size matched an approximate minimum area for a takahē' home range. This approximate minimum home range was estimated based on analyses conducted on offshore islands (Ryan and Jamieson, 1998; Baber and Craig, 2003), which appear to form the basis of minimum values stated in online

media (*Takahē Recovery Programme*, 2022; *The takahē's ecological niche*, 2022). However, such inference is questionable, as home-range analyses conducted on wild takahē in the Murchison Mountains produced far higher home range estimates (28-1677ha; Maxwell and Jamieson, 1997). For details of methods see Appendix A.1.1.

I then refined the 31 candidate predictors (Appendix Table A.1) in several stages. First, I used the removeCollinearity function in the virtualspecies package (Leroy et al., 2016) to identify correlation between candidate predictors based on Pearson's r correlation index (Appendix A.2). Predictors with a Pearson's  $r > 0.7$  were deemed to be overly correlated, and only one variable from these intercorrelated pairs/groups was retained (the variable that had the most plausible functional mechanism to impact takahē habitat suitability) for further consideration (Dormann et al., 2013). Next, I calculated Variance Inflation Factors (VIFs: a calculation of the severity of multicollinearity between model coefficients) for the remaining candidate predictors using the usdm package (Naimi et al., 2014) in R; any variables with a  $VIF > 3$  were excluded from further consideration (Appendix A.2; Zuur, Ieno and Elphick, 2010). Next, given the ecological and historical context of the Murchison Mountain takahē population, I removed any predictors displaying a clear altitudinal and/or latitudinal gradient, as these would produce erroneous correlations and generate misleading predictions when applied to Kahurangi NP. Finally, any remaining predictors that had only weak, marginal, or indirect effects in determining takahē habitat suitability (inferred from iterative trialling of putative models and sources such as Mills et al. 1984; Beauchamp & Worthy 1988; Trewick & Worthy 2001; Hegg et al. 2012) were also removed. This resulted in a finalised set of four environmental predictor variables for the relict distribution model that describe local factors understood to be the most important biologically in determining takahē habitat suitability:

1. Dominant Vegetation Cover – Included as takahē in the Murchison Mountains are preferentially tussock grazers (Mills et al., 1991). As such, vegetation cover determines food, cover and nesting resources that are key to survival and home-range selection (Mills, Lavers and Lee, 1984).
2. Soil Classification – Included as an indicator of soil drainage capacity/waterlogging tendency, soil pH and lithology. As members of the Rallidae, takahē prefer wet and boggy ground conditions (Hegg et al., 2012). Furthermore, acidity and lithology will impact the nutritional quality of takahē food plants that can grow in the soil (Rickebusch et al., 2008).

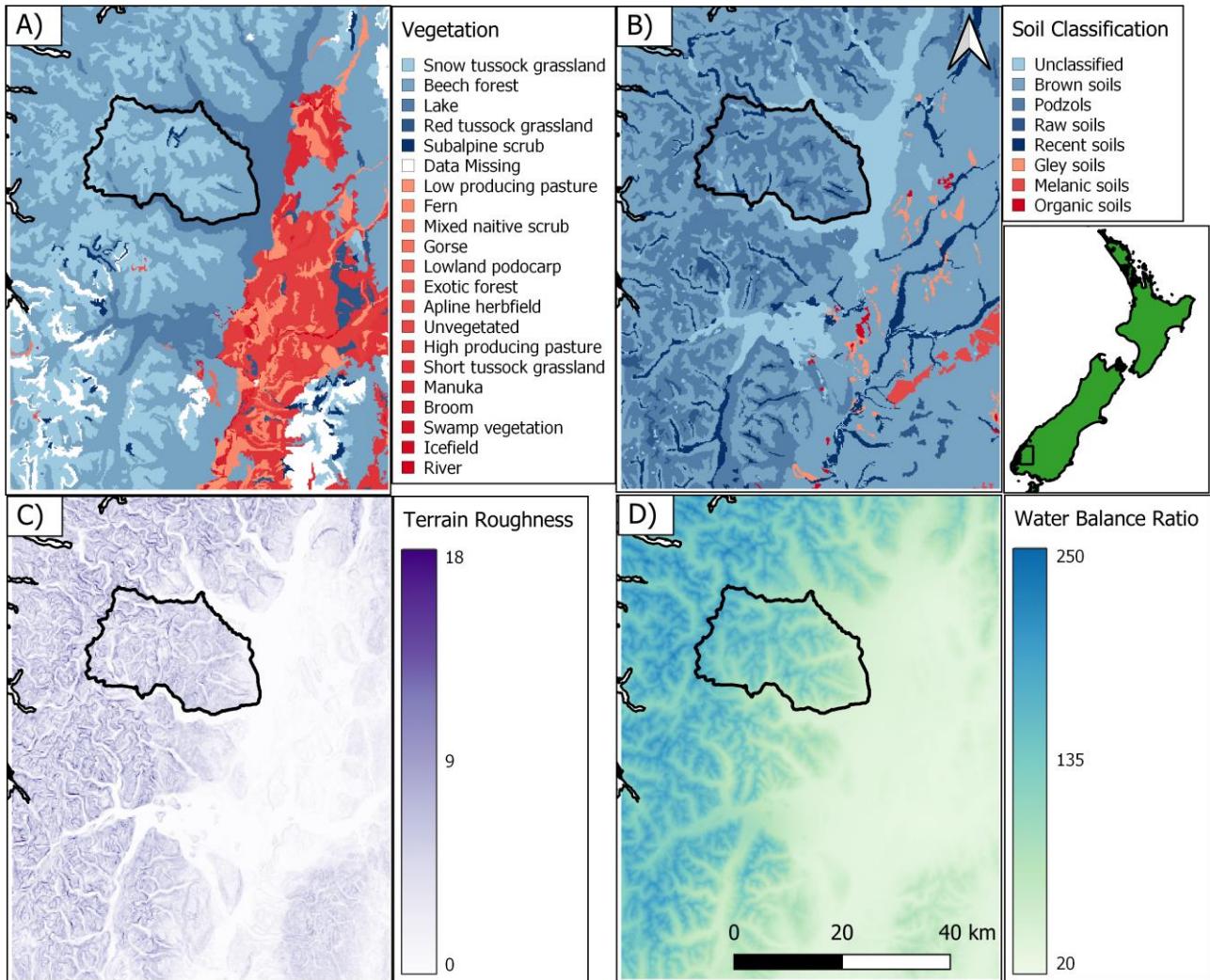
3. Terrain Roughness (Standard Error of 25 m DEM) – Included as a major source of mortality in the relict population is misadventure (largely falling off ledges and down slopes; Lee and Jamieson, 2001; TRG mortality records), and there is more risk of this in more uneven terrain.
4. Water Balance ratio – Included as a metric of environmental wetness and weather conditions. As mentioned, takahē are a rail species and as such are somewhat adapted to wet conditions (Beauchamp and Worthy, 1988; Trewick and Worthy, 2001). However, the extreme and heterogeneous rainfall and stormy conditions prevalent in the Fiordland region (Figure 4.2D; NIWA, [www.niwa.co.nz](http://www.niwa.co.nz)) exceed takahē' tolerance for both wet (e.g., western Fordland) and dry (e.g., eastern Murchison Mountains and east of Lake Te Anau) conditions. This understanding is supported by observed population concentrations shown in in Figure 4.1 and Lee and Jamieson (2001).

#### **4.2.4 Model Algorithm and Settings**

I chose the MaxEnt algorithm, recently shown to be analogous to inhomogeneous Poisson point process (Phillips, Anderson and Schapire, 2006; Phillips *et al.*, 2017), to create relict range habitat suitability models. MaxEnt was chosen because it operates with presence-only data such as those extracted from the takahē database; it has been shown to be relatively insensitive to violations of assumptions of unbiased samples from equilibrium populations compared with other correlative algorithms (Dudik, Phillips and Schapire, 2004; Elith, Kearney and Phillips, 2010; Fourcade *et al.*, 2014); and finally because MaxEnt is commonly used in the recent literature on species distribution modelling (Wollan *et al.*, 2008; Anderson and Raza, 2010; Breiner *et al.*, 2015; Mateo-Sánchez *et al.*, 2015; Galante *et al.*, 2018; Gomes *et al.*, 2018; Guevara *et al.*, 2018; Massaro *et al.*, 2018; Nüchel *et al.*, 2018; Thuiller *et al.*, 2020). However, despite the common usage of MaxEnt for habitat suitability modelling, several key criticisms have been levelled at the method, which warrant brief mention here. The maximum entropy principle that MaxEnt applies has been found to favour overly complex models, while also tending to overfit models to input data (which is addressed with an often arbitrary application of model regularisation; Warren and Seifert, 2011). Further, the correlative and presence-only nature of MaxEnt models means that it is possible to create models that fundamentally mis-represent species ecological responses, despite producing accurate predictions of range and distribution dynamics (Elith and Leathwick, 2009; Elith *et al.*, 2011). While the simplicity of application of the method does

attract a wide variety of users, this can also encourage models application without full understanding and critical evaluation of the modelling process (Phillips *et al.*, 2017).

MaxEnt is also sensitive to a variety ‘hidden’ factors, such as the grain-size of environmental inputs, though this is common to many modelling methods (Connor *et al.*, 2018; Chapter 3; Hunter-Ayad *et al.*, 2020).



**Figure 4.2** - Environmental Predictor variables prepared for The Te Anau Ecoregion considered for model fitting: A) Vegetation, B) Soil Classification, C) Terrain Roughness and D) Water Balance Ratio. Blue colours in A) and B) indicate categories that are represented in the buffer area in the Murchison Mountains (Figure 4.1), whereas red coloured categories are not represented in this area. For further consideration of non-analogue conditions see Appendix A.3. The black lines indicate the coastline and the boundary of the Special Takahe Area for spatial reference.

Several MaxEnt parameter settings can have a substantial impact on model predictions, and it is not recommended that automatic settings are used without consideration (Warren and Seifert, 2011). I therefore implemented MaxEnt models using the R package *ENMeval*

(Muscarella *et al.*, 2014), which creates a suite of MaxEnt models with a variety of parameter settings, comparing and evaluating these to identify the optimal model settings from tested candidates. Using *ENMeval* I created a suite of models combining three feature classes representing increasingly complex response functions (Linear, Linear and Quadratic, Linear Quadratic and Product; Phillips, Anderson and Schapire, 2006; Phillips and Dudík, 2008; Muscarella *et al.*, 2014). These feature classes were combined with 200 values of the regularization multiplier (between 0.05 and 10 in steps of 0.05), a model smoothing parameter, and used a “block” data partitioning method (as this option is recommended for models that will be projected across space, see Muscarella *et al.*, 2014 and Wenger and Olden, 2012 for details) for a total of 600 candidate models each for conservative and extrapolative modelling options.

Output metrics for candidate MaxEnt models give an indication of model performance (difference in sample-size-corrected Akaike information criteria, an indicator of model performance, relative to all others considered, hereafter delta-AICc, and area under the receiver-operator characteristic curve calculated using test data, hereafter test AUC, an indicator of performance relative to a perfect model) and overfitting (average difference in area under the receiver-operator characteristic curve, hereafter Average difference in AUC). Low delta AICc scores indicate better models, with AIC-optimal models having a delta AICc of zero (Muscarella *et al.*, 2014). Alternatively, high test AUC scores indicate better fitting models, where a score of 1 indicates perfect predictive accuracy and scores of 0.5 or below indicate that predictions are no better than random (Phillips and Dudík, 2008; Warren and Seifert, 2011). The average difference in AUC is a metric of model overfitting, it is the difference in AUC values when calculated with model training data and when calculated with model testing data (a subset of presence and background points withheld for evaluation during model building). A high difference in these two AUC values indicates that the model is overfitted to training data and thus is relatively less able to predict patterns in the testing dataset. In my models there was a 3:1 split of training to testing data and data was partitioned using the “block” method in ENMeval, whereby data is quartered into spatial blocks by partitioning down compass lines (Muscarella *et al.*, 2014). This partitioning method has been shown to be desirable for models intended to be projected across space (Wenger and Olden, 2012).

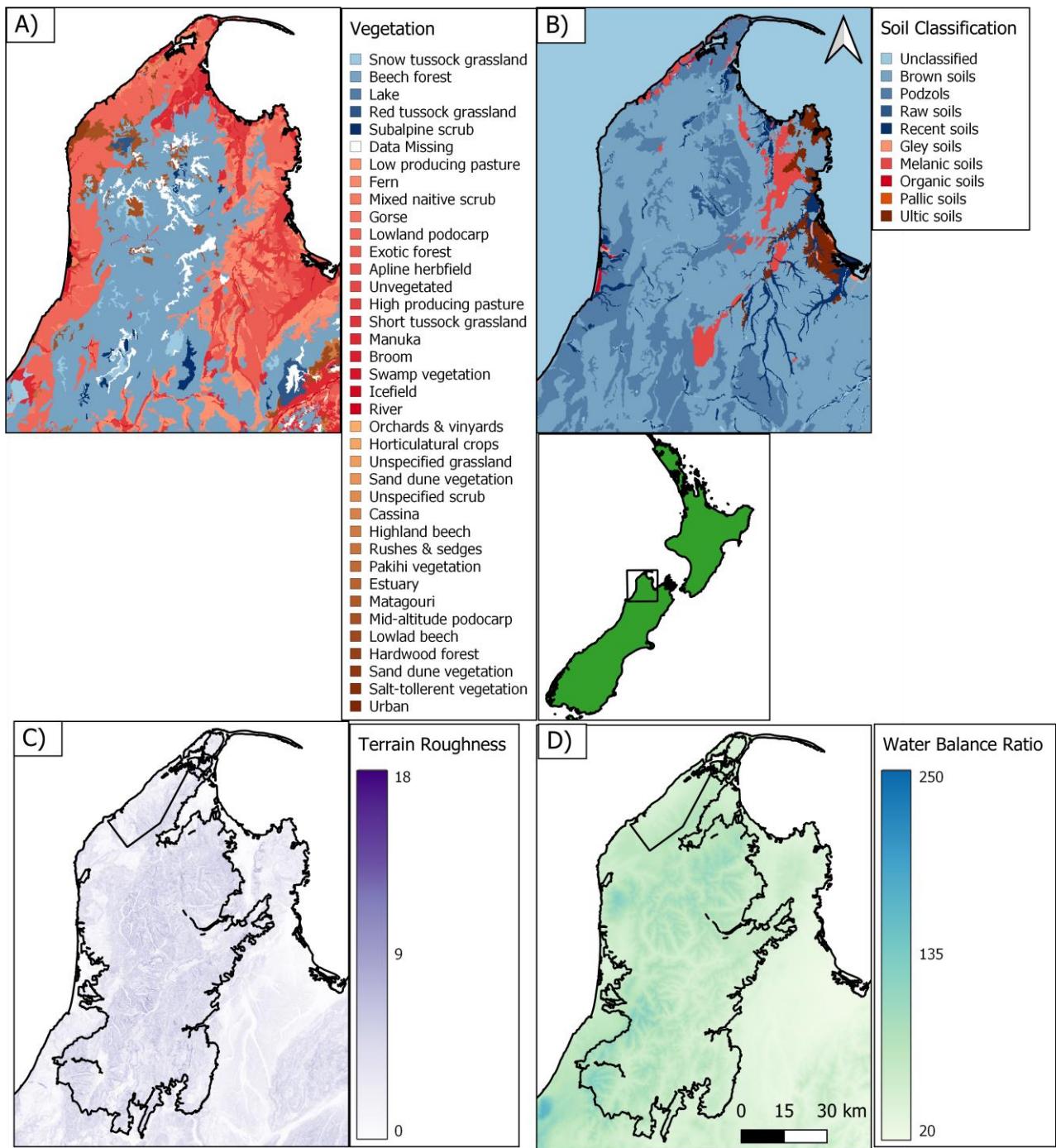
Optimal models were identified from the 600 candidate models based on the delta-AICc metric. A low delta-AICc is commonly used to identify the best model from a putative group

of models, and has been shown to be a better way of selecting optimal models for niche models than available alternatives (Warren and Seifert, 2011; Galante *et al.*, 2018; Norberg *et al.*, 2019). For each model replicate I selected the model with the lowest delta-AICc (by definition zero).

As described in section 4.2.1, the selection of background points can have a large impact on model outputs, and each individual run of ENMeval uses the same random sample of background points to fit all candidate models, thus making them potentially sensitive to biases inherent in any one random background sample. To reduce this bias, and ensure finalised models were not based on a single random draw of background points, I ran 40 replicates of the ENMeval optimisation run (which consist of 10 iterations per run, so, for clarity, in total I ran 400 model iterations, grouped into 40 replicates each using a separate random background sample for conservative and extrapolative models respectively; this was the maximum amount of replication that could be accommodated given the 8GB RAM capacity of the machine used for modelling). As each of the 40 replicates were based on a unique random draw of background points, I considered them to be independent model replicates (as opposed to separate models fitted to the same background sample, which I refer to as ‘iterations’). This resulted in 40 identified optimal models each for conservative and extrapolative options respectively, each fitted with a different random draw of background data.

#### **4.2.5      Habitat Predictions**

In order to predict habitat suitability and spatial structure for the takahē reintroduction in Gouland Downs, I projected optimal models to the extent of Kahurangi National Park. The models were projected onto environmental layers prepared in the same way as the environmental predictors (section 4.2.2; Figure 4.2), calculated this time for the extent of Kahurangi National Park (Figure 4.3).



**Figure 4.3** - Environmental projection variables prepared for the extent of Kahurangi National Park: A) Vegetation, B) Soil Classification, C) Terrain Roughness and D) Water Balance Ratio. Blue colours in A) and B) indicate categories that are represented in the buffer area in the Murchison Mountains (Figure 4.1), red coloured categories are not represented in this area, but are present in the Te Anau Ecoregion (Figure 4.2), brown colours indicate classes that are neither present in the Murchison Mountain buffer area nor the Te Anau Ecoregion. For further consideration of non-analogue conditions see Appendix A.3. The black lines indicate the coastline and the boundary of Kahurangi National Park for spatial reference.

Each of the 40 optimal models were projected using a complementary log-log (cloglog) transformation, specified within the *project* function, as is now recommended for MaxEnt models (Phillips *et al.*, 2017; the transformation is also examined in more detail in Appendix C.3, relating to analyses in Chapter 6). I then calculated means and standard deviations across the 40 habitat predictions generated for conservative and extrapolative options. I used these summarised outputs as finalised habitat suitability predictions and as a measure of the spatial stability of habitat predictions, respectively. The extent of extrapolation to non-analogous conditions in model projections is discussed (and assessed via Multivariate Environmental Similarity Surface, or MESS, maps for continuous predictors; Elith, Kearney and Phillips, 2010) in Appendix A.3. I also projected models in the same way described above to the Te Anau Ecoregion for the information of the takahē recovery group, although this projection is not of primary interest to this study, details are provided in Appendix A.4. Continuous model projections for Kahurangi were also binarized (using maximum sum of sensitivity and specificity threshold; Canran Liu, Newell and White, 2016) for the purposes of highlighting the different extent of habitat predicted by conservative and extrapolative model options (shown in Figure 2.4, for further details see appendix A.5). Limiting factor analyses (Elith, Kearney and Phillips, 2010) were also conducted to examine the driving factors creating the patterns of habitat suitability represented in model projections, with these described in Appendix A.6.

#### **4.2.6 Accounting for Dispersal**

While habitat suitability predictions for the reintroduction landscape are useful in isolation (e.g., for helping to estimate the extent and structure of suitable habitat and inferring carrying capacities based on this), they cannot be taken as direct predictions of space and resource use following the release of animals into new areas. This is because of the assumption inherent in the projection of the model that all areas are equally accessible and potentially utilisable for the focal species (Guisan and Thuiller, 2005). In the case of reintroductions this is clearly not the case, at least not until a self-sustaining population has been established and successive generations have had sufficient opportunity to colonise the whole landscape (Sun *et al.*, 2016).

Due to the limited time-frame available for the course of my study, I would be able to use only monitoring data from the initial 30 months following the initial release of takahē to the Gouland Downs (see Chapter 5, although birds had been released, post-release monitoring data were not available when the predictive modelling described here were undertaken). As

this is not nearly enough time for the population to reach a state of equilibrium with the environment, I expected that observations of the reintroduced population would include an inherent release-site bias over this recording period.

In order directly to predict the post-release space use of takahē in the Gouland Downs in the first 30 months following their reintroduction (which makes predictions more specific and thus easier to evaluate using post-release monitoring observations, see Chapter 7) I decided to modify habitat suitability predictions with simple dispersal models.

I calculated negative exponential dispersal kernels (Slone, 2011; Hassall and Thompson, 2012; Jordano, 2017; Hunter-Ayad and Hassall, 2020) for takahē in the Gouland Downs, assuming an exponential decay of probability of takahē presence with increasing distance from release sites (Fandos *et al.*, 2021; Chapter 5; Figure 5.2), using the following equation;

$$\text{Probability of presence} = e^{-a*d}$$

where  $e$  is the exponential constant,  $a$  is a coefficient modifying the rate of decay and  $d$  is the distance from release sites measured in metres. This equation relates the probability of an animals presence to the distance from a fixed point where the animal was known to start moving from, which, in the case of reintroductions, is the release site (Attum and Cutshall, 2015; Mertes *et al.*, 2019). The paucity of dispersal data and observations for takahē to prior to the Kahurangi NP reintroduction created a high degree of uncertainty regarding post-release dispersal from the Gouland Downs release site. The only other place where true dispersal has been possible is the relict Fiordland population (including the Stuart Mountains reintroduction), and monitoring there has been too course to detect any detailed movement patterns (Maxwell, 1995; Lee and Jamieson, 2001; Hegg *et al.*, 2012). To account for this uncertainty, I created separate conservative and extrapolative options for dispersal models, which represent plausible (though still highly uncertain) estimates of maximum and minimum expectations of post-release dispersal. I did this by modifying  $a$  in the above equation based on conservative and extrapolative dispersal scenarios.

Under the conservative dispersal scenario, only very limited dispersal is expected from release sites (thus limiting exposure to more novel conditions away from release sites; Chapter 2; Hunter-Ayad *et al.*, 2021), with median distance from release sites expected to be 1km over the first 30 months following reintroduction. The extrapolative dispersal Scenario however, predicted widespread long-distance dispersal from release sites, with median distance from release sites expected to be 5km over the first 30 months.

I selected suitable values for the coefficient  $a$  from the previous equation for conservative and extrapolative dispersal predictions such that the kernel predicted 50% probability of presence at estimated median dispersal distances. This was calculated as;

$$a = \frac{-\ln(0.5)}{d_{median}}$$

where  $d_{median}$  is the estimated median dispersal distance for conservative and extrapolative models.

I calculated distances from release sites for each individual release site (Figure 5.2) using the *distanceFromPoints* function in the *raster* package in R (using the same extent and 200m resolution as habitat predictions, Figure 4.3). Next, I projected dispersal kernels based on each of these layers, for conservative and extrapolative options, respectively. I then weighted the resulting projected dispersal kernels according to the number of birds released from each release site, before summing the kernels for each specific release site, for conservative and extrapolative options respectively, and linearly rescaling outputs such that the maximum presence estimate was 1.

In order to predict space-use of takahē in the Gouland Downs specifically in the first 30 months since their release, I combined dispersal predictions with predicted habitat suitability for conservative and extrapolative options. Predictions were combined via simple multiplication of the respective output raster layers. These combined predictions reflect predicted selective behaviour of reintroduced takahē to areas of high habitat suitability, while also accounting for dispersal limitations following release and incorporating expected biases towards increased takahē presence proximate to release sites. I suggest that these can be taken as predictions of the distribution of the reintroduced population 30 months following initial release.

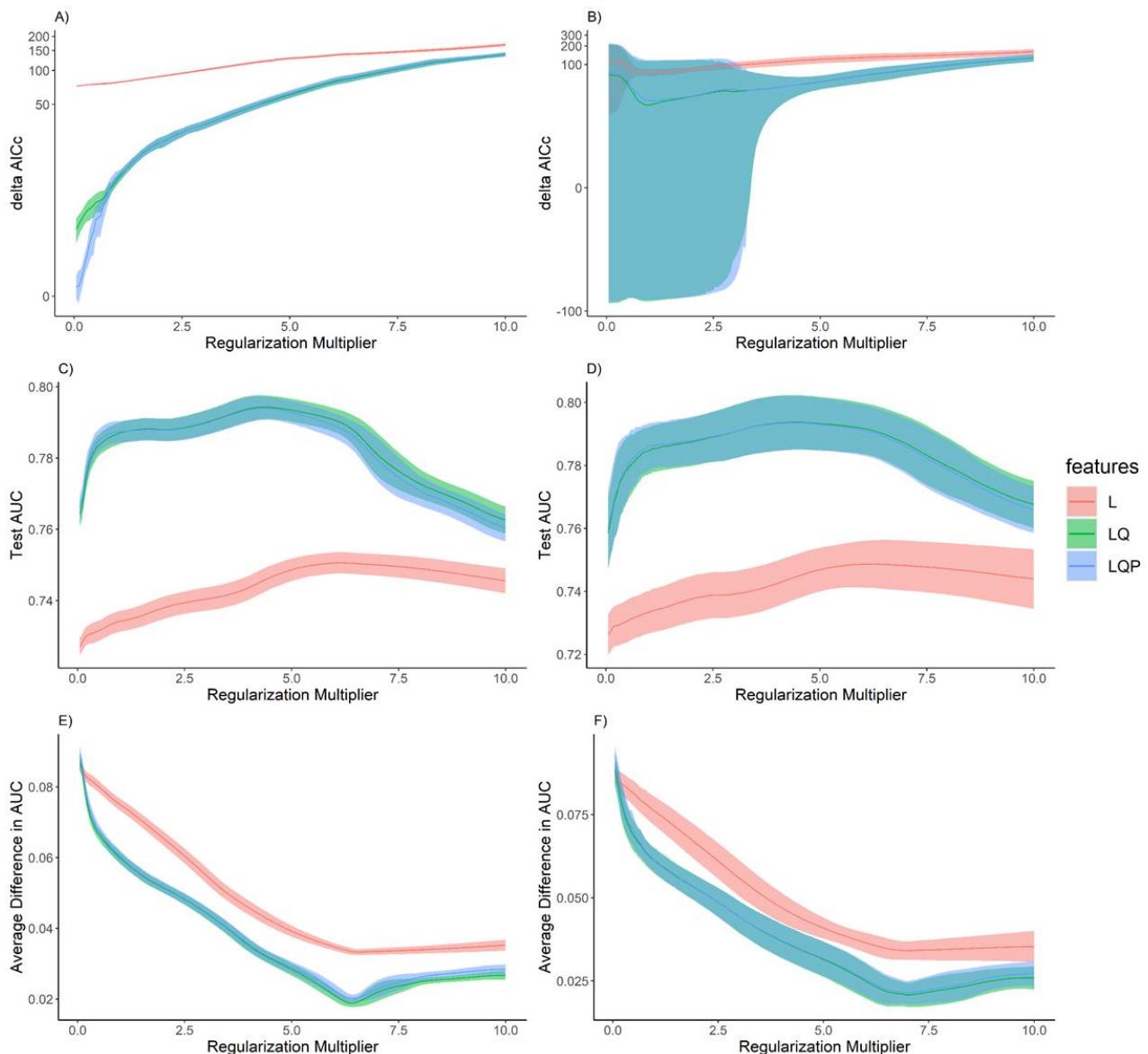
## 4.3 Results

### 4.3.1 Model Outputs

Both delta AICc and test AUC metrics indicated lower model performance for very low and very high values of the regularization multiplier (Figure 4.4 B, C and D, although A is an exception). The performance of models with Linear and Quadratic and Linear, Quadratic and Product feature classes was near indistinguishable for the metrics considered (Figure 4.4 and 4.5; for further details of model settings and outputs see [Digital Appendix 1.1](#)).

Optimal models from each run were selected based on delta AICc, with the finalised conservative and extrapolative model taken as the average of 40 optimal models. Test AUC and average difference in AUCs for optimal models are shown in Table 4.1 with full outputs provided in digital appendix 1.1 and 1.2 ([Digital Appendix 1](#)).

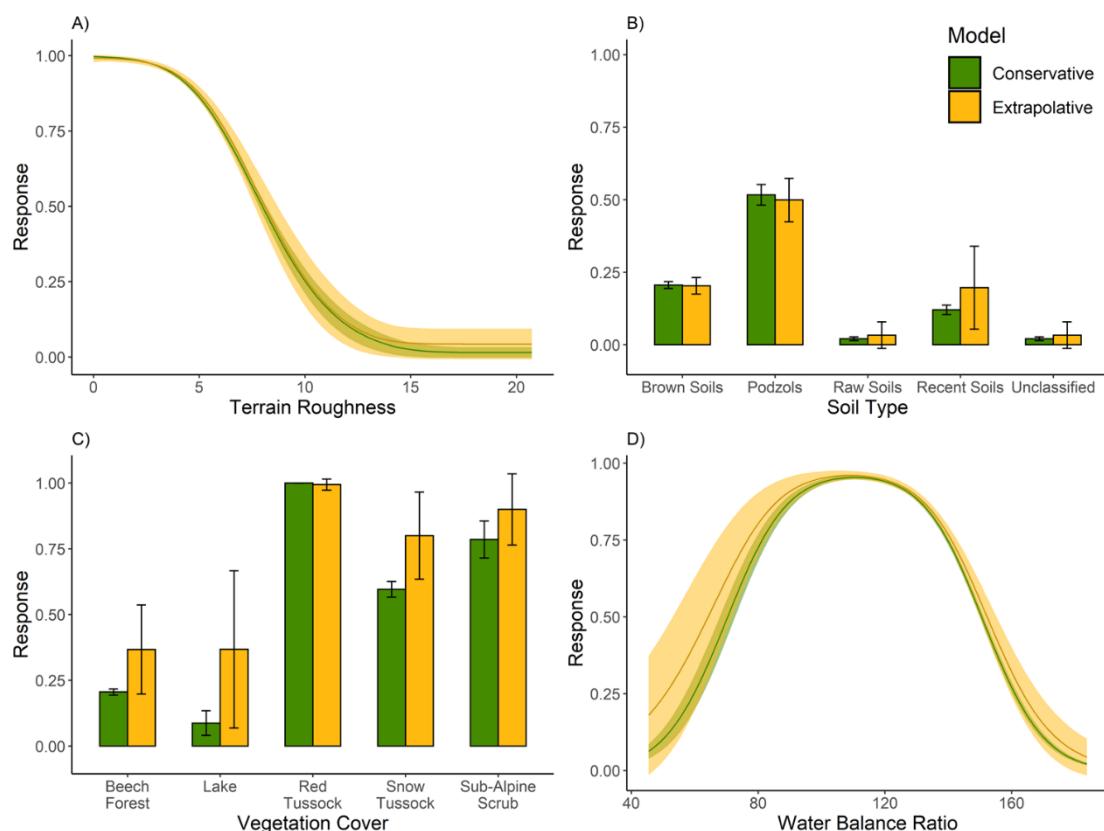
Response curves for MaxEnt models show the change in habitat suitability predicted with changes in the values of environmental inputs (Figure 4.5). While response curves are consistent across replicates for portions with high representation in input data (e.g., terrain roughness between 0.5-5, red tussock vegetation, brown soils and water balance ratios between 90-130), there is substantially higher variation (as indicated by larger standard deviations; Figure 4.5) between curves from different replicates in other areas. This largely relates to areas of the distribution that are less well represented in model input data, so there is more sensitivity to the placement of random background points, hence more variability and uncertainty in outputs. As expected, the conservative models are more consistent across replicates than the extrapolative models, reflected in lower standard deviations.



**Figure 4.4-** Average model evaluation metrics for 40 replicates of runs considering 600 variations of MaxEnt model settings for models trained on takahē presence data from the Murchison Mountains. The x-axis indicated the value of the regularisation multiplier (the MaxEnt smoothing parameter) applied. Colour indicates feature class settings (L= linear, LQ= linear and quadratic and LQP= linear, quadratic and hinge) and ribbons show  $\pm$  one standard deviation. A and B show delta-AIC (Akaike Information Criterion), C and D show test AUC (Area under the receiver-operator characteristic curve) and E and F show Average Difference in AUC. A, C and E show results for conservative models using a background sample of 5000 random points while B, D and F show results for extrapolative models using a background sample of 1000 random points.

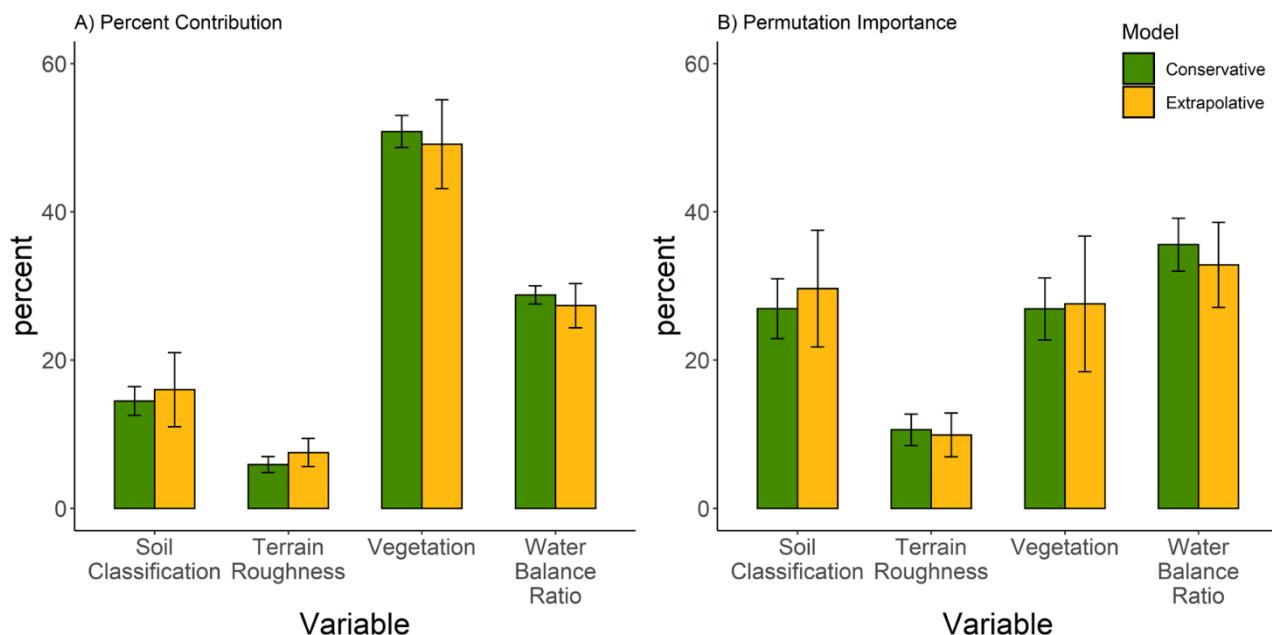
**Table 4.1-** Output metrics for final conservative and extrapolative versions of MaxEnt takahē habitat models trained with presence data from the Murchison Mountain relict population. Test AUC (Area Under the receiver-operator characteristic curve) scores are calculated based on testing data withheld during model training. Test AUC is an indicator of model accuracy. The average difference in AUC is the average difference in the value of the AUC characteristic when calculated using training and testing datasets respectively. Average difference in AUC is an indicator of model overfitting. All values are given to 3 sf.

Metric	Conservative model		Extrapolative model	
	Average	Standard Deviation	Average	Standard Deviation
Test AUC	0.770	0.00660	0.775	0.0126
Average difference in AUC	0.0845	0.00580	0.00755	0.0144



**Figure 4.5 -** Average environmental predictor response curves for the conservative (green) and extrapolative (yellow) versions of MaxEnt habitat suitability models for takahē trained with species presence data from the Murchison Mountains population. Error bars and shaded areas show  $\pm$  one standard deviation.

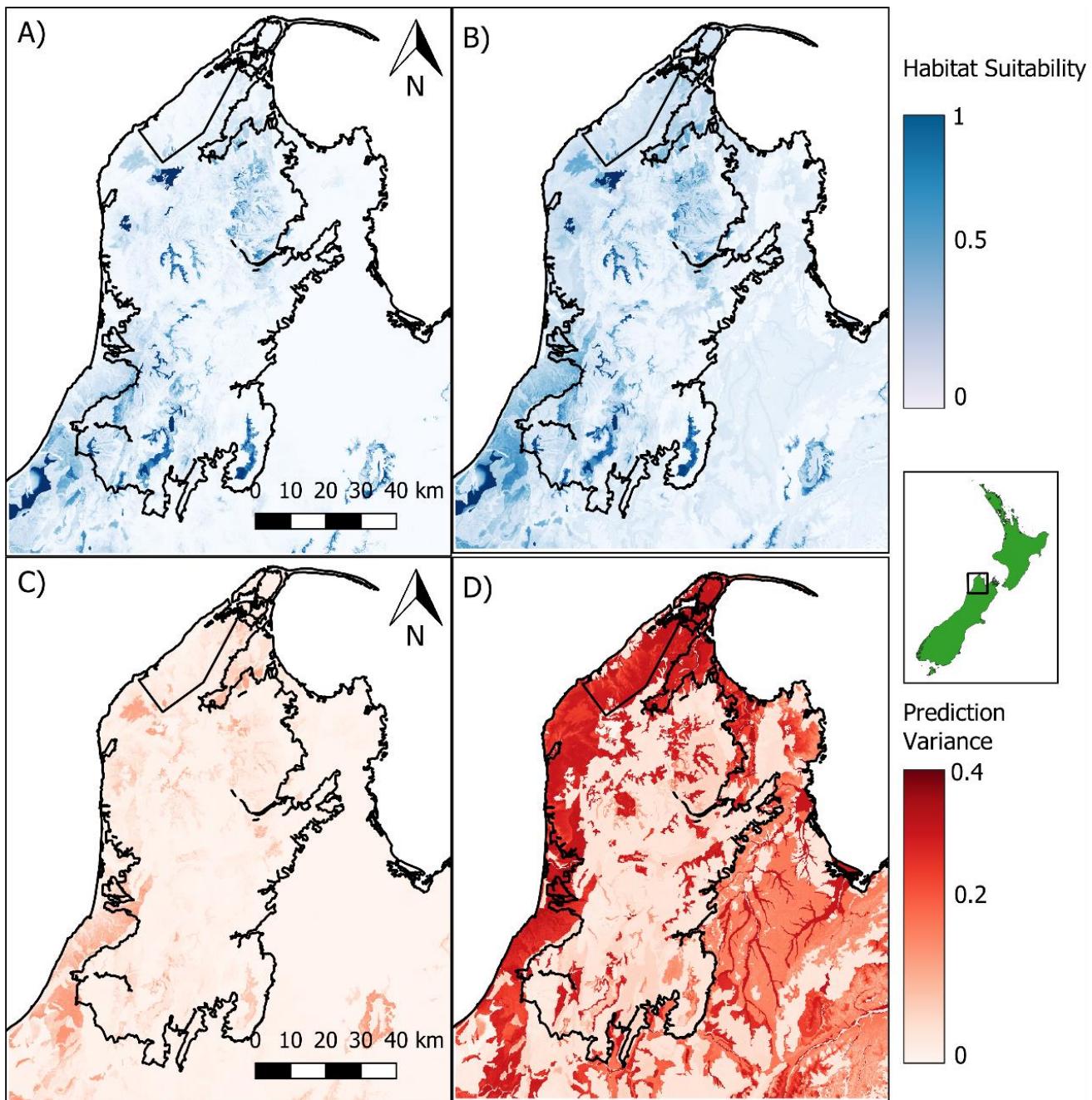
The weighting of environmental predictors is similar between conservative and extrapolative models, with more variation between different replicates of the extrapolative models (i.e., higher standard deviations; Figure 4.6).



**Figure 4.6** - Average variable importance for environmental inputs for conservative models (green) and extrapolative (yellow) versions of MaxEnt habitat suitability models for takahē trained with species presence data from the Murchison Mountains population. Panel A shows the percent contributions (weights) of each input variable, while panel B shows their permutation importance (sensitivity of model to changes in the values of the input variable). Error bars represent  $\pm$  one standard deviation.

### 4.3.2 Habitat Predictions

The final habitat maps (the average of the predictions of the 40 optimal MaxEnt replicates identified in *ENMeval*) show conservative and extrapolative habitat quality projections for Kahurangi National Park (Figure 4.7). While similar spatial patterns are evident in both conservative and extrapolative model options, overall habitat suitability predictions are higher in the extrapolative model. However, the higher habitat suitability predictions in extrapolative models are also associated with much higher uncertainty in many areas when compared with conservative predictions, as indicated by the standard deviations calculated for each model option (Figure 4.7 C and D).



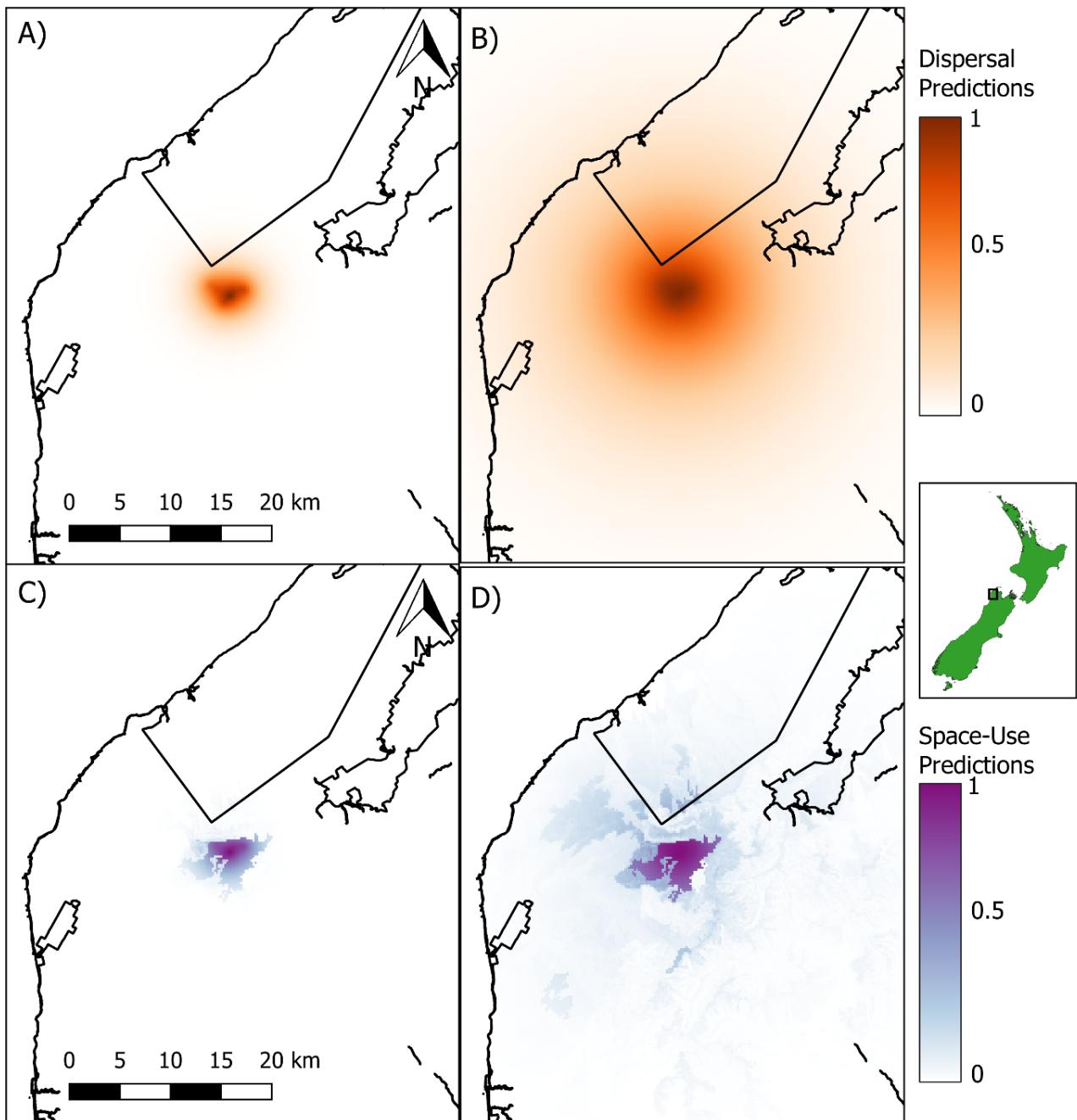
**Figure 4.7-** Habitat suitability projections for takahē in Kahurangi National Park. Projections are derived from MaxEnt habitat suitability models trained with takahē presence data from the Murchison Mountain population. Panels A and C show projections from conservative model fitting, while panels B and D show projections from extrapolative models. A and B show predicted habitat suitability while the C and D show the variance (standard deviation) across the 40 replicates used to generate final models.

#### 4.3.3 Accounting for Context of the Reintroduced Population

The projected and population-weighted dispersal kernels (Figure 4.8A and 4.8B) represent predictions of takahē distributions in Kahurangi National Park in the first 30-months

following releases based upon dispersal patterns and expected release-site biases. When multiplied by habitat suitability predictions (Figure 4.7A and 4.7B), a predicted population distribution is projected based upon the interaction between habitat selection and population radiation processes (Figure 4.8C and 4.8D, for conservative and extrapolative assumptions respectively).

Conservative dispersal models identify a restricted population distribution when compared with extrapolative models, reflecting a higher degree of bias towards release sites as birds are expected to disperse short distances (median 1km) from their release points. The much higher post-release movement predicted under extrapolative dispersal models (median 5km) results in a much wider predicted distribution, with birds expected to make use of a much larger area and to explore further from release sites. When accounting for predicted habitat structure in space-use predictions a more resolved and heterogenous distribution is predicted for the population, reflecting the interaction between dispersal and habitat selection behaviours (Figure 4.8C and 4.8D). Under the conservative distribution prediction (Figure 4.8C) takahē are expected to remain concentrated around their release sites in the central-northern area of the Gouland Downs. Whereas, under the extrapolative predictions (Figure 4.8D), although the Gouland Downs is still predicted to be a core area for the population, the population is less concentrated than under conservative predictions, with projected densities being relatively even across this area. Additionally, a low level of colonisation is predicted for areas surrounding the Gouland Downs release area in extrapolative models, as birds are predicted to make use of suitable habitat away from the immediate release area (Figure 4.7D).



**Figure 4.8-** Projected dispersal from release sites for takahē reintroduced to the Gouland Downs (A and B), under conservative, non-dispersive, (A) and extrapolative, highly dispersive, (B) assumptions. The output scale for dispersal is an index of relative probability of takahē presence in the first 30-months following release based on dispersal and expected release-site biases. C and D show predicted space-use of takahē in the same 30-month post-release period based on both dispersal and habitat suitability projections, under conservative and extrapolative assumptions respectively. The output scale for space-use predictions is an index reflecting relative probability of takahē presence based on both the expected habitat selection patterns reflected in habitat suitability predictions (Figure 4.7A and 4.7B) and expected dispersal and release-site bias (A and B).

## 4.4 Discussion

In this chapter I have developed correlative habitat suitability models to predict habitat suitability for takahē reintroduced to the Gouland Downs based upon patterns observed in the relict takahē population in the Murchison Mountains. I then incorporated predictions of post-release dispersal to elaborate these habitat suitability predictions and provide a prediction of the post-release population distribution for the reintroduced population. Two versions of predictive models were developed, providing both conservative and extrapolative model options.

### 4.4.1 Model Inferences from a Relict Population

The records from takahē monitoring in the Murchison Mountains are in many ways superior to those generally employed for correlative habitat suitability models in other studies (e.g., those from online databases and /or casual records; Galante *et al.*, 2018; Hunter-Ayad and Hassall, 2020). However, they are still limited by the specific context of the Murchison Mountain population, namely that this is understood to be a relict, or refugee population (Lee and Jamieson, 1997; Kerley, Kowalczyk and Crome, 2012; Chapter 2; Hunter-Ayad *et al.*, 2021). This meant that it was necessary to treat these records carefully, as using inappropriate environmental predictors and/or background records could easily create overfitted models, that infer niche limits based on coincidental or dynamic range boundaries (Jiménez-Valverde *et al.*, 2011; Breiner *et al.*, 2015; Chapter 3; Hunter-Ayad *et al.*, 2020). Therefore, in order to avoid identifying spurious relationships between environmental variables and takahē records in the Murchison Mountains I was careful in the selection and curation of input data and undertook extensive model selection and averaging processes. Further, I also presented two alternative models representing different interpretations of takahē ecology and attitudes to risk. I limited the scale of inference to within-population home range selection based upon environmental predictors understood to have a strong impact on habitat selection at this scale (Maxwell and Jamieson, 1997; Lee and Jamieson, 2001; Hegg *et al.*, 2012).

The overall patterns in fitted responses and predictor weightings are largely consistent between conservative and extrapolative model versions, with the main difference between them being the greater variance in fitted responses between model replicates (i.e., larger standard deviations) in the extrapolative models (Figure 4.5 and 4.6). This fits the definitions of conservative and extrapolative strategies (Chapter 2; Hunter-Ayad *et al.*, 2021) as the models identify the same overall trends in the data, but the extrapolative

models incorporate a broader range of potential responses fit to these patterns, and are thus less exclusionary when projected, identifying a wider area of potentially suitable habitat (Figures 2.2, 2.4 and 4.7).

The response curve for terrain roughness (Figure 4.5A) is an ecologically plausible pattern given current understanding of takahē ecology. As mortality and injury from misadventure are more likely in territories containing uneven terrain (Lee and Jamieson, 2001). It is then expected that as terrain roughness increases, habitat suitability should fall. The response to water balance ratio (Figure 4.5D) is similarly plausible, as takahē are in the rail family, a wetland group, they are not expected to do well in very dry conditions, but neither are they adapted for the extremely wet conditions that occur deep into the Fiordland ranges (NIWA niwa.co.nz; (Lee and Jamieson, 2001). Therefore, the “humpbacked” response curve for water balance ratio has ecological support, as it indicates that habitat suitability is highest at intermediate levels of wetness in the model-building region.

For the vegetation predictor variable (Figure 4.5 C) high suitability is predicted for tussock vegetation (both red and snow tussock) and sub-alpine scrub, which should all provide food, cover and nesting resources for takahē (Lee and Jamieson, 2001). Whereas lake and beech forest, which are only used transiently as seasonal and dispersal habitats by takahē, are identified as less favourable (Hegg, Mackenzie and Jamieson, 2013). The response to the ‘lakes’ category is the most variable (as there is a large difference between conservative and extrapolative models, and also a very high standard deviation for the extrapolative models; Figure 4.5 C). This may be explained by the tendency for takahē to feed and disperse along lake margins but also avoid deep water as they are not strong swimmers (Lee and Jamieson, 2001), leading to the variation in fitted responses between models and replicates (as the identified response is more sensitive to the specific locations of background points). While the fitted responses to vegetation overall match with current ecological knowledge for takahē, it must be noted that the predicted preference for red tussock over snow tussock runs counter to consensus. This likely spurious response appears to be an artefact of the relative rarity of red tussock in the model-building area (Figure 4.2A).

Plausible patterns can also be observed in the fitted responses to soil class predictor categories. The soil class that associated with the highest and most stable habitat suitability predictions are podzols (Figure 4.5B), strongly acidic soils with slow permeability (Manaki Whenua, 2020) and, as such, are associated with water-logged acidic grassland, which is

perceived to be suitable for takahē in the Murchison Mountains (Lee and Jamieson, 2001). Other soil classes predicted to be moderately unsuitable are recent and brown soils, which are both associated with moderate to high water availability and biological activity (plant and soil biota), meaning that they are likely associated with environments able to provide food and shelter for takahē (Manaaki Whenua, 2020). While the lowest-rated soil class is raw soils, which are associated with low-soil horizons and rocky surfaces (Manaaki Whenua, 2020), thus are unlikely to be associated with suitable resources for takahē habitat. Unclassified soil type most often occurs in deep water areas (e.g., Lake Te Anau, Figure 4.2B), so the strong negative effect on suitability predictions is thus expected.

Across replicates, vegetation is consistently identified as the input variable with the highest importance and weighting in determining habitat suitability for takahē (Figure 4.6A). This is to be expected, as the majority of takahē diet in the Murchison Mountains is made up of tussock grasses (Mills *et al.*, 1991; Hegg *et al.*, 2012), so the extent of grassland should be a strong driver of population distributions (Takahē Recovery Programme, 2016). The next ranked variables are water balance ratio and soil classification, again this makes sense as takahē are to some extent a wetland adapted species (Beauchamp and Worthy, 1988), and wetland conditions arise from a combination of high rainfall, low evaporation (i.e. water balance ratio) and low substrate drainage capacity (as indicated by soil class). Then, terrain roughness is overall the lowest rated input variable. This reflects that, while highly uneven terrain does limit habitat suitability, these highly uneven areas make up a minority of the landscape and for the most part terrain roughness is low-moderate across all the landscapes considered in this study (see Figures 4.2C and 4.3C). So, while in specific locations terrain roughness has a high impact on habitat suitability predictions, for overall predictions terrain roughness has the smallest influence (this is supported by limiting factor analyses, presented in appendix A.6).

Overall, the fitted models can be considered plausible representations of current ecological understanding of the Murchison Mountain takahē population (Mills, Lavers and Lee, 1984; Hegg, Mackenzie and Jamieson, 2013). However, when considering broader ecological understanding of takahē, i.e., incorporating evidence from subfossil records (Beauchamp and Worthy, 1988) and secure/captive populations (Jamieson, Wallis and Briskie, 2006; Greuber, Maxwell and Jamieson, 2012; Lees *et al.*, 2014; Greaves *et al.*, 2020), limitations of these models become evident. There are artefacts in the fitted responses, some of which may be confidently identified (e.g., the over-represented suitability of red tussock described

above), while others are more uncertain (e.g., the lower limiting boundary for water balance ratio, while plausible, also coincides with a hard boundary of the western shore of lake Te Anau, so could also be an artefact of this). A particular limitation is the inability to identify vegetation classes known to be utilised by takahē populations at secure sites, particularly exotic short grasses (Withers, 2014). Furthermore, while the selection and treatment of predictor variables were appropriate for the relict population, this likely represents only a portion of their pre-decline niche (Beauchamp and Worthy, 1988). Further exploration of subfossil records (shown in Figure 2.3) in conjunction with appropriate paleoclimate reconstructions (Fordham *et al.*, 2017) would be invaluable in overcoming this limitation.

As they currently stand, I suggest that models presented in this chapter can be useful in providing a data-driven, quantitative and projectable representation of habitat requirements of takahē in their relict range. However, as they currently stand, these will primarily only be relevant for environments at least broadly similar to those of the Murchison Mountains unless or until they can be supplemented with further analyses of secure site and/or subfossil data.

#### **4.4.2 Habitat Suitability Predictions for Kahurangi National Park**

The habitat suitability projections corroborate habitat identification by expert opinion prior to the reintroduction of takahē to the Gouland Downs (Takahē Recovery Program, 2016). The Gouland Downs reintroduction site been identified as an area of high habitat suitability (>0.8 on the MaxEnt cloglog scale; Figure 4.7 A and B) in the models. While additionally, the MacKay Downs to the North-West and Gunner Downs to the South-West of the Gouland reintroduction site (Figure 1.2) are also identified as areas of high habitat suitability in the models (though note the MacKay Downs is ranked lower than anticipated, with suitability ≈0.5 in extrapolative models and lower in conservative ones), matching expert opinion (Takahē Recovery Program, 2016). The spatial patterns in predicted habitat structure are qualitatively similar between the two models (Figure 4.7 A and B). However, when thresholds were applied to divide the landscape into habitat and matrix classes (as was done to produce the binary map shown in Figure 2.4) there was an 84% greater area of habitat predicted in the extrapolative model when compared with the conservative model (14,112ha in extrapolative models compared with 7644ha in conservative models; see Appendix A.5 for further details).

For extrapolative habitat projections, variance between replicates shows clear spatial patterns. These consist of low variance in areas of tussock and beech vegetation (which occurs within the model building buffer area) and much higher variance in areas with vegetation (and to a lesser extent soil class) categories that do not occur in the model training extent (Figure 4.7 C). While variance is generally much lower for the conservative model projections and bears no clear association with non-analogue predictor classes (Figure 4.7 D).

High variance under non-analogue conditions relates to areas where models necessarily extrapolate beyond the range of their input training data, so prediction uncertainty in these areas is expected. However, as the conservative models do not make inferences beyond known conditions (as defined using MESS maps and comparing novel classes for categorical variables; Appendix A.3), these novel areas are consistently identified as unsuitable, hence the lower variance in predictions. Additionally, the strong effect of vegetation in driving the observed patterns of variability in model outputs seems to derive from this being the most highly weighted environmental input in both conservative and extrapolative model versions (Figure 4.6 A).

#### **4.4.3 Accounting for Release Site Bias**

While estimates of habitat suitability and structure can be useful in isolation for conservation management in reintroduction landscapes, considering these in isolation can be somewhat limiting (Chapter 3; Hunter-Ayad *et al.*, 2020). For one thing, any assumed equivalence between habitat suitability and species presence will not be upheld in reintroduction landscapes, at least not until the reintroduced population has had the opportunity to expand and colonise habitat away from reintroduction sites (Sun *et al.*, 2016; Soriano-Redondo *et al.*, 2019). As this is will not be the case for takahē in the Gouland Downs in the initial years following reintroduction, the habitat suitability predictions in isolation cannot be used to directly predict the distribution of takahē in the landscape.

In order to generate specific predictions of the distribution of takahē over the initial 30-month period following their reintroduction to the Gouland Downs, I coupled habitat suitability projections with simple dispersal models. These dispersal models represent projected radiation of the reintroduced takahē populations from their release sites (Lalas and Bradshaw, 2003; Soriano-Redondo *et al.*, 2019). Given the uncertain expectations surrounding post release dispersal (Maxwell, 1995), I again created two model options, representing conservative and extrapolative scenarios, respectively (Figure 4.8A and 4.8B).

In the case of post-release dispersal, I considered that it was conservative to assume only limited post-release movements, with most animals expected to establish home ranges proximate to release sites. This followed the assumption that settlement close to release sites would act to limit the range of novel conditions reintroduced takahē encountered. On the other hand, I considered that wide-ranging expansion to be an extrapolative prediction, assuming that birds dispersing far from release sites would likely encounter a wider range of conditions and resources (which could present both opportunities and risks; Chapter 2; Hunter-Ayad *et al.*, 2021).

The predictions from dispersal models, when combined with their respective conservative and extrapolative habitat suitability predictions, produce specific predictions of space use by takahē in the first 30-months following their reintroduction (Figure 4.8C and 4.8D). The index scale of these predictions can be considered as a relative probability of takahē presence, incorporating consideration of both habitat suitability and dispersal patterns.

#### **4.4.4 Applications to Takahē Conservation**

The models and predictions presented in this chapter may usefully inform the current and future management of takahē populations in Kahurangi National Park and in the Murchison Mountains. The spatial projections of habitat predictions (Figure 4.7 and Appendix A.4) can be used to estimate total habitat area, fragmentation, and carrying capacity for takahē in projected landscapes (Kupfer, 2012; Villard and Metzger, 2014; Massaro *et al.*, 2018). These predictions are valuable for continued management of these populations as they can inform the choice of future release sites for follow-up reintroductions and reinforcements (Jarvie *et al.*, accepted; Clobert *et al.*, 2009; Stadtmann and Seddon, 2018). Additionally these predictions can inform targets for the eventual population sizes in reintroduction landscapes and direct management aimed at establishing metapopulation dynamics (Simonis *et al.*, 2018). These models can also be readily applied to candidate future reintroduction sites, aiding in the planning and management of these mooted interventions. While the incorporation of dispersal and population dynamics into these predictions (such as the dispersal dynamics incorporated in this chapter; Figure 4.8) can make these predictions more detailed, realistic, and specific (e.g., see Chapter 3; Hunter-Ayad *et al.*, 2020; Zurell *et al.*, 2021).

The predictions generated by models suggest that the Gouland Downs was the best choice of release site in Kahurangi NP (for discussion of why areas outside the NP are not considered suitable see Section 5.4.3), as models indicate that the Gouland Downs

represent the largest contiguous area of high suitability habitat within the national park boundary (Figure 4.7A and B; Table A.3). Given the high habitat suitability predicted (though also accounting for the recognised over-representation of red tussock suitability), this area could be expected to maintain population density of takahē equivalent to observed densities in takahē valley, Murchison Mountains (where Lake Orbell is located; Figure 1.1), as this area is also predominantly vegetated with red tussock (Figure 4.2A; Lee and Jamieson, 2001). I estimated takahē population density in takahē valley to be 0.0847 takahē per hectare, based on unpublished population data provided by the TRG (10-11 birds considered resident in the valley). This could provide a target for eventual population size (achieved through reinforcement translocations and breeding within the translocated population). Although more thorough surveying effort, including for example mark-recapture methods (Thomas *et al.*, 2010; Hegg *et al.*, 2012), is also necessary to arrive at a more reliable population and density estimate here.

To increase the overall population within the National Park, Gunner Downs, to the southwest of the Gouland Downs (Figure 1.2) appears to be the most suitable secondary release site. Despite being of considerably smaller in extent than the Mackay Downs area (Figure 1.2; Table A.3), models indicate that habitat quality is higher for the Gunner Downs (Figure 4.7 A and B), while predictions are also more stable than for the Mackay Downs (Figure 4.7 C and D). When considering dispersal and distribution predictions (Figure 4.8), it appears that releases directly into the Gunner Downs area may be necessary. Even the extrapolative predictions (Figure 4.8D) indicate that natural dispersal to this area from the Gouland Downs is unlikely, at least in the initial years following releases to the Gouland Downs. Although some other suitable habitat is predicted within the park boundaries, these are generally small, isolated and high-altitude areas south of the Gouland Downs and/or are located close to the National Park Boundary (Figure 4.7 A and B). Given this, these patches do not appear to be suitable for further releases, while their isolation from the Gouland Downs population means that takahē are unlikely to colonise these areas naturally, nor establish meta-population dynamics were any birds to be released to these areas (Figure 4.8)."

However, one drawback restricting the confident application of these models at this stage is the lack of effective model evaluation in reintroduction landscapes (Guisan and Thuiller, 2005; Jiménez-Valverde, Lobo and Hortal, 2008). Although internal model validation, based upon the ability of models to accurately predict patterns in a subset of species presence

data withheld during model fitting, indicate that the fitted models have a reasonable predictive accuracy (based upon test AUC scores; Table 4.2), the relevance of such scores when models are projected to regions beyond the training/testing datasets is questionable (Yates *et al.*, 2018). This can be seen as the test AUC scores are similar for both the conservative and extrapolative models presented (Table 4.2), despite the extrapolative model identifying an 84% larger area of suitable habitat when projected to the Kahurangi landscape (Appendix A.3). Indeed, this uncertainty is the reason that I presented multiple models in this chapter. This uncertainty, and the inability to assert which of the presented models has the better predictive accuracy when applied to reintroduction landscapes (the purpose for which they were constructed), will muddy the water when it comes to applying these models for takahē management. Therefore, it is important that this uncertainty is resolved, and the predictive accuracy of the models presented in this chapter are evaluated independently in the reintroduction landscape.

The reintroduction of takahē to the Gouland Downs represents a rare opportunity to collect truly independent data for the purposes of evaluating the predictions presented in this chapter. While these data should also be highly applicable for this purpose as they were collected under the conditions relevant to the purposes for which models were originally developed. Therefore, in order to collect a robust, detailed and accurate dataset to be used for *post-hoc* evaluations of these models (in addition to a more general evaluation of the reintroduction) post-release monitoring was heavily invested in. The details, methods, and preliminary results of this monitoring are presented in the next chapter, while chapter 7 uses these post-release monitoring data as the basis of *post-hoc* evaluations of the accuracy of model predictions presented in this chapter.

## Chapter 5

### **Independent Observation: Post-Release Monitoring of the Kahurangi Reintroduction**

In this chapter I evaluate the short-term outcomes of the reintroduction of 30 takahē to the Gouland Downs, Kahurangi National Park. I describe the releases and post-release monitoring of the reintroduction cohort for 30 months following initial releases. I then compare observed dispersal, survival, and productivity in the reintroduced population against targets based on observations of other takahē populations, identifying whether these patterns match pre-release expectations and understanding.

#### **5.1 Introduction**

The collection of robust field data is a key challenge in ecological research (Taylor *et al.*, 2017; Galante *et al.*, 2018; Ríos-Saldaña, Delibes-Mateos and Ferreira, 2018). As ecology is the study of complex, open, natural systems, taking data directly from these systems is often necessary in order to gain insights into fundamental processes (Ings *et al.*, 2009; Kissling *et al.*, 2012). However, the cacophony of interacting factors in ecological systems creates a major impediment to researchers seeking to gain specific insights. Numerous processes act across similar temporal and spatial scales and can act synergistically (to reinforce the effects of multiple processes), antagonistically (each process counteracting the effects of other processes to some degree), or neutrally with respect to one another (Baguette and Van Dyck, 2007; Wisz *et al.*, 2013; Chapter 3; Hunter-Ayad *et al.*, 2020). Thus, identifying which processes are responsible for an emergent pattern is a non-trivial challenge.

The need to collect and interpret ecological data accurately is perhaps felt particularly strongly in applied ecological disciplines, such as conservation ecology. This is because the findings in such applied studies are intended for application, and have potential and immediate real-world consequences, at least for the focal system (Chauvenet *et al.*, 2013; Taylor *et al.*, 2017). Effective, evidence-led, conservation management needs to be based on robust ecological understanding, and so collecting and interpreting these data should be a key component of management plans (Heer *et al.*, 2013; Svenning *et al.*, 2016). In addition, to allow adaptive management, where conservation plans are updated in response

to new evidence and emerging understanding, ecological data must be collected following management actions (Nielsen, Cranston and Stenhouse, 2009; Canessa *et al.*, 2015). This enables these actions to be evaluated effectively, while any unforeseen or sub-optimal responses to management actions can be detected and plans modified to avoid recurrence in the future (Snyder *et al.*, 1996; Canessa *et al.*, 2015).

Conservation translocations are a form of management conducive to adaptive management. Many conservation programs will include at least the possibility of multiple translocations, either to different locations, or to reinforce newly established populations (Lees *et al.*, 2014). Monitoring outcomes of previous translocations can enable the revision and refinement of practices in order to improve outcomes in subsequent translocations (Weeks *et al.*, 2011). Thus, any single translocation can be viewed as an ecological experiment, where monitoring the actions and behaviour of released animals creates an opportunity to develop an understanding of species' ecology and inform effective conservation going forwards (Seddon, Armstrong and Maloney, 2007).

Post-release monitoring of translocated animals involves some form of data collection from the re-establishing population. This monitoring can use any of numerous established ecological surveying methods, such as traditional visual surveys for animals or their field signs (Palomares *et al.*, 1996; Buckland, 2006; Massaro *et al.*, 2018). However, monitoring increasingly involves tracking movements of released animals by affixing tags that transmit and/or record animal locations over time (Lloyd and Powlesland, 1994; Tomkiewicz *et al.*, 2010). The oldest and simplest of these tags (hereafter radio-tags) contain Very High Frequency (VHF) radio beacons that emit pulses at a set frequency. However, there has been rise in the use of satellite tags (also referred to as GPS, or Global Positioning System, tags) to track animal movements. Satellite tags use an orbiting constellation of GPS satellites to triangulate and record tag locations. Several systems also allow the transmission of recorded locations via satellite relay, mobile telecommunications, or UHF (Ultra High Frequency) radio transmissions (Cagnacci *et al.*, 2010). I refer to these two distinct classes of tracking tags as radio and satellite tags, respectively, referring to the method used to locate animals used by each group (although some satellite tags transmit satellite-triangulated location data using radio frequencies). Both these classes of tags can allow the tracking of released animals with high spatial and temporal resolution, providing data that can reveal much about post-release behaviour and space-use, as well as identify when and where individuals die, are exposed to risk, or move out of managed areas.

Although many principles are shared between radio and satellite tags, in practice they operate and are used differently. Radio tags are often a lightweight, cheap, and reliable tracking option for ecological studies and can be deployed on a wide range and large number of species and individuals (He, Chen and Zhang, 2016; Bušina *et al.*, 2018; Marshall *et al.*, 2020). On the other hand, satellite tags often encounter unit weight and cost limitations, meaning that satellite tag tracking is often only feasible for tracking a small portion of populations of relatively large animals and is less commonly used for long field deployments (Forin-Wiart *et al.*, 2015). However, when operational, satellite tags have the capacity to record movement tracks that are finely resolved both temporally and spatially, revealing a level of detail in animal movement and behaviour that is often not achievable via radio telemetry (given limitation of person-hours that can be dedicated to tracking and the desire to reduce disturbance to tracked animals; Allan *et al.*, 2013).

In March 2018, takahē (*Porphyrio hochstetteri*) were reintroduced to the Gouland Downs, Kahurangi National Park, North-West Nelson, NZ. The Gouland Downs release site was chosen because it was believed to be able to provide similar resources to those in areas occupied by takahē within the Murchison Mountains, and due to the protections afforded within the national park (i.e., exclusion of livestock, extensive control of invasive mammal populations and limited human activity/encroachment; Takahē Recovery Program, 2016). This reintroduction attempted to create the first wild population of takahē outside of the species relict distribution in Fiordland for more than a century (Chapter 1; Lee and Jamieson, 2001). As this large-scale reintroduction was somewhat pioneering and extrapolative in scope, there were many unknowns and uncertainties regarding post-release behaviours and the chances of overall success for the reintroduction attempt (Chapter 2; Hunter-Ayad *et al.*, 2021). Therefore, post-release monitoring could potentially reveal unanticipated takahē behavioural and population patterns.

Following the release of takahē into the Gouland Downs, monitoring and tracking of the release cohort was a major component of management efforts. As for many reintroductions, this effort was necessary in order to enable effective evaluation of the relative success of the reintroduction attempt as well providing an opportunity to provide more data for research and evidence-based management practices (Kramer-Schadt, Revilla and Wiegand, 2005; Yott *et al.*, 2011; Mihoub *et al.*, 2014; Price *et al.*, 2020). Takahē reintroduced to the Gouland Downs were tracked with radio tags, using hardware and practices established through monitoring the relict takahē population in the Murchison

Mountains (Neill and Jansen, 2014). However, the reintroduction was also used as an opportunity to trial the use of satellite tags on takahē, as this technology had not previously been employed in the wild for this species. The radio and satellite tags deployed on takahē in the Gouland Downs formed the main basis of post-release monitoring effort.

The overall aim of this chapter is to describe the post-release monitoring of takahē released into the Gouland Downs in 2018. To illustrate the value of the ecological data collected by these means, I use data collected via radio and satellite tag tracking to provide an initial overview and evaluation of the short-term outcomes of the reintroduction (via comparison of patterns with ‘targets’ based on data and knowledge drawn primarily from the Murchison Mountain takahē population). The following patterns are investigated in the reintroduced population: dispersal, adult survival and population productivity.

## 5.2 Methods

### 5.2.1 Monitoring the Reintroduced Population

I define a study area of the Gouland Downs (Figure 5.2) and surrounding areas utilised by reintroduced takahē (a central-northern portion of Kahurangi National Park and adjacent regions; Figure 5.4). The Gouland Downs consist of a mid-altitude ( $\approx$ 700-750m) plateau dominated by red tussock (*Chinocloa rubra*) vegetation. The Downs are surrounded by peaks ( $\approx$ 900-1500m) with slopes covered by alpine beech forest (dominated by silver and mountain beech species, *Nothofagus menziesii* and *Fuscospora cliffortioides*; Kelly, 1991). The study period was defined as the 30-month (2.5 year) period immediately following the first release of reintroduced takahē (20<sup>th</sup> March 2018 – 20<sup>th</sup> September 2020).

All 30 takahē reintroduced into the Gouland Downs in 2018 were released in pre-established social groups (a mixture of established breeding pairs and sub-adult groups). All capture, handling, transport, and other activities impacting animal care and welfare were conducted under the stewardship, authority, and supervision of the Takahe Recovery Group. All birds were fitted with radio tags (Tx models, Lotek Ltd, Havelock North, New Zealand, Figure 5.1) following practices applied to monitoring the relict population of takahē in the Murchison Mountains (Lee and Jamieson, 2001; Neill and Jansen, 2014).

Additionally, the Gouland Downs reintroduction saw the first trial of satellite tags for a wild population of takahē. 16 birds were fitted with satellite tags (Pinpoint 120 avian tags, Lotek Ltd, Havelock North, New Zealand, Figure 5.1) in addition to their radio tags upon release.

These tags were programmed for 12-month deployments and had a pre-programmed schedule for triangulating tag locations, recorded spatial and temporal information are hereafter termed ‘fixes’ (see Table 5.1 for vocabulary clarification). Satellite tags were retrieved from captured birds when opportunity allowed after the estimated 12-month battery life of the tags to retrieve data for analyses.

**Table 5.1** Terminology used in thesis when referring to takahē management and tracking methods, with brief description and a summary of key properties. NP= National Park, VHF= Very High Frequency, GPS= Global Positioning System.

Thesis Term	Description	Key Properties
Release/ Reintroduction	Initial release of birds making up the reintroduction cohort.	Transferred into the Gouland Downs release site from a captive facility, Burwood Takahē Centre.
Internal translocation	Artificial relocation of takahē within Kahurangi NP.	Animal is captured and released to a new location within Kahurangi NP.
Radio tag	Animal tracking tag containing a VHF radio beacon.	Emits pulsing signals at a unique frequency (allowing different tags/animals to be differentiated).
On-the-ground record(s)	Spatio-temporal point recorded by tracking animals by following signals from their radio tag.	Data recorded during monitoring surveys, requiring an investment of man-hours in the field. Relatively low temporal and spatial accuracy and resolution.
Satellite tag	Animal tracking tag containing a GPS satellite signal receiver.	Records locations following a pre-determined schedule.
Fix(es)	Spatio-temporal point recorded by a satellite tag.	Data stored within satellite tags, meaning that tags need to be retrieved before data can be accessed. Relatively high temporal and spatial accuracy and resolution.

Both on-the-ground surveys tracking radio-tagged birds and satellite tag fixes provided locational data, giving indications of bird movement and activity, though with different spatial and temporal resolutions and different coverage across the reintroduction cohort (Appendix B.1). The use of radio tags meant that released animals could be tracked on-the ground following initial release. This allowed many indicators of the initial success of the reintroduction to be monitored, including; individual health/condition (via resighting and physical examination if/when birds were recaptured), breeding and mortality events, home range establishment, social dynamics and dispersal. While the spatially and temporally finer resolution records provided by satellite tags are a valuable resource for identifying finer

scale aspects of takahē ecology including diurnal activity (Appendix B.2), space-use and environmental preferences exhibited at the release site (Chapter 6).

### **5.2.2 On-The-Ground Records**

Post-release monitoring of takahē reintroduced to the Gouland Downs involved surveys roughly daily (weather and access permitting) for the first week following the initial release, decreasing in intensity to weekly (for roughly 1 month), bi-weekly (for roughly 2 months) then reducing to monthly surveys over the first 3 months of the reintroduction. Monthly surveys continued for the following 6 months, decreasing to approximately bi-monthly surveys from then on (the remaining 21 months of the study period). This decreasing intensity of monitoring reflected the easing of immediate risks and concerns that the reintroduced population might fail to settle or establish in the reintroduction area, as high release-site fidelity and stable survival and health were observed. On-the-ground monitoring intensity was increased between 14<sup>th</sup>-29<sup>th</sup> August 2020, as this was around the time of an aerial drop of the pesticide 1080 (Powlesland, Knegtmans and Marshall, 1999; Eason *et al.*, 2011) conducted as part of ongoing control of introduced mammalian predators within Kahurangi National Park. As takahē had never been exposed to this pesticide before their susceptibility was largely unknown. An exclusion zone was set around the reintroduced population to limit exposure to the poison and, as stated, monitoring intensity was stepped-up to identify any poison consumption and associated mortality.

On-the-ground surveys relied on VHF radio telemetry, using Yagi directional aerials and TR4 receiver units, to locate the released takahē (Neill and Jansen, 2014). Takahē were approached until trackers were able to confirm radio signals through direct observations of the tracked animals (whether visually, auditorily or both). During these surveys an approximate location was recorded for each recorded takahē (or group of takahē) using a handheld GPS device (Garmin inReach Explorer®+, Garmin Australasia Pty Ltd, Eastern Creek, NSW, Australia) carried to within approximately 25m of the animal (the distance at which birds generally started to move away from trackers). In addition to this locational data, mortality was also recorded; dead birds were identified (and where possible recovered so that necropsy could be conducted to determine a cause of death). During breeding seasons any discovered nests were also monitored, and fecundity data were collated from this monitoring. When surviving juveniles were large enough, they were fitted with leg bands, radio tags, and in some cases satellite tags and then monitored as for reintroduced adult birds. All birds that were caught for any reason (e.g., for satellite tag retrieval and/or

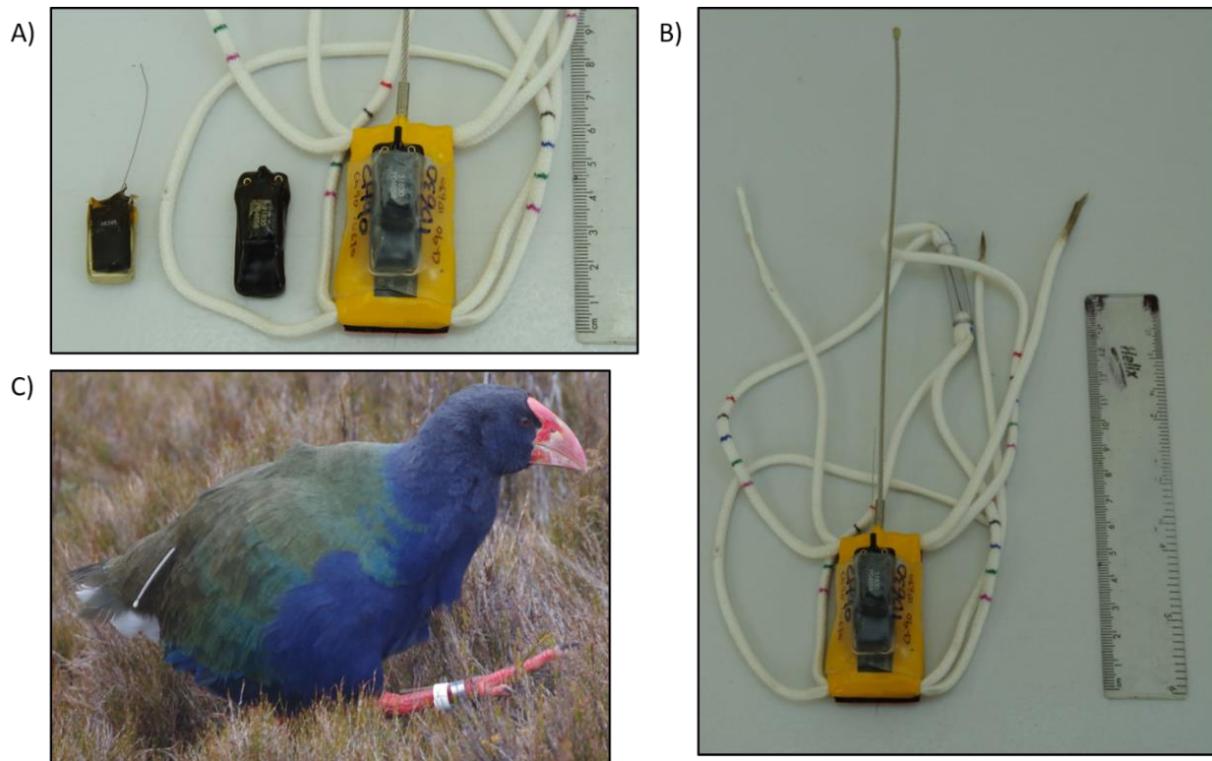
internal translocation within the release area) also had their weight and general physical condition recorded.

### **5.2.3 Satellite Tag Fixes**

The initially deployed satellite tags (Pinpoint 120 avian tags, Lotek Ltd, Havelock North, New Zealand, Figure 5.1) were programmed for 12-month deployments with fixes scheduled every 12-hours throughout this year. 22 arbitrary “frequent-fix” days were also scheduled, with fixes either every hour (two of the days) or every third hour (20 of the days). This schedule was developed to balance preserving battery life over a long deployment (12 months) while still providing fine-grain movement information on the “frequent-fix” dates.

On the 4<sup>th</sup> February 2019 an additional 15 satellite tags (Pinpoint 240 avian tags, Lotek Ltd, Havelock North, New Zealand, Figure 5.1) were acquired for deployment on takahē in Kahurangi NP. These tags were for attachment to birds when their originally fitted tags were removed for data extraction, recharging and reprogramming, with the intention of avoiding any gaps in coverage for satellite tracked birds. The newer tags had double the battery capacity of the initial 120 models, so while schedules were developed with the same strategy, fixes were scheduled more regularly, with daily fixes every six hours and 23 arbitrary “frequent-fix days” throughout the year with fixes scheduled either every 30 minutes (two of the days) or every 2 hours (21 of the days) on those dates.

All deployed GPS tags were “store-on-board” type, meaning they had no capacity to transmit recorded locations and thus tagged birds had to be recaptured and the tags removed for fixes to be downloaded. Approximately annual recaptures of released birds were planned for tag retrieval to minimise disruption of their natural behaviour as they established in the reintroduction area.



**Figure 5.1-** Takahē tracking tag equipment deployed in the Gouland Downs. A) From left to right; PinPoint 120 GPS tag, PinPoint 240 GPS tag (aerial missing), PinPoint 240 GPS tag attached to Tx radio tag and takahē chest harness (using shrink-wrap and adhesive), 15cm ruler shown for scale. B) PinPoint 240 GPS tag attached to Tx radio tag and takahē chest harness. Straps go around birds' wings and weak link sits across the breastbone. 15cm ruler shown for scale. C) Takahē in the Gouland Downs showing identification and monitoring equipment fitted. Aerial from Tx radio tag protrudes from feathers (tags sit beneath plumage on the back of the bird). Metal leg band marked with unique ID number and colour-coded leg band can also be seen on the birds' leg.

#### 5.2.4 Data Retrieval and Preparation

On-the-ground records were formed by collating spatio-temporal records from radio-based monitoring along with observational notes and additional information by Jason Van De Wetering, takahē ranger (DOC) which were provided for analysis here. Satellite tag data were downloaded from retrieved tags using a DLC-2 cable and PinPoint Host software (version 2.14.03, Lotek Wireless inc., Havelock North, New Zealand). The extracted data consisted of recorded fix attempts for each tag, containing time-stamped longitude-latitude coordinates (failed attempts did not include coordinates). These records were processed in R (R Core Team, 2020) using functions from the packages *sp* (Pebesma and Bivand, 2005), *stringr* (Wickham, 2019), *lubridate* (Grolemund and Wickham, 2011) and *tidyR* (Wickham and Henry, 2020) to produce outputs containing the combined records from all

tags, indexed by a unique tag ID and the name of the bird they were fitted to. As a first step, fixes not associated with free-roaming animals (i.e., from tag testing and calibration, birds in transit and following collection from birds) were removed from the dataset. Then all failed fixes were also removed. Next, any clear errors, based on inconceivable coordinates (not over land) or altitudes (hundreds of meters above or below ground) were removed. Finally, fixes were filtered based on the Horizontal Dilution of Precision (HDOP) and number of satellites associated with the location record, with fixes with HDOP >10 and number of satellites <4 removed (Rempel and Rodgers, 1997). Following this curation of the fix data and examinations of track animations ([Digital Appendix 2](#)), patterns of step-lengths, movement speeds and diurnal patterns seemed plausible, lending confidence to the accuracy of the satellite dataset and analyses based upon these data. This curated dataset is presented as summarised for each tracked bird in Appendix B.1.

### 5.2.5 Descriptive Analyses

On-the-ground records and satellite fixes were used to calculate the following rates: post-release dispersal, problematic dispersal, annual survival, breeding success, and daily activity using the methods given below.

Dispersal rates were calculated using on-the-ground records, excluding records from a 4 month ‘settlement period’ (within which locations were relatively oversampled and it was assumed that bird locations would be overly correlated with release sites), with post-release dispersal calculated as the straight-line distance of bird records from the release site of that bird (the distance “as the crow flies”). I then compared dispersal between single takahē (resulting from the breakdown of release groupings) and those associated with social groups (for full details of these methods see Appendix B.3). Finally, “problematic dispersal” was defined as the number of times a takahē was known to leave Kahurangi NP and enter private agricultural land.

For the estimation of the annual rates (survival and productivity) the study period was divided into three periods based on the date of the first takahē release (20<sup>th</sup> March 2018). This created two 1-year periods (20<sup>th</sup> March 2018- 19<sup>th</sup> March 2019 and 20<sup>th</sup> March 2019- 19<sup>th</sup> March 2020) and a 174-day period (approx. 6 months, 20<sup>th</sup> March 2020- 10<sup>th</sup> September 2020).

For each of these periods’ rates were calculated as:

Survival- One minus the number of mortalities during the period divided by adult (birds > 1 year old) population at the start of the period.

Productivity- Number of chicks fledged (identified during on-the-ground surveys) during the period divided by adult population at the start of the period.

These measures were then compared with the following targets arrived at through consultation with the Takahē Recovery Group (TRG) based on long-term average rates in the Murchison Mountain takahē population; zero problematic dispersal, at least 85% survival and up to 9.6% productivity (though expected less due to the main food source for takahē in the Gouland Downs release area being red tussock, *Chionochloa rubra*, which is understood to be a lower quality food source than the snow tussocks, *Chionochloa sp.*, that are the main food source of takahe in the Murchison Mountains; Mills *et al.*, 1991). These targets were used to provide an early evaluation of the relative success of the Gouland reintroduction. I also used the satellite fix dataset to investigate daily activity patterns in the reintroduced population, details of this are provided in Appendix B.2. Unless otherwise stated results given are means followed by  $\pm$  standard deviations and are given to three significant figures. All analyses and Figures were created in R (R Core Team, 2020) with the exception of map-based Figures, where QGIS was used (QGIS Development Team, 2017).

## 5.3 Results

### 5.3.1 Field Data

On the 20<sup>th</sup> March 2018, 18 takahē (12 females and 6 males, mean age 5 years old  $\pm$  3 years) were released into the Gouland Downs (Figure 5.2), with another 12 birds (7 females and 5 males, mean age 6 years  $\pm$  4 years) released on the 1<sup>st</sup> May 2018. The delayed release for the second cohort was to allow these 12 birds to complete their moult.

The collection of post-release monitoring data in the Gouland Downs was disrupted by several factors, both foreseen and unexpected. The expected issues included a level of tag loss from failure and damage in the field to either the tag itself or the harness to which it was affixed. Additionally, some irregularity was expected in the timing and frequency of on-the-ground monitoring trips as these were subject to weather and logistic constraints. In addition, the advent of the COVID-19 pandemic in 2020 meant that monitoring trips were reduced in scale and regularity. A further, somewhat unexpected, issue was the extent of

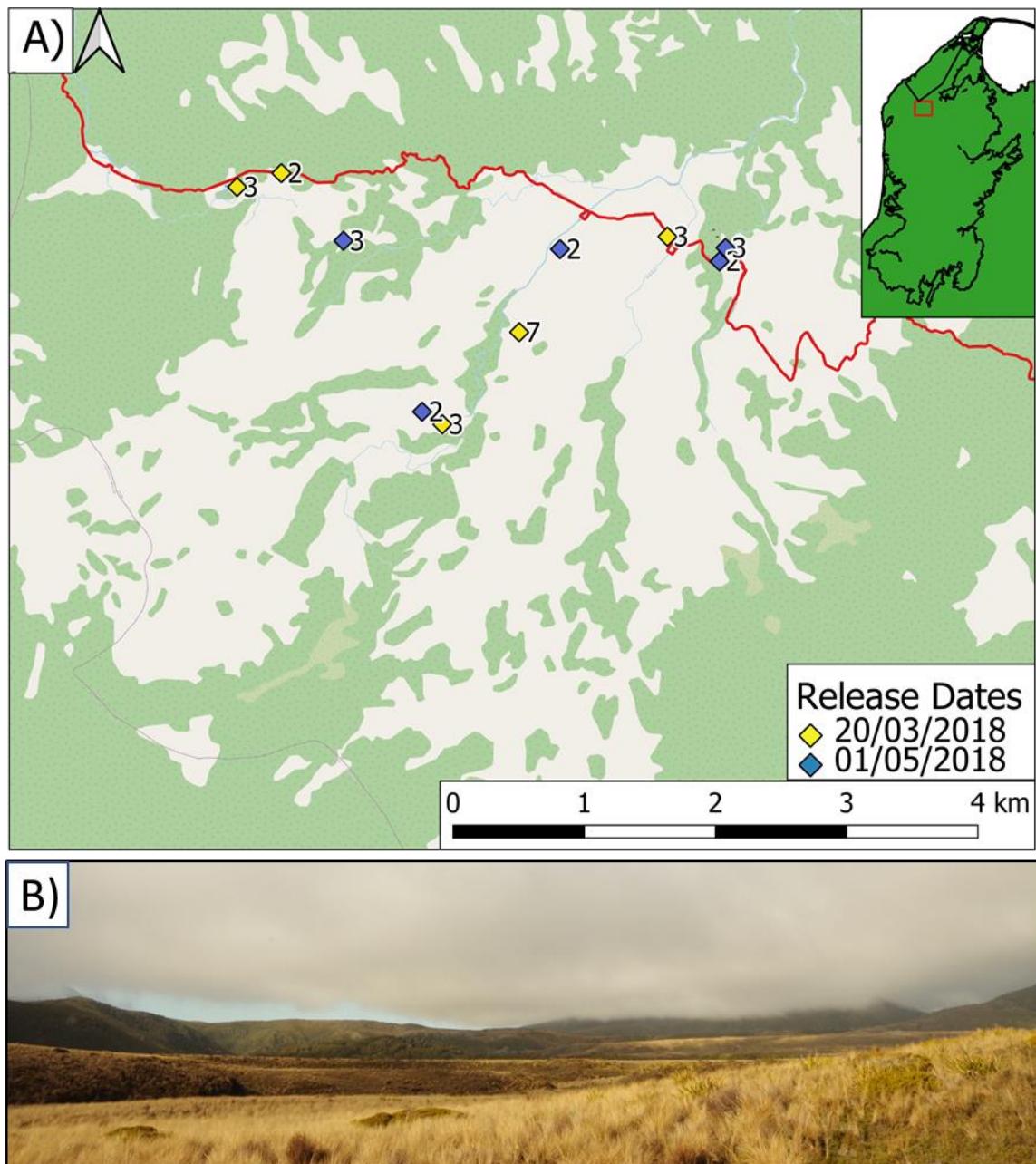
bird-damage to the satellite tags; 18 of the satellite tags deployed had lost their aerial wire by the time they were retrieved.

A total of 1237 on-the-ground records were collected. The mean records collected per bird were  $33.7 \pm 14.6$ . 32 radio tagged birds were tracked over the study period, with an average time covered per bird of  $745 \text{ days} \pm 207 \text{ days}$ . Of these records, 961 contained locational information (easting and northing coordinates in the New Zealand Transverse Mercator coordinate system).

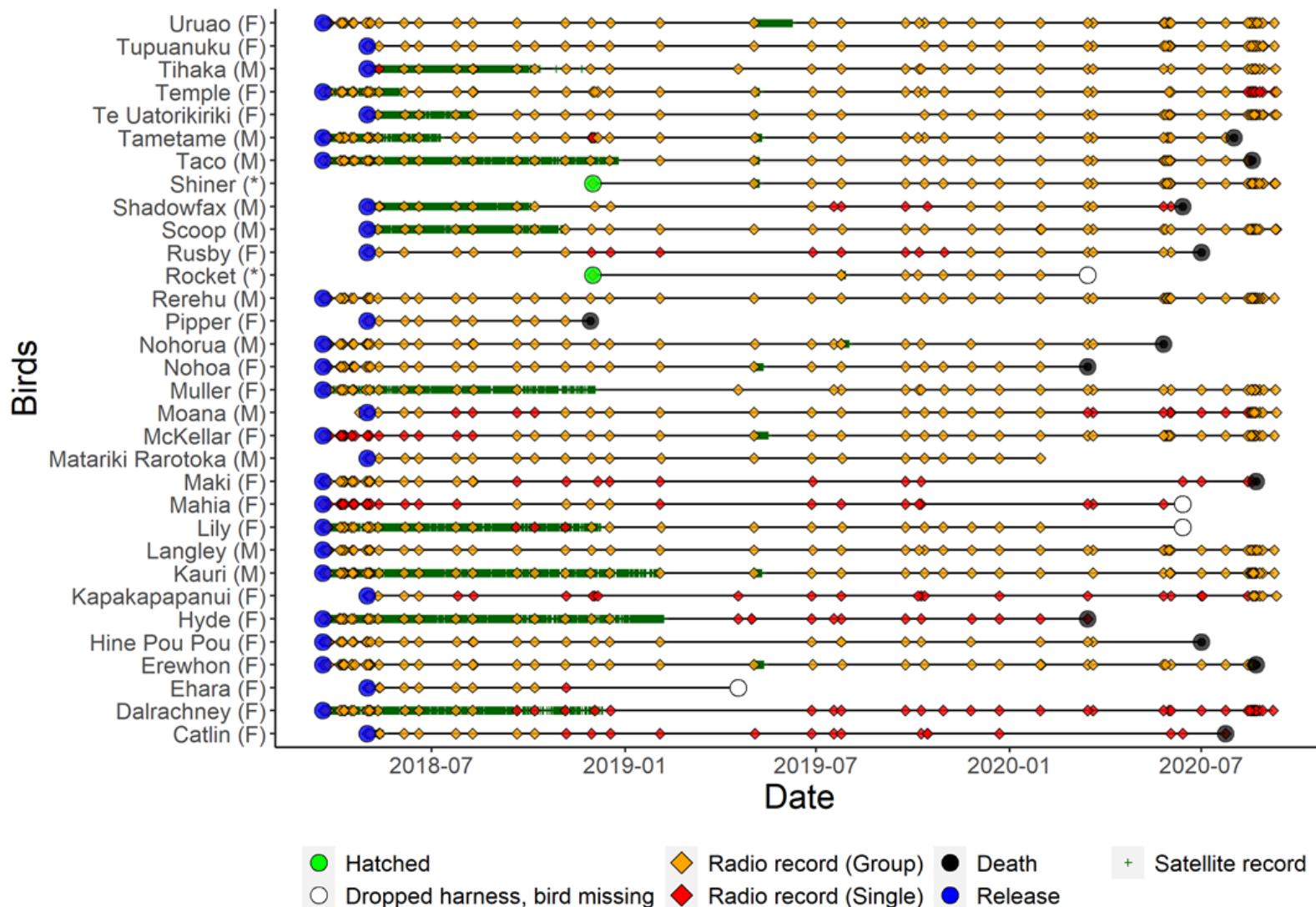
Over the same period, satellite tags made 29,873 fix attempts, though 23,438 of these attempts could not connect to enough satellites to record a location, the vast majority of these failures relate to tags with removed aerials and/or failing batteries. Following curation of the satellite data (section 5.2.4), 5641 satellite fixes were retained ( $282 \pm 203$  per bird for 20 satellite tagged birds) with an average time covered per bird  $188 \text{ days} \pm 165 \text{ days}$ .

Twelve mortality events were confirmed throughout the study period with causes being attributed to various factors based on context in which corpses were recovered and necropsies conducted at Massey University, Palmerston North, NZ. Two deaths occurred when birds dispersed outside of protected areas and were predated, one more bird was predated within the National Park, while four deaths were considered likely emaciation, three were put down to 1080 consumption and two were considered likely misadventure (unpublished mortality and necropsy reports). Five birds were also not monitored for the full study period as they dropped their harnesses with their tags affixed and so could not be tracked from then on (confirmed for four birds, with the fifth expected to have experienced failure of the radio tag; Figure 5.3). The loss of only five tags, and for only a portion of the study period, meant that on-the-ground data were available for the majority of the reintroduced population for the majority of the study period. This removed the need to rely on population estimation methods (e.g., mark-recapture; Panfyllova et al., 2016), although the unknown fate of these 5 untracked birds introduces uncertainty into the calculation of mortality and fecundity rates.

Two chicks were also successfully fledged in the 2018-19 breeding season, though total breeding failure was recorded for the 2019-20 season as flash flooding washed out all seven known nests. A summary of data collected over the study period is given in Figure 5.3 (full data provided in appendix Table B.1).



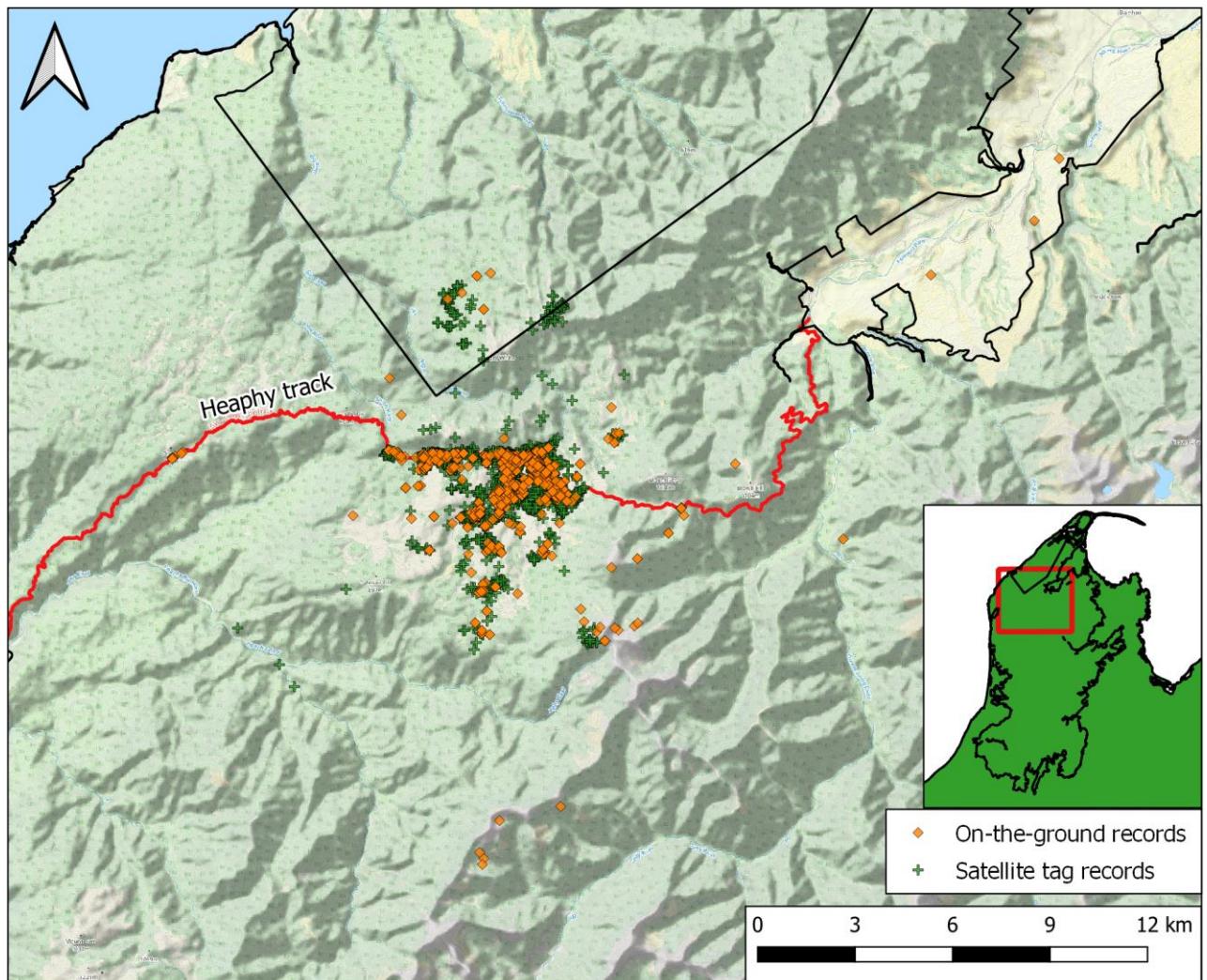
**Figure 5.2-** A) Release locations for takahē in the Gouland Downs, Kahurangi National Park (average elevation approx. 700m). Numbers next to points indicate the number of birds released from that location, while colour indicates the date of releases. The red line shows the path of the Heaphy Track, while the black line (inset map) shows the national park boundary. Green areas in the basemap indicate areas of forest cover, while white areas are open vegetation (mostly red tussock grassland) B) The Gouland Downs release area, characterised by extensive areas of red tussock.



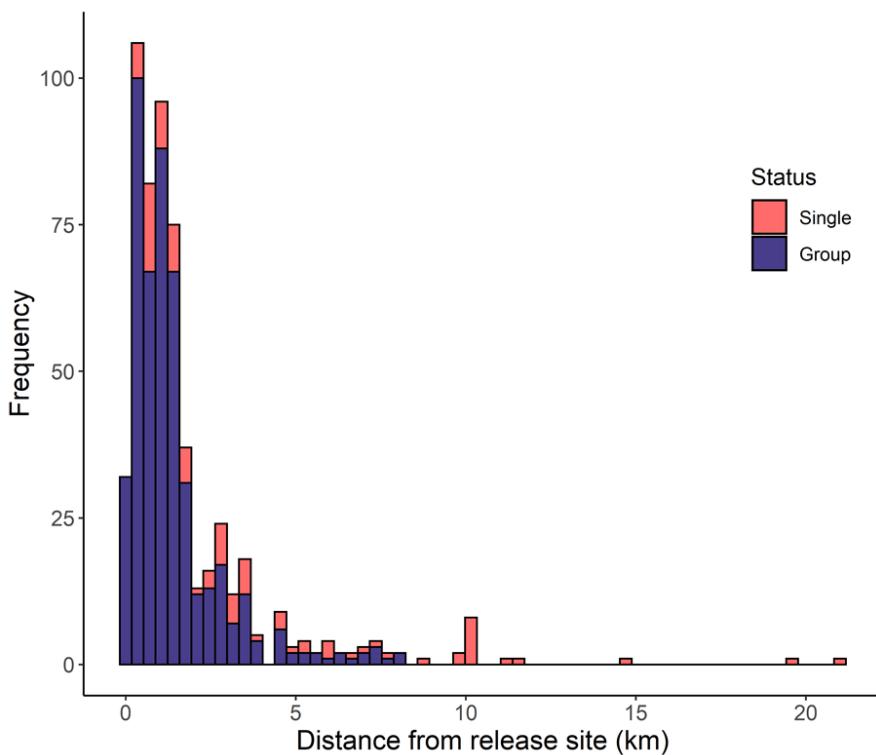
**Figure 5.3-** Temporal monitoring data from takahē, Kahurangi National Park, illustrating patterns in spatial data recording and key events for the takahē during a 30-month period following initial reintroduction. Individuals are identified by the names given to them by the Takahē Recovery Group, with sex indicated in brackets following, F= female, M= male and \*= unknown sex.

### 5.3.2 Post-Release Dispersal

Figure 5.4 shows the spatial distribution of bird locations from both on-the-ground and satellite tag tracking. Most records form a dense cluster around the Gouland Downs release sites (Figure 5.2), with most birds remaining in proximity to their respective release locations (median distance of record from release point 1.14km; Figure 5.5). However, five individuals dispersed >8km away from their release locations, with the furthest recorded dispersal at 21km (Figure 5.5).



**Figure 5.4-** Map of spatial records for takahe collected in Kahurangi National Park over 30 months following initial reintroduction. Orange diamonds show locations recorded by relocating the birds on the ground via radio telemetry, whereas green plusses show locations recorded by satellite tags, the red line shows the path of the Heaphy Track. The number of on-the-ground records shown is 961 and satellite records is 5641.



**Figure 5.5-** Distances of on-the-ground records for takahē from the release point of the bird recorded (includes both initial release locations and secondary release points of birds that were translocated within-site). Median distance from release-points = 1.14km. n= 569 on-the-ground records (474 records from individuals associated with an established breeding pair or social group and 95 records from single birds without established social associations).

Before conducting statistical tests I transformed dispersal distances by taking the natural logarithm of the dispersal distances in km to normalise the data distribution. The results of these tests indicate that single takahē dispersed significantly farther than those associated with a social group (Welch two sample t-test,  $t = -8.3926$ ,  $df = 132.91$ ,  $p < 0.001$ ).

### 5.3.3 Problematic Dispersal

Although the majority (28 out of 30) of the released birds remained within the borders of Kahurangi NP throughout the study period, the hope of all birds remaining within the national park was not realised. Birds dispersed outside of the parks borders on three occasions (involving two birds, as one bird, Catlin, dispersed twice by returning to agricultural areas following an internal translocation back within the National Park after her first foray outside park borders). Dispersing birds appeared to follow the route of the Heaphy Track to the park's borders and thence continue to travel into agricultural areas. As two of these dispersal events ended in predation, this highlights the danger to takahē of dispersing outside of the relative protection provided within National Parks.

### 5.3.4 Annual Survival and Productivity

Survival and productivity rates across the study period are summarised in Table 5.2.

Survival was high for the first two years of the reintroduction (97.7 % and 93.1%), exceeding the target 85% survival set by the TRG. However, as anticipated, productivity was low in these first two years (6.67% and 0%, respectively).

**Table 5.2-** Summary Table of annual vital rates for takahē following reintroduction to the Gouland Downs across the 30-month post-release study period.

Start date	End date	Time covered	Initial Population	Deaths	Lost Tags	Fledged young	% survival	% productivity
20/03/18	19/03/19	1 year	30	1	0	2	96.7	6.67
20/03/19	19/03/20	1 year	29	2	3	0	93.1	0.00
20/03/20	10/09/20	174 days	26	9	2	NA	65.4	NA

## 5.4 Discussion

The deployment of satellite tags on takahē allowed the collection of bird locations and description of post-release movements with a higher spatial and temporal resolution than for any previous spatial monitoring of this species. The data recorded by satellite tags can be used to investigate some questions regarding takahē ecology (such as the daily activity patterns investigated in Appendix B.2). While the fragmentary nature of the satellite dataset limits the questions that they can directly address, the on-the-ground records have much greater coverage of the population (covering a greater number of animals and for a longer time). However, the on-the-ground data is represented at a lower spatial and temporal resolution than the satellite fixes (Figure 5.3). This makes the on-the-ground records a valuable resource for identifying and evaluating general, longer-term trends in the reintroduced population. Given these patterns I have used the satellite and on-the-ground datasets to address different, complementary analyses of patterns in the reintroduced takahē population in order to provide a preliminary evaluation of the relative success of the reintroduction.

### 5.4.1 Satellite Tag Deployment Assessment

The satellite tag dataset was relatively small and highly fragmented due to a high rate of tag failure. Useful data were retrieved from satellite tags for fewer birds and for shorter time periods than planned. As satellite tags with damaged or removed aerials were unable to record locations effectively, the loss of aerials on 18 of the retrieved satellite tags greatly

reduced the effective tracking period and number of successful fixes recorded for satellite-tracked birds. Aerial damage was particularly severe and rapid for the PinPoint 240 tag models that were deployed in 2019, affecting all retrieved tags of this model and appearing to occur between 4 and 37 days following the tag being fitted. Pinpoint 240 Satellite tags were deployed in the field between 2<sup>nd</sup> May - 26<sup>th</sup> July 2019, with the latest suitable fix recorded on the 1<sup>st</sup> August 2019 (Figure 5.3). As these tags were intended to be collecting data until approximately July 2020, this damage to tags severely reduced the satellite-tracking period for the population and the number of satellite locations recorded overall. Most of the satellite data were recorded in 2018, as these pinpoint 120 models had a far lower rate and speed of mechanical damage experienced, even so, their battery life was lower than expected and no tag continued recording data for the full 12 months following release as intended (Figure 5.3).

#### **5.4.2 Post-Release Dispersal**

While the majority of released birds remained relatively settled close to their release site in the Gouland Downs (within 5km; Figure 5.5), and although some birds explored areas away from the Gouland Downs, a core population of resident birds quickly became established and has remained relatively stable in the Downs (Figure 5.4). This is promising, suggesting that the release site was appropriate as many birds have identified the area as providing suitable resources for the establishment of home-ranges and several have attempted to nest in these areas (Mihoub *et al.*, 2014; Sun *et al.*, 2016). However, five reintroduced takahē did disperse over 8km away from their respective release sites. This appears to be a suitable threshold for defining long-distance dispersal in the reintroduced population given the landscape structure (movements of 8km or more clearly leave the Gouland Downs plateau, considered the anchor site for the reintroduced population; Takahē Recovery Program, 2016) and the nature of birds dispersing above this threshold (all single animals rather than those associated with a social/breeding group, which can be considered a more dispersive class; Figure 5.5). Six individuals were internally translocated to bring them back into the core release area during the study period, predominantly when they dispersed into agricultural land or were at risk of exposure to 1080 poison baits (outside of the exclusion zone prior to the planned drop).

#### **5.4.3 Problematic Dispersal**

Long-distance dispersal was of specific concern only for those birds that moved outside of the national park, and so were exposed to increased predation risk. Protected areas

provide a refuge for many species from numerous potential threats, for example, human persecution/harvest (Schaub *et al.*, 2009; Peres *et al.*, 2016; Recio *et al.*, 2021), predation/competition from introduced and domestic species (Stüwe and Nievergelt, 1991; O'Donnell, Weston and Monks, 2017), physiological stress and reduced resource availability in anthropic landscapes (Wisler, Hofer and Arlettaz, 2008; Crooks *et al.*, 2017; Marshall *et al.*, 2020). This is the case for takahē in Kahurangi National Park, which benefit from protection, particularly from predation by introduced species (O'Donnell, Weston and Monks, 2017), while within the parks boundaries. Dispersal into the agricultural landscapes bordering the National Park were concerning as birds entering these landscapes were at much increased risk of mortality as they were not afforded the relative protection of the National Park.

Post-release dispersal can also be problematic even without the issues arising from leaving protected areas. Dispersal and population radiation creates a more diffuse population occupying a wide geographical space. This could have ramifications for the growth-potential of the reintroduced population as it creates a low density population that might be susceptible to Allee effects (Reynolds *et al.*, 2012). It was observed that dispersal in the Kahurangi NP takahē population did not appear to be in response to population pressure in the core occupied area, i.e., takahē dispersed despite apparently suitable unoccupied habitat in their current location. This could potentially cause an Allee effect as dispersal under these circumstances maintains a population density below the potential carrying capacity of the landscape.

Low population density alone is not enough to assert the existence of an Allee effect, as additionally a mechanism for positive density dependence in population growth at low densities, such as difficulty finding suitable mates, must also be identified (Chandler *et al.*, 2015). Considering the social and breeding ecology of takahē, which maintain social breeding groups (most commonly pair groups, often with yearling nest-helpers, but occasionally polygamous trios or quads) year round, the existence of a significant Allee effect seems unlikely (Williams and Miers, 1958; Ryan, 1997). Dispersal appeared to be heavily biased towards unpaired birds (predominantly female due to a gender bias in the release cohort) with single birds moving significantly farther from their respective release sites than those associated with social/breeding groups ( $p<0.001$ ; Figure 5.5). The motivation for exploration/dispersal thus appears to have been mate-seeking by single birds.

The heterogenous dispersal patterns (with most birds remaining close to release sites, while a few moved several kilometres away) can largely be attributed to breakdown of established release groups coupled with the female gender-bias in the reintroduction cohort. Due to the ‘single’ nature of dispersing animals, dispersal is expected to have minimal impacts on population growth. Any Allee effects created by mate-finding difficulty in a low-density population will apply only in the event of loss (through mortality or pair-breaking) of a female partner from established breeding pairs (i.e., any newly lone males may have difficulty re-pairing if most of the lone females have dispersed). It is therefore expected that at most dispersal from release sites will have a marginal impact on population growth for the Kahurangi NP population. However, although the presence of single animals within the reintroduced population might be expected to have only limited effects on population growth, this situation (itself arising from an uneven sex ratio) does mean that the effective population size of the reintroduced population is lower than might be apparent from population size alone (Xia *et al.*, 2013). Although an even sex ratio in the released cohort was intended for the Gouland Downs reintroduction, ultimately this was not realised due to limiting logistic and circumstantial factors in sourcing the reintroduction cohort (Section 1.3.3).

#### **5.4.4 Annual Survival**

Targets for reproduction and mortality in Kahurangi NP were largely based on observations in the only extant wild population of takahē in the Murchison Mountains. Targets were provided by the TRG based on their long-term monitoring of the Murchison Mountain population (>85% annual survival and ≤9.6% annual productivity, uncertainty values were not made available; TRG, unpublished data). Annual survival targets were realised in the first two years following release (96.7% and 93.1%, respectively). The low survival in the first approximately 6 months of the 2020/21 window is especially concerning, however. Even discounting the three deaths attributed to 1080 consumption, survival in this period was still low (76.9%). The remaining mortality events were predominantly unpaired females that exhibited dispersive behaviour and/or displayed ephemeral/semi-nomadic movements. This is reflected in the causes of mortality: predation, emaciation, and misadventure. Birds without a consistent home range are considered to have higher exposure to these factors (i.e., due to a higher likelihood of moving outside of protected areas where predator densities are higher and having a lesser knowledge of local food resources and/or dangerous topography and vegetation due to nomadic behaviour). High mortality in the start

of the third year of the reintroduction can then be put down to two factors: a novel threat from 1080 exposure and an apparent time-lagged impact of the gender demographics and resultant social patterns, movement and dispersal behaviours within the release cohort. However, it is possible that other unaccounted for factors including individual-level effects also had a role in this high death period.

#### **5.4.5 Annual Productivity**

Annual productivity was, as expected, lower in the Kahurangi NP over the first two breeding seasons following reintroduction (6.67% and 0.00%, respectively) than the 9.6% seen in the Murchison Mountains. However, despite fitting initial allowances for lower productivity resulting from lower nutrient quality in food plants, the overall productivity in Kahurangi NP is even lower than expected, particularly in the second breeding season which resulted in no chicks fledging. Despite this disappointing start, there is reason to believe that productivity this low will not become the long-term trend in the Kahurangi population, as specific atypical conditions impacted breeding in the first two years.

Social instability was evident prior to and during the first breeding season as many breeding groups that had been established and stable prior to release promptly separated once they were free to do so, leading to low nesting effort (only three nests detected). This is thought to have been particularly pronounced due to the destabilising effects of a female-biased release cohort. However, in the second breeding season, breeding group instability was no longer an issue, and accordingly a much higher nesting effort was observed (seven nests detected). But then flash flooding in the summer destroyed all known nests (such events are not known from other takahē populations), resulting in complete failure this season.

As neither social instability nor flash flooding is expected to be a regular or long-term problem in the population, low productivity in the initial two breeding seasons does not necessarily indicate the future potential productivity in this population. Therefore, at this stage nothing equivocal can be said regarding the potential productivity of the Kahurangi population, excepting that it is at least confirmed that it is possible for takahē to breed successfully at this site as evidenced by the fledging of two wild-born and reared chicks in the 2018/19 breeding season. Observations across more breeding seasons are required to detect any generalisable trends in the productivity of this population.

#### 5.4.6 Recommendations

From this initial evaluation of post-release patterns following the reintroduction of takahē to the Gouland Downs lessons can be learned to aid both the management of this and future reintroduced takahē populations. Firstly, the first field trial of GPS satellite tags deployed for takahē yielded much useful tracking data at a higher spatial and temporal resolution than has been collected for this species in the wild previously, and this despite high rates of tag damage and failure. I strongly recommend the continued use of satellite tag technology to aid monitoring and research of takahē into the future, though satellite tags purchased in future should have revised specifications, primarily to reduce the susceptibility to aerial loss (i.e., more robust, or potentially internal aerials). The continued use of satellite tags has high potential for this species, enabling continued research into takahē spatial ecology and further monitoring of takahē populations while reducing the required on-the-ground person hours needed to record these data (Tomkiewicz *et al.*, 2010; Neill and Jansen, 2014).

Deployment of satellite tags to the relict takahē population in the Murchison Mountains as well as other populations would also be valuable, as it would enable comparisons of the movements and spatial ecology exhibited between takahē populations in differing contexts.

Secondly, more effort needs to be put into ensuring that takahē do not ingest 1080 poison baits at Kahurangi or any future site, as despite attempted remedial measures (establishment of an exclusion zone where no baits were dropped and relocation of birds to be held within this zone as much as possible), six birds were exposed to the poison baits, of which three died, contributing to the 33.3% mortality observed across the reintroduced population in March-September 2020. Although this is a very small sample, and it is thus hard to draw conclusions regarding the absolute susceptibility of takahē to 1080, exposure to the baits clearly constitutes a risk to the birds. Exposure to 1080 needs to be strictly avoided, unless or until more information or countermeasures (such as bait repellents or aversion training for takahē) are available.

Thirdly, biases in post-release dispersal (that necessitated more active management to internally translocate dispersing animals back within the core population) and mortality biased towards lone birds emphasises the importance of an even gender balance in release cohorts. Although an even gender ratio was intended for this reintroduction, the final composition of the Gouland release cohort was predominantly determined by the availability of birds suitable for release. By chance (and ill-fortune, as several males intended for inclusion in the cohort died before the reintroduction could occur) this was a predominantly

female group (Section 1.3.3). While this was known to be non-ideal, it was also deemed acceptable as evidence from other sites (predominantly small islands; Chapter 1) indicated that an excess of females usually results in larger polygamous groups (2 females and 1 male), rather than increased incidence of lone birds (TRG, unpublished records). Based on post-release patterns observed in the Kahurangi NP it is hypothesised that the gender-biased release cohort led to both reduced breeding effort in the first year following release (put down to the separation of established breeding pairs in part due to the presence of excess females), as well as increased dispersal and mortality in the introduced population attributed to the mate-seeking behaviour of unpaired females. Although in some respects this could be considered a self-correcting issue (as excess females disperse away or die, correcting the gender bias in the core population), these patterns reinforce the known need to consider the demographic make-up of release cohorts (Xia *et al.*, 2013) and confirm that even sex ratios should remain the goal for future reintroductions of takahē whenever possible.

## 5.5 Conclusions

Despite the relatively short time frame since reintroduction, and the challenges of post-release monitoring (e.g., COVID disruptions and tag failures), preliminary evaluations of the reintroduction could be conducted based on monitoring of the reintroduced population of takahe in Kahurangi NP. There are many facets of the reintroduction that can be usefully evaluated, although disentangling these can be difficult as they are inter-related. Specifically, there are a series of unprecedented conditions in the Kahurangi reintroduction that can be considered as ecological and/or management trials/experiments for takahē including: the overall reintroduction (as it represents the first time that a large group of takahē have been released at a wild site outside of Fiordland); the deployment of Satellite tags on takahe, and the incidental exposure of takahē to aerial 1080 baits. Additionally, some post-release patterns are potentially impacted by more than one field trial, e.g., interactions between social/demographic make-up of the release cohort and exposure to 1080 (mediated through impacts on individual behaviour). In order to deal with this complexity in this chapter I have presented simple (*simplistic* even), targets/goals that can be assessed by considering the temporal and spatial patterns in monitoring datasets as independent (although these would be more accurately represented as movement data, with both temporal and spatial dynamics).

Although the analyses presented in this chapter can provide useful preliminary evaluations, little can be said with certainty at this stage regarding the success of the reintroduction or even the suitability of the chosen release site (Seddon, Armstrong and Maloney, 2007). More time and continued observation are needed, particularly breeding monitoring, before these assessments can be made and presented with a degree of certainty. However, while a complex overall evaluation of the Kahurangi NP reintroduction is not yet possible, much useful data have been collected from the monitoring of the reintroduced population and the combined deployment of radio and satellite tags. These can be used to examine and evaluate patterns of resource and space-use by takahē following release. Such analyses have the potential to provide new insight into takahē ecology which can usefully be applied to management efforts in future. These analyses will be the focus of the next chapter.

## Chapter 6

### Descriptive Models: Reconstructing Detailed Population Distributions by Combining “Patchy” Datasets

Post-release monitoring is an essential stage of any reintroduction programme and can provide much valuable information. But raw animal tracking data are often complex, fragmentary, and not readily interpretable in terms of ecological meaning or management value. Fitting models to ecological observations is often a crucial step in gaining insight and allowing useful application of monitoring data. In this chapter, I combine models fitted to satellite and radio telemetry datasets derived from post-release monitoring efforts to estimate post-release space-use, resource selection and distribution of takahē in the 30-month period following their release into the Goulard Downs.

#### 6.1 Introduction

Technological innovation and methodological advancement continue to provide new opportunities for field data collection in ecological studies (Lahoz-Monfort and Magrath, 2021). Innovation across disciplines allows ever-increasing detail and ever greater volumes of data to be collected, and new types of ecological management to be considered (Martinez *et al.*, 2020). From emerging DNA-based methods such as environmental DNA (Hering *et al.*, 2018) and metagenomics (Creer *et al.*, 2016), to increasing capacity for remote sensing (Lembrechts, Nijs and Lenoir, 2019), and movement and behavioural tracking (Kilshaw *et al.*, 2014; Kays *et al.*, 2015), there are a wealth of emerging options in data collection for ecological research and management.

The increasing opportunities in data collection are not without drawbacks, as data collected using new methods and technologies may not be directly comparable to historic records collected using other methods. Consistency in methodologies over long time periods is desirable to produce comparable datasets with a large temporal range (Barbet-Massin and Jetz, 2014). But, dynamism and adaptability in methodologies is also necessary to take advantage of emerging technologies and to increase the breadth and depth of data collected and hence the ecological knowledge accumulated (Ferrier *et al.*, 2006). As such, for species and systems which are the focus of long-term research and management, the choice of when, and how, to revise data collection methods is challenging.

Embracing new technologies is also risky. Early adoption of cutting-edge methods might fail to produce the desired results, with such methods often still requiring thorough field-testing, as unforeseen errors and issues can severely reduce the expected quality and quantity of data collected (Kouba *et al.*, 2013). Even adopting relatively well-established and thoroughly field-tested technology is not without risk, as many complications will be specific to the system to which they are applied. For example, tracking or monitoring devices are often custom designed for a single species and field-deployment period, e.g., camera traps deployed in sub-Saharan Africa need to be structurally robust as elephants (*Loxodonta africana*) may attempt to destroy them, whereas the lack of terrestrial megafauna in Scotland means camera traps would not need to be built nearly as strongly for deployment there. Any methodological updates should undergo a period of field-testing and refinement, during which time some useful data could be collected, but this cannot be relied upon until any bug-fixes have been implemented. This will often mean that as field-tests of new methods are conducted, established research and monitoring practices are carried out at the same time to act as a back-up in the case of emergent issues with the newer methods.

Additional reasons for simultaneous data collection with different methods include that some methods will collect multiple kinds of useful data, e.g., GPS tags can reveal patterns of movement (Recio *et al.*, 2010), but cannot assess an animal's health, or count the number of offspring in a nest, as a researcher tracking animals on the ground would be able to do (Panfyllova *et al.*, 2016). Such monitoring, primarily aimed at identifying individual health and breeding success, might produce spatial records as a by-product, nevertheless such spatial records can still have much utility.

This situation often results in managers and researchers having multiple measures of the same quantity, collected using different methods and of differing quality and bias. It will likely be the case that neither measure is ideal. If the established method were ideal, it would not be being revised; while field testing is required to identify the efficacy of newer methods (Hering *et al.*, 2018). Thus, faced with multiple non-ideal datasets upon which to make inferences, interpretation and integration of these data becomes a non-trivial challenge. However, there is potential to make the best of this situation by using overlapping datasets to cross-inform one another, identifying gaps and biases in one dataset that can be overcome to some degree by considering patterns in another dataset.

The post-release data collection for takahē (*Porphyrio hochstetteri*) in the Gouland Downs provides an opportunity to explore cross-informing analyses, specifically with regard to

spatial tracking data collected during post-release monitoring (Chapter 5). As reintroduced takahē were monitored with both radio and satellite tags, two spatial datasets are available based on radio-tracking (on-the-ground) records and satellite tag fixes, respectively. Due to high failure rates of the satellite tags the satellite dataset covered a much shorter timeframe than the on-the-ground dataset (Figure 5.3), but these short-term satellite data had much higher spatial and temporal resolution than on-the-ground records. The two spatio-temporal datasets are divergent, but complementary. Long-term on-the-ground data can identify movement patterns over the whole population and study period, associated with exploration, dispersal and home range establishment. Whereas high-resolution satellite data can identify resource selection and environmental drivers of space use at a finer scale, reflecting high-resolution resource use. Results from complementary analyses can then be combined to produce a best-possible estimate of takahē distribution in the Gouland Downs over the study period. These combined outputs can predict, for instance, the most heavily used areas within the broad areas that takahē have explored since their release. Combined outputs can potentially be more informative than constituent models in isolation, making the most of all the available spatio-temporal data. I term this hybrid analysis structure ‘interpolation-extrapolation’ as extrapolating from one (the high-resolution) dataset is used to add resolution to (i.e., interpolate) another (the long-term) dataset. The resultant combined predictions potentially have a resolution and spatial specificity that could not be achieved by considering the component datasets in isolation.

### *Aims and Objectives*

In this chapter, I use the complementary on-the-ground and satellite tag datasets provided by post-release monitoring of the Gouland Downs takahē to:

1. Identify long-term space use of takahē in the Gouland downs from the on-the-ground record dataset. This long-term space-use should identify patterns associated with exploration, dispersal and home range establishment over 30 months following initial releases.
2. Identify fine-resolution environmental drivers of movement decisions for takahē in the Gouland Downs based on the satellite tag dataset.
3. Combine outputs from the above steps to generate a hybrid ‘interpolation-extrapolation’ output where extrapolations from the high-resolution patterns are combined with interpolations of long-term patterns to predict the most heavily used spaces for the reintroduced population.

## Caveats

Several aspects of the methods presented in this chapter are, to my knowledge, novel. Particularly approaches to rescaling model outputs and then combining them must be considered explorative and experimental. While overall the ‘interpo-extrapolation’ approach has produced interesting and hopefully useful outputs, at this stage they can only be considered as a proof-of-concept. While the overall patterns in outputs presented are potentially informative, it is currently not appropriate to give weight to precise quantitative results (which are sensitive to many decisions regarding the post-processing rescaling and subsequent combination of model outputs). As such, the chapter results do remain untested, and the methodologies need development.

## 6.2 Methods

Temporal and spatial records collected from animal tracking can be extremely useful for examining animal movement behaviours. To do this, spatially-explicit time series data needs to be transformed into movement paths, where temporal information is used to arrange consecutive location records into a continuous path. When this is done additional, potential useful information is revealed, for instance, movement speed, direction and turning angles (Joo *et al.*, 2020). Spatial behaviours can also be shown dynamically by animations of these movement paths (Schwalb-Willmann *et al.*, 2020). For analyses in this chapter both the on-the-ground records and satellite tag datasets described in chapter 5 were converted from time-stamped locational data to create movement paths for all following analyses.

### 6.2.1 Long-Term Space Use Models (Brownian Bridge Movement Models)

The low and variable spatial (accuracy from radio-telemetry and the handheld GPS method ≈ 5-25m; Neill and Jansen, 2014) and temporal (temporal records only accurate to calendar date, time of day not included in database records, location interval 1-248 days, mean 26.4 days; Figure 5.3) resolution makes the movement paths created from these data highly uncertain, as the time between recorded locations (and the 24hr window attributed to individual location records) allowed birds opportunity to make substantial movements. Therefore, I modelled these movements in a way that accounted for the uncertainty associated with on-the ground movement tracks.

#### *Rationale*

Brownian Bridge Movement Models (BBMMs) are a method of analysing a discrete sample of animal movements (such as those generated by satellite or radio tracking) taking specific account of measurement uncertainty and tolerating variable time-intervals between locations (Kranstauber *et al.*, 2012). Brownian Bridge Movement Models estimate a continuous Utilisation Distribution (UD), reflecting intensity or probability of space-use, based on a discrete sample of animal movements. They do this by modelling the movements of animals in between recorded locations as a random diffusion process, with start and end points determined by recorded locations, generating an estimate of continuous space use from discrete time-series locations (Horne *et al.*, 2007). The most common use of BBMM's is to provide estimations of individual home-ranges via a binarization of the continuous UD based on confidence intervals relating to the probability of finding an animal within a defined boundary (Kranstauber *et al.*, 2012).

The concept of the home range is often a poorly defined idea (Powell and Mitchell, 2012), with one early definition being “That area traversed by an individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range” (Burt, 1943 in Powell and Mitchell, 2012). This idea creates problems in the context of a reintroduced population (at least in the initial period following reintroduction) as it implicitly assumes a level of stability (i.e., an established routine “normal activities”) and that the home-range is an area in which animals maintain a level of knowledge and familiarity. Animals released into an (initially) unfamiliar reintroduction landscape will necessarily take time to gather knowledge of their environment and establish a normal activity routine that includes a relatively stable pattern of space-use. Therefore, reintroduced animals cannot reasonably be asserted to maintain a home range until an (individually and contextually variable and indistinct) time has passed following release (Mertes *et al.*, 2019). However, it is still beneficial to assess post-release movement patterns and estimate utilisation distributions within such populations. Though given the ecological context it is best to avoid presenting these as “home range analyses”. Such analyses can be more broadly phrased as “space-use estimations”, which for a reintroduced population are understood to include innate biases towards release sites and much exploratory movement and dispersal arising from the reintroduced population radiating from and establishing around release sites.

The limitations of the post-release monitoring data for takahē in the Kahurangi NP (Chapter 5), prevent a clear-cut assessment of traditional home-ranges for individuals within this

population. Instead, I used utilisation distributions based on on-the-ground monitoring data to provide a broad estimation of space-use across the reintroduced population accounting for the substantial uncertainty regarding bird movements in between on-the-ground records and ecological processes of exploration and population radiation in the reintroduced landscape. However, as this is an atypical application of Brownian Bridge Movement Models, there are no directly comparable results from other studies, so results should be treated with caution until further validations are conducted.

### *Process*

The on-the-ground monitoring records collected by the Takahē Recovery Group (Chapter 5), provided long-term movement data for takahē following their reintroduction to the Gouland Downs. These records were processed to create movement-paths for released birds; first tracks for any birds that were internally translocated (e.g., to prevent their dispersal out of the National Park, or to contain them within a 1080 exclusion area; Chapter 5) were split into pre- and post-translocation tracks (such that no tracks contained human-mediated movements). Finally, tracks fewer than 3 location records were removed from the dataset, as BBMMs could not be fitted to such short tracks. However, this omission, in addition to the loss of tracking data from some birds when they lost their tags (Section 5.3.1), reduces the coverage of the reintroduced population in input data and introduces some error into the resulting distribution estimation (Figure 6.1).

I fitted Brownian Bridge Movement Models to on-the-ground movement paths in R using the BBMM package (Nielson, Sawyer and L., 2013). Utilisation Distributions were estimated over the rectangular extent of a 5km buffer area around the on-the-ground records and at a 25m resolution (higher spatial resolution than usually would be considered suitable given the resolution of input data, but necessary to match the resolution of satellite-based models so that these could be combined). BBMMs were calculated for each on-the-ground movement track individually with a location error set to 100m (accounting for the estimated 5-25m spatial error and inaccuracy from the variable times of the day at which records were taken), a time step of 1440 minutes (24 hours) to match the minimum recorded interval between on-the-ground records for any bird, and maximum time lag set to the maximum relocation interval for each track individually (13-248 days).

The continuous utilisation distribution raster outputs for each unique track were then summed to create an estimate of space-use across the whole reintroduced population.

However, the scaling of raw outputs of Brownian Bridge Movement Models (Figures C.5-C.7) were not considered plausible or intuitive representations of the post-release distribution of takahē in the Gouland Downs. Comparison with monitoring data revealed that most points fell in the lower half of the distribution of pixel values (Figure C.8A), meaning that models were considered to be unduly overfitted to input points (likely due to the very fine 25m resolution to which models were fitted, coupled with inherent release site biases). To counter for the observed right skew and extremely low pixel values in outputs (Figures C.5-C.8) the BBMM outputs were transformed using the following equation adapted from Nielsen, Cranston and Stenhouse (2009).

$$\text{Rescaled BBMM} = 1 - e^{-100000 \times \text{Population BBMM}}$$

This transformation produced a more intuitive output range (a 0-1 index of use intensity; Figure C.8B) and reduced the right-skew observed in the distribution of the outputs. Parameterisation of this transformation (i.e., the selection of the 100,000 constant) was arrived at iteratively and was pragmatically adjusted with reference to tracking data (both satellite and on-the-ground datasets; Chapter 5). This rescaling was experimental (and thus is in need of further development) but appears to be a better fit to observed points than untransformed outputs, as the majority of tracking data fall within the upper half of the transformed distribution (Figure C.8B). Based on this observation, a putative threshold of 0.5 is adopted for aiding interpretation as this threshold was taken to approximate a likely used/unused threshold.

### *Interpreting Outputs*

This rescaled BBMM output identified the key areas of space-use for the Kahurangi NP takahē in the first 30 months post release. However, this estimate contains a high degree of uncertainty and low spatial precision due to the relatively long time intervals between location records in the on-the-ground tracking data (Horne *et al.*, 2007). While further error is introduced by missing and removed location records for several birds (Section 5.3.1 and above). Additional to this uncertainty, these models take no account of environmental drivers of movements and space use, as they are purely descriptive (Kranstauber, 2019). This means that while the outputs from BBMMs do represent a useful estimate of the most likely areas of space-use in the long-term by takahē, this estimate has low spatial and temporal resolution and is not informed by the environment. Therefore, these course-scale model outputs could be usefully informed and refined through combination with

complementary models of high-resolution, environmentally informed and short-term movements.

## **6.2.2 High-Resolution Environmental Selection Models (Step Selection Functions)**

### **6.2.2.1 Model Fitting**

Whereas the on-the-ground records from the Gouland reintroduction are too spatially and temporally coarse to reveal the fine-details of takahē movements, data retrieved from satellite tags do have the necessary resolution and regularity to model such patterns. However, due to lack of coverage by satellite tags, and high rates of satellite tag failure, these high-resolution data cover only a portion of the reintroduced population for a limited time following fitting of satellite tags (Chapter 5). This means that, in isolation, satellite records cannot identify space use across the entire reintroduced population, nor over the entire study period. To make best use of the satellite tag data, I sought to identify environmental drivers of fine-scale movements based on the satellite dataset, and to extrapolate from these relationships to make inferences across the wider population and study period.

#### *Rationale*

Step Selection Functions (SSFs) provide an established method for identifying resource and spatial selection accounting for animal movement properties (Zeller *et al.*, 2016; Signer, Fieberg and Avgar, 2019). They were developed as an extension of resource selection functions, conditional logistic regressions that identify preferences by comparing ‘used’ (presence) to ‘available’ (absence/background) locations in a user-defined region around presence locations (Zeller *et al.*, 2018). SSFs expand this framework to account for temporal dependencies in animal movement paths (as the location of one record in a path is limited by the location of the previous record and the movement properties and ability of the animal). So, instead of discrete locations being considered as the model response, steps, or the explicit movement between two locations, are the modelled quantity, with semi-random “potential” steps (generated from a distribution of step lengths and turning angles fitted to observed steps, so that simulated steps reflect realistic alternative movements to observed steps) being compared with the actual movements represented in tracking data (Forester, Im and Rathouz, 2009). Predictor variables for SSFs describe environmental character and structure affecting animal movement decisions (Panzacchi *et al.*, 2016).

### Process

Satellite tag data (Chapter 5) were first separated by unique tag and bird IDs to create individual movement tracks recorded by each tag. These tracks were then animated using the *MoveVis* package (Schwalb-Willmann *et al.*, 2020) in R (R Core Team, 2020) to create mp4 video files showing the movements of each bird recorded (provided in [Digital Appendix 2](#)). These animations allowed movement patterns to be examined and hypotheses of movement behaviours and driving factors to be generated, influencing decisions regarding suitable models to be fitted to these data.

Satellite data were then prepared for analysis using the *AMT* (Signer, Fieberg and Avgar, 2019) and *adehabitatLT* (Calenge, 2006) packages in R. Tracks were defined by bird ID (birds that carried multiple tags over the study period had data collected from different tags merged together) so that time intervals between recorded locations could be summarised and data retention when tracks were resampled to regular time intervals could be examined. These factors informed decisions for how to fit models to these data.

I chose to focus on distance predictors based on animated tracks that indicated the birds appeared to be following linear habitat features and because of previous suggestions that takahē are edge-specialists (Trewick and Worthy, 2001). I fitted SSFs to the satellite tag tracks from the Gouland Downs using environmental predictors of; vegetation cover (binary measure, forest or open vegetation), distance to paths, distance to rivers, distance to forest edges and terrain slope (continuous measures, for details of data sources and preparation see Appendix C.1). Environmental predictor variables reflect aspects of landscape structure (both vegetation and topography) of potential importance in directing fine-scale takahē movements in the reintroduction area observed in animations. Predictor variables were processed to the same 25m resolution and cropped to the same extent as used for the BBMMs. As distance to linear features was only expected to impact takahē in close proximity of these features, distance predictors were transformed following the method of Nielsen, Cranston and Stenhouse (2009). This method creates an output on a 0-1 scale, with values of 0 at the feature and 1 over a certain threshold distance away from the feature (the distance beyond which it is assumed that the feature no longer impacts animal movement patterns). Values between 0 and 1 then represent distances close enough to the linear feature to impact movement decisions. The following equation was used to transform distance predictors (Nielsen, Cranston and Stenhouse, 2009);

$$\text{Transformed Distance} = 1 - e^{-a \times \text{Distance}}$$

where  $e$  is Euler's number, or the exponential constant, and  $a$  is a coefficient determining the rate of the exponential decay; this was set at 0.02 for forest edge and river distances and 0.04 for path distances (as takahe were expected to cease responding to paths more rapidly than the larger, more obvious landscape features). I then tested for collinearity between predictor variables and found levels of collinearity to be acceptable (Pearson's  $r < 0.7$  and Variance Inflation Factor  $< 3$ ; Dormann et al., 2013; Zuur et al., 2010, for full results see appendix C.2).

Following Muff et al. (2020) I resampled satellite data for each bird to create tracks with a consistent fix-interval of 3 hours (with a tolerance of  $\pm 15$  minutes and a minimum track length of 3 steps) using functions from the *AMT* package (Signer, Fieberg and Avgar, 2019) in R, removing any tracks which could not be resampled in this way (i.e., which did not have enough relocations suitably close together). Fitting SSFs as a Generalised Linear Mixed Model (GLMM), allowed environmental drivers of movement patterns to be estimated across the tracked cohort while accounting for individual-level variation in movement behaviour (Muff, Signer and Fieberg, 2020). I used this method to allow the pooling of data collected across individuals while accounting for individual variability. Modelling across individuals reduces autocorrelation in input data, as individuals are considered the sample unit instead of locations (Gillies et al., 2006; Muff, Signer and Fieberg, 2020).

I fitted a population-level SSF using functions from the *glmmTMB* (Brooks et al., 2017) and *AMT* (Signer, Fieberg and Avgar, 2019) packages in R based on code and methods provided in Muff, Signer and Fieberg (2020). I fitted models using the four predictor variables described above (vegetation cover, distance to paths, distance to rivers, distance to forest edges and terrain slope). To account for individual-level variation in movement behaviour I also included animal ID as a random factor in models, while step length was also included as a predictor to reduce bias in parameter estimates (Muff, Signer and Fieberg, 2020).

### 6.2.2.2 Model Projection

A linear projection of the fitted SSF model was then created using the equation below.

$$\text{Projection}_{\text{linear}} = a_1x_1 + a_2x_2 + a_3x_3 + a_4x_4 + a_5x_5$$

where  $a_i$  are model coefficient and  $x_i$  are the four predictor variables (in raster format) respectively.

#### *Rationale*

In most step selection function studies, the exponent of the linear projection is taken as the final output, with exponential values taken to represent values indicating the relative probability of use (Keeley, Beier and Gagnon, 2016; Muff, Signer and Fieberg, 2020; Smith *et al.*, 2021). However, in the case of this study an exponential projection was deemed unsuitable for several reasons.

Firstly, the use of several distance-based predictors meant that the ecological meaning of the exponential (or even linear) projection is questionable. As distance to paths, forests and rivers are all included as predictors, the linear projection assumes that proximity to multiple of these linear features will have an additive effect in terms of increasing probability of selection, with this cumulative effect becoming even more prominent in an exponential projection. However, it might be questioned whether animals are capable of following multiple linear features at the same time. It seems more likely that, to a large degree, animals will “choose” to follow one feature or another at any given time (Howard *et al.*, 2015; Dickie *et al.*, 2017). Given these considerations a logistic-type projection of the linear step-selection function is potentially more ecologically meaningful for SSF’s including multiple distance-based predictors. Logistic projections represent expected “diminishing returns” in terms of probability of space use for animals being in proximity to multiple linear features. This is more conceptually defensible given the observed linear-feature tracking behaviour of takahē (as proximity to multiple linear features increases the routes to that area, as birds can follow either forest edges or paths, for example, but does not inherently make the location more selected).

Secondly, and likely due to the conceptual issues outlined above, the scaling and sensitivity of the linear and exponential projections were not intuitive or informative for management purposes. High selection was only predicted in locations where optimal values for all predictors intersected (Appendix C.6). These projections excluded large areas identified as potential takahē habitat by expert assessment (Takahē Recovery Program, 2016) and habitat suitability models (Chapter 4; Figure 4.7 A and B), as they gave undue weight to very small areas that were simultaneously proximate to forest edges, paths and rivers. As stated, these weightings and sensitivities seem unrealistic and unwarranted given the low

likelihood that animals are even capable of responding to multiple linear features at the same time.

The above points suggest that a logistic-type projection of the fitted SSF should be more ecologically realistic and consequently more useful for management purposes than a linear or exponential projection of the fitted model. When it came to choosing the precise function to produce a logistic-type projection I chose a complementary-log-log (cloglog) function, for practical reasons. The projected SSF will later (in Chapter 7) be compared with the predictions of MaxEnt models produced in Chapter 4. As these MaxEnt predictions are represented as a cloglog projection (as is currently recommended for MaxEnt models; Phillips et al., 2017) applying a cloglog transformation for the SSF projection will ensure that MaxEnt and SSF outputs are represented with similar scaling and sensitivities, aiding their comparison. However, while this choice does aid comparison between the two model outputs, it cannot at this stage be asserted that the cloglog projection is the most suitable for the SSF in isolation, though, as argued above, there are reasons to maintain that some form of logistic transformation would be suitable for this SSF (and other similar models).

### *Process*

Before applying the cloglog transformation, the linear projection was rescaled using the following method.

$$\text{Projection}_{\text{rescaled linear}} = (\text{Projection}_{\text{linear}} + 1.5 - \text{Projection}_{\text{linear}}^{\max}) \times 1.333$$

Where  $\text{Projection}_{\text{linear}}^{\max}$  is the maximum value in the linear projection. This rescaling was performed so that the range of values for the rescaled projection was within the range of values that the cloglog function is sensitive to (approximately  $-5 < x < 2$ ). This ensured that outputs covered the full potential range of outputs from the cloglog function (0-1, see appendix C.4).

The cloglog projection of the SSF was generated using the following function from Phillips et al. (2017);

$$\text{Projection}_{\text{cloglog}} = 1 - e^{-(\text{Projection}_{\text{rescaled linear}})}$$

### *Interpreting Outputs*

This cloglog projection is a raster output covering the reintroduction area with cell values representing an index prediction of the relative likelihood of takahē to moving into that cell

(given the opportunity to do so). As cloglog outputs from MaxEnt models are considered to be predictions of “probability of presence” under equilibrium conditions, I suggest that the cloglog output of the fitted SSF can putatively be considered to represent a scale of “probability of use” under equilibrium population conditions. However, this assumption of equivalence requires further conceptual and statistical exploration to be confirmed.

While the projected SSF provides a highly detailed picture of landscape structure through a takahē-eye-view, the projection is time-insensitive and does not take account of the process of movement and diffusion from release sites following takahe reintroduction. As the SSF equation is applied equally across the projection landscape it is implicit in the projection that all areas are equally accessible to takahē, irrespective of population context or dynamic processes. In order to predict realised space-use intensity, these predictions of selection likelihood need to be combined with additional data.

### **6.2.3 Estimated Distribution (Combined Brownian Bridge Movement Models and Step Selection Function Outputs)**

#### *Rationale*

By combining outputs from BBMMs and SSFs described above I sought to arrive at an output representing an informed high-resolution estimate of the distribution of the takahē population in Kahurangi NP over my study period. The outputs from BBMMs (based on the on-the-ground dataset) represent long-term space-use patterns, identifying the broad areas that the birds have explored and established home ranges since their reintroduction. The SSF output (based on the satellite tag dataset), on the other hand, represents environmentally informed predictions of fine-grain resource selection accounting for movement properties and patterns. However, these two processes do not operate in isolation, it is the fine-grain movement choices that determine long term movements of birds, dictating the areas in which they will explore, disperse, and establish home ranges. There is, therefore, an opportunity to combine outputs focussing on these different ecological processes in order to generate more ecologically complete and realistic predictions by accounting for the interaction between both long and short-term movement patterns. Mechanistically, by combining the BBMMs with SSF I sought to extrapolate high-resolution patterns from a limited number of birds and a limited timeframe and use this to add useful resolution to coarse, long-term patterns identified across the entire reintroduced population.

### *Process and Interpretation of Outputs*

I combined the output rasters from the BBMM and SSF models by multiplying them together. Both of the combined outputs were represented on a 0-1 index scale, each relating to probability of use of any given landscape cell based on considering the gross movements of animals (in the BBMMS) and resource selection decisions (in the SSF) respectively. Therefore, the combined model outputs will also be represented on a 0-1 index scale, also representing “probability of use” but this time based on the combined effects of both fine-scale selection patterns and long-term diffusion, exploration, and home-range movements.

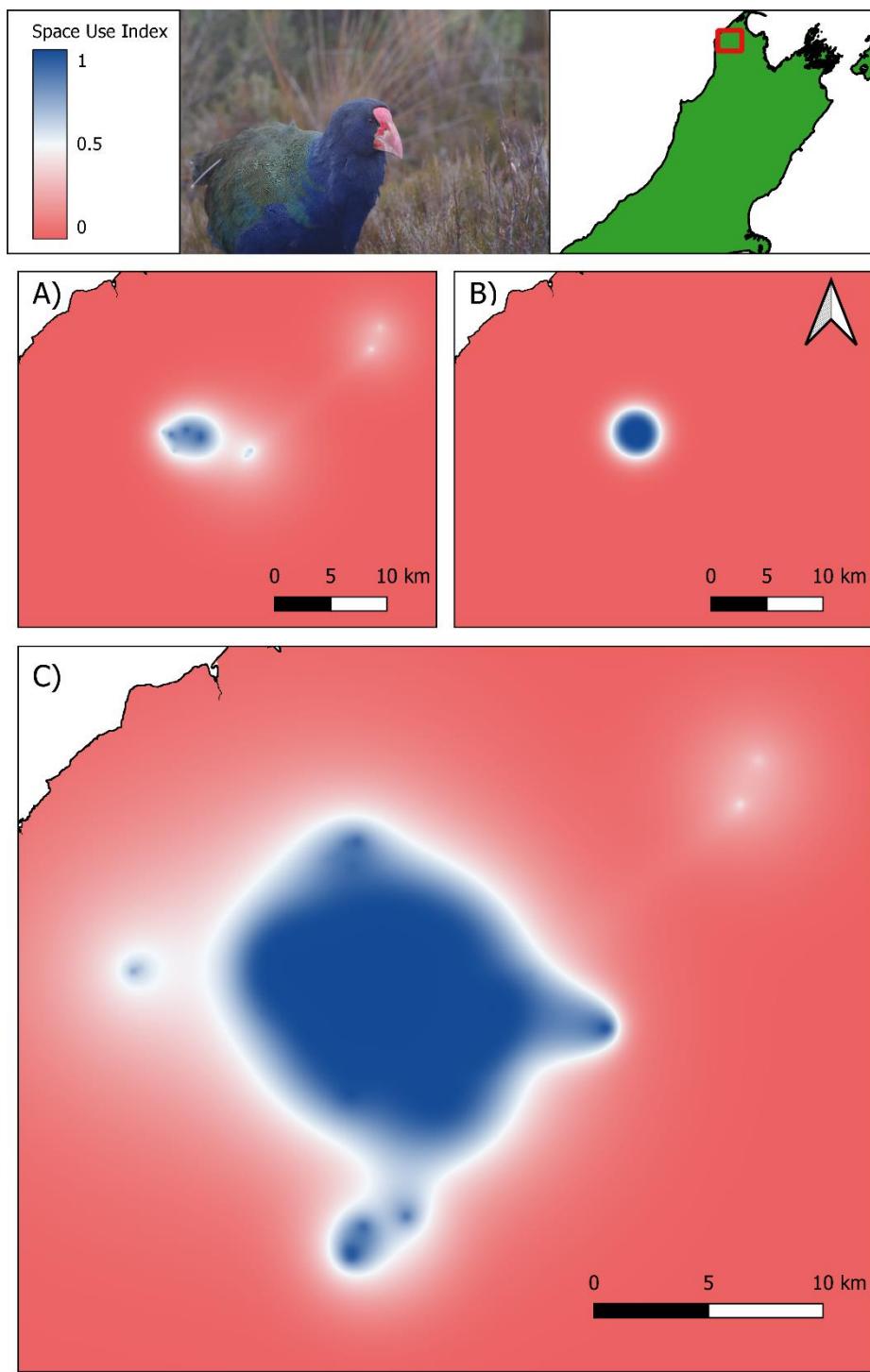
## **6.3 Results**

The on-the-ground and satellite monitoring data used in this chapter were collected from a reintroduced population of 32 takahē in Kahurangi NP. 971 on-the-ground spatial records were collected over a 30-month study period, these are split between all 32 birds in the population (Figure 5.3). Over the same period 5641 accurate satellite fixes were recorded, however these were split between only 17 birds from the reintroduced population and covered a fraction of the study period due to high instances of tag failure (Figure 5.3). For more details on this population and data collection see Chapter 5.

### **6.3.1 Long-term Space Use Models (Brownian Bridge Movement Models)**

Over the study period six birds were internally translocated (Catlin, Hine Pou Pou, Hyde, Kapakapapanui, Nohorua and Rocket) due to dispersal away from the core release site and outside of the 1080 exclusion area (Chapter 5). Movement tracks for these birds were split into pre- and post- translocation tracks. Following these divisions, two tracks were removed from the dataset as they consisted of too few location records to be analysed further (Catlin post-translocation: 3 locations, Rocket pre-translocation: 2 locations). Following these removals, the on-the-ground dataset consisted of 921 location records making up 36 movement tracks made up of between 4 and 45 relocations (mean 25.6; Appendix Table C.2).

The transformed Utilisation Distribution outputs from BBMMs fitted to the on-the-ground records are shown in Figure 6.1 for two individual birds and summed across the whole population. For the transformed index 0.5 is taken to be a putative threshold between core-



**Figure 6.1-** Transformed Utilisation Distribution probability density output from Brownian Bridge Movement Models for 36 movement tracks recorded from 32 takahē in the Goulard Downs, Kahurangi National Park. A and B are examples of Utilisation Distributions for single tracks belonging to A) Catlin (dispersive bird), B) Tupuanuku (settled bird). Panel C shows the whole population Utilisation Distribution (sum of all 36 individual-level outputs) cell values are an index representing the predicted space use of that cell.

use and non-used areas, based on reference to raw data (Figure 5.4). Although, given the high uncertainty in asserting use and non-use given the temporal resolution of input data and incomplete population coverage (Section 5.3.1), this should be interpreted as a “soft” boundary. Raw Utilisation Distributions (for every bird and summed across the population) are shown in Appendix C.3.

### **6.3.2 High-Resolution Environmental Selection Models (Step Selection Functions)**

The location data recorded for each bird is summarised in Appendix Table C.3. Animations of movements recorded by satellite tags are provided in [Digital Appendix 2](#).

Resampling the satellite data to provide a consistent time interval between fixes led to differing levels of data loss/retention depending on the fix interval selected, with maximum path lengths retained when data were resampled to 2-hour intervals, but a greater number of paths being retained overall at 3 and 12-hour intervals (Table 6.1).

**Table 6.1-** Number of movement paths for takahē reintroduced to Gouland Downs with consistent time intervals between successful fixes across the satellite tag dataset. Paths refer to continuous movement tracks with a consistent time interval between relocations. Path lengths indicate number of locations making up movement paths.

Fix interval	Number of paths	Minimum path length	Maximum path length	Mean path length
30 minutes	3	4	35	17.3
1 hour	62	3	49	9.24
2 hour	51	3	103	15.7
3 hour	181	3	58	7.07
6 hour	21	3	63	8.86
12 hour	502	3	59	6.17

The fitted SSF identified strong selection for open vegetation and proximity to forests and a lower, but still highly significant, selection for proximity to paths (Table 6.2). No significant preference for proximity to rivers was identified, despite this being expected to be another significant determinant of takahē movements based on observations of birds following water courses in MoveVis animations ([Digital Appendix 2](#)). The lack of an effect of river proximity seems to be due to spatial inaccuracy of the source data (as the river data used did not align well with water courses shown in base maps in QGIS; QGIS Development

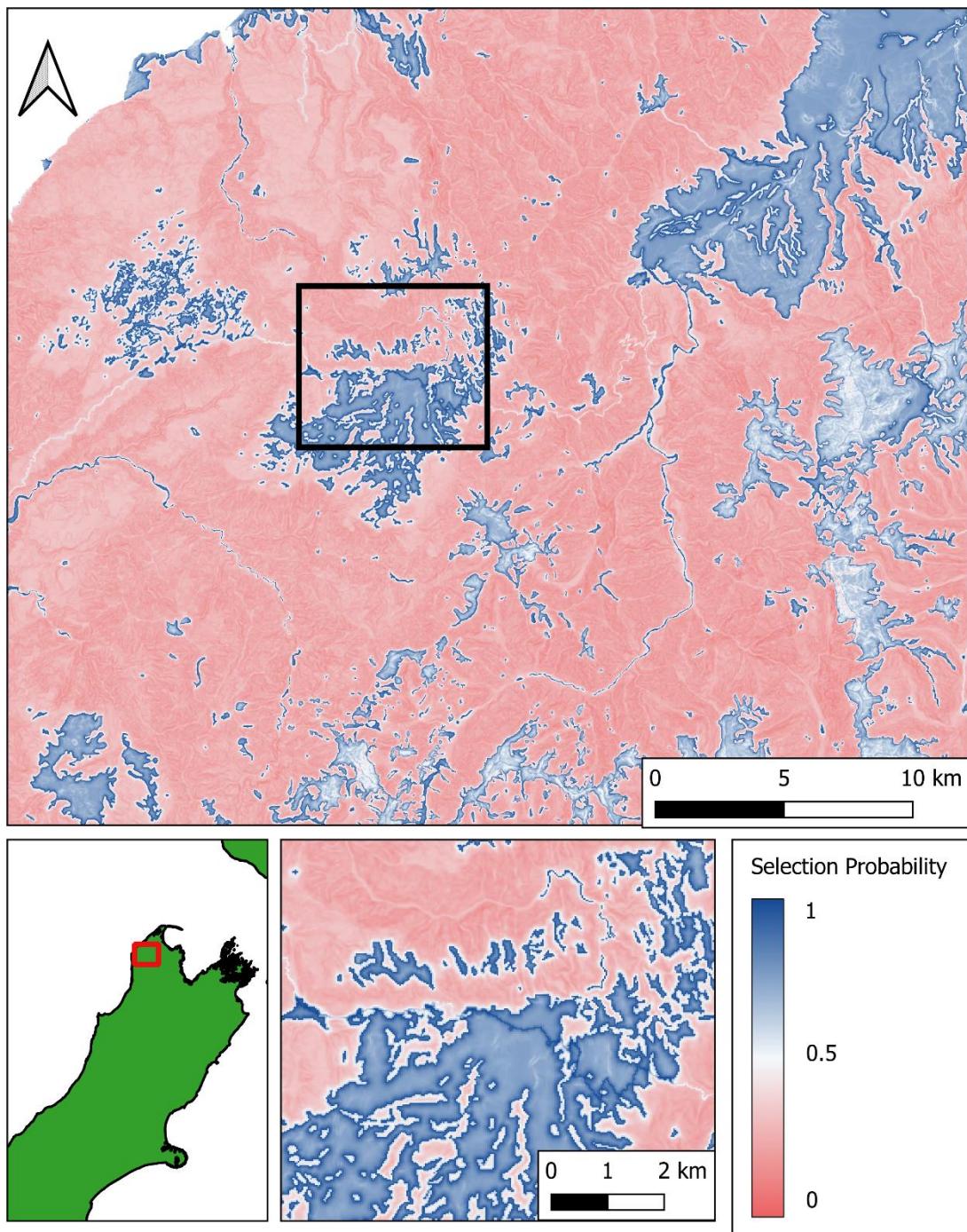
Team, 2017) and lack of metadata that could have aided in identifying more significant water courses to focus on (e.g., width or flow rate, as potentially only relatively large water courses influence takahē movements, while minor streams, that can be crossed with ease, likely have little impact). However, as model fit was marginally decreased when omitting non-significant predictors (distance to rivers and slope removed, delta-AIC=0.311), I chose to retain the full hypothesis-driven model, rather than make refinements based on model performance at this stage.

The cloglog projection of the fitted SSF is shown in Figure 6.4 (See Appendix C.6, Figure C.10 for a projection to the full extent of Kahurangi National Park and Figure C.11 for presentation of linear and exponential projections of the model for comparison). The cloglog scale is interpreted as “probability of use” with values >0.5 indicating positive selection for these areas (with increasing preference towards 1) and values <0.5 indicating negative selection, with increasing avoidance towards 0 (inferred from spatial correlations with tracking data; Figure 5.4). However, robust model validations are required to confirm this scaling and thresholding, which at this stage should only be considered as putative.

**Table 6.2-** Output from Step Selection Functions (SSFs) for takahē reintroduced to Gouland Downs. The SSFs were fitted as Generalised Linear Mixed Models with a Poisson distribution, with fixed effects for vegetation, distance to paths, distance to rivers, distance to forest edges, terrain slope and step length and a random effect for individual bird identity. The results of the SSF show estimated coefficients, with uncertainty and p-values.

	Estimate	Confidence Interval (2.5%)	Confidence Interval (97.5%)	Std. Error	z value	Pr (> z )	
Vegetation	-0.926	-1.32	-0.536	0.199	-4.66	0.000	***
Path Distance	-0.572	-1.05	-0.0896	0.246	-2.32	0.0201	*
River Distance	0.0404	-0.401	0.482	0.225	-0.180	0.858	
Forest Edge Distance	-1.09	-1.62	-0.559	0.271	-4.02	0.000	***
Slope	-0.00512	-0.0231	0.0129	9.17 x10 <sup>-3</sup>	-0.558	0.577	
Step Length	0.000587	-2.34x10 <sup>-4</sup>	1.41x10 <sup>-3</sup>	4.19 x10 <sup>-4</sup>	1.40	0.161	

Significance codes: 0.0001 = \*\*\*, 0.05= \*



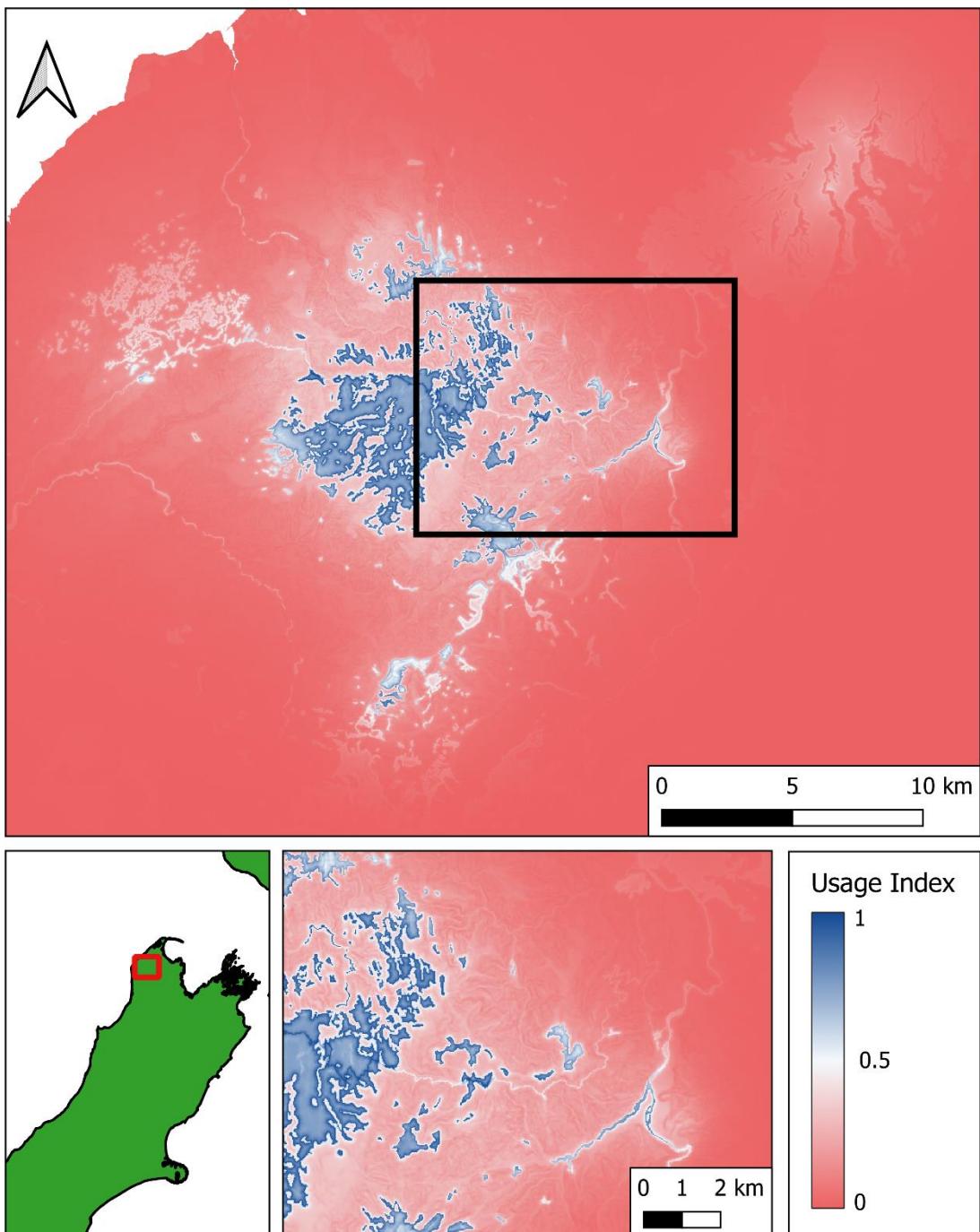
**Figure 6.2** – Complementary-log-log projection of a Step Selection Function fitted to satellite tag data collected from 17 takahē in Kahurangi National Park. Cell values represent the predicted preference of bird to move into that cell given the local conditions. Black box in the top Figure shows the extent of the inset map shown below.

### 6.3.3 Estimated Distribution (Combined Brownian Bridge Movement Models and Step Selection Function Outputs)

The BBMM's provide predictions of movements and space-use across the whole population and study period, albeit at a coarse manner, with much uncertainty due to the low temporal

resolution of the data input to these models. The SSF output, on the other hand, represents high resolution predictions of resource-use patterns in the reintroduced population, although these are presented without any context from population density and spatial structure. Therefore, combined predictions represent a complementary synthesis of these predictions, with the BBMM's providing the spatial population context over the study period while the SSF predicts the environmental response within this population context. The values of the usage index represent a prediction of space-use based on predicted resource-selection identified in the SSF within a limited spatial area defined by the BBMM's representing a detailed estimation of core areas utilised by the reintroduced population over the study period (Figure 6.3).

The combined models identify high use of the Gouland Downs release area concentrated around the North-East of the plateau where many of the birds were released (Figure 5.2). The Heaphy Track is identifiable in Figure 6.3 as it defines a line of relatively high use both in the context of open tussock (generally the blue areas) and in closed beech forest (generally red areas). While the Downs are predicted to be the most widely used area, several satellite patches are identified as actively used areas (Usage index >0.5). These are generally patches of open tussock above the tree line on the peaks surrounding the Gouland Downs plateau (although an area along the banks of a river is also identified as a used area to the east, while small portions of the Mackay Downs are also identified as used to the west; Figures 1.2 and 6.3).



**Figure 6.3** – High resolution distribution prediction for takahē population reintroduced to the Gouland Downs. Predictions were generated through multiplying spatial outputs of long-term movement models (Brownian Bridge Movement Models) and high-resolution environmental selection models (Step Selection Function). Cell values represent an index of probability of cell use informed by both long-term patterns and environmental preferences exhibited in fine-scale movement. The output scale is 0-1 index with cell-scores indicating the predicted use-intensity of the cell by takahē in the Gouland Downs during the study period. The Black line in the top panel indicates the extent shown in the inset panel below.

## 6.4 Discussion

In this chapter, I have shown how two limited tracking datasets from the Gouland Downs takahē reintroduction can be combined to provide a potentially more ecologically meaningful and detailed picture of takahē space-use than either could provide in isolation. Outputs from combining models of both on-the-ground and satellite tracking datasets reflect the synergy between long-term and short-term patterns identified by the constituent models. The on-the-ground records cover a long enough timeframe to be informative in identifying core-use areas for takahē, which variously reflect the areas that birds have established home-ranges and/or dispersed to and explored over the full study period. However, the long and variable intervals between locations recorded by researchers on the ground means that these data cannot provide adequate resolution to highlight important or well-used areas and resources. The satellite tag records have the inverse problem, as they recorded data at high spatial and temporal resolution, but over a limited duration (and for a subset of the population) due to high instances of tag failure and damage. By modelling each dataset appropriately for their given strengths, the maximum utility was realised for both, meaning that together they have the highest potential to inform takahē conservation management (Taylor *et al.*, 2017).

### *Long-term Space Use Models (Brownian Bridge Movement Models)*

Fitting BBMMs to on-the-ground records generated a prediction of space-use based on animal locations recorded via radio-telemetry tracking, while accounting for the coarse temporal resolution of the input data. Outputs fitted to individual tracks roughly estimate the core areas that birds used following their release into the Gouland Downs (Figure 6.1, appendix C.3). These estimates should capture key areas explored during home-range establishment, exploration, and dispersal for the reintroduced population (Kranstauber *et al.*, 2012). Relative space-use across the population was then estimated by a simple summation of the probability scores fitted to each individual movement track (Figure 6.1 C). Although these outputs are useful in identifying the key core areas used by takahē in the Gouland Downs, the coarse and irregular nature of the on-the-ground monitoring data used as input means that predictions include a high degree of uncertainty (Horne *et al.*, 2007). The raw outputs from BBMMs represent this uncertainty as very diffuse utilisation distributions, as very low usage probabilities are represented over a wide geographical area, especially for tracks that include long-range dispersal movements (Appendix C.3). These highly diffuse utilisation distributions prevent the identification of any detail or

resolution in the depiction of home-ranges, dispersal pathways, and/or resource selection, thus taken in isolation outputs from the BBMMs fitted to on-the-ground tracking data from takahē in Kahurangi NP are limited to coarsely identifying space-use intensity at broad spatial scales.

The high spatial resolution (25m) at which BBMM utilisation distributions were predicted is inappropriate given the coarse resolution of input data and uncertainty in outputs, and such fine-scale sampling of the utilisation distribution has resulted in extremely low probabilities of use in model outputs (appendix C.3). This high resolution was chosen as the outputs from BBMMs were ultimately combined with high-resolution patterns identified using the satellite tag dataset. I addressed the very low and skewed probabilities from BBMMs by transforming the outputs to arrive at a more intuitive index-range, representing relative space use (Section 6.2.1).

The method used to rescale the Utilisation Distribution was pragmatic, based on iterative manipulations considered with reference to input data (on-the ground records; Chapter 5) and supplemented with additional data (satellite records; Chapter 5). Although I am confident in asserting that the rescaling applied is a meaningful estimate for the population considered, the methods used to arrive at these outputs are not transparent nor easily transferable to other contexts and species. A more rigorous and conceptually transparent methodology for identifying ‘soft-boundaries’ around core-use areas would be beneficial, perhaps based on interpolating between contours defined by confidence intervals in the predicted Utilisation Distributions (Kranstauber *et al.*, 2012). At this stage, the rescaling method should only be considered a ‘proof of concept’, while future work will be needed to make the approach conceptually sound, transparent and reproducible.

#### *High-Resolution Environmental Selection Models (Step Selection Functions)*

Fitting SSFs to the satellite tag dataset allowed environmental drivers of fine-scale movement choices to be identified for reintroduced takahē, while animating the movement tracks ([Digital Appendix 2](#)) aided with generating hypotheses and selecting environmental predictors for these models. The spatial representation of this model identifies selected and avoided areas based on the landscape attributes of that location (Appendix C.1). By projecting this model across a landscape, predictions are generated reflecting the relative probability of animals visiting a given location (Muff, Signer and Fieberg, 2020). Habitat can be differentiated from the inter-habitat matrix based on these predictions as areas with

higher probability of use can be inferred to be suitable habitat (Forester, Im and Rathouz, 2009). In this way the projection of the Step Selection Function can be considered to be predicting a conceptually similar quantity to the habitat suitability models presented in Chapter 4 (although based on different input data and modelled with different methodologies). While a threshold of the SSF can be used to estimate a habitat/matrix threshold, the distribution of values of the projected SSF can also be used to identify relative quality of habitat as well as the relative resistance to movement offered by different areas within the habitat matrix (Panzacchi *et al.*, 2016).

The fitted SSF can also be projected onto any landscape for which equivalent environmental predictors can be collated, meaning the model has high value for takahē conservation as it can be used to predict the suitability across regions (although the context of the region must also be considered, as projections to non-analogue contexts, e.g., areas with high predator and/or human densities, will be highly questionable). While the high-resolution preference predictions can be useful to identify space-use in the reintroduced population, these inferences are made over only a portion of the population (17 out of 32 individual birds) and the short timeframes in which satellite tags were collecting data (figure 5.3; Table C.4). Therefore, application of these outputs across the whole population and the whole study-period requires model extrapolation, under the assumption that identified selection patterns are stable across time and across individuals (Elith, Kearney and Phillips, 2010).

Additionally, even if completely accurate, predictions of a species' environmental selection alone can be somewhat limited for purposes of describing attributes of a population, rather than simply interpreting the suitability of environments for a species (Forester, Im and Rathouz, 2009; Smith *et al.*, 2021). As the model projection is time and population-independent, it does not take account of temporal processes, spatial biases or population structure that impact the space-use of animals (Soriano-Redondo *et al.*, 2019). Therefore, to predict the realised space-use (or the population distribution) of takahē following reintroduction, these identified environmental preferences must be considered while taking account of other synergistic drivers of population distribution for the reintroduced population (e.g., release site bias, movement ability, diffusion processes and social/demographic pressures; Reynolds *et al.*, 2012).

*Estimated Distribution (Combined Brownian Bridge Movement Models and Step Selection Function outputs)*

I predicted the distribution of the reintroduced population in the Gouland Downs by combining a model of animal movements with a model of resource selection. This is a hybrid model framework, as I combined predictions from two independent models to make inferences from interactions between multiple processes (Parrott, 2011; Sun et al., 2016; Chapter 3; Hunter-Ayad et al., 2020). Similar frameworks have been applied to predict ecological connectivity (Hunter-Ayad and Hassall, 2020), range expansions (Cowley, Johnson and Pocock, 2015), and extinction risks under climate change (Keith et al., 2008) among other objectives. However, to my knowledge this is the first example of a hybrid model framework being applied to estimate a populations distribution by interpolating and extrapolating from two complementary datasets with different spatial and temporal coverage and resolutions.

The combined outputs map (Figure 6.3) represents a reconstruction of reintroduced takahē distributions in to the Gouland Downs achieved using differently “patchy” monitoring data that were collected from on-the-ground and satellite tag tracking (Chapter 5). In the combined predictions, the long-term core-use areas identified from the on-the-ground monitoring (figure 6.3) are combined with the detailed takahē-eye-view of the habitat structure predicted from modelling satellite data (Figure 6.2). This combination allows two of the key processes driving post-release space use in conservation translocations to be reflected; movement/dispersal ability (specifically resulting in population settlement around and radiation from release sites in the reintroduction context) and environmental preferences. The added detail this combination provides has much utility as likely dispersal pathways and colonised areas are easily identified in Figure 6.3 (especially in the inset box, the predicted likely routes taken out of the protected area will likely be of interest and use to the TRG). Further broad discussion on the methodology developed in this chapter is provided in Appendix C.7.

## 6.5 Conclusions

This chapter sought to arrive at a detailed spatial distribution for the takahē population in the Gouland Downs in the 30-month period following their initial reintroduction. This was challenging due to the high failure rate of the satellite tags applied to the birds meaning that high-quality movement data was only available for a fraction of the post-release study period. By identifying potential synergies in two individually patchy datasets (poor frequency, but long-term on-the-ground records from radio tracking, and high-frequency but

short-term satellite fix data) it was possible to analyse each dataset to focus on a different aspect of animal space-use (animal movement and diffusion patterns with BBMMs and environmental selection with SSFs). Then combining outputs to generate predictions representing patterns resulting from synergies between the two processes (i.e., space use by the reintroduced population), allowed an estimation of the population distribution at the high spatial resolution that was sought. This reconstructed distribution appears to be reasonably accurate, although currently it critically depends critically on inference-based steps in processing the model outputs requiring further validation and revisions (Appendix C.7). Chapter outputs can potentially be used to predict future patterns of resource selection and movement/dispersal in this and future reintroduced takahē populations. The observed patterns in fine-resolution movement patterns are novel and may be interesting to the TRG in helping to generate knowledge of fine-scale takahē movement behaviours. Further to this, the reconstructed distribution prediction will be used as an independent observational model of takahē movements to evaluate the predictive models developed in the chapter 4.

## Chapter 7

### Evaluating Predictions: Assessing the Accuracy of Predictive Models via comparison with Descriptive Model Outputs

Evaluating the predictive accuracy of models is challenging and is often overlooked as, in most cases, it is not possible to collect truly independent data with which to conduct evaluations. The reintroduction of takahē (*Porphyrio hochstetteri*) to Kahurangi National Park allowed a unique opportunity to evaluate models that predicted the space-use of the reintroduced population based on resource selection and dispersal limitations. These predictions, presented in Chapter 4, are here compared with descriptive models, presented in Chapter 6, which represent an independent estimate of space-use in the reintroduced population. The model outputs compared are similarly based on resource selection and dispersal processes but are derived independently based on data collected in differing contexts.

#### 7.1 Introduction

Although predictive models (As described in Section 1.4) are widely applied in ecology, effective evaluation of the predictions generated by such models is often lacking (Brook *et al.*, 2000; Vaughan and Ormerod, 2005; Brudvig and Catano, 2021). One of the major factors limiting effective evaluation of ecological models is a lack of suitable data with which to evaluate predictions. Model validation, or assessment of the ability of models to predict patterns, often relies on using a subset of model input data (designated testing data) that is withheld during model fitting (Dougherty *et al.*, 2017; Norberg *et al.*, 2019). However, such validation methods have questionable relevance when models are extrapolated across time and/or space (as is the case for predictive models in Chapter 4), as it cannot be assumed that patterns in model input data will be maintained in the context of the conditions to which the extrapolated model is applied (Hortal, Lobo and Jimenez-Valverde, 2007).

This is particularly relevant when modelling refugee species, which are often the focus of conservation translocations, as patterns observed in relict populations for such species are unlikely to reflect the full breadth of potential behaviours (Kerley *et al.*, 2012; Chapter 3; Hunter-Ayad *et al.*, 2020; Chapter 2; Hunter-Ayad *et al.*, 2021). Biased perceptions of species ecology are likely pervasive for many refugee species (Kerley, Kowalczyk and

Cromsigt, 2012; Britnell *et al.*, 2021). Thus, predictions based on patterns observed in a refugee species current distribution may be inaccurate (Kerley *et al.*, 2020; Britnell *et al.*, 2021). Therefore, the common method of internal model validation has limited power to detect these misidentified relationships as model testing datasets will likely include the same potentially misleading patterns as those of model training data (as they are subsets of the same original dataset). Therefore, for refugee species (or generally where models extrapolate from observations of populations in atypical situations), there is a danger that common model validation methodologies, rather than effectively demonstrate the accuracy of model predictions, will reinforce any misidentified relationships, and lend false confidence to predictions applied in contexts beyond model training populations.

When models are based on species data that are known or suspected to be biased, it is important that these models are critically evaluated based on data relevant to the context in which the models are applied. While this is widely appreciated by ecologists, such evaluations are often limited due to the scarcity of suitable evaluation datasets that meet these requirements (Jiménez-Valverde, Lobo and Hortal, 2008; Briscoe *et al.*, 2019).

Conservation reintroductions provide an opportunity to evaluate ecological models. Firstly, there is much desire and utility for accurate ecological models to guide management of translocated populations (Seddon, Armstrong and Maloney, 2007). Secondly, the establishment of reintroduced populations extends the contemporary distribution of a species. This can provide information to evaluate models built on data from within the prior, non-extended, distribution (Vaughan and Ormerod, 2005). And finally, there is commonly high investment in post-release monitoring of translocated populations in order to evaluate outcomes and to inform species management, beyond the evaluation of ecological models (Mihoub *et al.*, 2014; Price *et al.*, 2020; Smetzer *et al.*, 2021). This investment in monitoring of translocated populations means that not only can translocations provide an especially suitable source of evaluation data, but these data will often be uncommonly abundant and detailed compared with many ecological datasets (Chapter 3; Hunter-Ayad *et al.*, 2020, Chapter 5).

Following the reintroduction of takahē (*Porphyrio hochstetteri*) to the Gouland Downs, Kahurangi NP (Chapter 1; Takahē Recovery Program, 2016; Chapter 2; Hunter-Ayad *et al.*, 2021), predictive models were employed to predict the habitat suitability of the reintroduction area and the post-release dispersal and distribution of the reintroduced population (Chapter 4). Given the considerable uncertainty in predicting patterns in the

reintroduced takahē population based on data from the relict population, two versions of the models were developed, based on conservative and extrapolative interpretations of the input data (Chapter 4; Chapter 2; Hunter-Ayad *et al.*, 2021). However, common validations of the habitat models also failed to suggest a clearly superior model from the two options, despite the choice between conservative or extrapolative models having a large impact on the overall area of habitat predicted in the reintroduction landscape (Chapter 4). Post-hoc model evaluations using post-release monitoring data from the reintroduced population will then be valuable in identifying which of the conservative and extrapolative options provides the most accurate predictions.

The data collected through post-release monitoring are described in Chapter 5. Chapter 6 then develops descriptive models based on these data. These descriptive models produce estimates of ecological processes that can be considered as estimates relating to similar quantities to those predicted by models in Chapter 4. The long-term movement models described in Chapter 6 capture post-release dispersal in the reintroduced population, so should be able to be usefully compared with post-release dispersal predictions from Chapter 4. While the high-resolution environmental selection models predict detailed resource selection patterns that in theory should relate to habitat suitability, making them comparable to habitat predictions in Chapter 4. The combined outputs of the space-use and resource selection models in Chapter 6 then provide an estimate of the population distribution by considering interactions between long-term movement patterns and fine scale resource selection of the takahē population in Kahurangi NP. These estimates may be usefully compared with post-release distribution predictions based on the interactions between habitat suitability and post-release dispersal.

### *Aims and Objectives*

In this chapter, I will evaluate the predictive models estimating post-release patterns of; dispersal, resource selection and post-release distribution against putatively comparable estimates provided by descriptive models based on post-release monitoring data. I will then use these evaluations to suggest the suitable application and interpretation of predictive models for takahē management as well as suggest avenues for their further refinement and development.

### *Caveats*

For the purposes of the post-hoc validations presented in this chapter, I incorporate two key conceits; 1. That the descriptive models presented in Chapter 6 are assumed to be both true and accurate representations of the quantities they estimate, as they are here used as an observation dataset, taken to be a proxy of true patterns. And 2. That the predictive models presented in Chapter 4 are directly comparable with the descriptive models from Chapter 6.

I acknowledge that these are likely to be false assumptions, the descriptive models still require further development and represent only estimates of ecological quantities. Further, although the outputs of predictive and descriptive models can be considered to estimate related metrics (and so correlation between these outputs is expected), the direct equivalence of these metrics is unlikely due to differences in data type, quality and various assumptions made in each respective modelling process.

However, I also consider these assumptions suitable for the purposes of preliminary validations of the predictive accuracy of models presented in Chapter 4. A more common approach to such validations would be to use the ‘raw’ monitoring data presented in Chapter 5 as presence locations in a presence-background evaluative design (e.g., methods considered in Hirzel *et al.*, 2006). However, the challenge here would be accounting for the pseudo-replication, spatial autocorrelation, and release-site biases inherent in this dataset (Chapter 5, Figures 5.3 and 5.4). As the monitoring data cannot be treated simply as presence data, the challenge with using them as such would be to generate suitable background samples that effectively represent null hypotheses regarding takahē post-release movements while incorporating the biases and spatio-temporal autocorrelations inherent in the monitoring data.

## 7.2 Methods

### 7.2.1 Model outputs

#### *Predictive Models*

Six spatial outputs were produced in Chapter 4 for the Kahurangi takahē population, representing conservative and extrapolative predictions of; post-release dispersal, habitat suitability, and distribution, respectively. These layers were used as the predictions to be evaluated in this chapter (See Chapter 4 for details).

These outputs were prepared for comparison with the outputs from Chapter 6 in a number of stages. First, the post-release dispersal and habitat suitability layers were cropped to the more restricted study extent used in chapter 6. Following this, the habitat suitability predictions were rescaled so that the critical suitability thresholds used previously for these predictions (Maximum Sum of Sensitivity and Specificity, MaxSS, 0.322 for conservative and 0.350 for extrapolative models respectively; Appendix A.5) fell at 0.5 on a rescaled version designed to match the critical thresholds used in dispersal predictions and in all descriptive models (Chapter 6). The rescaled Habitat suitability predictions were generated using the following method.

$$H_R = (H_N \times \frac{0.5}{MT}) + ((H_P - MT) \times \frac{0.5}{1 - MT} + 0.5)$$

Where  $H_R$  is the rescaled habitat suitability prediction,  $H_N$  is the negative portion of habitat suitability predictions (i.e., predictions less than the MaxSS threshold), MT is the MaxSS threshold and  $H_P$  is the positive portion of Habitat suitability predictions (i.e., predictions equal to or greater than the MaxSS threshold).

Following this rescaling of the habitat suitability predictions the space-use predictions were re-calculated at the lower spatial extent and modified habitat suitability scaling by multiplying the rescaled habitat suitability rasters with the dispersal prediction rasters for conservative and extrapolative predictions, respectively.

#### *Descriptive Models*

Three spatial outputs were produced in Chapter 6 for the Kahurangi NP takahē population, representing estimates of long-term broad scale post-release movements, fine-resolution resource selection, and estimated distribution (based on the combination of the previous two predictions) respectively (see Chapter 6 for details). These layers were used as the evaluation dataset in this chapter, providing independent observations against which the predictive outputs described above were compared.

These outputs were prepared for comparison with the outputs from Chapter 4 in a number of stages. First, these outputs from descriptive models were aggregated to the same 200m (4ha) resolution at which the predictive models are projected, with cell values in the rescaled output calculated as the mean of the 64 cells from the original 25m projection of the descriptive model contained within the new 200m landscape cell. The aggregation process resulted in the truncation of the scale at which models were presented (as taking

means across several cells resulted in the ‘averaging out’ of outlying values). To rectify this, descriptive outputs were next rescaled to restore the full breadth of the 0-1 index scale using the following method.

$$Descript_{rescaled} = \frac{Descript_{aggregated} - Descript_{min}}{Descript_{max} - Descript_{min}}$$

Where  $Descript_{rescaled}$  is the rescaled descriptive output,  $Descript_{Aggregated}$  is the aggregated, 200m resolution version of descriptive model outputs and  $Descript_{max}$  and  $Descript_{min}$  are the maximum and minimum values of the aggregated rasters respectively.

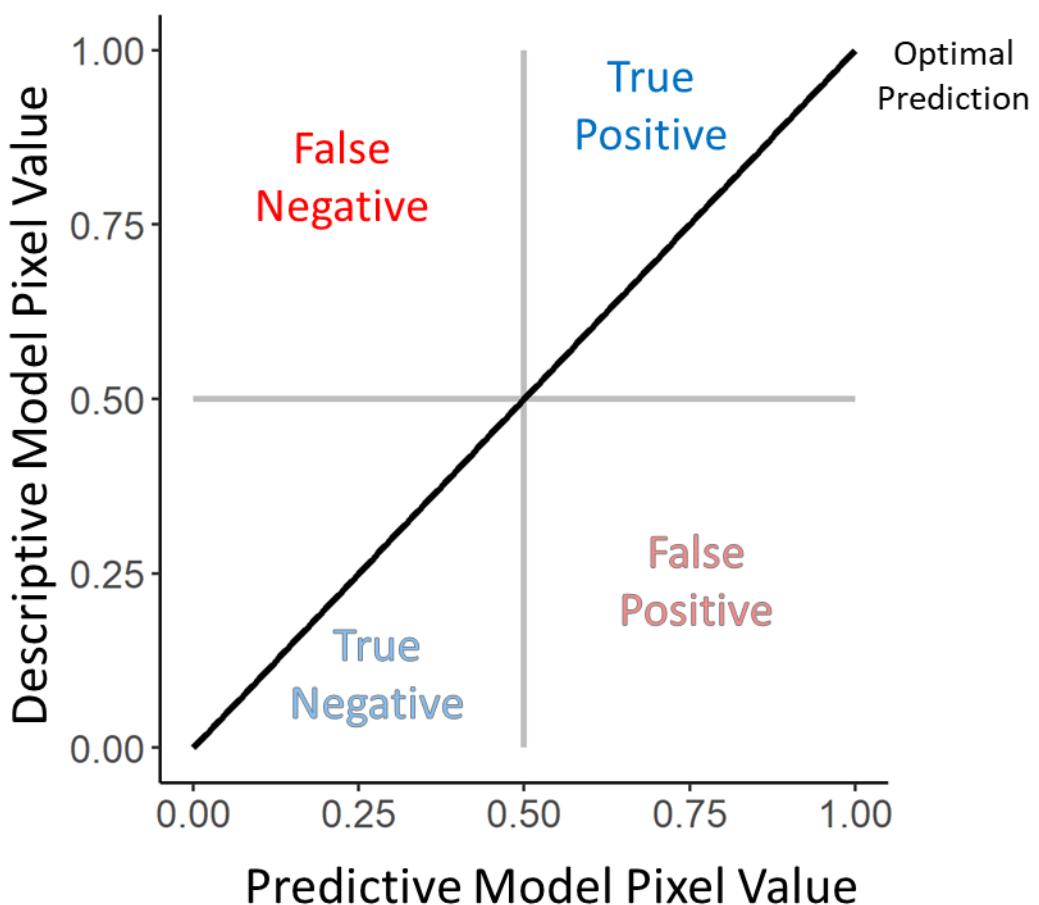
### 7.2.2 Prediction Error Rates

Following the above steps, the prepared raster data were sampled so that correlations between predictive and descriptive model outputs could be identified, and the predictive models evaluated based on these correlations. The correlations examined were: 1. post-release dispersal predictions (from conservative and extrapolative dispersal kernels) vs. estimated long-term post release movements (from Brownian Bridge Movement Models). 2. habitat suitability predictions (from conservative and extrapolative MaxEnt habitat suitability models) vs. resource selection estimates (from Step Selection Functions). 3. predicted distribution (from combinations of conservative and extrapolative post-release dispersal and habitat suitability predictions) vs. estimated distribution (from combinations of long-term post release movements and resource selection estimates).

In order to identify error rates, a confusion matrix (Liu *et al.*, 2005; Fang *et al.*, 2006) was used to separate predictions into correct (true positive and true negative) and incorrect (false positive and false negative) predictions based on the agreement of predictive and descriptive outputs (Figure 7.1). These divisions were based on dividing predictive and descriptive indices into +/- portions around a threshold of 0.5 on each index.

In these models the threshold is taken to represent slightly different quantities depending on the value estimated by the metric. For movement from release-sites the threshold should be taken to represent an estimated boundary of population expansion (over 30 months post-release). In the case of resource selection predictions, the threshold can be taken as a boundary between positive and negative selection (i.e., attraction and avoidance) for environmental features. While for estimates of space-use the threshold can be interpreted as an estimated presence/absence likelihood threshold.

The 0.5 threshold was taken to be appropriate given the treatment of models in previous chapters. The dispersal Kernels were designed to have a value of 0.5 at the predicted median dispersal distance (Section 4.2.6; Hunter-Ayad and Hassall, 2020). While the scaling and projection of all descriptive models was designed such that values of 0.5 represented an estimated used/unused threshold (or selected/avoided in the case of resource selection; see Chapter 6 for details). The exception to this is the habitat suitability models, which employed a different threshold value based on model validation analyses (see Appendix A.5 for details). However, as described above these outputs were rescaled such that the previously employed thresholds were represented as values of 0.5 for these analyses (enabling easier comparison with other outputs, as in this way thresholding was standardised across model outputs).



**Figure 7.1-** Confusion matrix used to assess predictive accuracy of predictive models through comparison with estimated values for equivalent processes in descriptive models. Predictions are separated into positive and negative predictions using a threshold of 0.5.

All models, both predictive and descriptive are biased towards the lower half of their output range, i.e., under the 0.5 threshold they predict more negative results than positive (Figure 7.2). So, in order to perform a balanced evaluation, that weighted the ability of predictive models to correctly estimate positive and negative values evenly, I took a stratified random sample of the data prior to calculating error rates. This resampling was based on the scale of the descriptive models, such that each quartile of the descriptive models output index (e.g., values between 0-0.25, 0.25-0.5, 0.5-0.75, 0.75-1) were evenly represented by a sample of 400 landscape pixels (for a total sample of n=1600) for the calculation of error rates. False positive, false negative and overall error rates were then calculated for these stratified random samples based on the proportions of the data attributed to each false prediction category based on the confusion matrix (Figure 7.1) and the sum of the individual error types respectively.

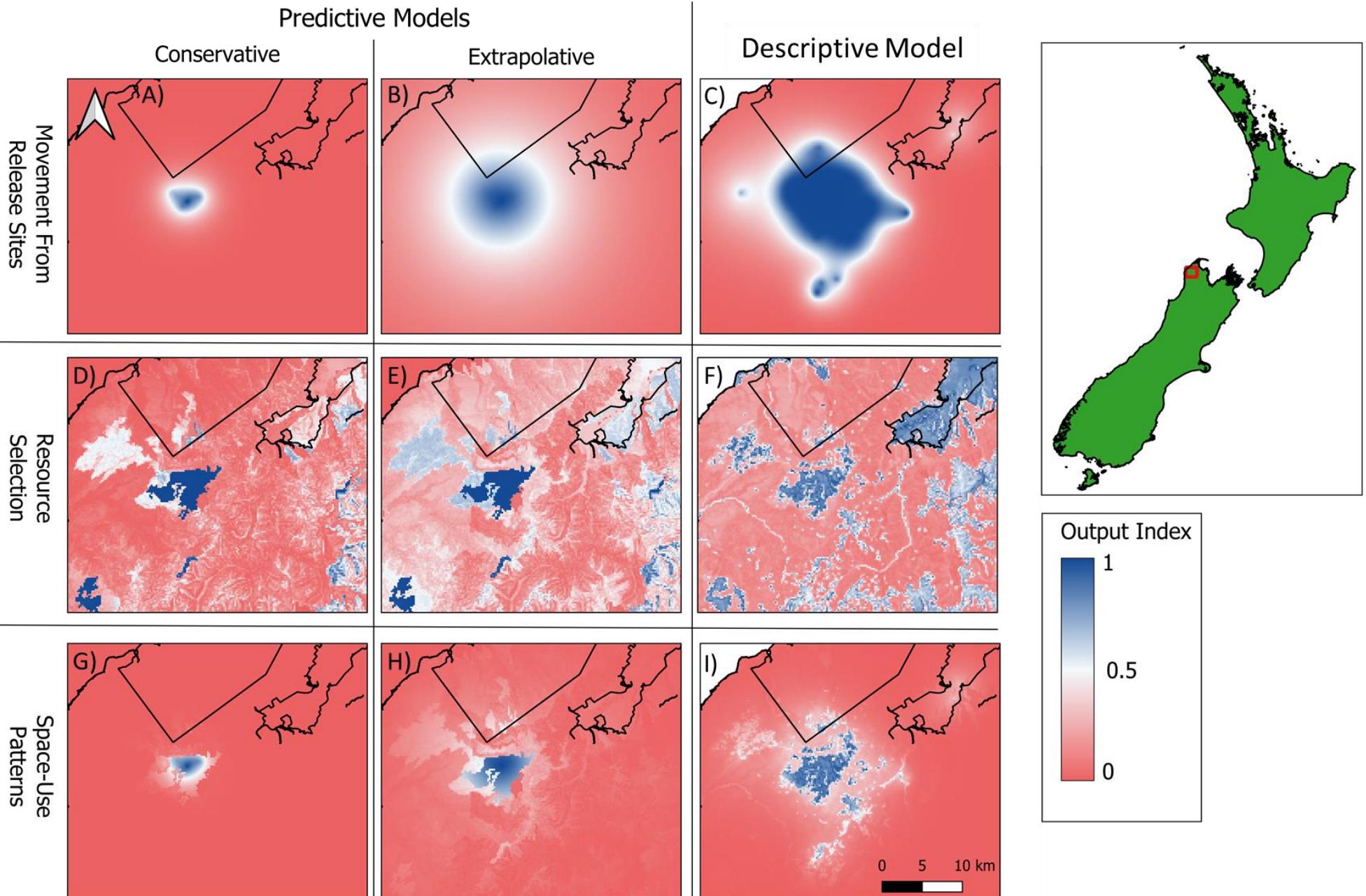
### **7.2.3 Prediction Error Maps**

To illustrate spatial patterns in prediction errors, the prediction accuracy categories (as determined by the confusion matrix; Figure 7.1) were plotted spatially for all predictive models. These maps should aid the interpretation of model accuracy and highlight potential specific issues with model predictions indicated by spatial patterns in prediction errors.

## **7.3 Results**

### **7.3.1 Model Outputs**

The outputs from predictive and descriptive models, following the rescaling described in section 7.2.1, are shown in Figure 7.2. Similar patterns are evident across the resource selection models, as the Gouland Downs is consistently identified as a high-quality area for takahē (Figure 7.2 D-F). The Gouland plateau is also expected to be a focal point for the population distribution due to both of limited post-release movements and positive selection by takahē (Figure 7.2 G-I). Compared with conservative predictions, outputs from extrapolative models have higher values for both post-release dispersal (Figure 7.2 B), and resource selection (Figure 7.2 E), resulting in a wider predicted distribution (Figure 7.2 H). Initial comparison with the outputs from descriptive models indicates that extrapolative models better predict patterns estimated in descriptive models. However, they still appear to underestimate both movement from release sites (particularly asymmetrical dispersal) and resource selection for areas outside of the Gouland Downs plateau (Figure 7.2).

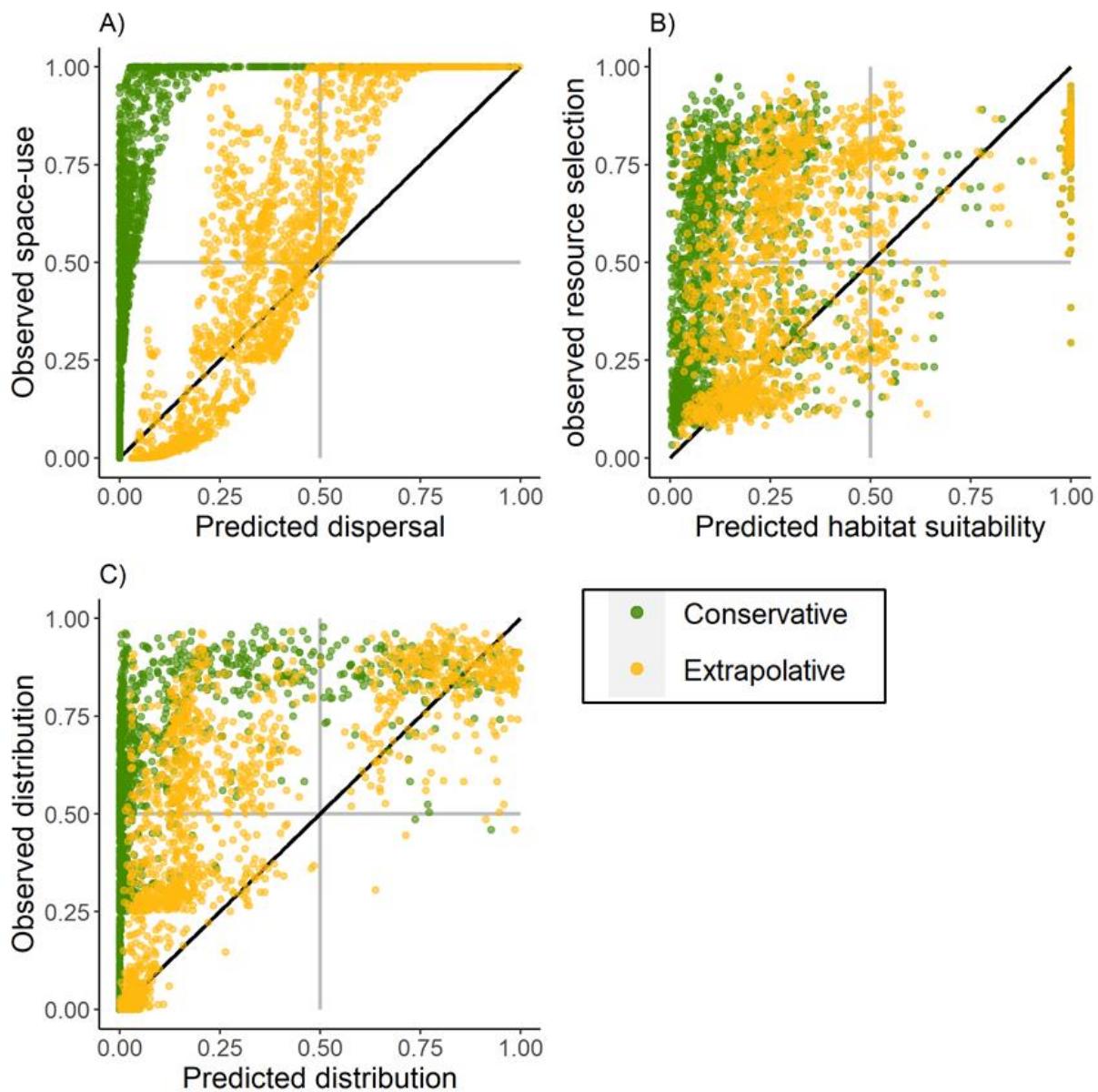


**Figure 7.2 (Previous page)-** Outputs from conservative and extrapolative predictive models (described in Chapter 4) and descriptive model outputs (described in Chapter 6) used to evaluate these predictions. The three plots on the left (A, D, and G) show outputs from conservative models, while outputs from extrapolative models are in the centre (B, E and H). The right-hand plots show outputs from descriptive models (C, F and I). The top row (A-C) shows outputs reflecting estimates of movements from release sites, while the second row (D-F) shows estimated resource selection patterns, and the bottom row (G-I) shows estimated space-use. All outputs have been scaled to a consistent 200m landscape cell size and to have a 0-1 index scale with values of 0.5 indicating the divide between positive and negative predictions.

### 7.3.2 Prediction Error Rates

Correlations between scores attributed to landscape cells in predictive and descriptive models are shown in Figure 7.3. The clearest relationship is evident between predicted and observed movements from release sites (Figure 7.3 A) where the lower prediction boundaries clearly describe a sigmoid curve for extrapolative predictions and a logarithmic curve for the conservative predictions. While there is much scatter around trends in the other two outputs (resource selection- Figure 7.3B and Distribution- Figure 7.3C) a positive correlation is evident. All predictive models generally underestimated scores of descriptive models (as the majority of points fall above the 1:1 line), though extrapolative models in general show better agreement with descriptive models, but also overestimated observed scores more commonly (i.e., more extrapolative model points fall below the 1:1 line).

Error rates calculated from the application of a confusion matrix are shown in Table 7.1. For all three output classes extrapolative models had higher predictive accuracy than conservative models. This improvement in predictive accuracy was associated with decreases in the proportion of false-negative predictions, though this was also accompanied in all cases by a small increase in the proportion of false positive predictions. Estimated prediction error in conservative models was consistently high (41.6-47.5%; Table 7.1). For extrapolative models, predictions of movements from release sites and space use were considerably more accurate than those for resource selection (error rates of 24.6% and 27.8% compared with 40.6%; Table 7.2). Overall, predictive accuracy was relatively low for all models, with the best predictions (extrapolative model predictions of movement from release sites) making accurate predictions for only 75.4% of landscape cells. Most prediction errors were false negatives, with very few false positive predictions made by any model. Predictive models therefore are inaccurate due to an overall underestimate of patterns, while they accurately predict negative values in descriptive models.



**Figure 7.3-** Correlations between outputs of predictive and descriptive models for a stratified random sample of 1600 landscape cells. A) predictions of animal movements from release sites, B) resource selection predictions and C) space-use predictions based on the interaction of diffusive animal movement and resource selection patterns. Conservative models are shown in green while extrapolative models are shown in yellow, grey lines indicate the quarters of the confusion matrix used to divide outputs into positive and negative predictions and the black line indicates the 1:1 relationship between predictive and observational outputs, reflecting the relationship that would be observed if predictive models perfectly matched outputs from descriptive models.

**Table 7.1-** Error rates calculated for conservative and extrapolative predictive models predicting movement from release sites, resource selection and space use. True and false predictions were established by comparison with patterns in the outputs of descriptive models following binarization of predictive and descriptive model outputs using a threshold of 0.5.

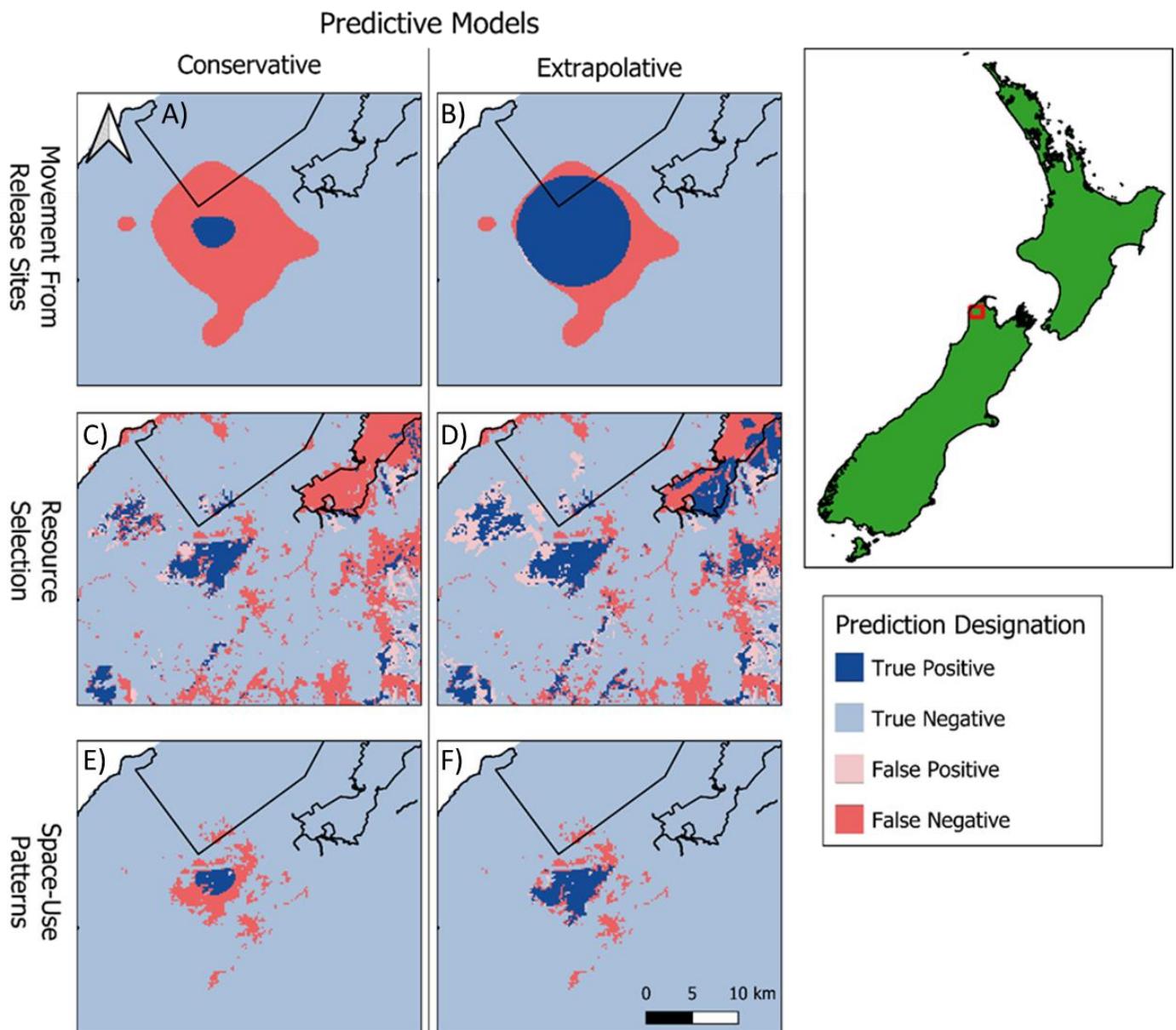
Pattern Estimated	Predictive Model	Error type	Error Rate, %
movements from release sites	Conservative	False negative	47.5
		False positive	0
		Overall error	47.5
	Extrapolative	False negative	24.5
		False positive	0.125
		Overall error	24.6
Resource Selection	Conservative	False negative	42.3
		False positive	1.63
		Overall error	43.9
	Extrapolative	False negative	36.6
		False positive	4.06
		Overall error	40.6
Population Distribution	Conservative	False negative	41.4
		False positive	0.125
		Overall error	41.6
	Extrapolative	False negative	27.6
		False positive	0.250
		Overall error	27.8

### 7.3.3 Prediction Error Maps

The spatial distribution of estimated true and false predictions is shown in Figure 7.4 for both conservative and extrapolative predictive models. For all predictions, the largest class by area is true negatives, while the size of other groups varies between conservative and extrapolative models. For all conservative models (Figure 7.4 A, C and E) the second largest class is false negatives, which demonstrates the widespread underestimation of all quantities in these models. In extrapolative models, on the other hand, there is a relatively even balance between true positives and false negatives in the maps (Figure 7.4 B, D and F), representing the better predictive performance of these models (while still overall underestimating patterns identified in descriptive models). The smallest class in all maps are false positives (Figure 7.4).

Compared with conservative models the higher area of true positive predictions in extrapolative models demonstrates a higher predictive accuracy, although overall they appear to underestimate both post release dispersal and resource selection beyond the

Gouland Downs. This also results in an underestimation of population distribution, with several patches of false negative predictions identified beyond the Gouland Downs plateau.



**Figure 7.4-** Estimated prediction accuracy classes associated with conservative (A, C and E) and extrapolative (B, D and F) models for takahē reintroduced to Kahurangi National Park (see Chapter 4 for details). The top row (A-B) shows accuracy of models predicting post release movement from release sites, while the second row (C-D) shows the accuracy of resource selection predictions and the bottom row (E-F) shows the accuracy of population distribution predictions. Prediction error is determined based on comparison with descriptive models fitted to post-release monitoring data (see Chapter 6 for details).

## 7.4 Discussion

By using the descriptive models in Chapter 6 as a proxy for true values, post-hoc evaluations of the predictive models developed in Chapter 4 demonstrate that extrapolative models have higher predictive accuracy than the conservative model options. This is beneficial information for further development and application of these models, as the prior internal model validations could not effectively separate the habitat suitability model options based on their relative accuracy (Table 4.1). As the extrapolative model predictions were consistently shown to have higher accuracy than conservative options, these models will be the focus of further discussion here.

The need to validate model predictions with independent data has long been recognised (Sutherst and Bourne, 2009; Hao *et al.*, 2019). However, examples of attempts to validate models with independent data are rare in the literature, though there are key examples (e.g., Greaves *et al.*, 2006; Fordham *et al.*, 2018; Hunter-Ayad and Hassall, 2020). A key example of independent validations in a conservation translocation context is provided by Draper *et al.* (2019), who evaluated the habitat suitability predictions for putative translocation sites for *Narcissus cavanillesii* (a critically endangered flowering shrub) using *in situ* germination trials. However, despite the few examples in the literature, a standardised methodology for conducting *post-hoc* validations is not forthcoming, with statistical analyses largely determined by the type of data used to validate models (e.g., field survey data in Greaves *et al.*, 2006, and Hunter-Ayad and Hassall, 2020, compared with germination trial data in Draper *et al.*, 2019). For this study the evaluation data available were animal tracking data, thus the methodologies employed in the above examples were not directly translatable, though the overall concepts and strategies employed are comparable.

There were considerable conceptual and methodological challenges inherent in the use of post-release monitoring data for this validation. Ultimately predictions were evaluated through comparison with independently derived model estimates, rather than through more common evaluation metrics (e.g., those described in Hirzel *et al.*, 2006) as the tracking data available were unsuitable for straightforward use in calculating these metrics (due to autocorrelation, pseudoreplication and release-site biases inherent in these data; Chapter 5).

For these comparisons, a direct equation of predictive and descriptive output metrics is questionable. However, it seems reasonable to expect these metrics to be correlated, given that they estimate somewhat similar quantities (movement from release-sites, resource selection and distribution respectively; Phillips et al., 2006; Forester et al., 2009; Reynolds et al., 2012; Nielson et al., 2013; Briscoe et al., 2019). While the descriptive models are still somewhat preliminary and require further development (Chapter 6), being based directly on post-release monitoring data (as opposed to data from years and geographic regions away from the landscape to which predictions are applied, as is the case for predictive models; Chapter 4) means that they can reasonably be assumed to be a relatively accurate proxy of true ecological patterns when compared with predictive models. Therefore, for the sake of these analyses, the closer predictive and descriptive model values (in a given landscape cell) are, the higher the estimated (and presumed) accuracy of the predictive model.

#### **7.4.1 Movement from Release Sites**

Of all of the model predictions examined, the extrapolative dispersal kernel predictions had the highest estimated predictive accuracy, successfully identifying patterns in the descriptive model 75.4% of the time. However, the extrapolative kernels did underestimate the area identified as ‘likely explored’ in the descriptive models (Table 7.1).

To improve the predictive accuracy of these models further, a first step would be to use a larger estimate of dispersal range, rather than the 5km estimate used for these kernels (Chapter 4), which appears to be an underestimate. Alternatively, a lower critical threshold could be used to separate positive and negative predictions in the confusion matrix. This is applying the same strategies as threshold selection methods targeting sensitivity and specificity (e.g., Maximum Sum of Sensitivity and Specificity and Equal Sensitivity and Specificity methods; Liu et al., 2005; Naimi and Araújo, 2016), albeit in a course manner. Adjusting the threshold in this way would be functionally equivalent to using a larger dispersal estimate for the purposes of these evaluations. Using a threshold of 0.35 instead of 0.5 for the predictive index (while still using 0.5 as the threshold for descriptive model outputs), would increase the predictive accuracy of these models from 75.4% to 78.8%. However, these changes would be associated with more false positive predictions being included in the estimated movements (increasing from 0.125% to 12.5% of predictions). This is due to the assumption of symmetric, radial dispersal from release sites that is inherent in the kernel predictions. This assumption means that asymmetric structure in population expansion will not be predicted using the kernel method applied in chapter 4,

leading to limited predictive performance from these models, as realised patterns of dispersal are unlikely to be symmetrical (as was the case in Kahurangi NP; Figure 7.2, Figure 7.4).

To predict asymmetric dispersal, more detailed and mechanistic models could be developed to replace the dispersal kernels applied here (e.g., Aben et al., 2016; Briscoe et al., 2019; Day et al., 2020). Methods that predict animal movements based on interactions between movement properties, landscape structure, and population structure will likely have the highest potential to accurately predict post-release movement patterns. Such methods could include individual-based simulations such as the Stochastic Movement Simulator (Palmer, Coulon and Travis, 2011), potentially embedded in a population model to account for the impacts of population dynamics on dispersal (Bocedi, Palmer, et al., 2014). Alternatively a circuit theory dispersal model could provide a method capable of capturing these processes in a probabilistic manner (Hanks and Hooten, 2013).

#### **7.4.2 Resource Selection**

Resource selection predictions had much lower estimated predictive accuracy than dispersal models, with positive predictions correlating with a positive result in descriptive models only 59.4% of the time. Like dispersal predictions, most of the inaccurate resource selection predictions were false negatives (Table 7.1).

As for dispersal predictions, considering a lower critical threshold for separating negative and positive selection would increase the predictive accuracy of MaxEnt models. Although the maximum sum of sensitivity and specificity threshold considered for habitat suitability models is a widely used threshold and is based on quantitative model validation procedures, other methods for deriving thresholds from model validations are available (Canran Liu, Newell and White, 2016). One alternative threshold is a ten percent training omission rate (Galante et al., 2018), calculated as 0.193 (standard deviation 0.0104) for the extrapolative habitat suitability models and equivalent to 0.278 on the modified MaxEnt output scale used in these evaluations. Therefore, a threshold for positive and negative habitat selection predictions of 0.278 can be considered as methodologically sound as the 0.5 threshold currently used. When considering this lower threshold, the estimated predictive accuracy of habitat suitability models increased from 59.4% to 69.4%. However, this increase in predictive accuracy was also accompanied by an increase in the false positive rate, which rose from 4.06% to 12.6%. Therefore, it appears that for these models a ten percent training omission threshold is more suitable than the maximum sum of

sensitivity and specificity threshold. However, even when adjusting the threshold used, habitat predictions are still relatively inaccurate, with an estimated error rate of 30.5%, with remaining errors likely due to data limitations/inaccuracy in the inputs of habitat suitability models.

The spatial prediction errors shown in Figure 7.4 provide some insight into the likely sources of error in resource selection predictions. The distribution of false predictions largely appears to align with differences between the vegetation predictor variables which were a major component in both predictive (Chapter 4) and descriptive models (Chapter 6). Different vegetation layers were derived for each model to best suit the spatial resolution of species data inputs (McGarigal *et al.*, 2016; Scales *et al.*, 2017). However, this meant that the vegetation predictors used in habitat suitability models (derived from the NZLRI Vegetation layer) had a lower spatial resolution and precision than the layer used in step selection functions, derived from the NZ Native Polygons (Topo, 1:50k) layer. The differences between these two vegetation layers appear to translate into most of the prediction error identified in these evaluations, as false positives (particularly to the west and north-west of the Gouland Downs) relate to over representation of suitable vegetation classes in the habitat suitability model input layer. False negative predictions, on the other hand, appear to be attributable to open areas, or gaps in forest cover, that were not identified, or were underrepresented in the vegetation input for habitat suitability models. The predictive accuracy of habitat suitability models could be improved most easily by replacing the vegetation layer currently used with a more spatially accurate layer, e.g., potentially one derived from the recently released LCDB v5.0 - Land Cover Database layer. Of note, however, is the area outside the boundary of Kahurangi NP, in the North-East of the study area. As this is a largely human-dominated, agricultural landscape, this region is non-analogous to the contexts of model inputs for both the predictive and descriptive models of resource-selection. Therefore, as both the predictive and descriptive models are likely unreliable in identifying suitability in this context, the evaluation of predictive accuracy is likely unreliable in this area (Elith, Kearney and Phillips, 2010; Guevara *et al.*, 2018).

Refinements in sensitivity and spatial accuracy of habitat models seem likely to maximise the predictive accuracy of habitat suitability models as they are presented here. However, as long as the species inputs are solely derived from the relict population in the Murchison Mountains these will still be restricted to predictions of resource-use based on landscape structure. Further development of habitat and resource selection models to incorporate a

broader spectrum of data sources (e.g., from subfossil records; Lentini *et al.*, 2017; Jarvie *et al.*, 2021 and/or from populations in secure sites; Chauvenet *et al.*, 2013) would enable models to account for climatic as well as landscape structural traits. This would likely improve the transferability of models, as they would be able to make meaningful predictions under a broader array of climatic conditions (currently these are limited to situations where climate and environments are broadly analogous to those in the Murchison Mountains).

#### **7.4.3 Population Distribution**

Space-use predictions were reasonably accurate, with an estimated 72.2% predictive accuracy. As for the dispersal and habitat suitability model's errors were highly biased towards false negatives. Which is unsurprising as predictions of space-use are based on the combination of post-release dispersal and habitat suitability models, it follows that error rates in these predictions are derived from cumulative errors in these component prediction elements (Table 7.1).

It then follows that predictive accuracy can also be improved for space use by considering a lower critical threshold to divide predicted “used” and “unused” categories. Reducing the threshold to 0.25 led to an increase of estimated prediction accuracy to 77.3%, although this was associated with an increase in the false positive rate from 0.25% to 3.37%.

The spatial patterns in prediction accuracy further demonstrate the combination of errors from component models (Chapter 3; Hunter-Ayad *et al.*, 2020), as false negative predictions are patchily distributed around the core-area of true positive predictions (Figure 7.4). False errors appear to be attributable to a combination of under-estimated post-release movements and unidentified habitat patches in component models (with a small number of false positive predictions arising from overestimated habitat extent). While the reduction in critical threshold used would overcome some of these erroneous predictions, further development of the constituent models, as suggested above, may be necessary to overcome the methodological constraints that currently limit the predictive accuracy of these models (Chapter 3; Hunter-Ayad *et al.*, 2020; Briscoe *et al.*, 2019; Zurell *et al.*, 2021).

### **7.5 Conclusions**

Overall, the model evaluations presented in this chapter clearly indicate that the extrapolative models presented in chapter 4 are more accurate than the conservative models and should be taken forward and developed for management. These models could

be usefully applied to the management of takahē in wild populations. They may be particularly useful for future wild site reintroductions, as here they can be applied in a similar context to the Kahurangi NP reintroduction, so can be expected to predict patterns with a reasonable degree of accuracy. Further refinement and development of these models has the potential to increase predictive accuracy further.

However, despite being nominally extrapolative, these models are likely to underestimate dispersal, resource selection and population distributions when applied to management scenarios. Meaning that, if applied without revision (i.e., making the changes suggested in the discussion above), predictions of post-release movements, habitat suitability, and resulting patterns of post-release distribution are likely to underestimate true values. This also means that estimates arising from these predictions, e.g., population radiation, carrying capacity, and potential population growth rates will also likely be underestimates. Therefore, even these nominally “extrapolative” models could be considered to be relatively conservative. The measures suggested in the discussion section to improve predictive accuracy should also have the effect of making the predictions more extrapolative. However, this might not always be desirable for management purposes, as when conservative management agendas are being pursued, the likely underestimations of model predictions would be necessary to maintain a low ratio of false-positive predictions and reduce exposure of threatened species to novel conditions and potential stressors.

## Chapter 8

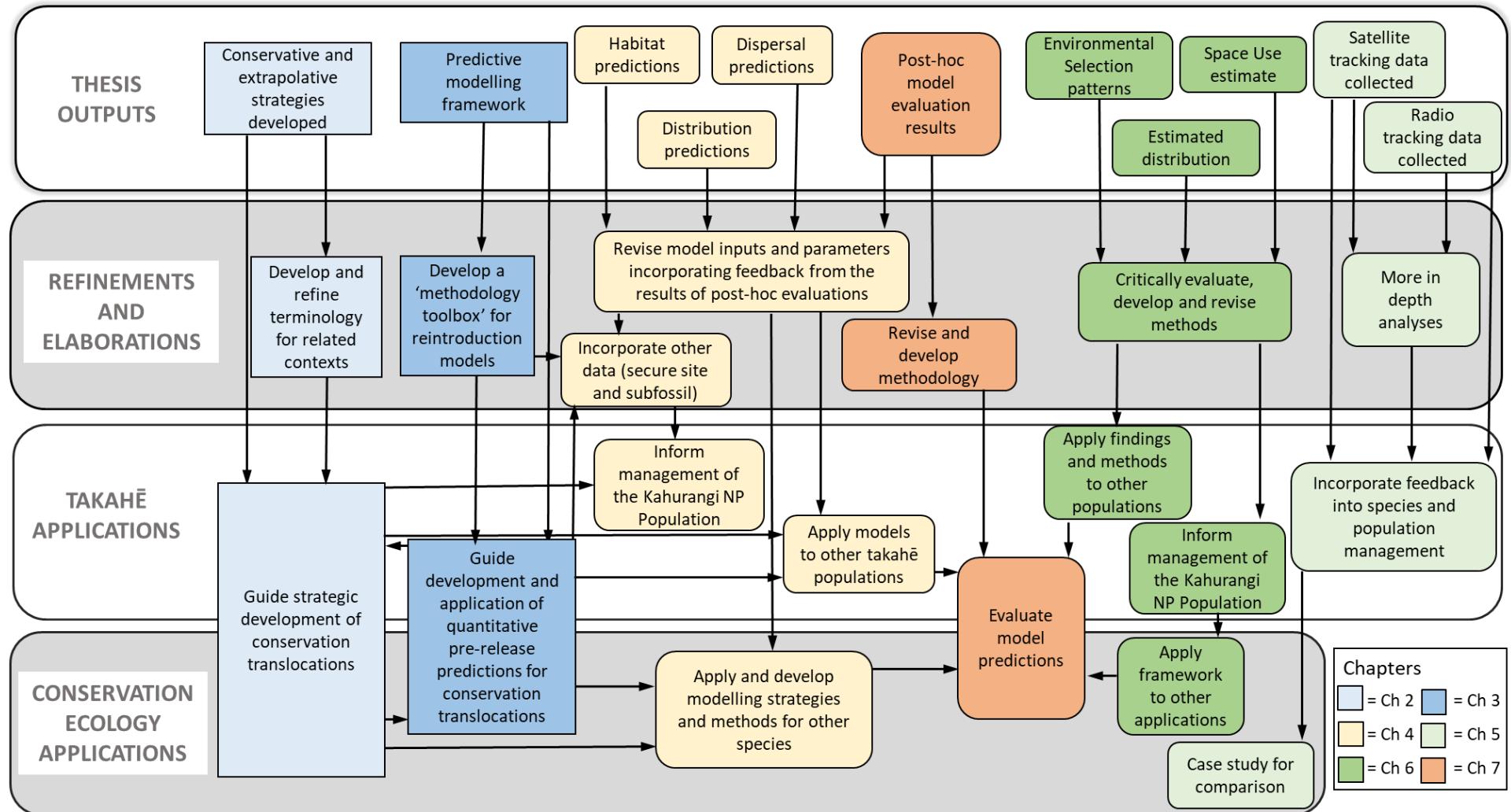
### General Discussion: Reintroduction Management Applications and Future Directions

This thesis has a consistent focus on the development of an ecological evidence base and applied framework to inform the conservation management of takahē translocations. Thesis chapters provide a number of outputs that have potential value when applied to conservation translocation programs for takahē and other species around the world. Here I discuss the current applications and scope for future development of the thesis outputs developed in previous chapters, focusing this discussion around three core areas; the conceptual contributions to conservation translocation management, including strategic and methodological framing; the use of predictive models to inform reintroduction attempts, and the development of resources aiding adaptive management in conservation translocations.

In this general discussion I discuss the themes and outputs of the thesis and provide recommendations for their further development and application both for takahē conservation and conservation ecology more generally. A summary figure illustrating the suggested developments and applications is provided as Figure 8.1. This is designed to complement and follow on from Figure 1.4, which illustrates the work presented within this thesis.

#### 8.1 Reintroduction Concepts

While primarily focusing on applications to applied conservation management, I have presented a variety of outputs covering conceptual, strategic, methodological, analytical, and evaluative aspects of evidence-based translocation management. The literature-based chapters develop both strategic and methodological frameworks that can be used to provide context and guidance for the management of conservation translocations. The data chapters then demonstrate the application of these strategies and methods to the focal case-study system, the reintroduction of takahē (*Porphyrio hochstetteri*) to the Gouland Downs, Kahurangi NP.



**Figure 8.1-** Summary flow chart illustrating recommendations for refinements and development of thesis outputs and applications both for takahē management and conservation ecology more broadly. Coloured boxes indicate chapters providing the output indicated (or the primary chapter being developed). Arrows indicate the movement of an output to be an input in the following process (starting at inputs and ending at the process). Large greyscale boxes are used to categorise outputs and actions.

### *Applications for takahē*

My literature-based Chapters, 2 and 3 (Hunter-Ayad *et al.*, 2020; Hunter-Ayad *et al.*, 2021), provide a strategic and methodological framework within which takahē conservation and research efforts focusing on translocation management can be placed. This should have utility in contextualising the management and research around the Kahurangi NP reintroduction that was the focus of this thesis, as well as providing useful perspectives that can be applied to both historic management actions (e.g., secure site and genetic management discussed in; Jamieson, Wallis and Briskie, 2006; Greuber, Maxwell and Jamieson, 2012; Lees *et al.*, 2014), and research projects (e.g., Hegg *et al.*, 2012; Merow *et al.*, 2014; Stadtmann, 2019). Further to this I hope that these outputs will help to guide and informing future work with takahē, e.g., through an explicit adoption of the conservative-extrapolative framework (developed in chapter 2; Hunter-Ayad *et al.*, 2021) at a strategic planning level. The conceptual framework laid out in Chapter 2 discusses strategies for approaching uncertainties that are inherent in translocating takahē. This perspective should be useful in clarifying and contextualising current ecological understanding of takahē as a species and the uncertainty around inferences drawn from the relict and the other small, highly managed, extant takahē populations. While this context is well understood currently incorporated into takahē management practice (Lees *et al.*, 2014; O'Donnell, Weston and Monks, 2017; Greaves *et al.*, 2020) historically the biased interpretations and research arising from the “species stereotype” paradigm discussed in Britnell *et al.*, (2021) have been evident. For example, the interpretation of takahē as obligate grassland specialists put forward by Mills, Lavers and Lee (1984) was later rejected by Beauchamp and Worthy (1988) as this interpretation was considered to be a consequence of shifting baselines arising from an historical range contraction. The framework proposed in Chapter 2 should help to inform the continued development of takahē conservation management and research with a specific consideration of the context and state of current ecological understanding of the species. Chapter 3, on the other hand, provides an overview of the current state-of-the-art in predictive modelling methods and their integration, as well as highlighting important caveats and considerations when using these methods for conservation translocations. This framework should be applied to past (Hegg, Mackenzie and Jamieson, 2013; Stadtmann, 2019), current, and future efforts to develop predictive models designed for use in informing takahē translocation efforts. For example, I applied this framework to habitat and dispersal modelling in Chapter 4, which is

also used to illustrate the application and importance of the conservative and extrapolative assumptions described in Chapter 2 (Hunter-Ayad *et al.*, 2021) during model fitting.

Looking ahead, the literature chapters (Chapters 2 and 3) presented in this thesis can be used as a roadmap for developments in the translocation management of takahē. Based on the arguments put forward in Chapter 2 (Hunter-Ayad *et al.*, 2021), I advocate for takahē management transitioning to a more extrapolative approach than is currently being pursued. The increased scope for extrapolative management actions is largely based on the recent population growth and reduced extinction risks that have been achieved through captive-breeding and secure site management (Chapter 1 and 2). This increased security for the species provides the flexibility to pursue more experimental species management without necessarily increasing the vulnerability of the species to population declines and extinctions (so long as the current captive populations are maintained). Further to this, ongoing takahē conservation efforts are increasingly inhibited by the limited capacity of current approaches (relying on captive breeding and maintenance of small populations at secure sites) to accommodate the increasing global population of takahē (Department of Conservation, 2019). The emerging threat of climate change is also likely to also impact the efficacy of current management strategies over the coming decades (Pecl *et al.*, 2017; WWF, 2020). Temperature increases and associated climatic fluctuations could render the northernmost secure sites (i.e., those situated in the Hauraki Gulf, Figure 2.3; Lees *et al.*, 2014) inviable if niche thresholds for takahē are surpassed. As northern takahē populations are already known to exhibit signs of climate-induced stress (considered to be primarily caused by prolonged droughts; TRG, unpublished data), these thresholds might be surpassed in the relatively near future. The combination of limited capacity for current management strategies and emerging threats from global climate change then provide an impetus for takahē management to transition to a more extrapolative approach to management, particularly with regard to translocations to large mainland areas (Chapter 2; Hunter-Ayad *et al.*, 2021).

The main factor limiting a transition to more extrapolative management strategies is the substantial risk to takahē posed by exposure to invasive mammalian predators (Chapter 5; Lee and Jamieson, 2001; Hegg *et al.*, 2012; O'Donnell, Weston and Monks, 2017). The majority of otherwise suitable translocation sites for takahē are currently rendered unsuitable due to the presence of mammalian predators, and/or due to the type of predator control strategies employed (particularly the use of aerially deployed poison baits).

Therefore, there is currently limited scope to pursue further mainland reintroductions for takahē. Conservation efforts for takahē can then be considered to be at an impasse, with an increasingly pressing need to develop more extrapolative approaches to conserve the species and restore populations throughout its' pre-human distribution, but with very limited opportunities to do so. Although ambitious predator-eradication programmes such as the national "Predator Free 2050" programme can offer some hope that, should these be successful, the number of viable takahē translocation sites should rise in the not-to-distant future (Parker et al., *Pre-print*).

#### *Applications for other species*

The literature-based chapters in this thesis (Chapters 2 and 3) are intended to provide information that can be usefully applied across a range of species and contexts, although both are primarily focused on conservation translocations, particularly reintroductions (Sarrazin and Barbault, 1996; Seddon et al., 2014). The conservative and extrapolative frameworks developed in Chapter 2 (Hunter-Ayad et al., 2021) are applicable to many species in the same way as they are for takahē. The suggestion explicitly to consider novel conditions for species translocations, and to apply a context-based approach when determining suitable levels of exposure to these novel conditions, can potentially help refine conservation plans for several species (Seddon, Armstrong and Maloney, 2007). Thus far, the media and academic interest in the published paper indicate the broad appeal and utility of the framework developed in this chapter (Appendix D). Similarly, the methodological overview and framework presented in Chapter 3 (Hunter-Ayad et al., 2020) can provide a useful resource for conservation managers and ecological researchers seeking to develop predictive models (Zurell et al., 2021), particularly when these are intended for application to conservation reintroductions (Stadtman and Seddon, 2018). Feedback following the publication of the paper indicate that this review has been a useful resource for postgraduate students and other researchers at the early stages of project development, as it helps to clarify the methodological options and decisions ahead of them. Citations of this paper over the past several months also indicate that the review has provided a useful overview and resource for the academic community interested in developing and applying models for conservation translocations (Appendix D).

While my literature-based chapters are both published, and so constitute relatively complete and refined pieces of work, future work could still build on the premises that these chapters have established. The conservative-extrapolative framework presented in Chapter

2 (Hunter-Ayad *et al.*, 2021) could be usefully developed and extended to differentiate and classify conservative and extrapolative definitions with regard to strategy, methods, models and predictions. This would allow these concepts to be more readily applied and translated into conservation research and management programmes. Similarly, the broad methodological overviews provided in Chapter 3 (Hunter-Ayad *et al.*, 2020) could be further developed to provide a more specific “methodological toolbox”, where the details of potential and available algorithms, methods and platforms are examined for the groups of models identified in this chapter (e.g., similar to the review of Joo *et al.*, 2020, which applied to analytical methods that can be applied to movement data).

## 8.2 Predictive Modelling

A key component of species reintroductions is predictive modelling of habitat suitability at the release site (Mihoub *et al.*, 2014; Massaro *et al.*, 2018), while further modelling of post release dispersal is less common, but also potentially useful (Palmer, Coulon and Travis, 2011; Reynolds *et al.*, 2012; Attum and Cutshall, 2015; Alexander *et al.*, 2016; Mertes *et al.*, 2019; Fandos *et al.*, 2021). As the methods available for such modelling are covered in the conceptual work discussed in the previous section, I focus here on the application of these methods in my data chapters.

### *Applications for takahē*

The home-range scale predictive habitat suitability models developed in Chapter 4 (and evaluated in Chapter 7) should be useful in the ongoing management of takahē in Kahurangi NP. These could have a material contribution to efforts to establish a self-sustaining metapopulation within the National Park boundaries, which is a current long-term management goal (conditional on resolving current limitations due to use of 1080 poison baits in Kahurangi NP; Section 5.4.6). For example, by identifying potentially suitable habitat that had not been found previously and estimating the relative quality of habitat patches, which should be valuable information for the TRG. Further, the models can be readily projected to any putative reintroduction areas proposed currently or in the future, giving them utility beyond applications to the Kahurangi population. The spatially explicit habitat suitability predictions produced by the models could inform decisions regarding choice of reintroduction areas and release sites (Chauvenet *et al.*, 2013; Stadtmann and Seddon, 2018). Further to this, they should indirectly inform decisions regarding suitable sizes of release cohorts and estimates of carrying capacities based on habitat extent and

quality identified in proposed reintroduction areas (though this would depend on comparisons between suitability estimates and observed population densities in extant populations; Massaro et al., 2018; Hunter-Ayad and Hassall, 2020). The evaluations of these models provide key information to inform the relevant interpretation and application of model predictions (Jiménez-Valverde, Lobo and Hortal, 2008), as well as providing useful feedback of how models could be usefully refined and developed in future work (Miller et al., 2019). These outputs, both in isolation and in combination, have much potential use when applied to guide and advise the suitable management of takahē translocations now and into the future (Grimm et al., 2014).

As takahē conservation, particularly with regard to translocation management, faces substantial challenges in the near future there is a clear role for development of predictive models to inform and guide conservation efforts. The framework described in Chapter 3 (Hunter-Ayad et al., 2020) should continue to be a useful tool in guiding the development of these models. Research to date has developed models of habitat suitability (Chapter 4; Stadtmann, 2019) and population dynamics (Hegg, Mackenzie and Jamieson, 2013). In this thesis, research has begun to incorporate dispersal models to refine predictions (Chapter 4), and the use of satellite tag tracking in the Gouland Downs (Chapter 5) should provide a valuable data source for the further development of more realistic and nuanced dispersal models (Graves et al., 2014; Coulon et al., 2015). While all predictive models developed for takahē thus far can usefully be developed and refined in isolation (see discussion in Chapter 7), further integration of data from other sources (e.g., subfossil distributions and secure site records) would also contribute greatly to improving predictions. A step-change towards enhancing the utility of these models could be achieved through effectively integrating them as components of spatially explicit dynamic metapopulation models (Chandler et al., 2015; Fournier et al., 2017; Hunter-Ayad and Hassall, 2020; Chapter 3; Hunter-Ayad et al., 2020). Further modelling developments could then focus on providing species interaction models that predict the dynamic impacts of both invasive predators and predator mitigation strategies on translocated takahē populations (Duffy et al., 2007; Conlisk et al., 2012). Although major challenges are inherent in the development of multi-species models, if these could be developed and integrated with other models of takahē ecology they would provide an extremely useful tool (Driscoll et al., 2014; Albert et al., 2017; Zurell, 2017). Multi-species ecological models can potentially provide the most nuanced and detailed guidance in navigating challenging, complex and controversial

decisions regarding the most suitable management to continue to protect, conserve and restore takahē populations into the future (Chapter 3; Hunter-Ayad et al., 2021).

#### *Applications for other species*

The predictive modelling chapters in this thesis, although focusing exclusively on takahē can be considered as case-studies, as many aspects of their methods and approaches can be effectively translated to other studies to their advantage. For instance, although habitat suitability modelling is a well-established field (Gomes et al., 2018), the thorough and considered approach to developing the habitat predictions used in Chapter 4 can provide guidance for the development of these models in other projects. Throughout the development of these models, key consideration was given to the conditions under which model input data were collected and the setting to which model predictions were applied, namely a reintroduction landscape. Further to this, the development of two alternate models, and the subsequent evaluation of these alternatives in chapter 7, as a response to uncertainty regarding the suitable strategy towards model fitting (based on arguments in Chapter 2; Hunter-Ayad et al., 2021), is an approach that could usefully be applied in other contexts to both communicate and resolve uncertainties regarding model-fitting decisions (Briscoe et al., 2016; Sun et al., 2016; van der Vaart, Johnston and Sibly, 2016).

Development of the predictive modelling work presented in Chapter 4 could take advantage of the broad array of model settings used during model development (for regularisation and feature classes; Chapter 4). While *post-hoc* evaluations (Chapter 7) suggest that this approach produced effective and meaningful predictions, uptake of the procedures followed in this work could be inhibited by a general lack of time and resources to run large numbers of model iterations during model development. Future work could use sensitivity analyses based on this approach and produce advice and guidelines on the suitable model settings to consider, streamlining this process (Morris and Doak, 2002). While independent validations of predictive ecological models remain rare in the literature (Hijmans et al., 2005; Jiménez-Valverde, Lobo and Hortal, 2008; Sutherst and Bourne, 2009), the methodologies employed in the few studies that do attempt independent validations remain diverse, with the approach taken largely depending on the type and format of data in the evaluation (observation) dataset (Jiménez-Valverde, Lobo and Hortal, 2008; Draper, Marques and Iriondo, 2019; Hunter-Ayad and Hassall, 2020). Therefore, the model correlation approach presented in Chapter 7 (to resolve complexities in evaluating models with highly autocorrelated tracking data) should provide fertile ground for the further

development, refinement, and standardisation of *post-hoc* prediction evaluations. As the need for the effective evaluation of model predictions has been recognised by several authors (Vaughan and Ormerod, 2005; Seddon, Armstrong and Maloney, 2007; Phillips and Dudík, 2008; Brudvig and Catano, 2021), this rare example of putting this need into practice should be of interest to a diverse audience and could have a role in developing principles and recommendations for these kinds of model evaluations going forward.

### **8.3 Adaptive Management Resources**

The adoption of effective adaptive management frameworks in conservation science and management is increasing (Dimond and Armstrong, 2007; Weeks *et al.*, 2011; Ziolkowska *et al.*, 2016). Adaptive management is an approach whereby data is collected following either coincidental changes in management practices, or deliberate manipulations of management over time, to gain information to improve ecological understanding and to inform practice (Smith, Werner and Kelcey, 2012). While adaptive management is certainly desirable, in order to be effective, a strong evidence base must be established and management practices be continuously evaluated and revised (Doherty and Ritchie, 2017; Simonis *et al.*, 2018; Zurell *et al.*, 2021). The post-release monitoring and analysis work presented for takahē in my thesis can potentially contribute such an evidence base for ongoing takahē conservation, while also being an example and case-study that can be considered when designing monitoring and management programmes for other species' translocation management.

#### *Applications for takahē*

The initial data collected from the Kahurangi reintroduction presented in Chapter 5 is a valuable resource for ongoing takahē research and evidence-based conservation management (Seddon, Armstrong and Maloney, 2007; Price *et al.*, 2020). The post-release monitoring dataset described has been used to provide a preliminary evaluation of the relative success of the reintroduction in Chapter 5, providing a source of feedback for the TRG (Maxwell *et al.*, 2015; White *et al.*, 2015). The analysis of these data in Chapter 6 provides insight into the post-release movements of takahē (both the population radiation from release sites and fine-grained resource selection) that should be useful for continued management of the population as it reveals patterns and trajectories of population establishment (Mihoub *et al.*, 2014; Massaro *et al.*, 2018). Inferences from the Kahurangi data collection (both the "raw" patterns in Chapter 5 and the fitted models in Chapter 6)

should also be applied to the management of other takahē populations, in order to predict post-release patterns in future reintroduced populations, and to infer patterns in current populations where monitoring provides much lower resolution data than in Kahurangi NP (i.e., the Murchison Mountain takahē population and some of the secure sites; see Sections 1.3 and 2.7). Observations from the Kahurangi NP translocation can also be used to inform expectations and risk-analysis in subsequent translocation efforts (Fernández, Kramer-Schadt and Thulke, 2006). For instance, the greater than expected dispersal observed away from the Gouland Downs put some birds at risk from predation when they moved outside of protected areas (Chapter 5). This should be taken into account in future, potentially leading to a greater requirement for geographic isolation and/or dispersal barriers for putative translocation sites to reduce this risk (Knox and Monks, 2014; Mertes *et al.*, 2019).

Further analyses of the satellite tag dataset would also likely prove valuable for ongoing management efforts. As this was the first time that satellite tag tracking has been used for takahē, the data collected from this population currently constitute a unique resource for the investigation of takahē spatial ecology and movement behaviour, and so should be exploited to their full advantage. The satellite dataset is, however, somewhat limited in coverage due to high rates of tag failure (Chapter 5), so I recommend that further deployments of satellite tags be considered (with improved tag specifications to ensure tags are more robust to damage, particularly aerial loss) to expand this dataset, increasing the potential analyses that these data could be used for (Jacoby and Freeman, 2016; Joo *et al.*, 2020). It would be especially beneficial for satellite tracking (and data collection in general) to be conducted in parallel across multiple takahē populations so that data collected in differing contexts can be directly compared, providing greater analytical power and increasing the confidence with which specific conditions can be inferred to be driving observed patterns.

#### *Applications for other species*

The preliminary evaluation of the takahē reintroduction to Kahurangi NP presented in Chapter 5 can provide a useful comparison for many conservation translocation projects, as such evaluations have been somewhat rare in the literature, particularly in the initial periods following translocations (Seddon, Armstrong and Maloney, 2007; Armstrong and Seddon, 2008). The models developed from the post-release monitoring data (Chapter 6) should also be of interest to researchers, both as an example of investigating the spatial dynamics

of translocated populations (Reynolds *et al.*, 2012; Mihoub *et al.*, 2014) and of pragmatic methods to combine multiple, individually limited datasets (Miller *et al.*, 2019; Hunter-Ayad and Hassall, 2020). Overall, the specific methods applied to takahē research and the strategies behind these approaches can be applied to a broad range of species and translocation contexts.

The goal-based management evaluation in chapter 5 could also be developed and implemented across a range of studies. While not particularly analytically complex, these evaluations represent a key step in adaptive management processes, where outcomes or progress are critically compared with prior expectations (Armstrong and Seddon, 2008). As many conservation interventions are somewhat open-ended, with only vague goals and timeframes defined for interventions undertaken (Soorae, 2016), such evaluations are often overlooked. These preliminary evaluations then can be used to promote and emphasise the benefits of this framework, demonstrating the need for these evaluations to facilitate effective, evidence-based, adaptive management programmes and clarify decision frameworks for a range of species (Armstrong and Seddon, 2008; Taylor *et al.*, 2017). The much more involved spatial analyses of post-release monitoring data presented in Chapter 6 can be used as a proof-of-concept for developing an integrative analysis framework for combining multiple fragmented movement datasets (Galante *et al.*, 2018). This framework is based on the recognition of complementarity and synergies between the datasets that are combined. Although the framework developed in the chapter requires further conceptual and methodological development, refinement, and validation, it has the potential to be developed into a tool that can provide ecologically meaningful estimations from relatively poor input data (Hunter-Ayad and Hassall, 2020; Chapter 3; Hunter-Ayad *et al.*, 2020). Such a framework is likely to have applications for many ecological studies.

## **8.4 Limitations**

Each of the data chapters in this thesis were impacted by issues with the quality and quantity of data available for analyses. This has meant that much of the analytical effort in the thesis has been expended on attempting to counteract low quality data inputs via methodological adjustments and elaborations. Such methodological exploration is of interest and provides much scope for further development. However, the often unusual or restricted application of analyses does reduce the confidence that can be placed in results, while also reducing the number of studies with which they can be effectively compared.

In Chapter 4 the species presence data available, while valuable, were also somewhat restrictive. As takahē monitoring in the Murchison Mountains is relatively infrequent (censuses every 3 years; Section 4.2.1) due to the inaccessibility of the site, this limited the analyses that could be considered to presence-only methods. More frequent monitoring could have allowed presence-absence methods to be used in chapter 4 (Zeller *et al.*, 2017), while also allowing more detailed analyses of takahē home ranges to be conducted. This would be valuable for resolving the questionable inferences combining secure site and wild site analyses highlighted in Section 4.2.3 (Maxwell and Jamieson, 1997; Ryan and Jamieson, 1998; Baber and Craig, 2003; *The takahē’s ecological niche*, 2022; *Takahē Recovery Programme*, 2022). As it was I deemed monitoring data of insufficient quality for analyses using anything more than the presence-background methods such as the MaxEnt (Phillips, Anderson and Schapire, 2006) modelling settled upon. Furthermore, the relict status of the population in the Murchison Mountains, and the uncertainties to ecological inferences from such a population, meant that additional effort was put into selection of predictor variables, model parameterisation and model selection. In addition, the creation of conservative and extrapolative versions of fitted models was also necessary to account for the uncertainty in ecological inferences made from this population. Finally in Chapter 4, the near complete lack of any clear dispersal estimates for wild takahē predating the Kahurangi NP reintroduction (Maxwell, 1995), severely limited the complexity of dispersal models and predictions that could be considered. Ecological theory, via the concept of the dispersal kernel (Fujiwara *et al.*, 2006; Fandos *et al.*, 2021), had to be relied on to generate patterned predictions around highly uncertain estimates of minimum and maximum plausible values.

The data collection described in Chapter 5 ultimately resulted in far fewer data being collected than was intended. The deployment of GPS satellite tags was intended to overcome the limitations of previously developed VHF radio tracking and provide far more detailed tracking data than had ever been available before. While this was technically realised, the excessive failure of and damage to deployed satellite tags meant that this was to far less a degree than planned. The short duration of satellite tracking prohibited the use of such data for many purposes, including detailed home range analyses and individual-level movement comparisons, as these would not be expected to produce meaningful or reliable results (Joo *et al.*, 2020; Forrest, 2021). While on-the-ground monitoring was more intensive than in the Murchison Mountains (i.e., Section 5.2.2 compared with Section 4.2.1), data from this monitoring were still too course for detailed movement or home range

analyses (especially considering the dynamics of the establishing translocated population). Comparisons with course data and targets from the Murchison Mountains were used to give context and feedback from the monitoring data in Chapter 5. But the majority of tracking data analyses were removed to Chapter 6 owing to the complex analytical framework that was required to incorporate and draw ecological inferences from the relatively poor datasets.

The fragmented datasets described in Chapter 5 necessitated considerable effort to model and recombine in Chapter 6. The rarity of comparable analyses in the literature also meant that I resorted to experimental adaptation of existing methods to fit this purpose. Such adaptation and developments may, with development, provide much utility in other ecological research where data quality is low. But as such methods are currently underdeveloped and require much revision and validation effort, meaning that the results as presented are highly questionable, as they critically depend on many experimental manipulations and methods.

Similarly to Chapter 6, Chapter 7 incorporates much experimental methodology and is dependent on both assumptions regarding the accuracy of input data (specifically the outputs from Chapter 6 which are used as observation data) and the suitable treatment of input datasets (i.e., the outputs from Chapter 4 and 6). While the methods are suitable for preliminary evaluations, and do provide valuable insights, I suggest a full methodological overhaul is necessary to make these analyses robust. Specifically, the outputs of Chapter 4 should be tested with the ‘raw’ monitoring data described in Chapter 5, provided a suitable evaluative methodology is utilised.

## **8.5 Conclusions**

Overall, I consider that my thesis has successfully fulfilled its’ stated objectives (Section 1.6). I have presented outputs that will be useful resources for the ongoing conservation management of takahē, with many of the approaches developed readily translatable to the conservation management of other species. All thesis chapters should be able to be employed for this purpose in their current states. However, further development of the concepts, methodologies, and analyses presented in this thesis will also increase their utility for application to conservation management, both for takahē and other species around the globe.

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## **List of Abbreviations**

BBMM- Brownian Bridge Movement Model

DEM- Digital Elevation Model

DOC- Department of Conservation

ESRI- Environmental Systems Research Institute

GPS- Global Positioning System

IUCN- International Union for the Conservation of Nature

LENZ- Land Environments of New Zealand

LRIS- Land Resource Information Systems

NIWA- National Institute of Water and Atmospheric Research

NP- National Park

NZ- Aotearoa New Zealand

SSF- Step Selection Function

TRG- Takahē Recovery Group

UD- Utilisation Distribution

VHF- Very High Frequency

VIF- Variance Inflation Factor

## **Appendix A- Supporting Information for Correlative Habitat Suitability Models**

Appendix A provides supplementary and supporting materials for chapter 4: Predictive Modelling: Relict Distribution Model.

### **A.1 Candidate environmental predictors prepared for relict distribution correlative model**

#### **A.1.1 Rescaling Method**

To standardise extent and resolution across environmental predictors I first generated an empty “fishnet” raster at the selected extent, cell size and coordinate system (New Zealand Transverse Mercator) in R using functions from the *raster* package (Hijmans, 2016).

Following this the processing of cropped, raw data depended on the source format:

- I rescaled and projected raster data to the scale and extent of the fishnet raster using a combination of functions in the R packages: *sp* (Pebesma and Bivand, 2005; Bivand, Pebesma and Gomez-Rubio, 2013), *plyr* (Wickham, 2011), and *raster* (Hijmans, 2016). As part of this rescaling process I used QGIS (QGIS Development Team, 2017) to run an intersect function for intermediary ESRI shapefile layers. For raster data where source layers had cell sizes larger than 200 m (i.e., NIWA data, received at 500m resolution), I used bilinear interpolations to calculate cell values for the 200m output cells. For raster data where source layers had cell sizes smaller than 200m I calculated the values in the rescaled raster as the mean value of all cells in the source layer whose centroid fell within the same cell of the fishnet raster.
- I rasterised ESRI Polygon shapefiles to the scale and extent of the fishnet raster based on the variable of interest in their attribute Table using the *rasterize* function in the package *raster* in R (Hijmans, 2016).
- I also rasterised ESRI Polyline shapefiles to the scale and extent of the fishnet raster the *rasterize* function in the package *raster* in R (Hijmans, 2016). Here I based the rasterisation on the intersection of line sections with raster cells such that values output raster reflected presence or absence (one or zero) of the linear feature in that cell.

All candidate predictor variables came from separate source layers with the exception of terrain predictors (altitude, altitudinal range, terrain roughness, aspect and slope) which were generated from processing of the Digital Elevation Model for the South Island (LRIS, accessed 20<sup>th</sup> August 2018). Altitude, altitudinal range and terrain roughness predictors were calculated in R using the *plyr* (Wickham, 2011) and *raster* (Hijmans, 2016) packages, while slope and aspect were generated using the DEM (terrain models) toolbox in QGIS.

**Table A.1-** Candidate environmental predictor variables prepared for MaxEnt correlative habitat suitability models for takahē using species records from their relict distribution in the Murchison Mountains

#	Candidate Predictor	Source Layer	Download	Data Provider	Format
			Source and date		
1	Altitude	NSDEM South Island 25 metre	LRIS, 20 <sup>th</sup> August 2018	Manaaki Whenua – Landcare Research	25m raster (GEOTIFF)
2	Altitudinal Range (DEM)	NSDEM South Island 25 metre	LRIS, 20 <sup>th</sup> August 2018	Manaaki Whenua – Landcare Research	25m raster (GEOTIFF)
3	Mean Annual Temperature	LENZ- Mean annual temperature	LRIS, 20 <sup>th</sup> August 2018	Manaaki Whenua – Landcare Research	25m raster (GEOTIFF)
4	April Soil Temperature	Mean April Soil Temperature (South Island)	LRIS, 20 <sup>th</sup> August 2018	Manaaki Whenua – Landcare Research	25m raster (GEOTIFF)
5	Aspect	NSDEM South Island 25 metre	LRIS, 20 <sup>th</sup> August 2018	Manaaki Whenua – Landcare Research	25m raster (GEOTIFF)
6	Biotic Composition	GDM Classification of New Zealand Biotic Composition for All Forest Plants	LRIS, 20 <sup>th</sup> August 2018	Manaaki Whenua – Landcare Research	100m raster (GEOTIFF)
7	Landcover	LCDB v4.1 - Land Cover Database version 4.1	LRIS, 20 <sup>th</sup> August 2018	Manaaki Whenua – Landcare Research	ESRI polygon shapefile

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8	Mean Minimum Temperature	LENZ - Mean minimum temperature of the coldest month	LRIS, 20 <sup>th</sup> August 2018	Manaaki Whenua – Landcare Research	25m raster (GEOTIFF)
9	Median Annual Total Rainfall	Median Annual Total Rainfall	NIWA, 4 <sup>th</sup> October 2018	NIWA National Climate Database	500m raster (ASCII)
10	Median Annual Number Wet Days	Median Annual Number Wet Days	NIWA, 4 <sup>th</sup> October 2018	NIWA National Climate Database	500m raster (ASCII)
11	Median Annual Mean Daily Air Temperature	Median Annual Mean Daily Air Temp	NIWA, 4 <sup>th</sup> October 2018	NIWA National Climate Database	500m raster (ASCII)
12	Median Annual Average Daily Solar Radiation	Median Annual Average Daily Solar Radiation	NIWA, 4 <sup>th</sup> October 2018	NIWA National Climate Database	500m raster (ASCII)
13	Median Annual Average Daily Wind Speed	Median Annual Average Daily Wind Speed	NIWA, 4 <sup>th</sup> October 2018	NIWA National Climate Database	500m raster (ASCII)
14	Median 9am Soil Temperature	Median 9am Soil Temperature	NIWA, 4 <sup>th</sup> October 2018	NIWA National Climate Database	500m raster (ASCII)

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15	Median Annual Total Sunshine Hours	Median Annual Total Sunshine Hours	NIWA, 4 <sup>th</sup> October 2018	NIWA National Climate Database	500m raster (ASCII)
16	Minimum Temperature	LENZ - Mean minimum temperature of the coldest month	LRIS, 20 <sup>th</sup> August 2018	Manaki Whenua – Landcare Research	25m raster (GEOTIFF)
17	Rivers	NZ River Centrelines (Topo, 1:50k)	LINZ, 20 <sup>th</sup> August 2018	Land Information New Zealand	ESRI polyline shapefile
18	Roads	NZ Roads: Road Section Geometry	LINZ, 20 <sup>th</sup> August 2018	Land Information New Zealand	ESRI polyline shapefile
19	Slope (DEM)	NSDEM South Island 25 metre	LRIS, 20 <sup>th</sup> August 2018	Manaki Whenua – Landcare Research	25m raster (GEOTIFF)
20	Slope (NZLRI)	NZLRI South Island, Edition 2 (all attributes)	LRIS, 20 <sup>th</sup> August 2018	Manaki Whenua – Landcare Research	ESRI polygon shapefile
21	Soil Classification	FSL New Zealand Soil Classification	LRIS, 20 <sup>th</sup> August 2018	Manaki Whenua – Landcare Research	ESRI polygon shapefile
22	Soil Temperature Regime	FSL Soil Temperature Regime	LRIS, 20 <sup>th</sup> August 2018	Manaki Whenua – Landcare Research	ESRI polygon shapefile
23	Solar Radiation	LENZ - Mean annual solar radiation	LRIS, 20 <sup>th</sup> August 2018	Manaki Whenua – Landcare Research	25m raster (GEOTIFF)
24	Terrain Roughness (std. dev.)	NSDEM South Island 25 metre	LRIS, 20 <sup>th</sup> August 2018	Manaki Whenua – Landcare Research	25m raster (GEOTIFF)

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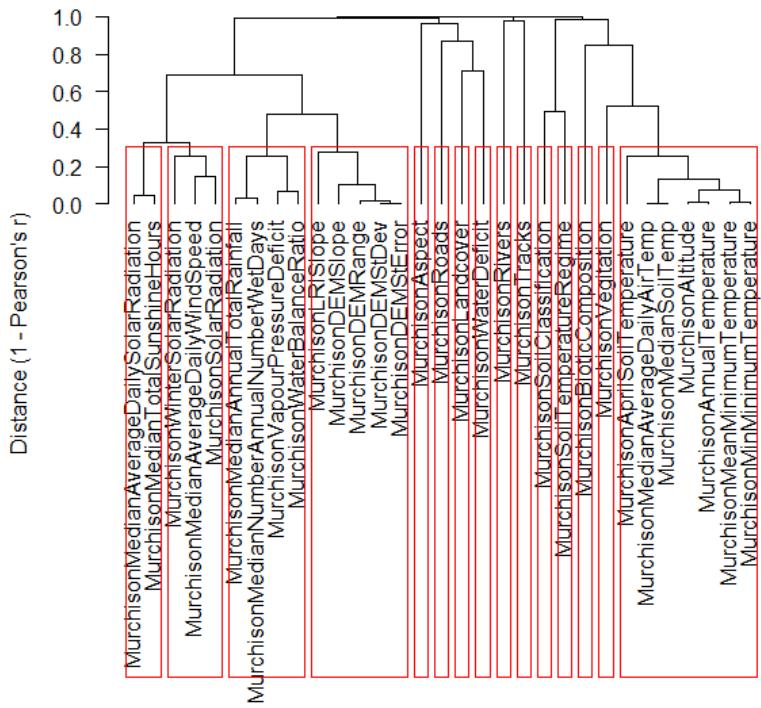
25	Terrain Roughness (std. err.)	NSDEM South Island 25 metre	LRIS, 20 <sup>th</sup> August 2018	Manaaki Whenua – Landcare Research	25m raster (GEOTIFF)
26	October Vapour Pressure Deficit	LENZ - October vapour pressure deficit	LRIS, 20 <sup>th</sup> August 2018	Manaaki Whenua – Landcare Research	25m raster (GEOTIFF)
27	Vegetation	NZLRI Vegetation	LRIS, 20th August 2018	Manaaki Whenua – Landcare Research	ESRI polygon shapefile
28	Walking and Biking Tracks	NZ Walking and Biking Tracks	LINZ, 20 <sup>th</sup> August 2018	National Tracks	ESRI polyline shapefile
29	Monthly Water Balance Ratio	LENZ - Monthly water balance ratio	LRIS, 20 <sup>th</sup> August 2018	Manaaki Whenua – Landcare Research	25m raster (GEOTIFF)
30	Annual Water Deficit	LENZ - Annual water deficit	LRIS, 20 <sup>th</sup> August 2018	Manaaki Whenua – Landcare Research	25m raster (GEOTIFF)
31	Winter Solar radiation	LENZ - Winter solar radiation	LRIS, 20 <sup>th</sup> August 2018	Manaaki Whenua – Landcare Research	25m raster (GEOTIFF)

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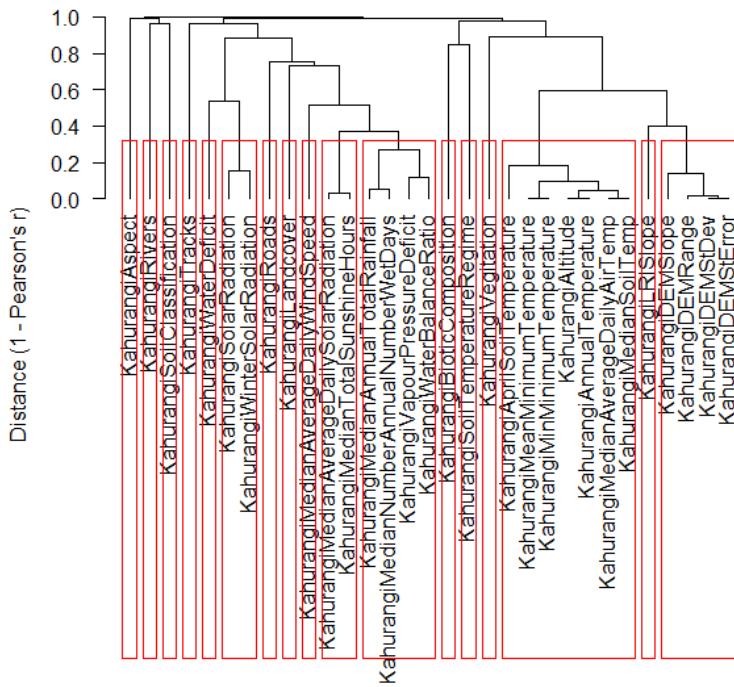
## A.2 Restricting Choice of Environmental Predictors

### A.2.1 Pearson's Correlation Coefficients

Figures A.1 and A.2 show the Pearson's correlations of candidate environmental predictors in the Te Anau Ecoregion and Kahurangi National Park study areas respectively using the virtual species package in R (Leroy *et al.*, 2016). As can be seen there are 5 groups of correlated variables in each study area that show much overlap between the regions.



**Figure A.1-** Autocorrelation indicated by Pearson's correlation coefficient for environmental predictors in the Te Anau Ecoregion. Red boxes indicate groups of variables that are significantly autocorrelated (as defined by a 0.7 Pearson's r threshold).



**Figure A.2-** Autocorrelation indicated by Pearson's corelation coefficient for environmental predictors in the Kahurangi National Park. Red boxes indicate groups of variables that are significantly autocorrelated (as defined by a 0.7 Pearson's r threshold).

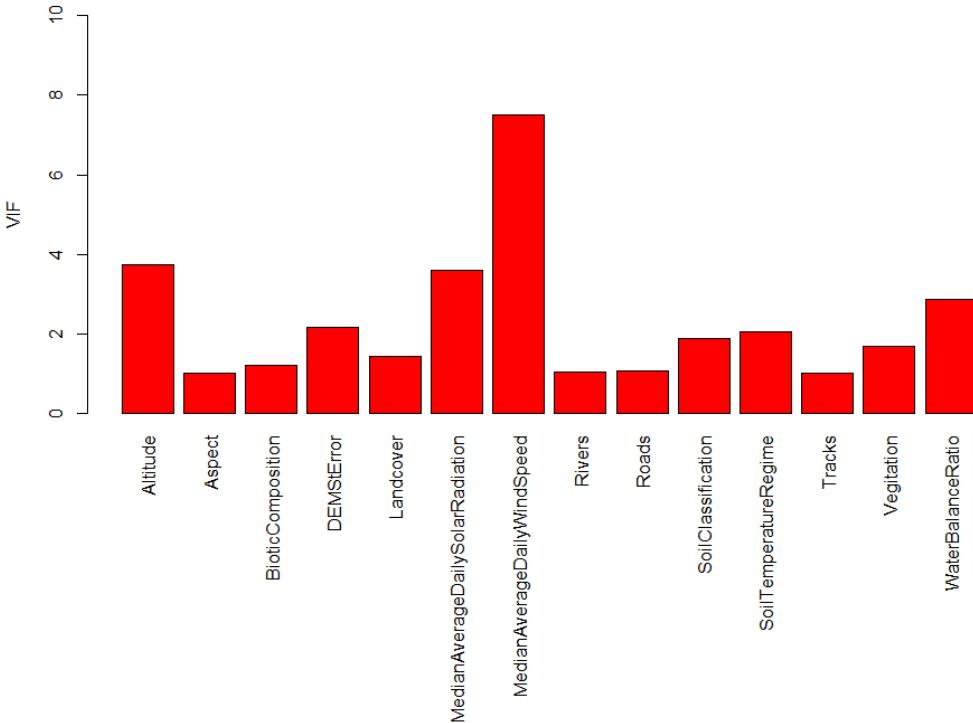
Based on these correlations the following 17 environmental variables were excluded from further consideration.

- Annual Temperature
- April Soil Temperature
- Terrain Roughness (DEM Range)\*
- DEM Slope
- Terrain Roughness (DEM Standard Deviation)\*
- LRI Slope
- Minimum Temperature (Mean)\*
- Median Annual Total Rainfall
- Median Average Daily Air Temperature
- Median Annual Number Wet Days
- Median Soil Temperature
- Median Total Sunshine Hours
- Minimum Temperature (Minimum)\*
- Solar Radiation
- Vapour Pressure Deficit
- Water Deficit
- Winter Solar Radiation

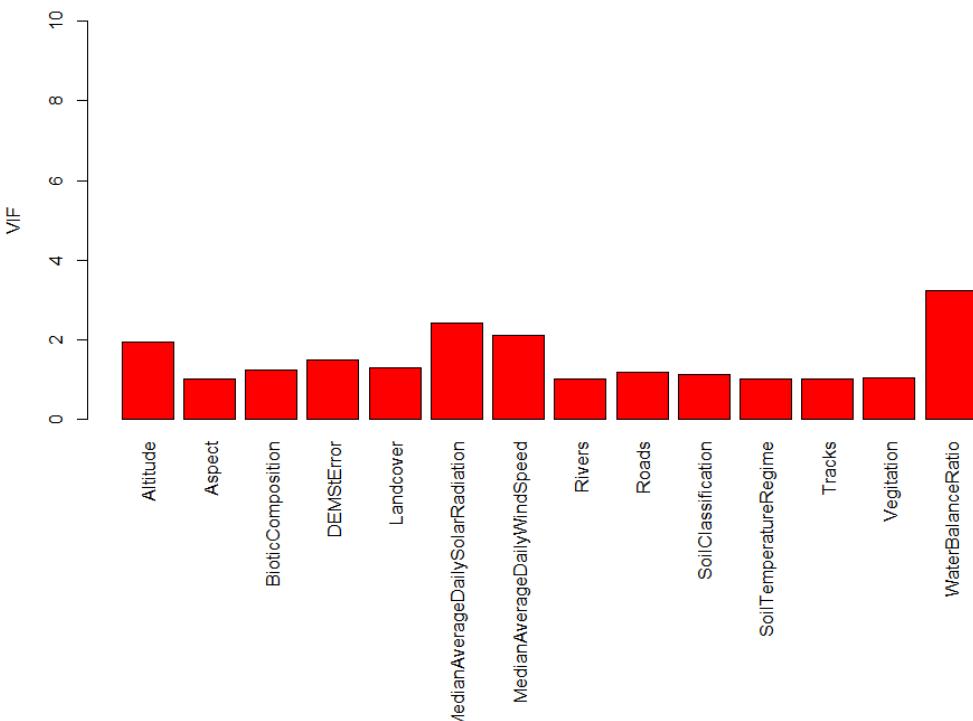
\* Brackets refer to the calculation/rescaling method for these variables

### A.2.2 Variance Inflation Factors

Figures A.3 and A.4 show the Variance inflation factors calculated for the remaining 14 variables calculated using the *usdm* package in R (Naimi *et al.*, 2014) for the Te Anau Ecoregion and Kahurangi National Park study areas respectively.



**Figure A.3-** Variance Inflation Factors (VIF) for candidate environmental predictors to be used in habitat suitability models for takahē. VIFs are calculated for the extent of the Te Anau Ecoregion.



**Figure A.4-** Variance Inflation Factors (VIF) for candidate environmental predictors to be used in habitat suitability models for takahē. VIFs are calculated for the extent of the Kahurangi National Park.

Based on the highest VIF values for Attitude, Average Daily Solar Radiation and Average Daily Wind Speed in the Te Anau Ecoregion, these predictors were removed from further consideration and the VIF's calculated again. This resulted in VIFs for the remaining factors being acceptably low (all under 3; Zuur, Ieno and Elphick, 2010, see Table A.2).

**Table A.2-** Variance Inflation Factors (VIF) for the restricted set of candidate environmental predictors to be used in habitat suitability models for takahē. This restricted set was arrived at following the removal of previously considered candidate variables based on autocorrelations identified via Pearson's and VIF analyses

Predictor Variables	Variance Inflation Factors	
	Te Anau Ecoregion	Kahurangi National Park
Aspect	1.022284	1.002945
Biotic Composition	1.129972	1.155351
Terrain Roughness (DEM Standard Error)	1.79881	1.34841
Landcover	1.358059	1.304173
Rivers	1.044791	1.01066
Roads	1.064234	1.187345
Soil Classification	1.874259	1.044574
Soil Temperature Regime	1.882524	1.108108
Tracks	1.010581	1.036508
Vegetation	1.401973	1.037755
Water Balance Ratio	2.080664	1.246687

Next, after removing all variables for which autocorrelation would likely have led to poor model transfer, the remaining eleven variables were considered for their merit as model predictors. Firstly, there remained several categorical variables, likely as Pearson's and VIF statistics have less power to identify duplicated information in categorical raster layers. As Biotic Composition, Landcover and Vegetation layers were likely to be too functionally similar to warrant their inclusion as predictors in the same model, only the Vegetation layer was retained from these three. Further variables were excluded based on their limited weighting in preliminary model versions, these were Aspect and Soil Temperature Regime. Finally, raster layers representing linear features were removed, as roads and tracks are largely absent from focal takahē areas and further linear features were likely more

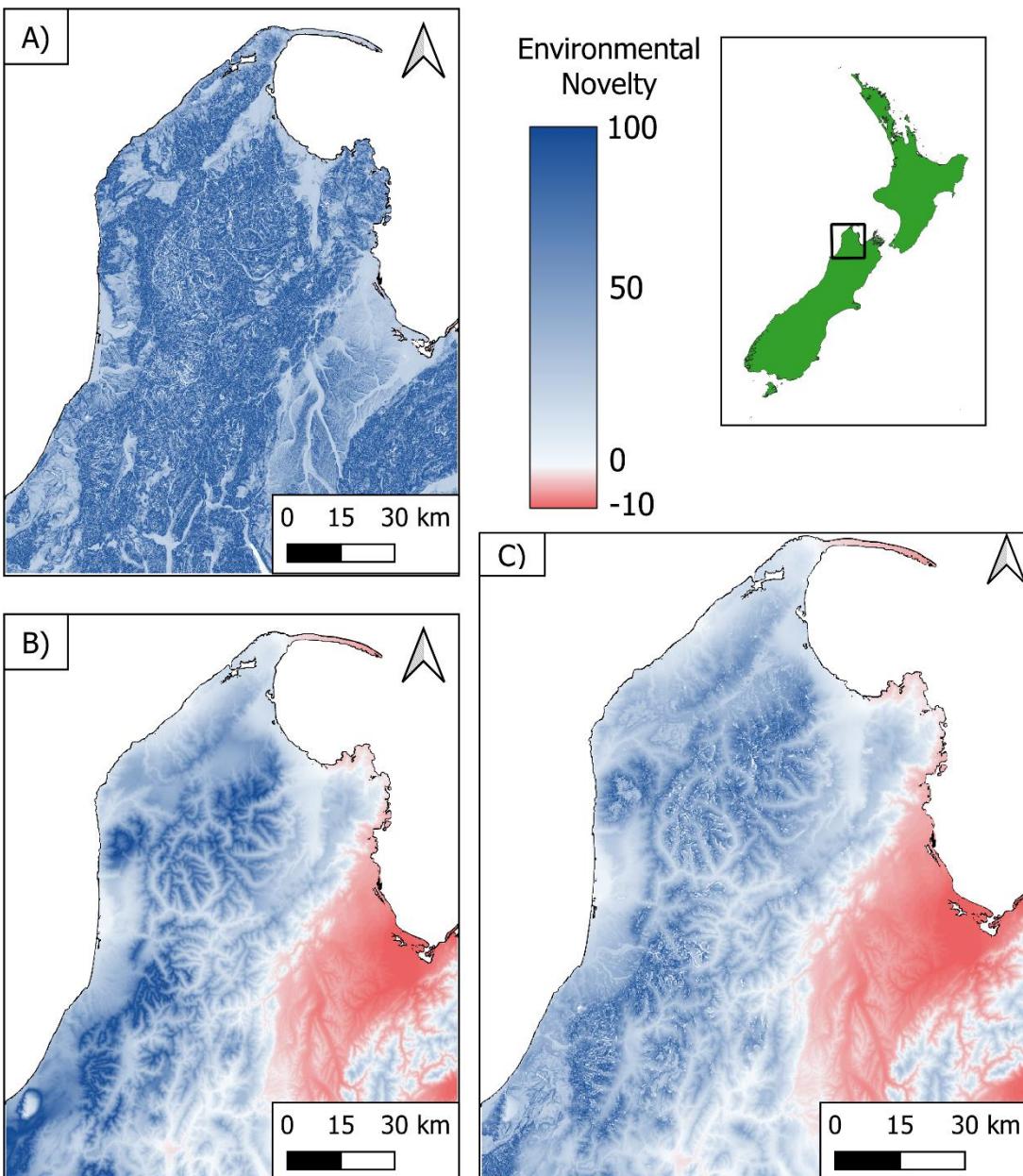
significant for habitat connectivity (which it was hoped would be included in this research at one point), rather than home range selection as such, and thus they were removed from the final set of environmental predictors.

This left me with four environmental predictors which were expected to be significant drivers of takahē home range choice (see 4.2.2).

### A.3 Non-Analogous Conditions in Model Projections

The spatial habitat predictions of MaxEnt models presented in chapter 4 and appendix A.4 represent spatial extrapolations of the fitted models, as they are applied to landscapes outside of the model fitting region (Figure 4.1). However, while spatial and temporal projections of models can be uncertain (Barbet-Massin and Jetz, 2014), model predictions are particularly questionable when they are applied to novel environmental conditions, as this requires extrapolations beyond the range of model training data (Elith, Kearney and Phillips, 2010; Norberg *et al.*, 2019; Chapter 2; Hunter-Ayad *et al.*, 2021). I therefore examined the areas with conditions outside of the range of training data in my model projection landscapes in order to identify the regions in which environmental extrapolation is necessary, aiding in the interpretation of model predictions.

I first considered novel conditions for continuous environmental predictors by calculating Multivariate Environmental Similarity Surface (MESS) maps (Elith, Kearney and Phillips, 2010) using the *mess* function from the *dismo* package in R (Hijmans *et al.*, 2017). These summarise the differences between continuous environmental variables in different regions, providing an output where positive values reflect conditions that are observed in a reference landscape (the model training extent in the case of my models) and negative values are novel, i.e., not observed in model training areas. These outputs also scale, so that the more negative a value is the further outside of the range of conditions in the reference landscape it is, while the more positive the value, the better represented these conditions are in the reference landscape. I calculated MESS maps based on a full sample of the 5km buffer area used to extract background points in the Murchison Mountains, which were then applied to Kahurangi National Park (Figure A.5) and Te Anau Ecoregion (Figure A.7) projection extents respectively.

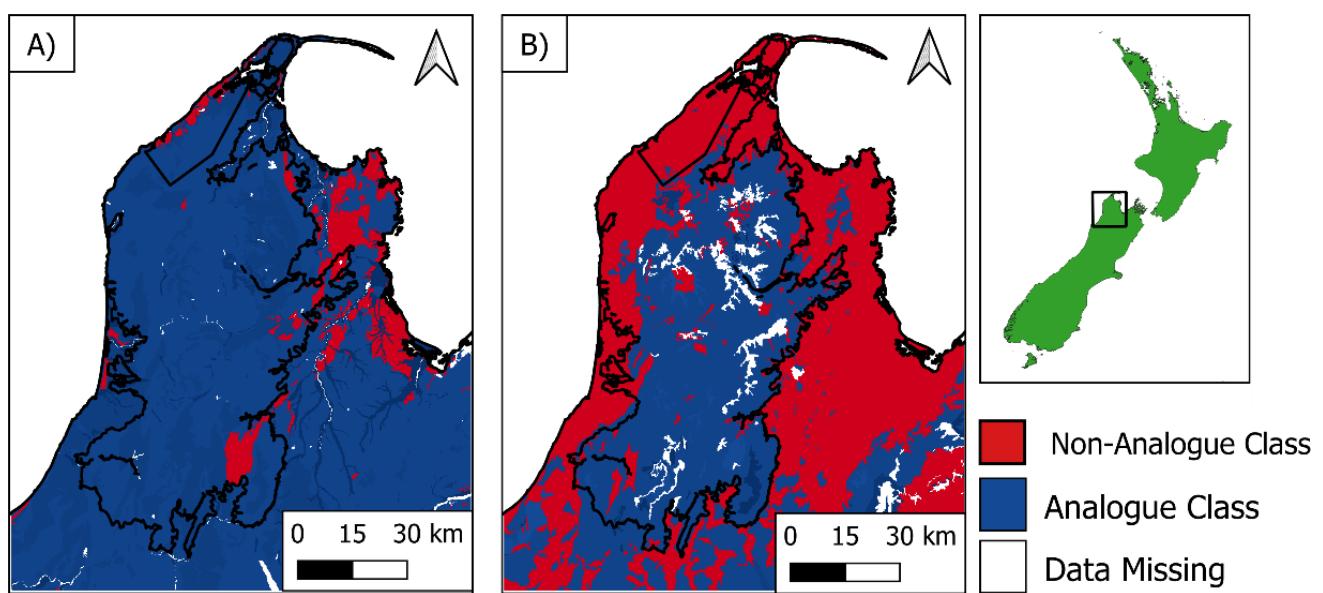


**Figure A.5-** Multivariate Environmental Similarity Surfaces (MESS) identifying non-analogue conditions for continuous environmental predictor variables in Kahurangi National Park, compared to the model training landscape in the Murchison Mountains (Figure 4.1). Panels represent MESS maps for Terrain Roughness (A), Water Balance Ratio (B) and a combined summary of both these maps (C), with positive values representing conditions observed in the model training area and negative values representing novel conditions compared with the model building area.

As MESS maps are not suitable for the consideration of categorical variables, I summarised novel conditions in categorical environmental variables simply by highlighting categorical classes that are not represented within the 5km buffer area from which background points

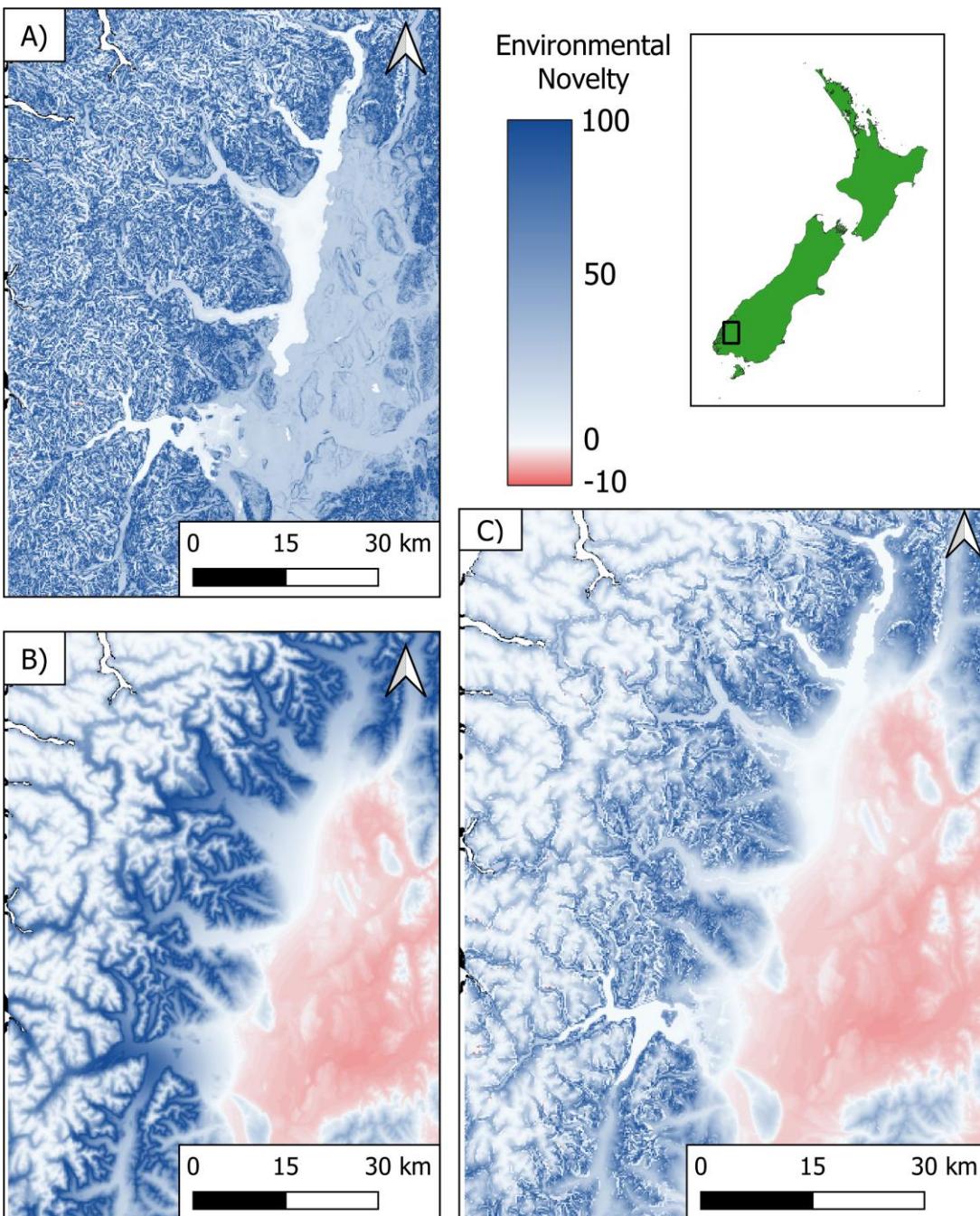
were drawn for both Kahurangi National Park (Figure A.7) and Te Anau Ecoregion (Figure A.8) model projection extents respectively.

For the continuous variables, no areas in either projection extent represent novel conditions in terms of terrain roughness (Figure A.5A and A.7A). However, this is not true for water balance ratio, with novel conditions introduced by considerably drier conditions in the South-West portions of each training extent (Figure A.5B, A.7B 4.2D and 4.3D). These regions are relatively low-lying and sheltered for each projection extent, representing a shallow valley between Motueka and Nelson and the Te Anau Downs on the Western side of Lake Te Anau, respectively.



**Figure A.6-** Summary of non-analogous classes of categorical predictor variables (i.e., those not present in the buffer area around takahē records; Figure 4.1) for the Kahurangi National Park prediction extent. Panels show summaries for soil classification (A) and vegetation cover (B) respectively. Blue indicates that the class is represented in the Murchison Mountains model training area, while red indicates that a class is considered novel, i.e., not represented in the model training area.

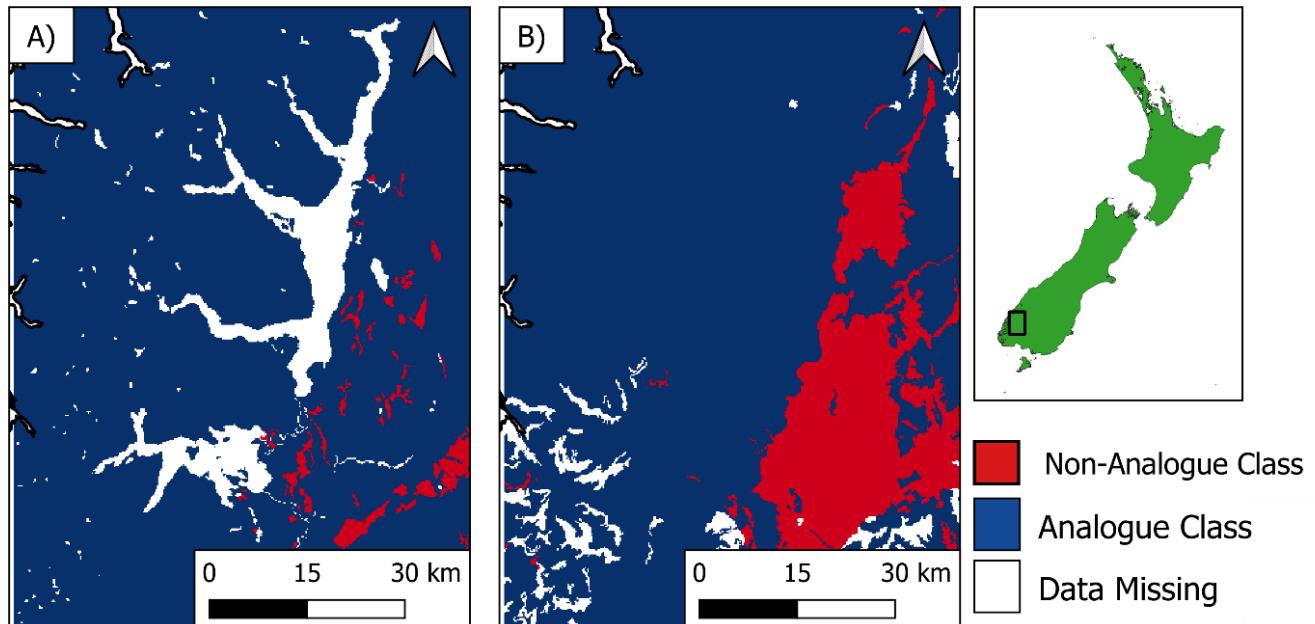
With regard to the categorical variables, there is a relatively limited extent of novel soil classes represented in each projection extent, mostly associated with anthropogenic activity away from core takahē areas (Figures A.6A and A.8A). While there is a similar association between anthropogenic (usually agricultural) activity and non-analogue vegetation classes, these are also much more widespread in both projection landscapes (Figure A.6B and A.8B), as there are also some novel vegetation classes that are not generated by human activity (e.g., Icefields and Manuka) present in each landscape (Figure 4.2A and 4.3A).



**Figure A.7-** Multivariate Environmental Similarity Surfaces identifying novel conditions for continuous environmental predictor variables in the Te Anau Ecoregion, compared to the model training landscape in the Murchison Mountains (Figure 4.1). Panels represent MESS maps for Terrain Roughness (A), Water Balance Ratio (B) and a combined summary of both these maps (C), with positive values representing conditions observed in the model training area and negative values representing novel conditions compared with the model building area.

Overall, novel conditions (meaning that extrapolation is inherent in habitat predictions for these areas) are not present in the core takahē areas for either landscape (e.g., the

Gouland Downs release area in Kahurangi National Park and the Murchison Mountains in the Te Anau Ecoregion). However, novel environmental conditions become more common away from these areas (e.g., coastal and low-lying areas in Kahurangi National Park and Western and Southern Portions of the Te Anau Ecoregion), making predictions in these areas more uncertain.



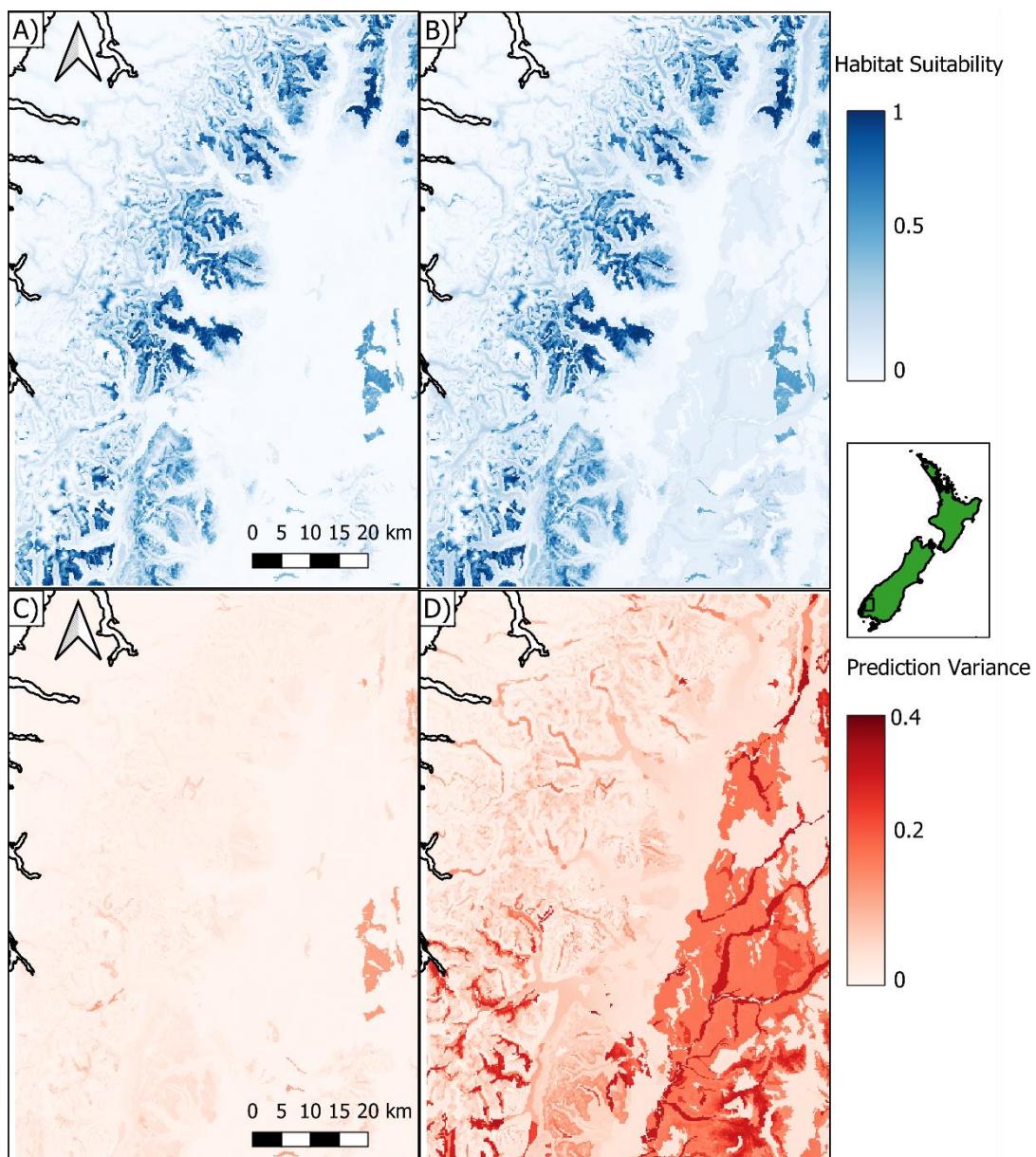
**Figure A.8-** Summary of novel classes of categorical predictor variables for the Te Anau Ecoregion prediction extent. Panels show summaries for soil classification (A) and vegetation cover (B) respectively. Blue indicates that the class is represented in the Murchison Mountains model training area, while red indicates that a class is considered novel, i.e., not represented in the model training area.

#### A.4 Projections to the Te Anau Ecoregion

The habitat suitability models presented in Chapter 4 are primarily intended to be used to inform reintroductions of takahē to landscapes beyond their relict distribution in Fiordland (which has directed many choices during model construction). However, as the takahē population in the Murchison Mountains is still the focus of much conservation management and monitoring (Lee and Jamieson, 2001; Hegg *et al.*, 2012; Hegg, Mackenzie and Jamieson, 2013), the habitat suitability models may be of additional use when applied to the landscape of the takahē relict population.

I projected the fitted conservative and extrapolative models to the Te Anau Ecoregion as for the projections to Kahurangi National Park projections presented in chapter 4 (Figure 4.7), with plots depicting estimated habitat suitability along with the variance, representing prediction uncertainty associated with these predictions (Figure A.9). I did not incorporate

dispersal limitation in these predictions as the relict population does not have specific source points in the form of release locations. However, for this projection, habitat suitability cannot be considered equivalent to probability of presence, as takahē are likely absent from all areas outside of the Special Takahē Area covering the Murchison Mountains (Figure 1.1) and are limited from accessing predicted habitat outside of this area by the dispersal barriers posed by Lake Te Anau and the topography of Eastern Fiordland.



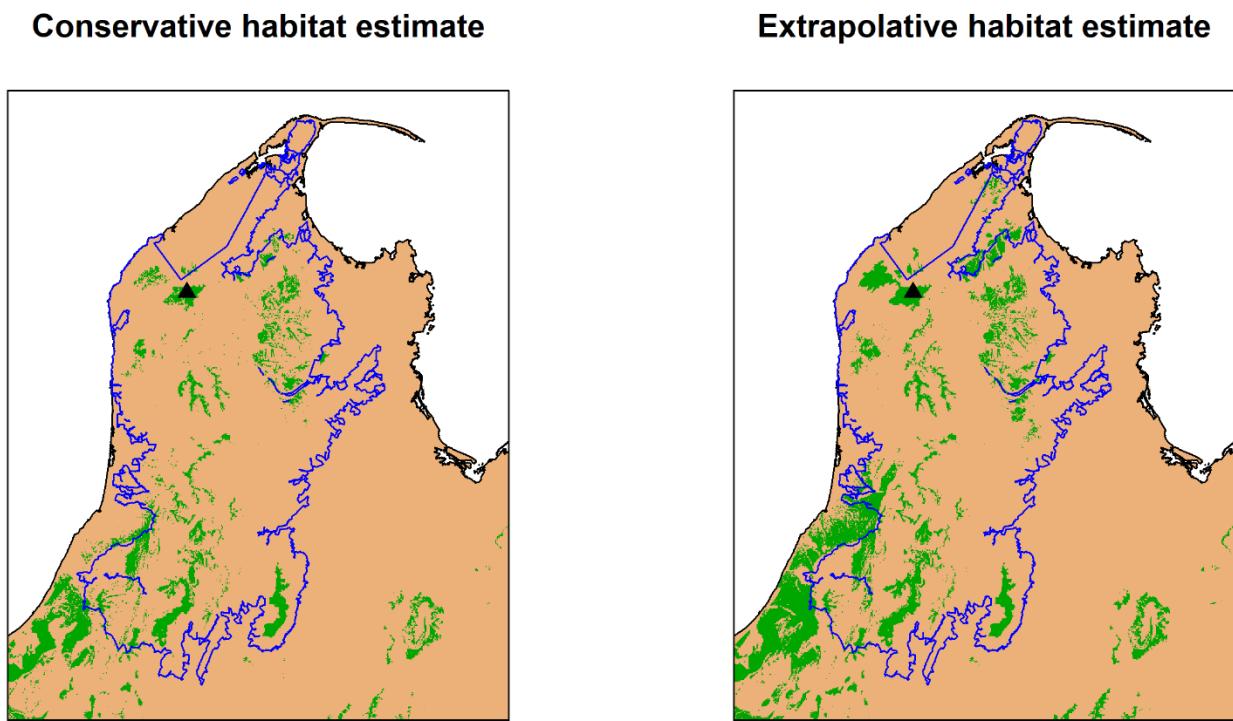
**Figure A.9** - Habitat suitability projections for Te Anau Ecoregion, for both conservative (A and C) and extrapolative (B and D) MaxEnt models. A and B show predicted habitat suitability while the C and D show the variance (standard deviations) across the 40 replicates used to generate final models.

The conservative and extrapolative models both predict a band of suitable takahē habitat covering the eastern side of the Fiordland ranges in the Te Anau Ecoregion, with predicted habitat suitability low on the east side of Lake Te Anau and the western reaches of Fiordland (Figure A.9A and A.9B). While spatial patterns are similar between both models, the extrapolative model predicts generally higher habitat suitability across the projection. The predicted habitat suitability scores were spatially consistent between replicates for the conservative model, resulting in a low variance in habitat suitability scores (Figure A.9C). The extrapolative model on the other hand has much greater variation in suitability scores between model runs (Figure A.9D), especially in the Southern and Eastern portions of the Te Anau Ecoregion, which coincides with the regions of environmental novelty (Figures A.7 and A.8).

## A.5 Summarising Conservative and Extrapolative Predictions

In order to present a simple illustration of the additional habitat predicted by the conservative model when compared with the extrapolative model, the habitat suitability rasters for each were converted into binary, habitat and matrix classes via a threshold conversion. For this, all values equal to and above a specific threshold were considered to be predictions of suitable habitat, whereas those below the threshold were considered to be inter-habitat matrix. The threshold chosen was the Maximum Sum of Sensitivity and Specificity (MSS), as it has been shown to have a high performance for this purpose (C Liu, Newell and White, 2016). The MSS threshold, calculated in *ENMeval* (Muscarella *et al.*, 2014), for each model was; 0.322 for the conservative and 0.350 for the extrapolative model respectively.

Figure A.10 shows the binary predictions for each model following conversion using the reclassify function from the *raster* package in R (Hijmans, 2016). As expected, the extrapolative prediction also includes all of the habitat identified in the conservative model, meaning they could be overlaid on the same axes without losing information, is shown in Figure A.11 for convenience and also in Figure 2.4 in the main thesis text.



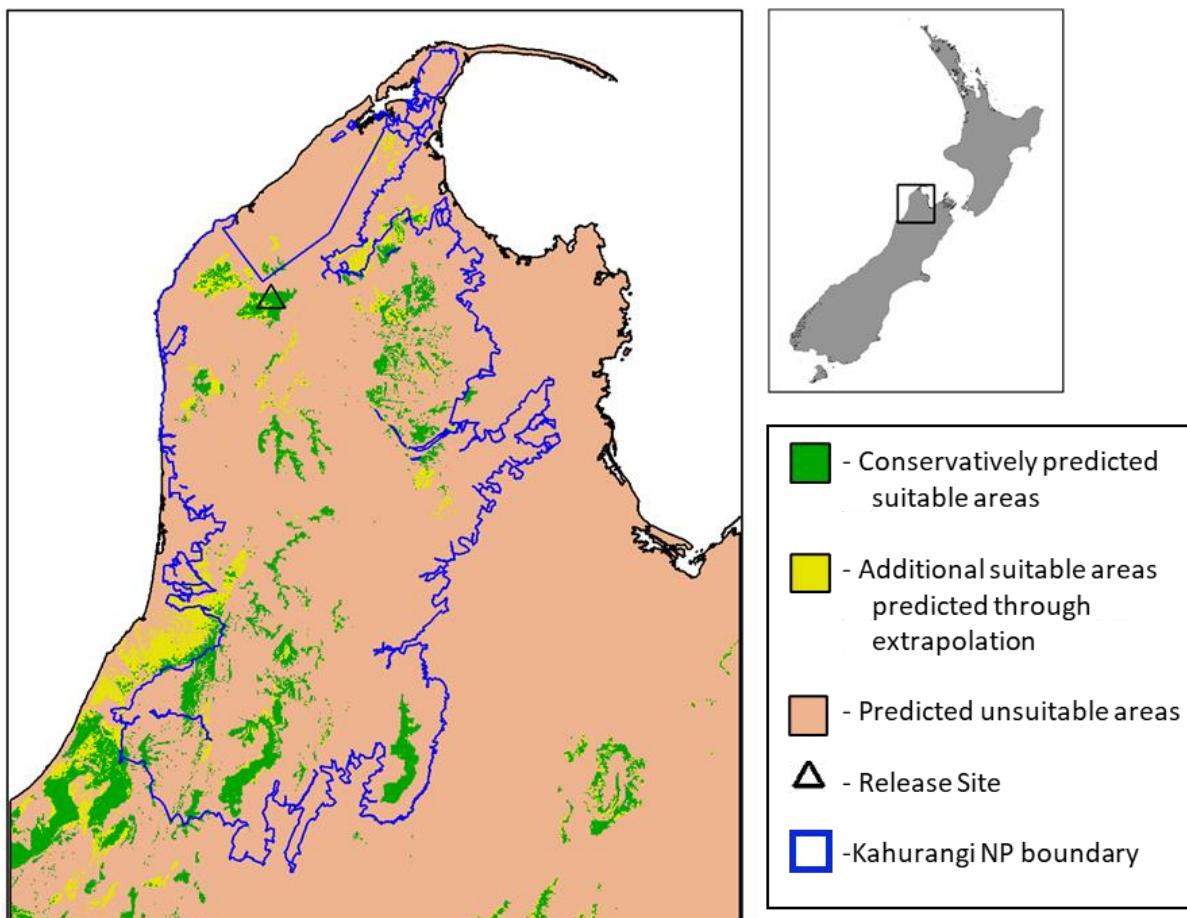
**Figure A.10-** Binary habitat predictions from conservative (left) and extrapolative (right) models. Green areas are predicted to be suitable habitat for takahe by each model, while orange/pink areas are predicted to be non-habitat. The blue line shows Kahurangi National Park boundary and the black triangle shows the Gouland Downs release site.

Following thresholding 1911 landscape cells were classified as habitat in the conservative model, while 3528 cells were classified as habitat in the extrapolative model. As each landscape cell is 4ha in area (Section 4.2.3) this represents a predicted total area of habitat of 7,644ha in conservative models and 14,112ha in extrapolative models.

These binary predictions were also used to provide estimates the extent habitat available for takahē in the three key suitable regions identified in the site selection report (Takahē Recovery Program, 2016): the Gouland Downs, Mackay Downs and Gunner Downs. To do this, binary predictions (Figure A.10) were cropped to the approximate extent of each of the ‘Downs’, before habitat area was calculated, as described in the above paragraph. Results of these calculations are shown in Table A.3.

**Table A.3-** Habitat area predicted by conservative and extrapolative MaxEnt habitat suitability models for three key regions identified in Kahurnagi National Park.

Key suitable region	Conservative prediction of habitat available/ Ha	Extrapolative prediction of habitat available/ Ha
Gouland Downs	2944	3688
Mackay Downs	1292	3492
Gunner Downs	924	1796



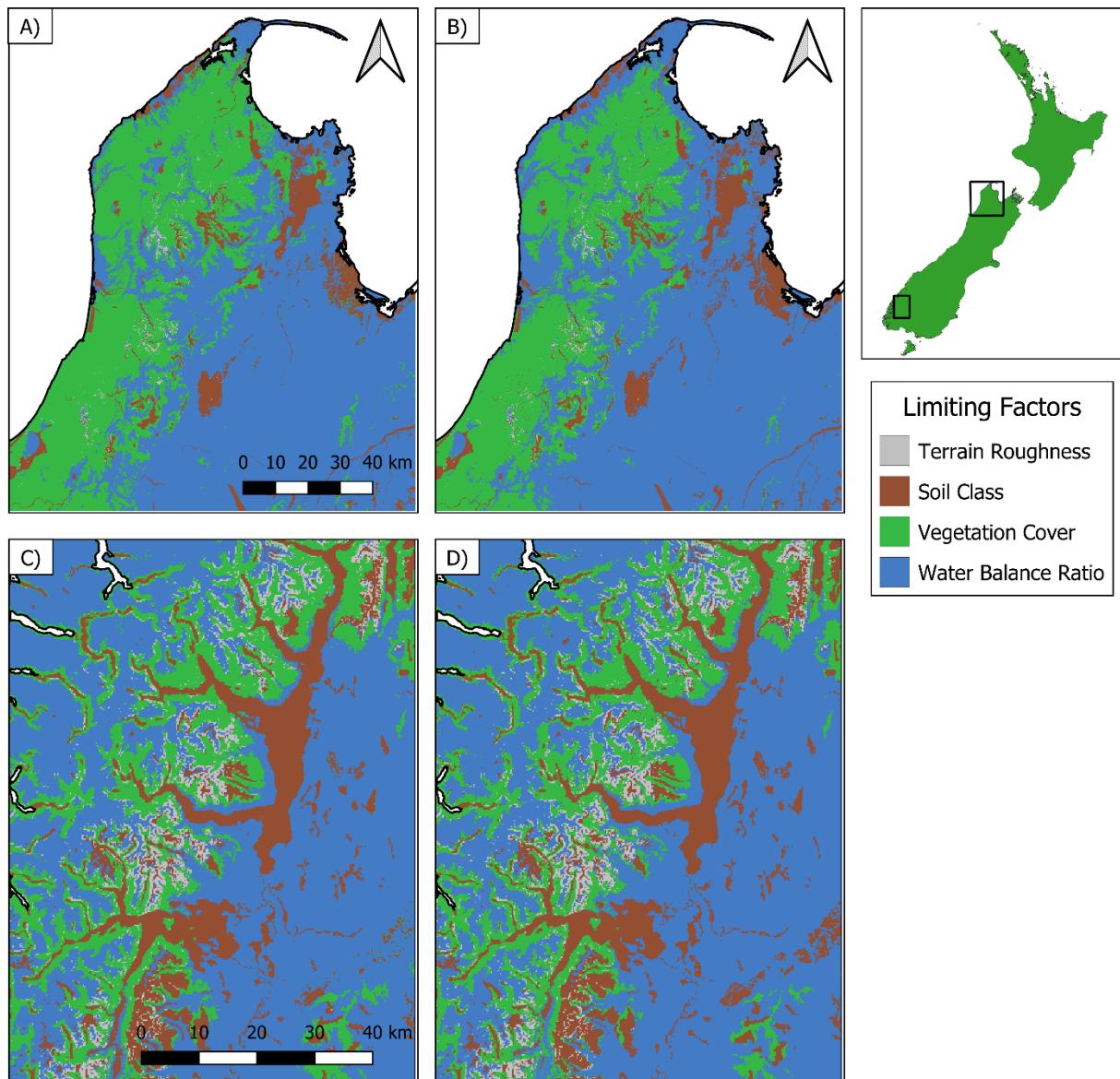
**Figure A.11-** Map of current environmental suitability from a maximum entropy model (Phillips, Anderson and Schapire, 2006) trained with records from South Island takahē (*Porphyrio hochstetteri*) relict population (Figure 2.3). Green areas were identified as suitable by a conservatively fitted model, whereas the yellow areas show the additional space predicted to be suitable when the model fitting was relaxed to allow a greater degree of extrapolation. The conservative model only identifies habitat in environments analogous to those occupied in the models' input data, whereas the extrapolative model focuses on excluding areas only because they are analogous to unused areas in the species training data.

## A.6 Limiting Factor Analyses

In this section are the results of limiting factor analyses for the habitat maps produced in chapter 4. Limiting Factor analysis identifies the input variable that imposes the greatest restriction on habitat suitability predictions for each raster cell of a model projection (Elith, Kearney and Phillips, 2010). The limiting factor maps were produced using the *limiting* function in the *rmaxent* package in R (Baumgartner and Wilson, 2020). As this function could only be applied to single model objects it was applied to each of the 40 optimal models identified from each ENMeval replicate, rather than the averaged model output. The

below Figures show the limiting factor for the 50<sup>th</sup> percentile across the forty model replicates for conservative and extrapolative models respectively. The quantile score was used due to difficulty in dealing with the categorical raster outputs; ideally the mode, or most common value, should be used as it would be the most meaningful way to average across replicates, but I was unable to calculate this for raster format data (I simply could not figure out a method in R or GIS that would perform the required calculation). The 50th percentile values should be a close analogue, although by treating the categories as ordinal data this metric is biased towards middle values (Soil type and vegetation). The limiting factor plots and rasters for each replicate are provided in Digital Appendix 1.3, though patterns across all replicates are consistent.

As can be seen in Figure A.12 within the Special Takahe Area, and in general in the eastern Fiordland ranges, all four input variables are shown to limit habitat suitability in different areas, with terrain roughness limiting habitat suitability in more topographically uneven areas, while vegetation is the limiting factor in areas covered by beech forest, while soil type and water balance ratio constrain predictions in other areas. However, outside the Special Takahē Area, to the East and West water balance ratio becomes the limiting factor as conditions become mostly too dry to the east and too wet to the west (Figure 4.2). For projections to Kahurangi National Park vegetation cover limits habitat suitability over much of the National Park, these areas are either beech forest, as in the Te Anau Ecoregion, or Lowland Podocarp, which is not found within the 5km buffer area sampled for model building (Figure 4.1). In the central and south-eastern regions of Kahurangi and outside of the National Park low water balance ratios are the most limiting factor restricting habitat suitability predictions (Figure 4.3), while terrain roughness and soil class limit predictions towards the peaks of the mountains south of the Gouland Downs (Figure 4.3).



**Figure A.12-** Limiting factors for MaxEnt habitat suitability models for takahē trained with presence data from their relict population in the Murchison Mountains. Limiting factors relate to projections to Kahurangi National Park (A and B) and Te Anau Ecoregion (C and D) for conservative (A and C) and extrapolative (B and D) versions of habitat models respectively. Colours indicate the environmental variable constraining habitat suitability predictions in each landscape cell.

## Appendix B- Animal Tagging Records

Appendix B provides supplementary and supporting materials for chapter 5: Independent Observation: Monitoring the Gouland Downs Reintroduction.

### B.1 Monitoring Data from the Kahurangi Reintroduction

**Table B.1-** Summary of monitoring records per bird in Kahurangi National Park. Birds with no tag info were not GPS tagged. “Unknown” fate is recorded for birds with lost/failed radio tags, so they could not be located on the ground.

Bird Name	Sex	Bird age (in 2018)	First on-the-ground Record	Last on-the-ground Record	Number of on-the-ground records	On-the-ground tracking period/ Days	First satellite tag Record	Last satellite tag Record	Number of satellite tag records	Satellite tag tracking period(s)/ Days	Fate as of the end of the study period
Catlin	Female	13	1/05/2018	15/10/2019	22	532	2/05/2018	16/05/2018	78	14	Dead - 2020-07-24
Dalrachney	Female	2	20/03/2018	7/09/2020	53	902	21/03/2018	10/12/2018	384	264	Alive
Ehara	Female	2	1/05/2018	18/04/2019	14	352	NA	NA	NA	NA	Unknown - 2019-04-18
Erewhon	Female	2	20/03/2018	22/08/2020	53	886	2/05/2019	12/05/2019	96	10	Dead - 2020-08-22
Hine Pou Pou	Female	7	20/03/2018	25/07/2019	29	492	NA	NA	NA	NA	Dead - 2020-07-01
Hyde	Female	8	20/03/2018	1/05/2019	28	407	21/03/2018	5/02/2019	525	321	Dead - 2020-03-15
Kapakapapanui	Female	3	1/05/2018	14/08/2020	26	836	NA	NA	NA	NA	Alive
Kauri	Male	2	20/03/2018	8/09/2020	54	903	21/03/2018	10/05/2019	729	415	Alive
Langley	Male	8	20/03/2018	8/09/2020	57	903	NA	NA	NA	NA	Alive

Lily	Female	9	20/03/2018	13/06/2020	36	816	21/03/2018	8/12/2018	414	262	Unknown - 2020-06-13
Mahia	Female	3	20/03/2018	13/06/2020	36	816	NA	NA	NA	NA	Unknown - 2020-06-13
Maki	Female	2	20/03/2018	22/08/2020	37	886	NA	NA	NA	NA	Dead - 2020-08-22
Matariki Rarotoka	Male	12	1/05/2018	30/01/2020	24	639	NA	NA	NA	NA	Alive
McKellar	Female	3	20/03/2018	8/09/2020	61	903	2/05/2019	16/05/2019	129	14	Alive
Moana	Male	2	24/04/2018	10/09/2020	43	870	NA	NA	NA	NA	Alive
Muller	Female	2	20/03/2018	9/09/2020	44	904	22/03/2018	3/12/2018	342	256	Alive
Nohoia	Female	7	20/03/2018	15/03/2020	38	726	3/05/2019	12/05/2019	108	9	Dead - 2020-03-15
Nohorua	Male	8	20/03/2018	25/07/2019	31	492	26/07/2019	1/08/2019	24	6	Dead - 2020-05-26
Pipper	Female	8	1/05/2018	29/11/2018	13	212	NA	NA	NA	NA	Dead - 2018-11-29
Rerehu	Male	9	20/03/2018	8/09/2020	59	903	NA	NA	NA	NA	Alive
Rocket	unknown	0	1/12/2018	25/07/2019	2	236	25/07/2019	29/07/2019	15	4	Unknown - 2020-03-15
Rusby	Female	10	1/05/2018	1/07/2020	26	792	NA	NA	NA	NA	Dead - 2020-07-01
Scoop	Male	2	1/05/2018	10/09/2020	43	863	2/05/2018	3/11/2018	401	185	Alive
Shadowfax	Male	10	1/05/2018	13/06/2020	27	774	2/05/2018	3/10/2018	371	154	Dead - 2020-06-13
Shiner	Unknown	0	1/12/2018	9/09/2020	35	648	2/05/2019	8/05/2019	71	6	Alive
Taco	Male	2	20/03/2018	18/08/2020	53	882	21/03/2018	8/05/2019	626	413	Dead - 2020-08-18
Tametame	Male	8	20/03/2018	1/08/2020	48	865	21/03/2018	10/05/2019	243	415	Dead - 2020-08-01
Te Uatorikiriki	Female	7	1/05/2018	10/09/2020	47	863	2/05/2018	5/05/2019	295	368	Alive
Temple	Female	2	20/03/2018	10/09/2020	55	905	21/03/2018	8/05/2019	114	413	Alive
Tihaka	Male	6	1/05/2018	9/09/2020	40	862	2/05/2018	21/11/2018	380	203	Alive
Tupuanuku	Female	2	1/05/2018	8/09/2020	46	861	NA	NA	NA	NA	Alive
Uruao	Female	8	20/03/2018	8/09/2020	57	903	2/05/2019	8/06/2019	296	37	Alive
Total					1237	23835			5641	3769	
Mean					38.7	745			282	188	
St.Dev					14.6	207			203	165	

## B.2 Daily Activity Patterns

Here I present an additional analysis of the data collected from post-release monitoring of the reintroduced population aiming to assess daily activity patterns of takahē in Kahurangi NP. These were represented by average movement speeds calculated from fix data.

### *Methods*

Daily activity patterns were calculated by finding the lateral groundspeed between fixes 1-hour apart for birds based on satellite tag data from tracking days with 1-hour or finer fix-intervals. While this metric is not an ideal index of activity (as non-movement activity and any movements up and down elevational gradients are not represented) it should broadly correlate with the relative activity of birds. Plotting patterns of these average groundspeeds against the hours of the day allowed identification of trends in gross animal movements (taken as an indicator of general activity levels) across a 24-hour period (Recio *et al.*, 2010).

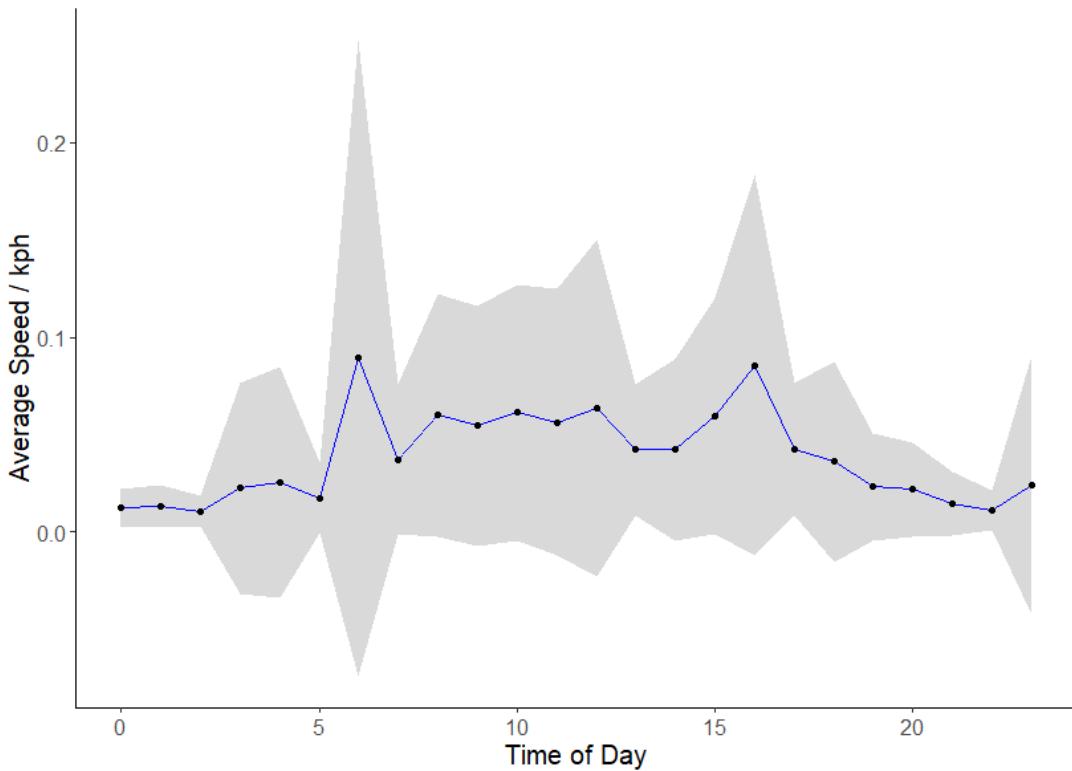
### *Results*

Figure B.1 shows the relationship between lateral groundspeed and time of day, revealing a crepuscular pattern, where activity is highest around dawn and dusk, although activity in daylight hours is also higher than that measured at night. The high variation observed around these patterns is likely due to natural variation in activity patterns between individuals and between days, but also to the likely variable correlation between lateral movement speed and non-movement based activity (e.g., feeding, fighting, mating etc.).

### *Discussion*

For assessments of daily activity patterns based on satellite tag data, no monitoring data from the Murchison Mountains has the resolution to enable calculation of comparative daily activity patterns. However, general activity levels, and daily activity patterns revealed through these analyses appear to be plausible and reasonable for wild takahē. This is encouraging as any unexpected patterns might suggest that the reintroduced population was potentially experiencing chronic stress (Teixeira *et al.*, 2007) or were exhibiting potentially maladaptive behaviour, i.e., foraging at times that increased risk of predation (at least to native predators, though crepuscular activity may increase exposure to invasive mammalian predators that are also active at dawn and dusk, although such predators are

controlled to low densities in Kahurangi National Park; Hoare, 2006; Takahē Recovery Program, 2016; O'Donnell et al., 2017).



**Figure B.1-** Daily activity patterns for takahē reintroduced to Gouland Downs from GPS records with hourly fixes (429 movement steps from 23 satellite tags and 21 birds). Black dots indicate the 'on-the-hour' values, the blue line shows the overall trend by joining these hourly values and the grey shaded area indicates  $\pm 1$  standard deviation.

The evidence to date suggests that crepuscular activity is a natural baseline in takahē that is preserved both in both wild and captive settings. However, this cannot be claimed with certainty as the Kahurangi population was initially reintroduced from captive stock, so it could still be that these behavioural patterns are ingrained in captivity and have been maintained post-release in Kahurangi. Considering these preliminary analyses, I suggest that further research is needed into activity patterns in takahē in order to confirm and resolve inferences presented herein. It would be useful to investigate activity patterns further by placing satellite tags and/or activity loggers on wild takahē that have never been in captivity (i.e., in the Murchison Mountains) and non-tussock grazing takahē (i.e., those feeding on introduced grasses and fallen fruits at some secure sites) to see if these patterns are conserved across further populations in different contexts.

### B.3 Details of Dispersal Calculation and Data Curation

Before assessing post-release dispersal distances for reintroduced takahē, the on-the-ground records were filtered. Firstly, records from birds fledged in the Gouland Downs were removed prior to any within-site translocations as they did not have a release site associated with them. I then removed records for which bird status was listed as dead or unknown ( $n=8$ ), retaining only records for birds listed as alive at the time the record was taken. Next, I removed records taken before 24<sup>th</sup> July 2018 ( $n=353$ ). This was because the population was oversampled in the first months following initial releases relative to the rest of the study period (section 5.2.2, Figure 5.3). Furthermore, the birds had only a limited opportunity to acclimatise to the release area and/or to disperse in the initial months following reintroduction, so I considered that these earlier records would be overly autocorrelated with release sites. I then split birds based on their social context, comparing dispersal in birds recorded as “single” with those indicated to be associated with a social and/or breeding group (combining recorded categories of ‘pair’, ‘trio’, ‘juvenile’, ‘subadult’, ‘breeding’ into a single category, ‘group’). The dispersal distances recorded, following this restriction of the on-the-ground record data are shown in Figure 5.5.

## **Appendix C- Descriptive Analysis Input Data, Output Treatment and Methodological Discussion**

Appendix C provides supplementary and supporting materials for Descriptive Models: Reconstructing Detailed Population Distributions by Combining “Patchy” Datasets.

### **C.1 Environmental Predictor Data Sources and Processing**

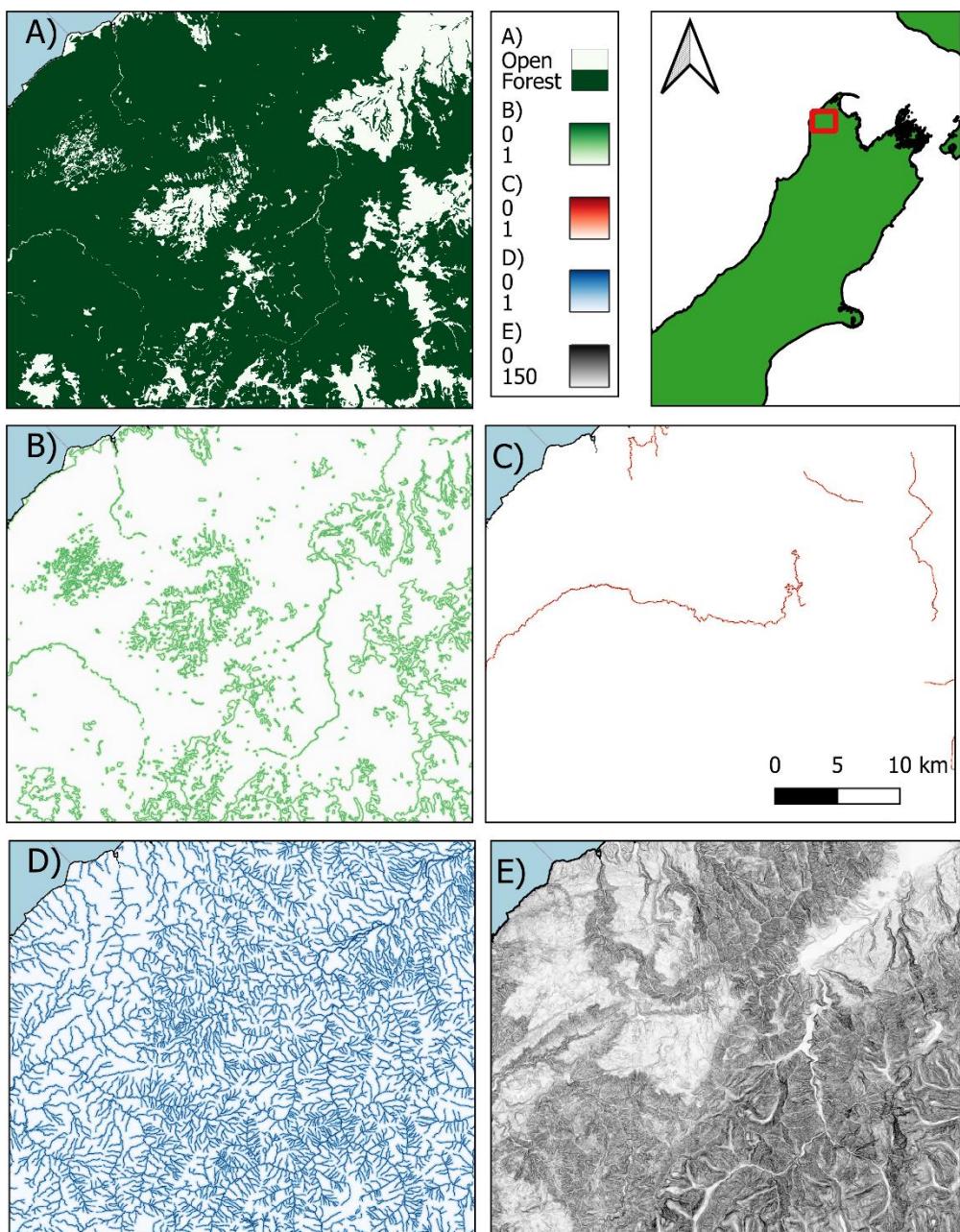
Details of the source files used to create environmental predictor layers for Step Selection Function (SSF) presented in Section 6.3.2 are shown in Table C.1.

**Table C.1-** Environmental predictor variables prepared for environmental preference Step Selection Functions.

Predictor	Source Layer	Download	Data Provider	Format
Source and date				
Vegetation	NZ Native Polygons (Topo, 1:50k)	LINZ, 7 <sup>th</sup> December 2020	Land Information	ESRI polygon shapefile
				New Zealand
Distance to forest edge	NZ Native Polygons (Topo, 1:50k)	LINZ, 7 <sup>th</sup> December 2020	Land Information	ESRI polygon shapefile
				New Zealand
Distance to paths	NZ Walking and Biking Tracks	LINZ, 20 <sup>th</sup> August 2018	National Tracks	ESRI polyline shapefile
Distance to rivers	NZ River Polygons (Topo, 1:50K) / NZ River Centrelines (Topo, 1:50k)	LINZ, 28 <sup>th</sup> January 2021 / 20 <sup>th</sup> August 2018	Land Information New Zealand	ESRI polygon shapefile / ESRI polyline shapefile
Terrain slope	NSDEM South Island 25 metre	LRIS, 20 <sup>th</sup> August 2018	Landcare Research	25m raster (GEOTIFF)

Source data were processed by first cropping them to the focal area for analyses (the rectangular extent of a 5km buffer area around all on-the-ground records). Following this all layers (excluding terrain slope) were rasterised to a 25m resolution using the NZDEM South Island layer as a template, cells in the raster output had a value of 1 if their centroid

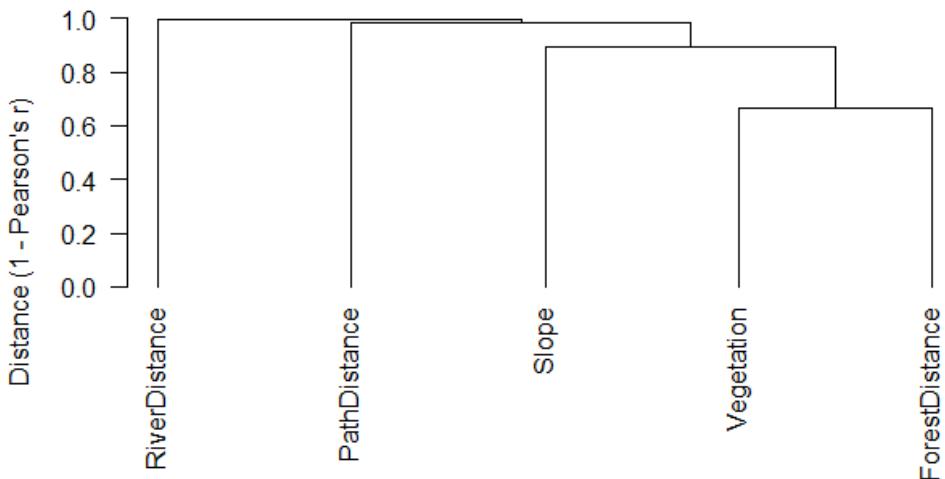
overlapped a feature in the shapefile input, else they had a value of 0. No further manipulations were performed for the vegetation predictor, so it remained a binary raster layer. For the distance to feature predictors, a distance raster was calculated from the binary rasters in QGIS using the Proximity (raster distance) function (QGIS Development Team, 2017). To generate the distance to forest edge predictor this was also performed on an inverted binary raster layer, producing an output reflecting distances within forest polygons, distance to forest edge was then taken by summing “outside forest distance” and “inside forest distance” rasters. Terrain slope was also calculated in QGIS using the slope function in the DEMTools menu. Non-land areas were then masked from all predictor rasters using the Ids NZ Coastlines and Islands Polylines (Topo 1:50k) shapefile from LINZ. This was done in R using the *raster* (Hijmans, 2016) and *sp* (Pebesma and Bivand, 2005) packages such that cell values in marine areas were replaced with NA. Finally, the distance rasters were transformed using the negative exponential formula described in Section 6.2.2. Finalised SSF environmental inputs are shown in Figure C.1.



**Figure C.1-** Environmental predictor variables used in Step Selection Functions with satellite tag records from takahē in the Gouland Downs. A) Vegetation B) Distance to Forest Edge C) Distance to Paths D) Distance to Rivers and E) Terrain Slope. B, C and D are inverse negative exponential transformations of metre distances.

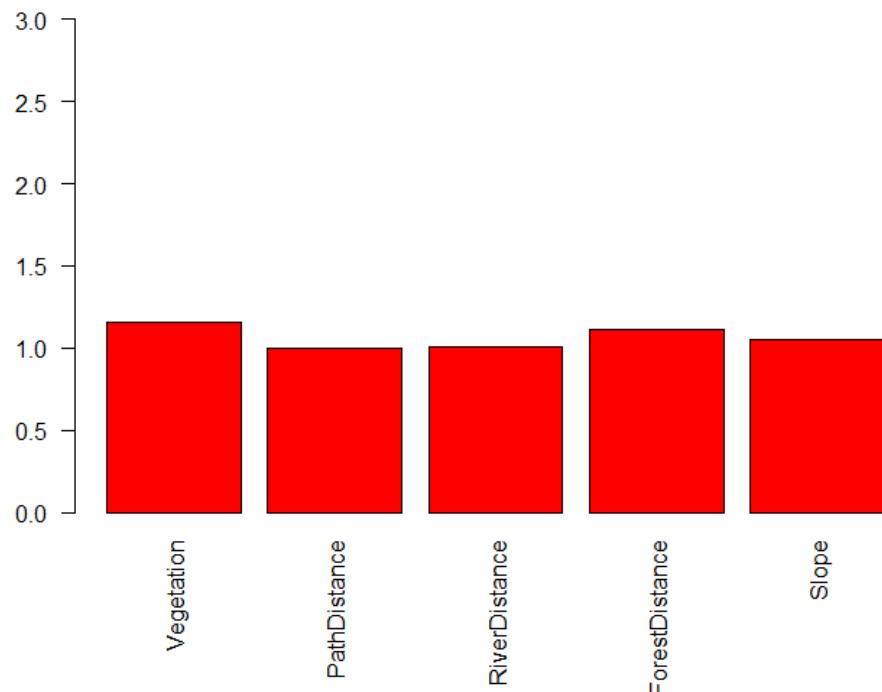
## C.2 Collinearity Testing

Figures C.2 shows the Pearson's correlations of environmental predictors in the Gouland Downs study area using the virtual species package in R (Leroy *et al.*, 2016). As can be seen, based on a 0.7 Pearson's threshold, no predictor variables are considered too correlated to be fit in the same model.



**Figure C.2-** Collinearity indicated by Pearson's correlation coefficient for Step Selection Function environmental predictors in the Gouland Downs.

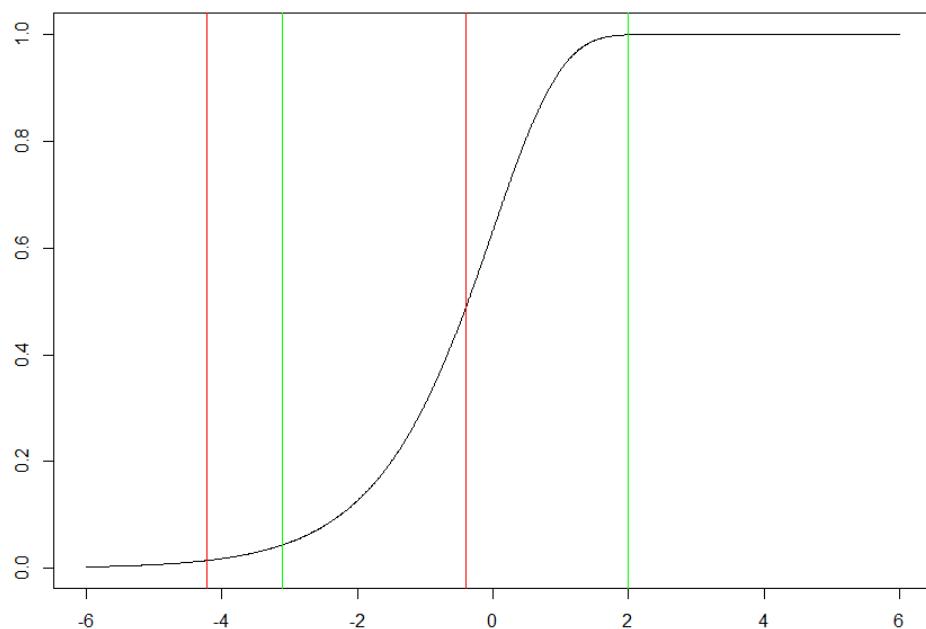
Figure C.3 shows the Variance Inflation Factors calculated for environmental predictor variables calculated using the *usdm* package in R (Naimi *et al.*, 2014) for the Gouland Downs study area. As can be seen the Variance Inflation factors are low (less than 1.5) for all predictor variables. Therefore, based on both the low Pearson's r and VIF scores, I determined that all predictor variables could be included in the fitted SSF without collinearity compromising model fitting.



**Figure C.3-** Variance Inflation Factors for candidate environmental variables for Kahurangi National Park.

### C.3 Complementary-Log-Log Transformation

Before application of the complementary-log-log (cloglog) transformation to the linear projection of the fitted SSF the linear projection was rescaled so that, when transformed, the cloglog projection would cover most of the theoretical range of values that the cloglog function can theoretically output (the cloglog function has limits at 0 and 1). Figure C.4 shows the cloglog function, with vertical lines showing the maximum and minimum values of the linear (red) and transformed linear (green) projections. From this the increased range of values that were returned from a transformation of the rescaled linear projection relative to the raw linear projection can be seen. This scaling was chosen to ensure that, as much as possible, the full theoretical range of the cloglog function was returned in the cloglog projection. The cloglog-transformed projection was found to produce an intuitive range of outputs, when compared with alternatives (Figure C.11). From comparisons with raw data it was considered that a threshold of 0.5 effectively partitioned the landscape into estimates of habitat and inter-habitat matrix.



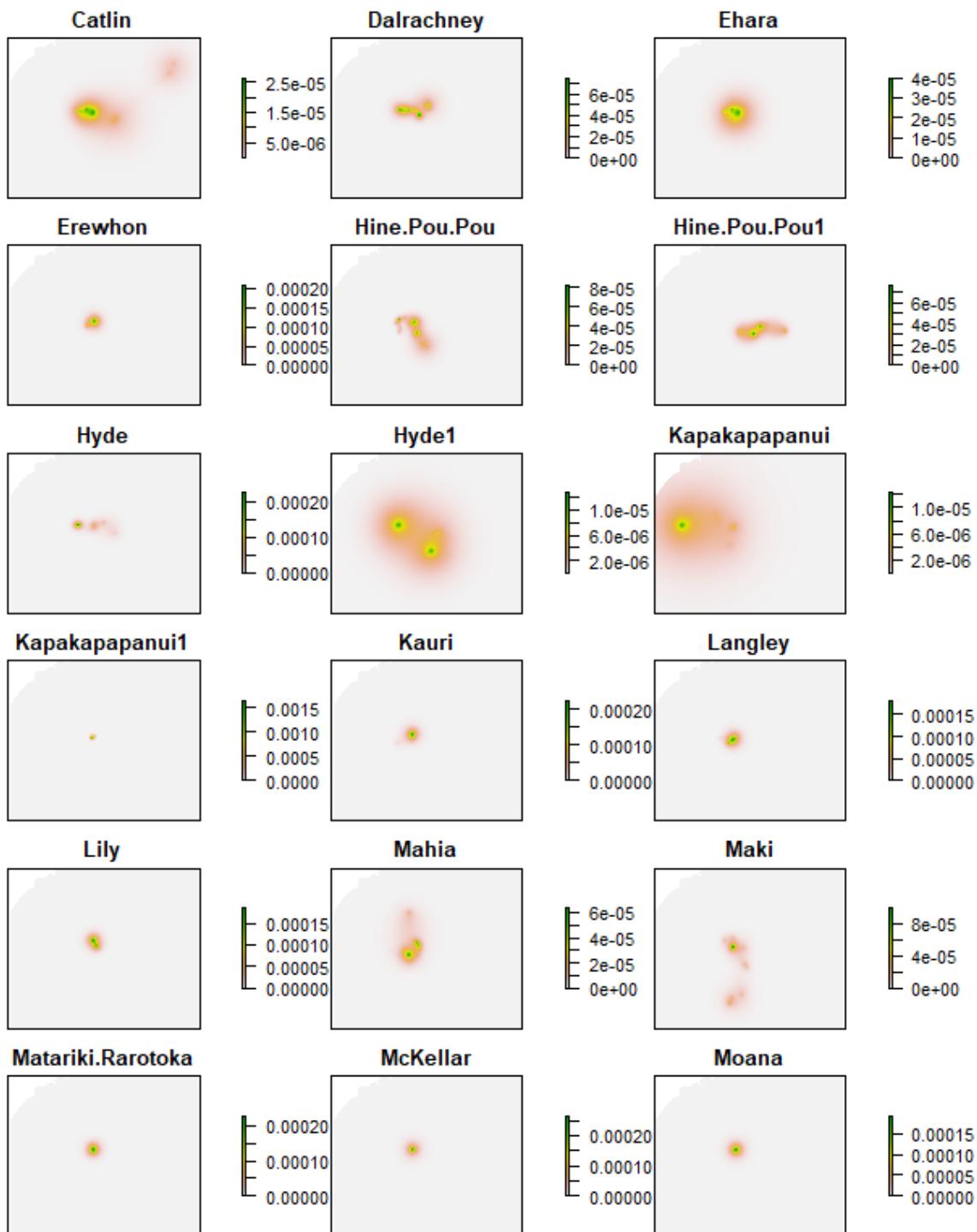
**Figure C.4-** Plot of the complementary log-log function used to transform the linear projection of Step Selection Function. The black line is the complementary-log-log function ( $y = 1 - e^{-x}$ ), red lines indicate the range of the linear projection of the fitted Step Selection Function (maximum and minimum values), while green lines show these maximum and minimum values of the rescaled linear projection.

## C.4 Brownian Bridge Movement Model Inputs

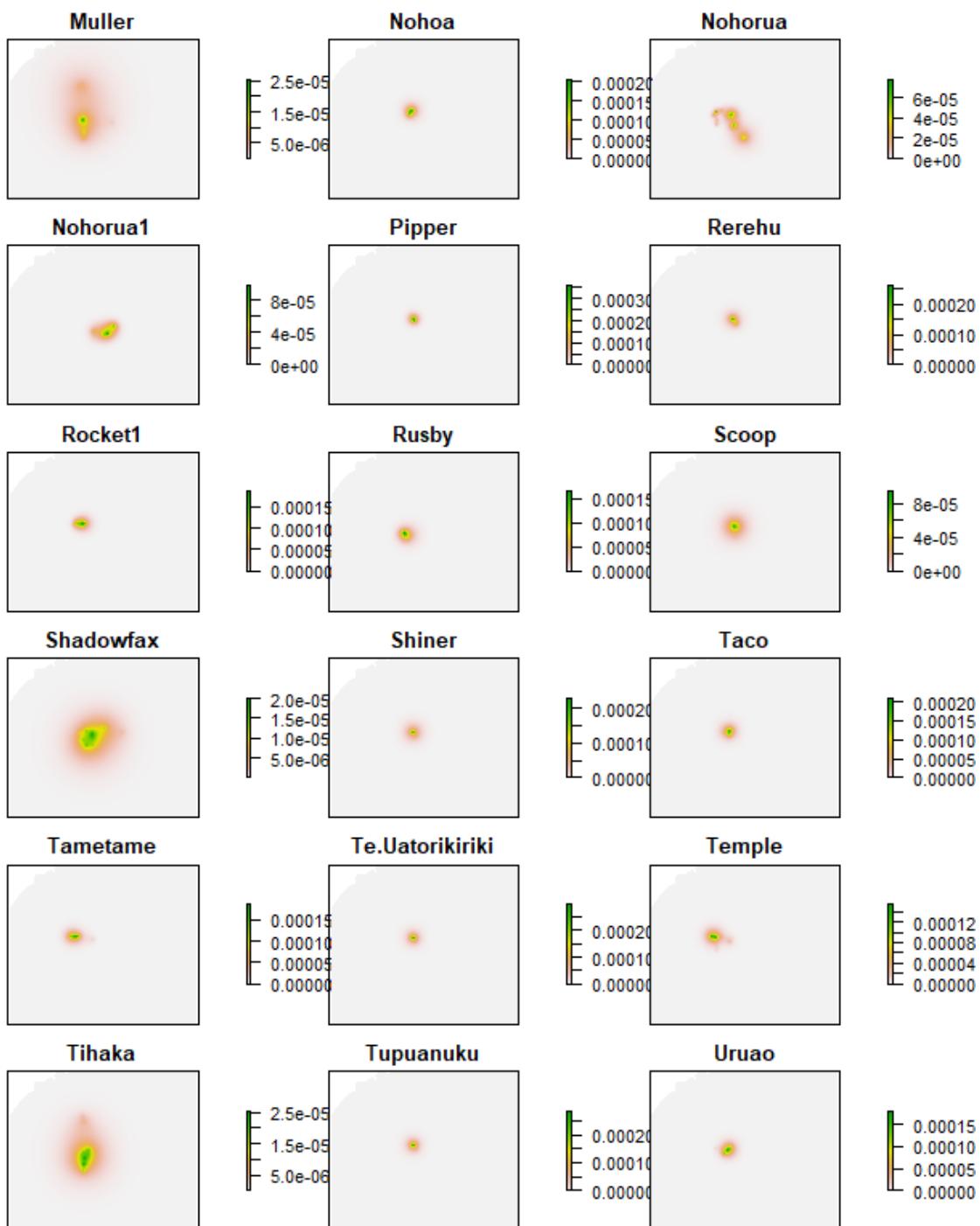
**Table C.2-** Summary of on-the-ground tracks for takahē in Kahurangi National Park used for Brownian Bridge Movement Models. Tracks are identified by bird names, those suffixed by '1' indicate this is a post-translocation track. Brownian motion variance values were calculated from fitted models.

Track	Track Start	Track End	Location Records	Brownian Motion Variance
Catlin	2/05/2018	15/10/2019	17	5.36
Dalrachney	21/03/2018	7/09/2020	40	1.00
Ehara	2/05/2018	18/04/2019	10	10.25
Erewhon	22/03/2018	22/08/2020	40	1.00
Hine Pou Pou	21/03/2018	25/07/2019	23	1.30
Hine Pou Pou 1	9/10/2019	1/07/2020	4	1.00
Hyde	21/03/2018	1/05/2019	24	1.00
Hyde 1	27/06/2019	30/01/2020	7	17.80
Kapakapapanui	2/05/2018	14/08/2020	16	19.80
Kapakapapanui 1	18/08/2020	10/09/2020	6	1.00
Kauri	22/03/2018	8/09/2020	36	1.00
Langley	22/03/2018	8/09/2020	42	1.00
Lily	21/03/2018	30/01/2020	30	1.00
Mahia	22/03/2018	26/05/2020	24	1.67
Maki	22/03/2018	22/08/2020	28	1.00
Matariki Rarotoka	2/05/2018	30/01/2020	20	1.00
McKellar	22/03/2018	8/09/2020	41	1.19
Moana	2/05/2018	10/09/2020	26	1.00
Muller	22/03/2018	9/09/2020	31	9.58
Nohoia	22/03/2018	30/01/2020	26	1.00
Nohorua	21/03/2018	25/07/2019	24	1.31
Nohorua 1	9/10/2019	26/05/2020	4	1.00
Pipper	2/05/2018	29/11/2018	11	1.00
Rerehu	21/03/2018	8/09/2020	45	1.00
Rocket 1	6/10/2019	30/01/2020	5	1.00
Rusby	2/05/2018	1/07/2020	18	1.00
Scoop	2/05/2018	10/09/2020	35	3.91
Shadowfax	2/05/2018	2/06/2020	17	6.29
Shiner	3/05/2019	8/09/2020	22	1.00
Taco	22/03/2018	18/08/2020	37	1.00
Tametame	21/03/2018	31/05/2020	36	1.00
Te Uatorikiriki	2/05/2018	10/09/2020	35	1.00
Temple	21/03/2018	10/09/2020	38	1.00
Tihaka	2/05/2018	9/09/2020	27	5.45
Tupuanuku	2/05/2018	8/09/2020	34	1.00
Uruao	22/03/2018	8/09/2020	42	1.00
Mean			25.6	3.00
Standard Deviation			12.1	4.49

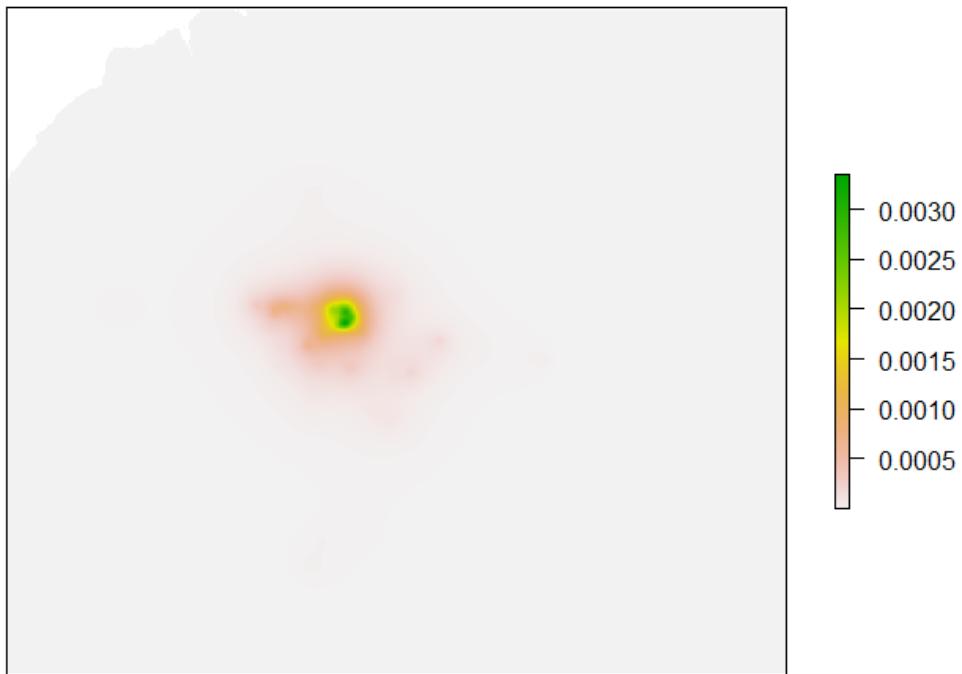
### C.5 Individual-level Brownian Bridge Movement Model outputs



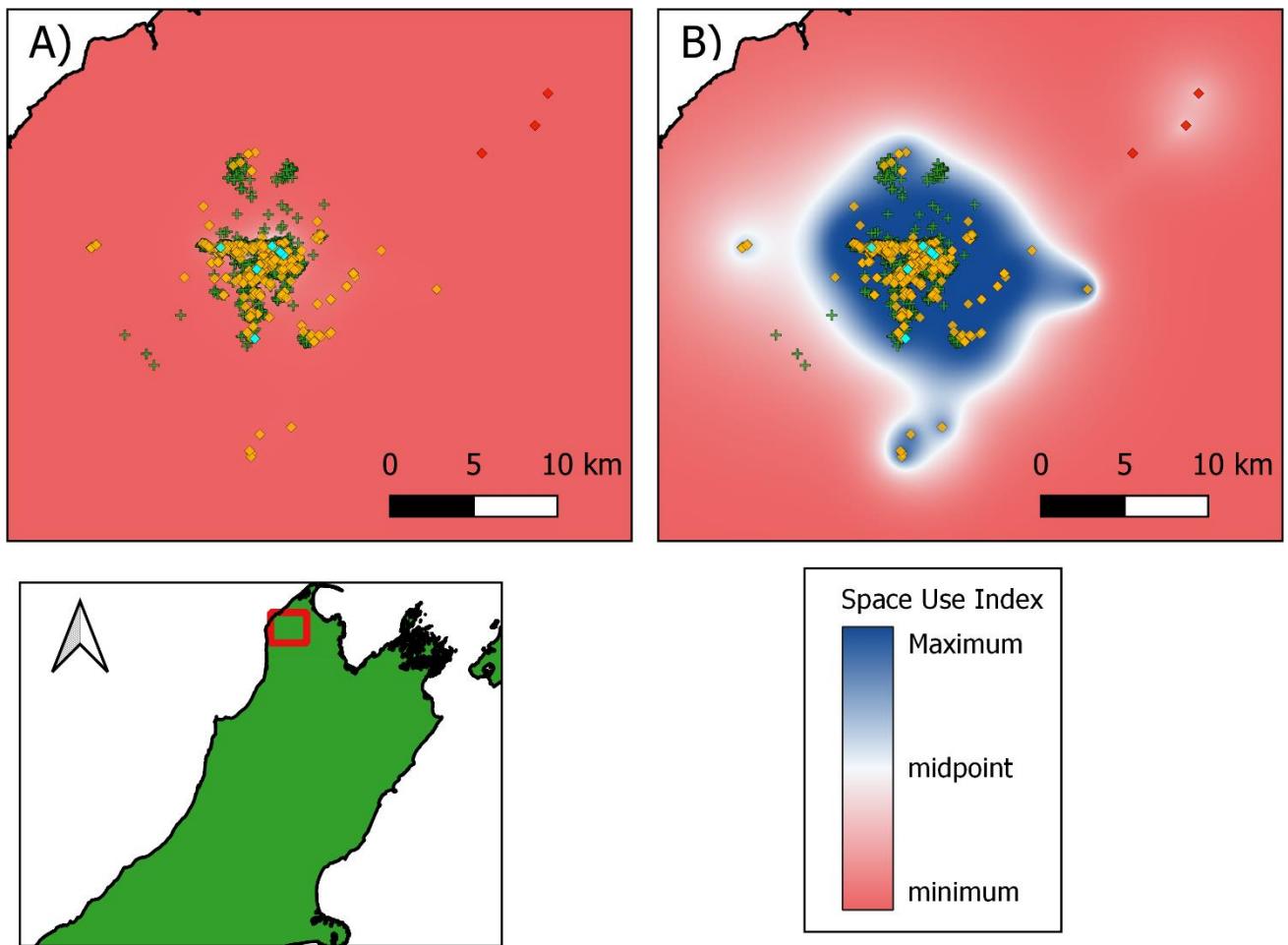
**Figure C.5-** Utilisation distributions for the first 18 tracks fitted to on-the-ground records of takahē movement in the Kahurangi National Park by Brownian Bridge Movement Models. Plots are titled by bird names. Titles ending with a 1 indicate that the bird was subject to an internal translocation and that the plotted utilisation distribution was calculated for the recorded movements following this internal translocation.



**Figure C.6-** Utilisation distributions for the second 18 tracks fitted to on-the-ground records of takahē movement in Kahurangi National Park by Brownian Bridge Movement Models. Plots are titled by bird names. Titles ending with a 1 indicate that the bird was subject to an internal translocation and that the plotted utilisation distribution was calculated for the recorded movements following this internal translocation.



**Figure C.7-** Population utilisation distribution generated by summing the individual-level outputs (Figures C.5 and C.6) from on-the-ground records of takahē movement in Kahurangi National Park.



**Figure C.8-** Post release monitoring data overlaid on population summed Brownian Bridge Movement Model outputs from takahē reintroduced to the Gouland Downs. A) shows the unmodified population-summed output (minimum= 0, midpoint= 0.00140, maximum= 0.00280), while B) shows the transformed population summed output (minimum= 0, midpoint= 0.5, maximum= 1). Diamonds indicate on-the-ground tracking points (from VHF radio tracking) while green plusses indicate satellite records (from deployed GPS tracking tags).

## C.6 Step Selection Function Inputs

A summary of the satellite tag tracks collected for the Gouland Downs population, following the data curation described in Chapter 4, is provided in Table C.3. Table C.4 shows an equivalent summary for the tracks retained following a resampling of the data, retaining only tracks with a consistent 3-hour fix interval, as described in Section 6.2.2.

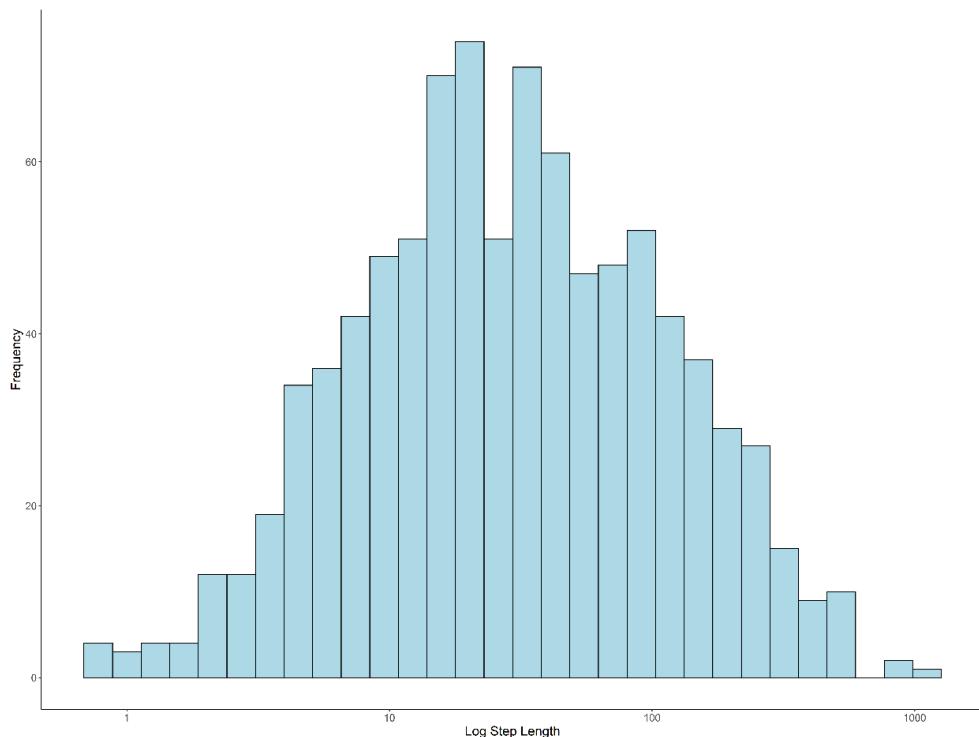
**Table C.3-** Summary of track attributes for satellite tag dataset for takahē reintroduced to Kahurangi National Park.

Bird name	Interval between successful fixes (hours)					Successful fixes
	min	Median	Mean	Max	SD	
Hyde	1.0	12.0	14.7	96.0	11.8	524
Muller	1.0	12.0	18.0	228.0	17.5	341
Dalrachney	1.0	12.0	16.6	120.0	12.8	383
Nohoa	1.0	2.0	2.0	6.0	0.8	107
Tametame	1.0	12.0	15.2	57.0	11.7	175
Kauri	1.0	12.0	13.7	2131.0	79.3	728
Lily	1.0	12.0	15.3	72.0	11.0	413
Te Uatorikiriki	1.0	6.0	30.1	6386.0	372.0	294
McKellar	1.0	2.0	2.6	24.0	2.4	128
Tihaka	1.0	12.0	12.9	588.0	36.0	379
Taco	1.0	12.0	15.9	3072.0	122.8	625
Scoop	1.0	12.0	11.1	72.0	9.1	400
Shadowfax	1.0	12.0	10.0	48.0	7.5	370
Erewhon	1.0	2.0	2.5	22.0	2.9	95
Catlin	1.0	3.0	4.3	30.0	3.7	77
Uruao	0.5	2.0	3.0	12.0	2.5	295
Shiner	1.0	2.0	2.0	20.0	2.3	70

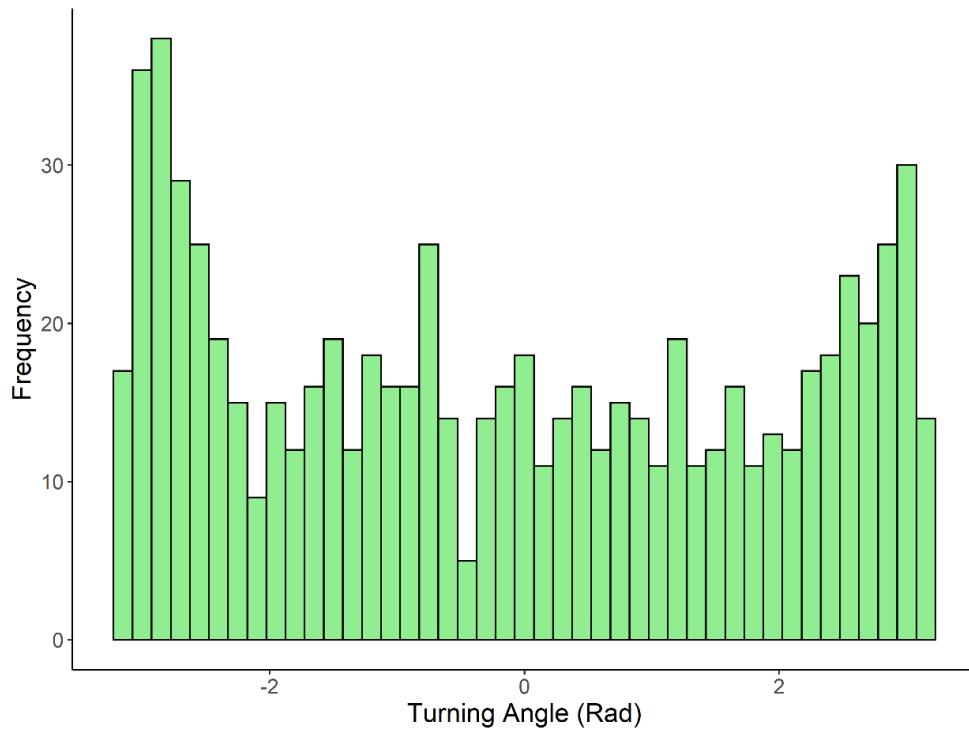
**Table C.4 -** Summary of track attributes for satellite tag dataset for takahē reintroduced to Kahurangi National Park following data resampling.

Bird name	Interval between successful fixes (hours)					Successful fixes
	min	Median	Mean	Max	SD	
Hyde	3.0	3.0	97.8	1482.0	313.2	78
Muller	3.0	3.0	157.7	1452.0	359.2	28
Dalrachney	3.0	3.0	139.6	2181.0	397.7	42
Nohoa	3.0	3.0	3.0	3.0	0.0	6
Tametame	3.0	3.0	143.1	1440.0	402.0	17
Kauri	3.0	3.0	57.6	2131.0	256.5	170
Lily	3.0	3.0	112.1	1449.0	294.5	52
Te Uatorikiriki	3.0	3.0	84.3	6551.0	648.5	104
McKellar	3.0	3.0	3.2	4.0	0.4	5
Tihaka	3.0	3.0	30.9	726.0	132.1	118
Taco	3.0	3.0	62.3	3606.0	333.7	157
Scoop	3.0	3.0	34.9	720.0	142.3	126
Shadowfax	3.0	3.0	29.1	720.0	128.5	125
Erewhon	3.0	3.0	3.0	3.0	0.0	7
Catlin	3.0	3.0	5.4	57.0	8.2	51
Uruao	3.0	3.0	29.7	670.0	133.4	25
Shiner	3.0	3.0	3.0	3.0	0.0	6

The step lengths and turning angles observed in 3-hour satellite tracks are summarised in Figures C.9 and C.10 respectively. Step-lengths calculated over 3-hour fix intervals are right-skewed, as is typical of movement data, representing many short-range movements within a home range with occasional longer range exploratory/dispersal movements (Figure C.8). The turning angles associated with takahē movement steps also indicate that the majority of movements are likely within home range movements, as the low directional persistence (no observed bias towards turning angles  $\approx 0$ ) indicates that the birds are generally not moving in a directed fashion. The relatively high frequencies of steps with a high turning angle indicates that the birds were often doubling back on themselves, perhaps indicating foraging behaviour along linear features (Figure C.10).



**Figure C.9-** Distribution of step lengths recorded across takahē movement tracks recorded by satellite tags following resampling to consistent 3-hour relocation intervals. Step lengths are presented on a log10 axis scale. Median step length = 28.2m.

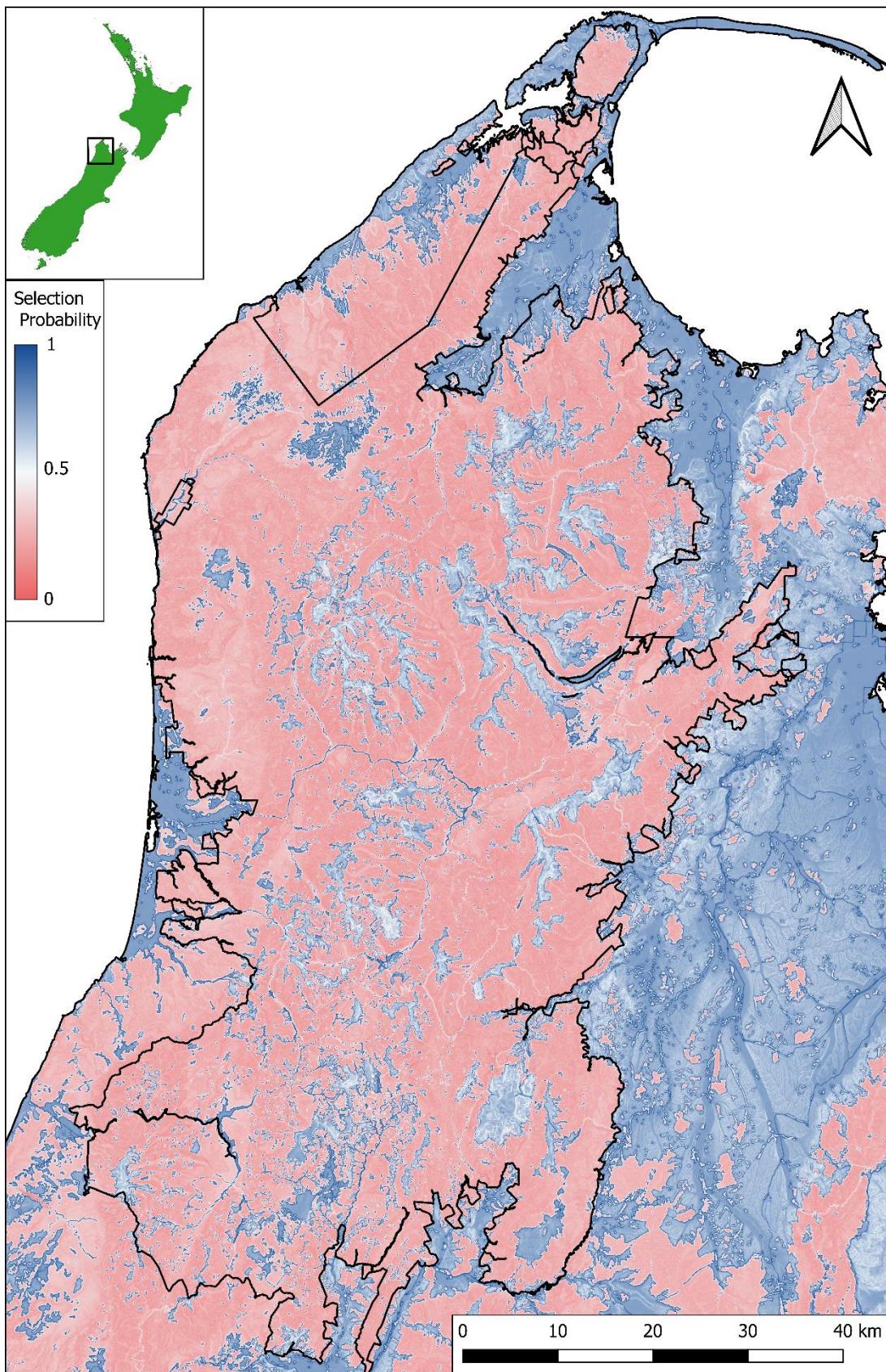


**Figure C.10** - Distribution of turning angles recorded across takahē movement tracks recorded by satellite tags following resampling to consistent 3-hour relocation intervals.

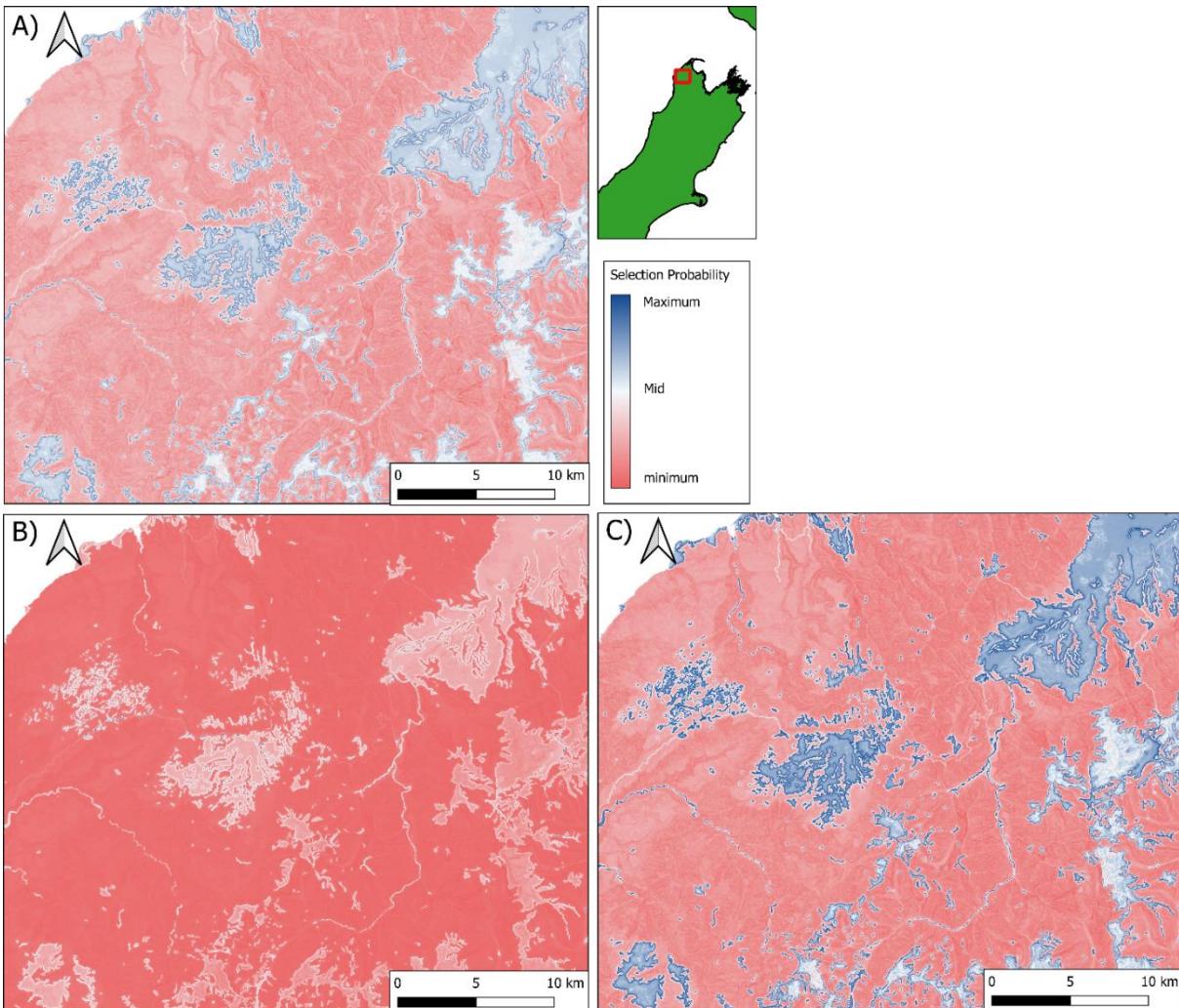
## C.7 Step Selection Function Projections

The cloglog projection of the fitted SSF are shown in Figure C.11 for the full extent of Kahurangi National Park. This projection should be a useful resource for the management of takahē within Kahurangi National Park into the future, as the National Park is considered the management unit for the long-term stewardship of the population (TRG, unpublished strategies).

Different projection options (linear, exponential and cloglog) are compared in Figure C.12. The distributions in the linear and exponential projections (panels A and B) are considered to be the result of assuming unrealistic synergies between the distance-based predictors (i.e., high scoring areas are close to both paths and forest edges, especially in the exponential projection). The cloglog projection appears to be more ecologically realistic, as in this projection proximity to linear features is interpreted as having a more marginal impact on inferred selection probability. I strongly suggest that, at least of these three options, the cloglog projection should be most informative and useful for takahē management purposes.



**Figure C.11-** Projection of the Step Selection Function based on satellite tag data from birds reintroduced to the Gouland Downs. The projection covers the extent of Kaurangi National Park.



**Figure C.12-** Projections of the Step Selection Function fitted to satellite tag data of takahē reintroduced to the Gouland Downs. A) linear projection, B) exponential projection and C) complementary-log-log (cloglog) projection. For all projections, colours are indexed to the range of values represented in the projection (red for minimum represented values, white for middle values and blue for maximum values), so that the projections are comparable in terms of indicating the distribution of the data in relative terms. Minimum, middle and maximum values for each projection are as follows: linear projection; -3.51, -1.97, -0.437, exponential projection; 0.0299, 0.338, 0.646, cloglog projection; 0.109, 0.554, 0.999.

## C.8 Methodological Discussion and Considerations

While the methods applied in this chapter were chosen to be appropriate for analyses of the Gouland Downs datasets, alternative methods could have been used in a similar general framework to generate outputs predicting similar quantities to those reflected in the combined model map (Figure 6.3).

*Long-term Space Use Models (Brownian Bridge Movement Models)*

One interesting option would have been to replace the BBMMs with a circuit theory model (Hanks and Hooten, 2013). In this application, the on-the-ground records could have been modelled as nodes, connected by a conductivity surface generated from the SSF output, current could then be stimulated between nodes representing subsequent on-the-ground location records with a voltage inversely proportional to the time interval between the two locations. In such a way movements between on-the-ground location records would be directly simulated and interact with the environmental selection identified in the SSF (Mateo-Sánchez *et al.*, 2015). This could be an advantage over the methods I employed in Chapter 6, where movement paths were more indirectly indicated by a simple weighting process, while maintaining the benefits of the BBMM method (paths/space-use more diffuse with increasing temporal separation and/or reducing spatial separation). However, as this would be an atypical application for a circuit theory model, it is likely that a significant amount of time would need to be spent building and applying a suitable modelling procedure.

Further approaches are available to model takahē space-use based on the on-the-ground records, particularly as the BBMM method applied could be considered overly complex given the coarseness of data they were fitted to. Simpler methods for identifying core-use areas include, for example, minimum convex polygons, which identify home ranges through linear connections between location records (Calenge, 2006). However, while such methods are analytically simpler than BBMMs, and may seem more appropriate for the coarse on-the-ground dataset, they do not take account of animal movement processes, nor uncertainty in these movements and inaccuracy in location records (Tatman, Stevens-Wood and Smith, 2000). Furthermore, the space-use predictions generated by alternate methods are most commonly binary (based on defining polygons representing core-use, or home range, areas, with utilisation distributions identified by BBMMs also commonly being binarized; Joo *et al.*, 2020). Binary estimations of core space-use areas were avoided for these analyses as these coarse delimitations can mask uncertainty in estimates of space-use (Horne *et al.*, 2007). This was particularly important given the poor temporal resolution of the on-the-ground data available to model space use, as it was appropriate to consider the high uncertainty in defining and separating used from unused areas when presenting model outputs. By transforming the predicted utilisation distributions, I was able to present predictions with a scaling that effectively separated likely used from unused areas, but still

presented these as probabilistic estimates with ‘soft edges’ which reflect the considerable uncertainty regarding this delimitation (Figure 6.1).

#### *High-Resolution Environmental Selection Models (Step Selection Functions)*

Although the SSFs used here are arguably the most suitable method for identifying environmental selection based on the satellite data, other methods were available. In cases where different kinds of species data is available other methods might be more relevant, for instance if temporal information for fixes were unknown (or otherwise inaccurate, unreliable or inconsistent), resource selection functions (McGarigal *et al.*, 2016) or habitat suitability models (Guisan *et al.*, 2013; Norberg *et al.*, 2019) could be appropriate methods to predict species’ environmental selection and identify habitat suitability.

Furthermore the SSFs developed in this chapter have the scope to be developed and refined further, as multi-model inference (Harrison *et al.*, 2018) and model averaging (Dormann, Calabrese, *et al.*, 2018) could be used to develop models and maximise their fit to the data. Following this, validation of the developed model would be useful for assessing the ability of the model to accurately predict patterns, which will inform the weight that should be given to these predictions (Peters *et al.*, 2015). As this work has not yet been done, the SSF’s presented in this chapter are again best considered as ‘proof of concept’ demonstrations, and they can be usefully refined and improved in later work.

Finally, the cloglog projection method, employed for the SSF requires further conceptual and practical refinement. There was both a conceptual (expected marginal effects of multiple linear features) and practical (the exponential scaling was implausible given knowledge of the populations distribution; Figure 5.4; Appendix C.6) basis for selecting this scaling for the model projection over the commonly used exponential scaling. However, the adoption of the cloglog transformation is not recommended anywhere in the literature for SSF’s and so must be treated with caution. Although the transformation is recommended for MaxEnt habitat suitability models (Phillips *et al.*, 2017) which have considerable similarities to SSFs (both estimate resource selection using a presence/background approach), there are also considerable practical, methodological and conceptual differences between them (e.g., MaxEnt uses species locations whereas SSF’s use movement data as the species input). This means that, although the transformation seems practical and intuitive for these outputs (Appendix C.6) and facilitates the comparison with predictions developed by MaxEnt models in Chapter 4, the assumed equivalence and

conceptual validity of this is questionable. Further work investigating this issue would be fruitful and may yield alternative, more conceptually sound, methods for projecting the SSF and comparing it with MaxEnt-based predictions. However, for the time being there is reason to believe that this treatment, pragmatic as it may be, has yielded useful preliminary outputs. Although it must be considered that, similar to other more experimental aspects of the work presented in chapter 6, that they are best treated as a proof-of-concept until more work is done to develop and refine these methods.

*Estimated Distribution (Combined Brownian Bridge Movement Models and Step Selection Function outputs)*

A key consideration when developing the hybrid framework employed in chapter 6 was the specific aims of the study, i.e., to reconstruct the distribution of the Gouland takahē population from two patchy datasets. For further applications of similar hybrid frameworks study aims should be similarly considered, particularly whether these are predictive or observational, as defined in Chapter 1, i.e., is the focus on pre-management prediction or post-management analysis. Here I sought to be analytical and fitted relationships to observed data. However, there are many instances, especially in reintroduction management and conservation planning more generally, where predictive models can have high value (chapter 3; Hunter-Ayad *et al.*, 2020). For predictive studies, observational data is not available in the area and/or time to which the model is to be applied. This means that information of environmental preferences and animal behaviour will need to be identified outside of the study area and then applied within it. This is very common and straightforward when it comes to environmental suitability/preferences, as these can be readily projected across both space (Jiménez-Valverde *et al.*, 2011) and time (Jarvie *et al.*, 2021) once they are identified. Though questions remain as to the relevance of such projections where the ecological context of the projected space and/or time differs significantly from the context of the data used to identify ecological relationships (Araújo and Peterson, 2012). When it comes to demographic and behavioural projections however, these will often need to be simulated based on observations in other areas, as they cannot be directly projected in predictive models (Palmer, Coulon and Travis, 2011; Bocedi, Palmer, *et al.*, 2014).

The general framework in chapter 6 has potential for further use and development as it was apparently able to overcome the limitations inherent in two incomplete and “patchy” datasets by identifying synergies between them and using them to cross-inform one

another. Although the predictions generated through this approach require validation, the idea seems to have potential for further development. Similar frameworks could be applied to other datasets by adapting the model components used to best suit the specific aims and context of particular studies. This is not specific to reintroduction, nor even conservation ecology, as the core principle of the approach I have taken, paraphrased as; “Identify synergies and complementarity between datasets and analytical methods, then combine analyses to achieve these synergies”, can be applied broadly across ecology (Hunter-Ayad and Hassall, 2020) and many other fields, particularly applied and social sciences. I consider that this approach and mindset has potential to draw the maximum use and potential out of even fragmented, incomplete, or otherwise low-quality data. There are many instances where multiple, individually limited datasets can be used to cross-inform one another, synergising and realising much greater potential together than the sum of their parts.

## **Appendix D**

### **Reception of Thesis Published Outputs at Time of Submission**

Appendix D provides information on the published outputs from this thesis and their response/reception at the time of thesis submission.

**Table D.1-** Details of published outputs from thesis, including links and citations, at time of thesis submission.

Thesis Chapter	Publication Details	Links	Citations
Chapter 2	Hunter-Ayad, J. et al. (2021)	<a href="#">Altmetric</a> (score 14,	8 (dimensions
Practical Context:	'Novel Conditions in	12/11/2021)	12/11/2021)
Novel Conditions in Conservation Translocations	Conservation Translocations: A Conservative-Extrapolative Strategic Framework', <i>Frontiers in Conservation Science</i> , 2(July), pp. 1–14. doi: <a href="https://doi.org/10.3389/fcosc.2021.691714">10.3389/fcosc.2021.691714</a> .		
Chapter 3	Hunter-Ayad, J. et al. (2020)	<a href="#">Publication Impact</a>   0 (12/11/2021)	
Methods Review:	'Reintroduction modelling: a	<a href="#">(frontiersin.org)</a>	
Predictive Models for Reintroductions	guide to choosing and combining models for species reintroductions', <i>Journal of Applied Ecology</i> , 57(7), pp. 1233–1243. doi: 10.1111/1365- 2664.13629.	<a href="#">Altmetric</a> (Score 26, 12/11/ 2021) <a href="#">Otago Daily Times</a> <a href="#">Online News</a> <a href="#">(odt.co.nz)</a>	