Behavioural mechanisms affecting the success of translocations. An investigation using New Zealand's rarest ratite, the rowi.

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Behavioural mechanisms affecting the success of translocations. An investigation using New Zealand's rarest ratite, the rowi. Ph.D.

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Abstract

Translocations are increasingly being used for conservation management of threatened species (Sarrazin & Legendre, 2000). Outcomes are influenced by a range of factors including effects of early rearing experience, conspecific familiarity, density of resident conspecifics, and habitat quality at the release site, all of which may impact on the behaviour of released individuals and subsequent survival and fitness (Law & Linklater, 2007; Linklater & Swaisgood, 2008; Sarrazin & Legendre, 2000). Conservation success, defined as the realisation of goals set out at the start of a project, can be improved by detecting factors causing suboptimal outcomes and identifying potential solutions (Buner et al., 2011; Green et al., 2005; Mihoub et al., 2011).

I aimed to expand current knowledge on factors influencing translocation outcomes by investigating the conservation management of the rowi (*Apteryx rowi*), the rarest species of kiwi. Current rowi conservation practices provide an opportunity to investigate this type of translocation management model. I provide new evidence and knowledge of behavioural mechanisms driving translocation success, include an expansion of current home range cognitive mapping theory relevant to conservation translocations, and present the first study of rowi home range behaviour (defined as the pattern of space use which leads to the emergence of a stable home range). Rowi conservation management involves removing eggs from the wild, hatching chicks in captivity, rearing on a predator free island until they are large enough to no longer be at risk of predation by stoats (*Mustela erminae*), then translocation back into the single remaining mainland population at Ōkārito forest. Over three years, experimental releases (n=66) were undertaken into both the existing population of rowi at South Ōkārito, and into an adjacent but unoccupied area of their former range at North Ōkārito. After intensive post-release monitoring, the effects of various elements of the translocation process on post-release survival, dispersal, conspecific association, habitat selection and home range behaviour were examined.

An investigation into the effects of season of release, conspecific density, sex, and release group size on survival during the 90 day critical period following release, found release season and release group size are the most likely factors to influence post-release survival, with highest survival in spring, and for large release groups of four or more birds per release site. Habitat quality throughout the Ōkārito forest was estimated using invertebrate biomass as a proxy. A Geographic Information Systems (GIS) layer showing relative estimated invertebrate biomass was created and used to provide values of habitat quality at release locations and within home ranges. An investigation of the influence of habitat quality on post-release dispersal, conspecific association and home range behaviour found maximum dispersal distance was affected by the release site (North or South Ōkārito), and the interaction of release site and the estimated invertebrate biomass at the release location. Mean home ranges (± SE) of translocated rowi (3.35 ± 0.37 km^2), were larger and of lower habitat quality than those of wild rowi (1.06 ± 0.09 km^2). No effects of release group size on dispersal distance or conspecific association rates post-release were found.

The effects of early rearing experience are proposed as a key factor influencing translocated rowi behaviour. By monitoring the survival, dispersal, conspecific association and home range behaviour resulting from the translocation of rowi reared in a non-natural social situation, I highlight the potential impact of prior social experience and social memory on cognitive mapping and home range establishment. This innovative approach has the potential to be a valuable expansion to current home range cognitive mapping theory, and warrants further study.

Translocation is a vital tool in conservation, and has undoubtedly been instrumental in improving the situation of rowi since the first application to rowi conservation in the 1990s. This study has demonstrated that further improvements in the effectiveness and efficiency of translocations for conservation can be gained through sound scientific analysis of factors affecting the mechanisms leading to translocation success. Ongoing monitoring, analysis and reassessment of translocation management practices are recommended to ensure optimal conservation outcomes.

“We have to continually be jumping off cliffs and developing our wings on the way down”

Kurt Vonnegut

For Dad,

Jim Abbott

(1951 – 2012)

I wish you were here to see this. I hope I make you proud.

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1 General Introduction

1.1 Early rearing experience and translocation practices in conservation

Translocations[1] are increasingly being used for conservation management of threatened species (Sarrazin & Legendre, 2000). However, many release attempts fail to meet their goals or to optimise success due to lack of information regarding how behaviours are affected by the management processes (Bernardo et al., 2011; Fischer & Lindenmayer, 2000; Hardman & Moro, 2006; Ryckman et al., 2010). Translocation outcomes are influenced by a range of factors including effects of early rearing experience, release strategy, conspecific familiarity within release group, age, sex ratio, density of resident conspecifics, habitat quality at the release site and structure of release cohort, all of which may impact on the released individuals behaviour (Law & Linklater, 2007; Linklater & Swaisgood, 2008; Sarrazin & Legendre, 2000). Conservation success, defined as the realisation of goals outlined at the start of a project, can be improved by identifying factors causing suboptimal outcomes and potential solutions (Buner et al., 2011; Green et al., 2005; Mihoub et al., 2011), yet factors influencing this are rarely empirically tested (Hardman & Moro, 2006; Moorhouse et al., 2009). I investigated a range of release strategy factors on post-release survival and behaviour, using the management model of an endangered kiwi species, the rowi (*Apteryx rowi*).

There are many examples of the variety of effects early rearing conditions can have on the behaviour and development of birds and mammals prior to translocation for conservation (Cristinacce et al., 2008; Hansen & Slagsvold, 2004; Horwich, 1989; Maxwell & Jamieson, 1997; Utt et al., 2008; Van Heezik et al., 2005).

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[1] Throughout this thesis I use the definition of translocation outlined in the IUCN guidelines for reintroduction and other conservation translocations (IUCN/SSC, 2013) that states conservation translocation is the intentional movement and release of a living organism where the primary objective is a conservation benefit, and recognises the following types of translocation: A) Population restoration is any conservation translocation to within indigenous range, and comprises two activities: i. Reinforcement is the intentional movement and release of an organism into an existing population of conspecifics. ii. Reintroduction is the intentional movement and release of an organism inside its indigenous range from which it has disappeared. B) Conservation introduction is the intentional movement and release of an organism outside its indigenous range. i. Assisted colonisation is the intentional movement and release of an organism outside its indigenous range to avoid extinction of populations of the focal species. ii. Ecological replacement is the intentional movement and release of an organism outside its indigenous range to perform a specific ecological function.

Early social environment and experiences can have profound long lasting effects on subsequent behaviour (Chapman et al., 2008; Evans et al., 2014; Hansen & Slagsvold, 2004; Harvey et al., 2002; Horwich, 1989). Particularly important effects may include those relating to dominance (Hansen & Slagsvold, 2004) and social learning ability (Chapman et al., 2008). For example,in Takahē (*Porphyrio hochstetter),* captive rearing in the absence of adults may result in the sub-dominance of captive reared individuals in comparison to wild reared individuals (Maxwell & Jamieson, 1997).

Captive breeding can lead to the selection of individuals displaying genetic and phenotypic traits best suited to captivity (Ford, 2002; Snyder et al., 1996). Such traits include adaptability to high levels of human interaction, limited breeding opportunities, constraints on social interaction and restricted food types (Griffin et al., 2000; Harvey et al., 2002; McDougall et al., 2006). The long term result of this type of selection is often domestication of a species, accompanied by the loss of key behavioural traits and physiological features necessary for survival in the wild (O'Regan & Kitchener, 2005; Price, 1999). For example, in early black footed ferret (*Mustela nigripes*) reintroductions, released ferrets had low survival rates because they lacked the correct behavioural repertoire required for post-release survival and were unable to hunt effectively (Biggins et al., 1998; Vargas & Anderson, 1999).

Elements of release processes can affect the behaviour of animals following release and in turn can impact on demographic and spatial characteristics of the population and long term success of the translocation (Ryckman et al., 2010). Sex and age at time of release had a significant effect on the outcome of reintroductions of harpy eagles (*Harpia harpyja*), with lower survival for the younger age (5-7 months old) group compared to the older age group (18 - 22 months old), (Campbell-Thompson et al., 2012). Red-cockaded woodpecker (*Picoides borealis*) translocations were most successful with adult female cohorts (Allen et al., 1993). Ungulate reintroductions were more successful when larger numbers of animals were released, up to a maximum of 20 individuals, when an asymptote was reached (Komers & Curman, 2000). Age of released individuals may influence dispersal distance, as demonstrated in reintroductions of elk (*Cervus elaphus*), which had higher dispersal distances when released animals were adults compared to juveniles (Ryckman et al., 2010; Yott et al., 2011) and Griffon vultures (*Gyps fulvus*), which had lower dispersal rates when adults were released compared with juveniles (Gouar et al., 2008). Dispersal following release away from a carefully selected release site can undermine the objectives of the translocation and may prevent successful population reestablishment as animals may move away from potential mates and suitable habitat (Skjelseth et al., 2007; Van Heezik et al., 2009; Yott et al., 2011). The process of dispersal itself may also increase the risk that released animals face as they traverse unfamiliar habitat without knowledge of resource availability, predation risks or refuge sites (Devillard & Bray, 2009; Di Fiore et al., 2009). Habitat quality may affect dispersal decisions, with individuals released in lower quality habitat forced to disperse further to locate better quality areas for establishing a home range (Bennett et al., 2012; Enfjall & Leimar, 2009). Existing population density can also effect dispersal, recruitment and survival of translocated individuals, and has been investigated for many species, including red cockaded woodpeckers (Allen et al., 1993), least flycatchers (*Empidonax minimus*), American redstarts (*Setophaga ruticilla*) (Fletcher, 2007), and black rhinoceros (*Diceros bicomis*) (Linklater & Swaisgood, 2008). Fisher et al (2009) investigated the “social fence effect” (Hestbeck, 1982), which occurs when dispersing individuals of translocated water voles (*Arvicola terrestris*) are sub-dominant to resident territory holders and as a result are prevented from immigrating into the existing colony. Recruitment into the existing population was negatively correlated with population density, thus supporting the “social fence effect” hypothesis, and suggesting that, in the case of translocations for conservation, social fencing may hinder recruitment into, and genetic rescue of, threatened inbred populations. Elements of the translocation process that affect home range behaviour[2] and habitat selection are another important consideration for conservation managers. Home range behaviour, temporal movement dynamics and habitat selection cues are of central importance to population and behavioural ecology (Spencer, 2012; Villegas-Ríos et al., 2013). The home range of an animal is determined by the availability of food resources, mates and nest sites, and therefore has fundamental consequences for ecological processes such as growth, reproduction and ultimately survival and fitness (Börger et al., 2008).

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2. Throughout this thesis I define home range behaviour as the pattern of space use which leads to the emergence of a stable home range.

Translocations are considered to have three stages, the establishment phase, the growth phase, and the regulation phase (Sarrazin, 2007). Measures of translocation success depend on which phase is being monitored and the relevant goals set within each phase. Within the establishment phase, goals may relate to factors affecting the initial population growth, such as mortality of released individuals or delays before reproduction, and success is considered low mortality and/or fast time to reproduction (Caughley, 1994). In the growth phase, success occurs when the range expands or increases until the population reaches carrying capacity. Success in the regulation phase is characterised by an equilibrium between mortality and reproduction/recruitment. Overall there are many factors that influence translocation success at all phases of the translocation, yet arbitrary or expedient approaches to conservation management and translocation release strategy are often used (Sarrazin & Legendre, 2000). Rigorous testing that would yield biologically meaningful conclusions in order to improve release outcomes has been repeatedly recommended (Scott & Carpenter, 1987), but this still rarely occurs. Behavioural studies may offer a way to investigate and improve the effect of conservation management and translocation procedures on conservation outcomes.

1.2 Review of behavioural studies in conservation

1.2.1 The history of behaviour in conservation; behavioural ecology and conservation biology

The study of animal behaviour and its incorporation into conservation biology, a field now known as conservation behaviour, has been evolving over the last 50 years. Having its basis in behavioural ecology, this development began during the 1960s and 70s (Owens, 2006). During this era a group of scientists set out to understand why behaviour is adaptive (Gross, 1994). As a result, a series of ground breaking papers were published, documenting studies of animal behaviour in relation to individual and species fitness (e.g. (Hamilton, 1964; MacArthur & Pianka, 1966; Williams, 1966). Tinbergen's 1963 paper on the aims and methods of ethology is one such notable example. Principles Tinbergen outlined almost half a decade ago are still commonly referred to and used as the basis for the development of current behavioural ecology and conservation behaviour concepts, (see Linklater (2004)). By the 1980s behavioural ecology had been established as a discipline with theoretical framework and strong underlying concepts, and was considered at the time to be the premier field for understanding why organisms behave as they do (Gross, 1994). The culmination of this development was the publication of the first behavioural ecology textbook, “An Introduction to Behavioural Ecology”, by Krebs and Davies (1981), which synergised many theories on the multiple ways behaviour contributes to survival and reproduction.

At the same time as behavioural ecologists were developing their field, global concern began mounting over the increasing loss of species diversity (Thomas & Pletscher, 2000). An immediate response was necessary to halt the decline and preserve biodiversity. This led to the rapid rise of conservation biology, a field that emerged as a panic response to a crisis situation (Soulé, 1985). Conservation biology was built on many years of previous work by applied scientists in forestry and landscape management, wildlife biology, as well as older philosophical traditions (Meine et al., 2006; Young, 2000). At its outset, the structure of conservation biology was synthetic, eclectic and multidisciplinary and this continues to be the case as the discipline matures (Justus, 2002; Soulé, 1985).

The integration of behavioural ecology into conservation management began in the 1990s (Gross, 1994). At this time many scientists began recognising the implicit benefit that additional behavioural knowledge could add to species conservation and calls were made within the literature for the two disciplines to work together (Caro, 1999; Curio, 1996; Reed & Dobson, 1993; Sutherland, 1998). These articles outlined how conservation of species preserves the ability to conduct behavioural research, and state that conservation problems offer opportunities for novel behavioural studies, and that behavioural studies could help to improve conservation success, as potential benefits of such a union.

While many authors over the past 30 years have hailed the advantages of combining the knowledge that can be gained from behavioural ecology studies into conservation management planning and practice, as a stand-alone field, conservation behaviour is a nascent discipline, with its role and application still being developed by its pioneering scientists (Buchholz, 2007). Just how beneficial this integration is, or has potential to be, remains a continuing area of debate. While an influx of papers calling for further integration between the two fields occurred during the late 1990s and early 2000s, along with these came the sceptical voice of some scientists who felt too much emphasis was being placed upon a discipline with relatively limited practical application (Caro, 2007). To date there are still discussion papers being written by authors both eschewing and promoting the usefulness of the emerging field known as conservation behaviour (Angeloni, 2008; Anthony & Blumstein, 2000; Buchholz, 2007; Caro & Sherman, 2011, 2013; Keogh, 2009). The primary concern of Caro in his 2007 paper was that the application of behavioural studies must result in empirical findings of benefit to conservation for conservation behaviour to be worthwhile. He commented that behavioural studies have proven of little use for conservation, and the knowledge gained has been primarily for the benefit of expanding the field of behavioural ecology and is therefore not recognised as useful by the conservation community. This idea is disproven by evidence of the application of behavioural mechanisms guiding species management for many years (Harcourt, 1999; Moore et al., 2008). An example of this is Moore et al.'s 2008 paper summarising the successful integration of behaviour into New Zealand conservation management, in which the authors provide unequivocal evidence that behavioural studies can be a key component of the conservation manager's toolbox.

It is important to note that the study of behaviour is however, a single tool in a very big toolbox. It is necessary to take a step back from the narrow focus of "behaviour in conservation", to the broader concern, which is how best to solve conservation problems. It is not necessary to use behavioural studies in every conservation project (Sutherland, 1998). Many conservation problems require simple non-behavioural solutions. Behaviour studies should instead form part of a pragmatic approach to conservation, where the most effective technique for dealing with the issues at hand are identified and used. Using conservation money for behavioural studies without direct feedback of significant conservation value is in fact, worse than doing nothing at all (Sutherland, 1998).

1.3 The rowi (*Apteryx rowi*)

I conducted this study into factors affecting post-release behaviour and subsequent translocation success on rowi as the current conservation management of rowi provided an opportunity where behavioural studies could be used to improve conservation success and provide insight into and development of theoretical paradigms of factors affecting translocation outcomes.

Rowi are the rarest kiwi species, with the current population comprising just 350 to 400 birds (Holzapfel et al., 2008, DOC kiwi managers pers. comm., 2014). This represents an increase from the 2006 estimate of 250 (DOC, 2006) and a doubling from just 150 individuals in the 1990s (Holzapfel et al., 2008). However the total population is still well below the 500 effective individuals or total population of approximately 1500 individuals required for a minimum viable population targeted in the 2008 species recovery plan (Holzapfel et al., 2008). The species is not currently listed on the International Union for Conservation of Nature and Natural Resources (IUCN) Red List, but is classified as nationally critical (conservation dependent, recruitment failure and single location) by the New Zealand Threat Classification System (Robertson et al., 2013).

Rowi are the second smallest of the five recognised kiwi species (Burbidge et al., 2003), with an average height of 38 cm and weighing on average 2.5 kg for females and 1.9 kg for males. Their plumage is a soft greyish brown, occasionally with white patches around the head and neck (Peat, 2006). Rowi form monogamous pairings, with pairs sharing a single territory (Bennett & Owens, 2002; McLennan, 1988; Sales, 2005). Egg care is shared by both the male and female, with the male providing the majority of time on the egg (Bennett & Owens, 2002). Due to the shy nature of kiwi, which are cryptic, predominantly nocturnal and tend to inhabit rugged, inhospitable terrain (Huynen et al., 2003; Taborsky & Taborsky, 1999), the application of direct observational behaviour studies in the field is extremely difficult (Herbert & Daugherty, 2002), and much of the rowi's behavioural ecology, including an accurate estimate of lifespan, remains unknown.

Rowi have been in gradual decline since the first arrival of humans to New Zealand (DOC, 2006). Once common from the Haast Pass throughout the upper South Island, and the southern North Island up to Hawkes Bay, they are now restricted to Ōkārito forest, on the west coast of the South Island (Figure 1.1) ((Holzapfel et al., 2008; Shepherd & Lambert, 2008). While recent efforts have been made to protect the remaining habitat of the rowi, it is widely acknowledged that the main threats now facing the species are reduced population size, leading to loss of genetic diversity and inbreeding risks, and vulnerability to localised stochastic events (Holzapfel et al., 2008). The primary cause of the decline of the rowi population is predation of eggs and chicks by stoats (Basse & McLennan, 2003; Holzapfel et al., 2008; Peat, 2006). Due to a lack of native mammals, kiwi evolved no behaviours or defence mechanisms against introduced predators (McLennan et al., 1996). As a result, while adult survival is fairly high, chick survival has been shown to be less than

5%, resulting in a very low recruitment rate (McLennan et al., 1996; Rickard, 2002; Robertson, 2004). The Ōkārito stoat population varies in density over time, with peaks correlated with an increase in rat numbers, brought on by mass rimu tree (*Dacrydium cupressinum)* seeding events (masts) approximately once every five years (DOC, 2006; Peat, 2006). Subsequent to the rimu mast, rat numbers decline again, forcing an increased number of stoats onto other food sources, including predating heavily on kiwi eggs and chicks (DOC, 2006).

Rowi have been actively managed by DOC since 1992 (Rickard, 2002). In 2000, the Ōkārito Kiwi Sanctuary was established, comprising 10000 ha of lowland and costal podocarp-rātā forest of the South Ōkārito forest (Figure 1.1). North Ōkārito (Figure 1.1), is not part of the kiwi sanctuary, but was historically part of the rowi range, and prior to this study had no evidence of rowi presence since the 1980s. Ōkārito is now the full extent of the current rowi mainland range[3], and is located within the 98000 ha South Westland National Park, situated between Hokitika and Fox Glacier (Colbourne, 2002; DOC, 2006; Peat, 2006). Ōkārito is a cold temperate lowland costal wetland forest ecosystem ranging from sea level to 520 m.a.s.l. (Christie et al., 2006). The topography of Ōkārito is rugged and varied, with a combination of flat areas, undulating slopes and ridges (Christie et al., 2006). South Ōkārito is largely unmodified native podocarp-hardwood forest (Murphy et al., 2008). The predominant canopy vegetation is rimu (*Dacrydium cupressinum*), miro (*Prumnopitys ferruginea*), and southern rātā (*Meterosideros umbellata*) , with a subcanopy of quintinia (*Quintinia acutifolia*) and kāmahi (*Weinmannia racemosa*) (Rickard, 1996; Warburton et al., 1992). North Ōkārito was similar in vegetation structure and composition and topography to South Ōkārito until it was selectively logged at 25% of total merchantable volume in the 1970s and 1980s, resulting in a series of logging tracks throughout the area, and regenerating vegetation (Pearce & Griffiths, 1980; Piskaut, 2000). The control of stoat numbers was the main focus of DOC for conserving rowi for many years. This was done throughout the kiwi sanctuary using both trapping and sodium flouroacetate (1080) poisoning (Holzapfel et al., 2008; Robertson, 2003). Despite this intensive stoat management for over six years, predation risk was still high.

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3. An offshore island backup population of rowi was established on Mana Island, off the coast of the North Island, in 2013.

Only two years between 2003 and 2008 resulted in chicks surviving to adulthood in the wild, and rowi recruitment did not increase as hoped (Colbourne et al., 2005; DOC, 2006; Holzapfel et al., 2008). This is in comparison to other similarly managed populations on the North Island, where predator alleviation actions have resulted in a chick survival rate of around 70% (DOC, 2006). In response to the continued low recruitment, attention shifted to rowi productivity and it was decided that a new tactic was needed to work alongside the ongoing predator control (Colbourne et al., 2005; Robertson, 2003). The idea for an egg and chick management procedure, now known as Operation Nest Egg (ONE), was hatched in 1994 (Colbourne et al., 2005).

1.3.1 Operation Nest Egg

Once a kiwi reaches around 1.2 kg, the threat from stoats is greatly reduced. At this size either they appear physically too large for a stoat to take on, or are large enough to fight off or escape from predators (Robertson, 2004). Building on this discovery, the ONE practice involves removing eggs or chicks from the wild, hatching young in captivity and earing them on a predator free “crèche” island, Motuara Island, in the Marlborough Sounds (Figure 1.1) until they are large enough to no longer be at risk from stoats, and can be translocated back into the source population (Colbourne et al., 2005). Kiwi lend themselves to this type of management, being semi-precocial and largely independent within days of hatching (Colbourne et al., 2005; Jolly, 1991; Robertson & Coulbourne, 2003).

1.3.2 Concerns with captive rearing and translocation in the conservation of rowi

The New Zealand Biodiversity Strategy sets out a clear goal of maintaining viable populations of indigenous species (DOC, 2000). The key element of this is the fact that the populations need to be self-sustaining in order to be viable in the long term (DOC, 2000). While it is of primary importance to prevent extinction of species by bolstering population numbers, it is also of great importance that all the possible consequences of management procedures that may affect long term population persistence, such as limited recruitment, selection of sub-optimal habitat, and lowered genetic hetrozygosity, are understood in order to reach these long term conservation goals and maximise the conservation output of management procedures (Armstrong & Craig, 1995; Scott & Carpenter, 1987).

ONE has been effective at increasing the rowi population size, however there remain a number of concerns arising from the potential for the captive rearing and translocation processes to impact behavioural mechanisms that could have negative effects on both the immediate success of translocations and long term population persistence (Ebenhard, 1995; Griffin et al., 2000; Griffith et al., 1989; Linklater & Swaisgood, 2008). While the collection of eggs from the wild reduces the risk of domestication occurring, there is still the chance that rearing in captivity or non-natural settings selects for those individuals best suited to the captive/crèche environment on both a physiological and behavioural level. Within the rowi population, one significant life history trait yet to be investigated is the extended maternal association period, where a juvenile rowi is permitted by its parents to remain within the maternal territory, thus delaying dispersal for significant amounts of time, sometimes up to seven years, with juveniles possibly remaining even in the presence of younger siblings (Colbourne et al., 2005; DOC, 2006). It remains uncertain what purpose this tolerance of offspring for such a long time within the parental territory of otherwise highly territorial birds may serve (Colbourne et al., 2005). Possibilities include non-genomic trans-generational behavioural transfer of important skills required for successful survival, such as predator avoidance or selection of premium foraging areas, as documented in several other bird and mammal species (Griffin et al., 2000). Alternatively, the extended association may include provisioning of resources when local resource competition is high as a result of high population density, or protection from predators and aggressive conspecifics, as proposed in the "offspring defences" hypothesis of maternal territoriality in solitary and semi social mammals (Wolff & Peterson, 1998). Since the exact function of this parental association period within rowi is unknown, it remains unclear what effect missing this interaction may have on ONE rowi (Colbourne et al., 2005).

South Ōkārito forest may be close to carrying capacity, and this may be the cause of low fecundity within the population (Holzapfel et al., 2008). There are currently around 40% of breeding age birds that do not attempt to breed (Holzapfel et al., 2008). Hence there is significant concern that sub-dominance due to captive rearing combined with a high existing population density may be resulting in ONE birds facing low recruitment levels and be being forced into edge territories of sub-optimal habitat. Given current knowledge of the effects of such changes on other animals, it is reasonable to hypothesise that there may be subsequent behavioural effects of the management process and translocation practice on ONE rowi that may affect long term population viability. To date there has been no comprehensive study on the effects of early rearing experience, release strategy, conspecific familiarity within release group, age, sex ratio, density of resident conspecifics, habitat quality at the release site and structure of release cohort on the success of rowi conservation.

1.4 Thesis aims

The overarching aim of this study was to expand the current knowledge of factors influencing translocation outcomes by providing new evidence and understanding of behavioural mechanisms driving translocation success. I investigated the impacts of current conservation management on rowi behaviour and translocation success, using a series of behavioural studies. The thesis is written as a series of independent manuscripts intended for publication, and as such there is unavoidably some repetition, particularly in the introductions of chapters. I am the lead author on all papers, with my supervisors, Dr Ben Bell and Dr Nicky Nelson as co-authors on all chapters.

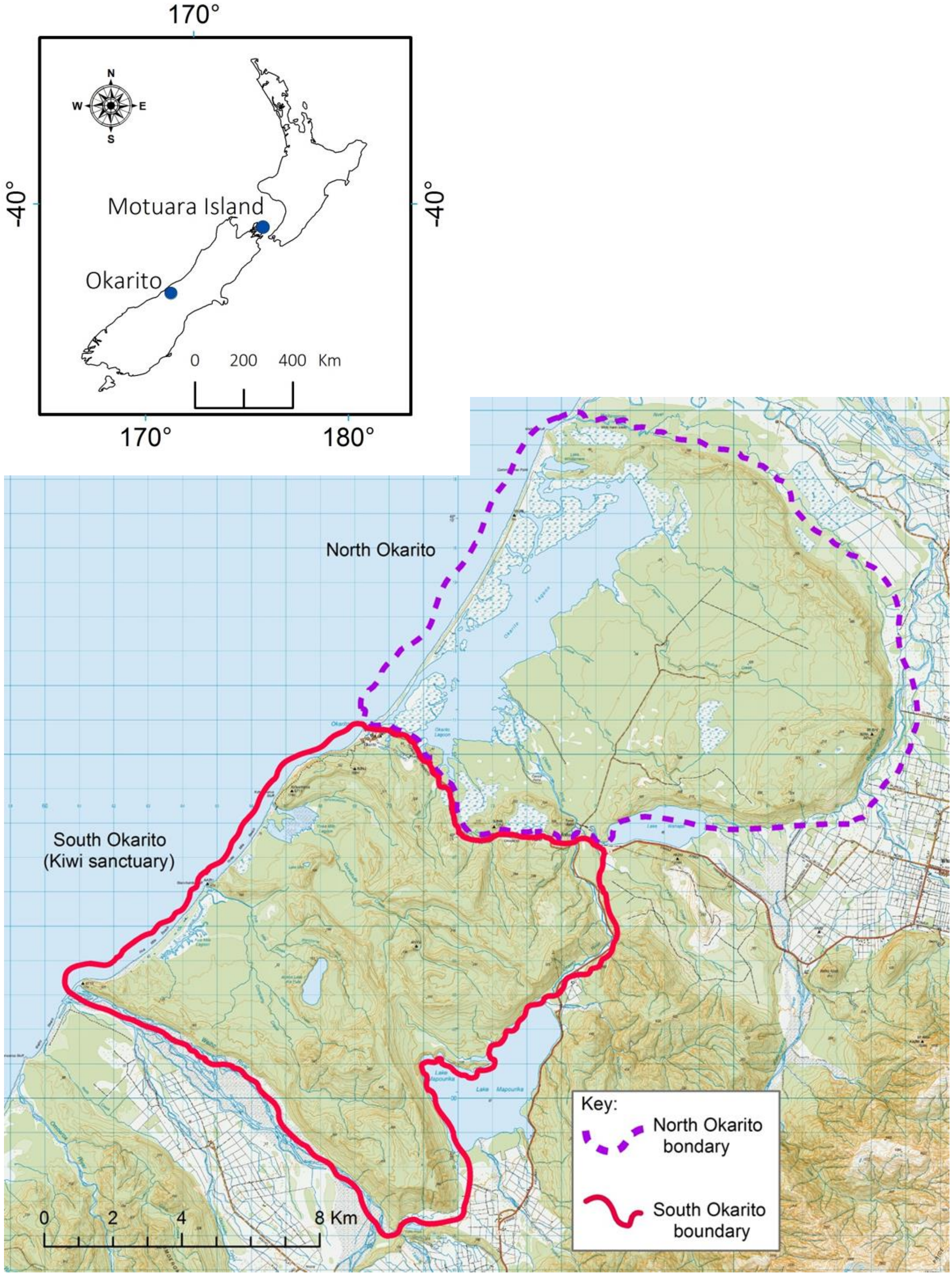

Figure 1.1. Inset: Map of New Zealand showing location of the kiwi sanctuary at Ōkārito and the crèche island of Motuara. Main picture: Detailed map of Ōkārito area, with the South Ōkārito kiwi sanctuary and North Ōkārito study area outlined. N.B There is no physical barrier around either North or South Ōkārito, the boundaries follow the coast, and rivers and roads that can both be traversed by rowi.

1.5 Thesis structure

I investigated elements of the release protocol that have an effect on the success of rowi translocations, with the aim of analysing and maximising the efficiency of rowi conservation management (Chapter 2). I measured translocation success as survival following release during a 90 day critical period, and answered the question "What factors affect translocation success?". Specifically, I analysed the post-release survival effects of:

1) Release season,
2) Sex of released birds,
3) Release group size,
4) Release site population density,
5) A landscape scale application of 1080.

I investigated biomass of invertebrates in rowi habitat and analysed corresponding habitat variables to establish a predictive model for relative invertebrate biomass as a proxy for habitat quality across the rowi range (Chapter 3). I used this model to produce a GIS layer and map of relative habitat quality throughout the study area that was used in subsequent chapters to address questions regarding the selection of home ranges based on habitat quality, of released and wild rowi, as well as to investigate the effects of release site habitat quality on translocation success.

I investigated impacts of the release strategy on dispersal and association rates following release (Chapter 4), including:

1a) Does release group size have a significant effect on the maximum dispersal distances during the critical period following release?
1b) What other factors affect the maximum dispersal distances during the critical period following release?
2a) Does release group size have a significant effect on the rate of association following release?
2b) What other factors affect the association rate of rowi following release?

I investigated what factors affect rowi home range and identified factors that influence rowi movement behaviour following translocation in Chapter 6. In doing so, I expand the current theory on home range behaviour. I specifically asked:

1) Do ONE rowi differ from wild rowi in their home range size and habitat quality?
2) What factors predict the size and habitat quality of an ONE rowi home range?
3) Does time since release affect site fidelity of ONE rowi?

In Chapter 7, I summarise the findings from this thesis, and present management recommendations and areas for further investigation.

2 Release group size affects post-release survival of rowi (*Apteryx rowi*)

2.1 Introduction

Translocations, restocking and reintroduction are increasingly being used for conservation management of threatened species (Sarrazin & Legendre, 2000). While conservation management practices are always well intentioned, they are often based on untested assumptions rather than strong scientific fundament (Gusset et al., 2010). Various hypotheses for translocation success exist, relating to a variety of elements within the translocation process such as release group size or sex ratios. Many of these hypotheses are based on theoretical relationships between fitness and elaborate combinations of socio-ecological predictors, but few have been tested experimentally (Deredec & Courchamp, 2007; Linklater et al., 2011). On many occasions this lack of empirical evidence on factors affecting translocation outcomes has led to misguided practices with sub-optimal, or negative effects (Conroy et al., 2006; Gusset et al., 2010; Karanth et al., 2003; Morrison et al., 2012). Early black-footed ferret (*Mustela nigripes*) reintroductions had low survival rates because the ferrets lacked the correct behavioural repertoire required for post-release survival and were unable to hunt effectively (Biggins et al., 1998; Vargas & Anderson, 1999). Incorrect assumptions regarding minimum habitat requirements led to Florida panther (*Puma concolor coryi*) releases occurring in areas later found to be suboptimal (Beier et al., 2006). Incorrect habitat specifications and false assumptions on minimum group size resulted in a nailtail wallaby (*Onychogalea fraenata*) reintroduction failing due to the fragmented nature of preferred habitat within the release site and small release group sizes (Kingsley et al., 2012). A lack of understanding of mesopredator release by predator eradication caused a reintroduction of brush-tailed bettongs (*Bettongia penicillata)* to fail due to predation by cats (*Felis catus*) following a fox *(Vulpes vulpes*) eradication programme (Priddel & Wheeler, 2004). It has long been recognised that more rigorous scientific input into conservation management practices are required (Armstrong & Seddon, 2011; Fischer & Lindenmayer, 2000; Seddon et al., 2007; Whitehead, 2010).

Translocation outcomes are influenced by a range of factors including release strategy, conspecific familiarity, age, sex ratio and structure of release cohort (Law & Linklater, 2007; Linklater & Swaisgood, 2008; Sarrazin & Legendre, 2000). Organisms are most vulnerable during the early phase following release and an initial high period of mortality often occurs (Armstrong et al., 1999; Letty et al., 2007; Letty et al., 2000; Tavecchia et al., 2009; Wilson et al., 1992), although see Armstrong et al (1999) for an example where this is not the case. A 15 year study of brown kiwi (*Apteryx mantelli*) by Robertson et al. (2011), found that of the 26 recorded deaths, nine (35%) were in the first month after release of captive-reared birds to the wild. Success of translocations may be improved if factors affecting survival during this critical period can be identified and adjusted. Sex and age at time of release had a significant effect on the outcome of reintroductions of harpy eagles (*Harpia harpyja*), with lower survival for the younger age (5-7 months old) group compared to the older age group (18 to 22 months old), (Campbell-Thompson et al., 2012). Ungulate reintroductions are more successful when larger numbers of animals are released, up to a maximum of 20 individuals, when an asymptote is reached (Komers & Curman, 2000). Yet arbitrary or expedient approaches to reintroduction release strategy are often used (Sarrazin & Legendre, 2000). Rigorous testing that would yield biologically meaningful conclusions in order to improve release outcomes has been long called for (Scott & Carpenter, 1987), yet this still rarely occurs.

While monitoring has become commonplace within translocation projects and throughout wider conservation management practices, a large number of datasets fail to be rigorously analysed (Holland et al., 2012). Standardised reporting of findings will enable improvements in not just the focal project, but also may hold relevant in other similar translocation projects (Sutherland et al., 2010). Analysis of data collected during post-release monitoring may shed light on elements of the release protocol influencing the translocation outcomes, which will enable formation of hypothesis regarding release procedures and translocation success. When experimentally tested, these may lead to vast improvements in the efficiency and effectiveness of a great many conservation projects. Strategic monitoring based on the needs of the species being translocated provides targeted answers to pertinent questions, whereas monitoring conducted without a specific aim defined make analysis of data and interpretation of results challenging (Parker et al., 2013). Translocations of rowi kiwi (*Apteryx rowi)* in New Zealand, provided an example of a long term (17 year) project with post-release monitoring and a large data set which had not been strategically defined at the outset of data collection, nor had it been extensively analysed prior to this study.

Case study: Rowi (Apteryx rowi)

Kiwi are the national icon of New Zealand. They are flightless ratites endemic to New Zealand. There are five recognised species of kiwi (Burbidge et al., 2003), all under threat from a range of anthropogenic issues, including habitat destruction and introduced predators and competitors (DOC, 2006). Kiwi (along with New Zealand's other bird fauna) evolved in the absence of terrestrial mammals, and thus have no effective defence mechanisms against predators such as cats (*Felis catus*) and stoats (*Mustela erminae*) introduced by human settlers (McLennan et al., 1996; Sales, 2005). Nationwide kiwi conservation efforts have led to a range of management practices being implemented at various times. These include predator control, dog aversion training schemes, establishment of kiwi sanctuaries and captive breeding and rearing programmes, such as Operation Nest Egg (ONE) (see below in this section). Translocation has become a crucial part of kiwi conservation management. Kiwi have been monitored following releases for over 17 years, resulting in a large dataset of release information and subsequent monitoring data. This presented an opportunity to explore the effects of release protocols on a critically endangered species.

Rowi, the rarest species of kiwi, are classified as "nationally critical" (Hitchmough, 2002). The current species range is 10000 ha area of lowland podocarp forest within the 98000 ha South Westland National Park, situated between Hokitika and Fox Glacier on the West Coast of the South Island of New Zealand (Figure 1.1), (DOC 2006, Peat 2006, Coulbourne 2002, DOC 2006). This area is a vast reduction from the historic range of rowi, which previously spanned the top of the South Island, and areas of the North Island up to Hawkes Bay (Holzapfel et al., 2008; Shepherd & Lambert, 2008). The current population is thought to number between 350 and 400 individuals (Holzapfel et al., 2008) (DOC kiwi managers pers. comm., 2014), representing an increase from 150 individuals in the 1990s (DOC, 2006), which has come about through intensive management practices.

The primary cause of the decline of the rowi population is predation of eggs and chicks by stoats (Basse & McLennan, 2003; Basse et al., 1999; Holzapfel et al., 2008). While adult survival is around 91% annually, without intervention chick survival is less than 6%, resulting in a very low recruitment rate (McLennan et al., 1996; Rickard, 2002; Robertson, 2004; Robertson & de Monchy, 2012). Rowi have been actively managed by the Department of Conservation (DOC) since 1992, (Rickard, 2002). Translocations have been a core part of their conservation management since 1996 (Robertson, 2003). Once a rowi reaches around 1 kg, the threat from stoats is greatly reduced. At this size it is thought they appear too large for a stoat to target, or are large enough to fight off or escape from predators (Robertson, 2004). Building on this discovery, the conservation management practice known as Operation Nest Egg (ONE) involves removing eggs or chicks from the wild, hatching the young in captivity, rearing juveniles in predator free locations until they are over 1.2 kg and no longer at risk from stoats, and then releasing them back into the source population (Colbourne et al., 2005). Kiwi lend themselves to this type of management, being semi-precocial and largely independent within days of hatching (Colbourne et al., 2005; Jolly, 1991; Robertson & Coulbourne, 2003). During the early years of ONE (1994 to 1997), captive hatched rowi chicks were reared entirely in captivity before release back into Ōkārito forest. From 1998 onwards, chicks were transferred between the age of 1 - 22 weeks from the hatchery facility onto Motuara Island (Figure 1.1 inset), a predator free "crèche" island in the Marlborough Sounds, before being transferred to Ōkārito forest as subadults weighing over 1.2 kgs (Colbourne et al., 2005). Traditionally, many of these releases took place with individual or pairs of birds at each release site to mimic the adult rowi social system, where birds form highly territorial monogamous pairs (Colbourne et al., 2005; Taborsky & Taborsky, 1999) (D. Kay pers. comm., 2012). Larger groups of birds were released together on a few occasions, including one release in 2002 of 14 birds at one site. The release timing in relation to season was initially unspecified by the management plan, and early releases took place in all seasons. Mortality rates during early years were high, with 61% (n=13) mortality within the 90 day period following release in 1996 and 1997. This was speculatively attributed to releases in autumn/winter being seasonally unsuitable, although this assumption was never experimentally verified. Early releases also took place in close proximity to resident birds, and many (six out of 18) of the rowi released between 1995 and 1998 were killed by territorial resident rowi soon after release. Colbourne et al (2005) suggested that this may be because the released rowi "behave inappropriately" due to the ONE process.

Management practice changed in 1998 to ensure that releases took place away from territorial birds (Colbourne et al., 2005).

Predator control occurred at irregular intervals between 1996 and 2011 throughout the Ōkārito area. Landscape scale predator trapping took place from 2001 to 2005, with 2144 stoats and 11,331 rats (*Rattus rattus*) killed, but trapping was ineffective at increasing rowi numbers. Stoat predation remained the main cause of mortality, with only 15% of chicks surviving to six months old, leading to a population increase of just 0.6% per annum (Robertson & de Monchy, 2012). Landscape scale poisoning by aerial application of sodium flouroacetate (compound 1080) occurred twice, once in 1999 and again in 2011. 1080 is a highly toxic vertebrate pesticide that causes inhibition of the Krebs cycle, (Eason et al., 2011; Eason et al., 1999). While the main risk of predation by stoats is mitigated by the ONE process, stoats and rats compete with rowi for food resources, with the frequency of invertebrates in stoats diets in Ōkārito classified as “high”, occurring in 52.4% of examined stoat guts (Murphy et al., 2008). Therefore 1080 operations may be of indirect benefit via reduced resource competition in addition to a reduction in predation.

Currently around 40% of breeding age rowi do not attempt to breed (Holzapfel et al., 2008). South Ōkārito kiwi sanctuary may be close to carrying capacity, and this may be the cause of low fecundity within the population (Holzapfel et al., 2008). Despite the rowi population doubling between 1990 and 2011, the range of rowi has not expanded. The current density of rowi in South Ōkārito is approximately one bird per 28 ha.

Study Aims

I investigated elements of the release protocol that have an effect on the success of rowi translocations, with the aim of analysing and maximising the efficiency of rowi conservation management. My timeframe was too short to measure reproductive output, so as with similar translocation studies, I measured success as survival following release (Bodinof et al., 2012; Burnside et al., 2012; Campbell-Thompson et al., 2012; Faulhaber et al., 2006; Hare et al., 2012). I set out to answer the following question: What factors affect translocation success? Specifically, I investigated the effects of release season, sex, group size, release site population density and a landscape scale application of 1080, on post-release survival.

2.2 Methods

Study site

The entire range of rowi was designated as one of five national kiwi sanctuaries in 2000. This does not mean the area is enclosed by fencing, rather the area is afforded extra legislative protection (exclusion of dogs), and funding from both the New Zealand government and corporate sponsorship through "Kiwis for Kiwi" (formerly the "BNZ Save the Kiwi Trust").

From 1992 - 2010, the entire range of rowi was encompassed by the South Ōkārito area. North Ōkārito was formerly part of the rowi range, but there had been no evidence of rowi there since the 1980s. In 2010 and 2011 I undertook experimental releases in both South Ōkārito and North Ōkārito (Figure 1.1). (Christie et al., 2006). South Ōkārito is largely unmodified native podocarp-hardwood forest (Murphy et al., 2008). North Ōkārito was selectively logged at 25% of total merchantable volume in the 1970s and 1980s, resulting in a series of logging tracks throughout the area, and regenerating vegetation (Pearce & Griffiths, 1980; Piskaut, 2000). The suitability of North Ōkārito as a rowi release site was assessed by the Department of Conservation, in 2010.

Rowi releases

Data were available on all 217 rowi released since ONE began in 1996. Released rowi were fitted with VHF transmitters (Sirtrack Ltd), attached following guidelines set out in the Kiwi Best Practice Manual (Robertson & Coulbourne, 2003), in order to locate them and estimate survival. The transmitters had a battery life of approximately 12 to 15 months (Keye et al., 2011; Robertson & Coulbourne, 2003), and were changed as required through the first year, then yearly, as recommended in guidelines set out in the Kiwi Best Practice Manual (Robertson & Coulbourne, 2003). Ground based monitoring was conducted using a hand held TR4 receiver (Telonics^{TM}) and Sika receivers (Biotrack Ltd), along with three-element folding Yagi antennas (Sirtrack Ltd). Ground monitoring was supplemented by use of a remote aerial monitoring system attached to light aircraft (Wildtech New Zealand Ltd). Monitoring effort and type of data collected varied over the course of ONE (1996 to present), severely limiting the strength of conclusions that can be drawn from analyses. Information available for most birds included release date and location, subsequent monitoring dates and recapture locations, dates of transmitter failures or removals, and mortalities detected within the monitoring periods. Only those ONE birds with a complete record were included in analyses, (n=153). Of the 153 birds with complete records, four were censored from the analyses as they were killed by cars, and it was felt that fatalities from car strikes were not relevant to this investigation since they are a result of human behaviour and only affect those birds close to roads, meaning the risk is not equal across subjects or throughout the study area. Of the remaining 149 birds in the sample, 35 mortalities occurred during monitoring, and the remaining 114 birds were monitored until their transmitter was removed, or their transmitter failed meaning the bird was no longer able to be found (Table 2.1). The amount of time these birds were monitored following release varied between 25 and 4,797 days.

Date of death was estimated using the midpoint between the last date the animal was known to be alive and the date on which the animal was confirmed dead if the visits are 15 days or fewer apart, or the date after 40% of the interval between visits if the visits were more than 15 days apart (Miller & Johnson, 1978; Robertson & Westbrooke, 2005). This provided a more conservative estimate of time alive than methods suggested by other authors such as Heisey and Fuller (1985) which calculate date of death as 50% of the time since final live sighting to confirmation of death. If the bird was not detected dead during its monitoring, the time alive since release was calculated up to either the last date it was known alive before transmitter failure, or the date of transmitter removal, upon which it was then right-censored from the sample (i.e., excluded from the analyses) (Pollock et al., 1989).

Sex was determined either by DNA sampling of feathers or blood, or through morphological measures, or a combination of both. Within the analyses there were 88 birds of known sex, 44 females and 44 males. Release groups were defined as those birds which were released on the same date, within 1 km proximity of one another. Rowi are able to hear one another's calls over a range of approximately 1 km (R.Colbourne pers. comm. 2012), so sites within this distance were not considered separate.

In order to establish whether an early elevated mortality rate occurred in rowi translocations, I visually explored the overall patterns of survival estimates following release from all the available data using the Kaplan-Meier method, and I went on to investigate the duration of this critical period for mortalities following release by observing the trend in the Kaplan-Meier graph of survival rates. I investigated the effects on survival of i) release year, ii) release season, iii) sex, iv) release group size, using data on all 149 rowi in the sample.

Releases in 2009, 2010 and 2011 (n = 66) were manipulated to experimentally test the relative effects of the following covariates on survival: i) release group size, ii) conspecific density, iii) predator/competitor density (via 1080 operation) (Figure 2.1). Release group sizes were pre-defined, locations were selected to vary conspesific density (South Ōkārito vs. North Ōkārito), and a 1080 operation took place after the 2010 releases and prior to the 2011 release to vary the predator/competitor density. Constraints imposed by several factors, including the small number of rowi available for release, the limited availability of suitable release sites within the release areas, logistical restrictions on access to sites within the release areas, the number of trained kiwi handlers which were available to conduct concurrent releases resulted in a suboptimal experimental design, where variables were not able to be fully crossed. Subsequently, conclusions able to be drawn from this data are limited.

Data analyses were conducted in SPSS 18 (PASW 18, July 2009), and R version 2.15.2. Estimates of cumulative survival probability were calculated using Kaplan-Meier analysis and covariates were compared with a log-rank test (Pollock et al., 1989; White & Garrott, 1990; Winterstein et al., 2001). As with previous studies of survival following translocation, I conducted the analyses without staggered entry (Pollock et al., 1989) since I was investigating survival following release, rather than survival during specific time intervals (Ben-David et al., 2002). Kaplan-Meier analysis is a product-limit estimator that requires no assumption about the constancy of daily survival probabilities, and can account for changing sample size (e.g., right-censoring at death, emigration or transmitter failure) (Davis et al., 2011; Winterstein et al., 2001). All of the assumptions of this test were met by the data.

To investigate the relative effects on survival of: release year, season, and small or large group (Heurich et al., 2012) on the full dataset I constructed a series of models and conducted a Cox proportional hazards analysis (Cox & Oakes, 1984; Winterstein et al., 2001) using all available data (n=149). I investigated the results of the 2009-2011 experimental manipulation subset of data using a Cox proportional hazards analysis to identify the relative effects of small or large group size, predator/competitor density and conspecific density on post-release survival. Due to the small sample size it was not possible to investigate interaction effects in either Cox proportional hazards analysis. I used Akaike's Information Criterion corrected for small sample size (AIC_c) for model selection (Burnham & Anderson, 2002) using package MuMln. I considered models with a delta AIC_c values ≤2 as competing models (Price et al., 2010).

Table 2.1. Number of rowi released (1996 to 2011) by season and percentage mortality within the critical period of 90 days following release.

Year[1]	Number of rowi released[2]					% mortality within critical period
	Spring	Summer	Autunm	Winter	SUB TOTAL	
1996	2			1	3	66.6
1997		4	2	4	10	60
1998		11			11	27.3
1999	5				5	0
2000	8	6	1		15	20
2002		13			13	23.1
2005	3	6			9	11.1
2006				1	1	0
2007		2			2	0
2008	6	8			14	0
2009[3]	17				17	35.3
2010[3]	34				34	26.5
2011[3]	15				15	0
				TOTAL	149	

[1] Only includes years where ONE releases took place.

[2] Only includes rowi that have a "full record" on the database and excludes those censored due to being hit by cars.

[3] Experimental release years. These data are included in the main analyses, and analysed further to explore the effects of group size, predator/competitor density and conspecific density (Figure 2.2).

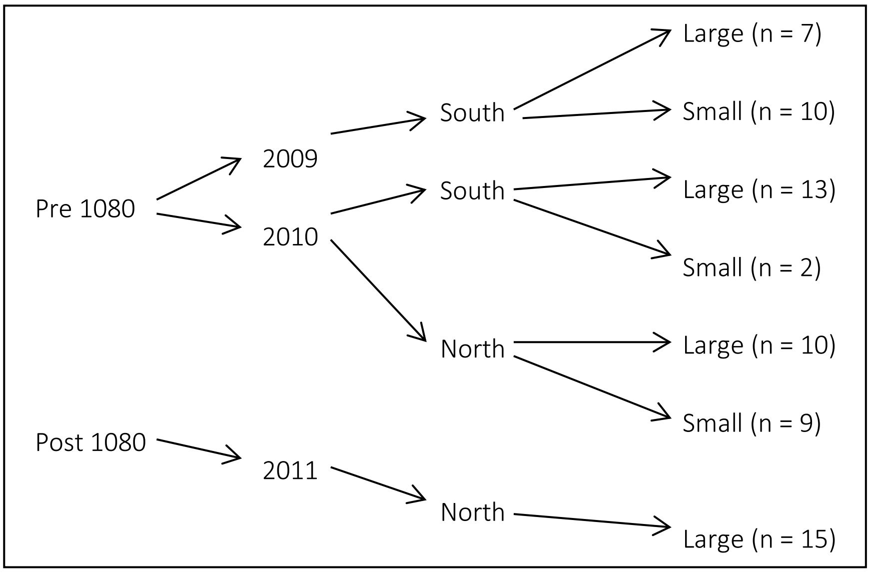

Figure 2.1. Diagram of experimental releases groups showing distribution of individuals among covariates of pre or post 1080 operation, year, release site and group size. Note that post 1080 there were only large release groups. This may have confounded the data as either a positive effect of predator control could positively influence the effect of large group size, or the effect of large group size could positively influence the effect of predator control. In order to control for this, a survival estimate by group size for releases only prior to the predator control was also conducted, and Cox proportional hazard regression with model selection using AIC_c was used to investigate the relative importance of covariates.

2.3 Results

Critical time period for increased mortality following release.

Thirty five rowi died during their monitoring period. The mean duration from release to death was 183 days, and 77%, of the mortalities recorded occurred within 90 days of release. The Kaplan-Meier analysis of survival showed a steep decrease in survival probability during the first 90 days, followed by a markedly slower decrease after 90 days (Figure 2.2). Mortalities that occurred after 90 days occurred between 150 to 2878 days post-release. Therefore, the initial 90 days following release was considered the critical period for rowi survival following release. All subsequent measures of survival following release refer to the survival rate within this critical period.

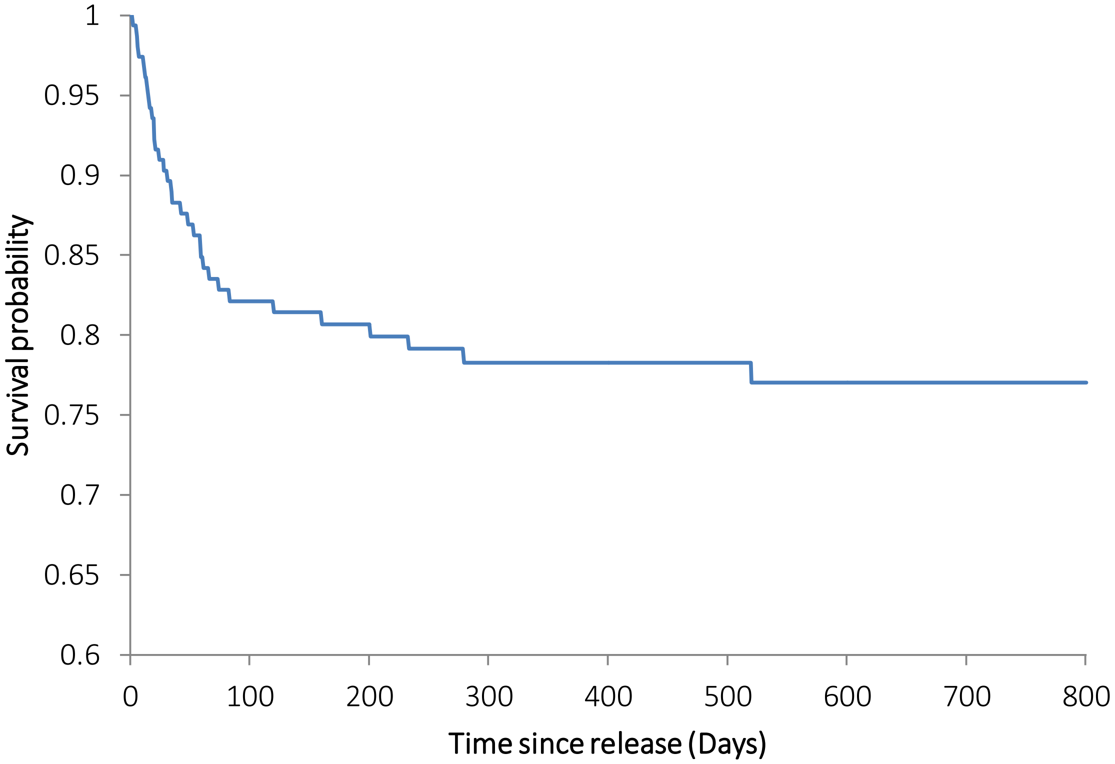

Figure 2.2. Survival probability of rowi following release between 1996 and 2011 (n=149). There was an initial steep drop in survival probability from 1 to 0.812 at 90 days post release, followed by a slower decrease for the remaining monitoring time. The critical period for rowi was therefore considered to be the first 90 days following release.

Release Year

The number of rowi released each year between 1996 and 2011 varied from none in 2001, to 20 in 2009 (Table 2.1). The percent of mortalities within the critical period following release varied between years from zero (1999, 2006, 2007, 2008) to 66.6% (1996) (Table 2.1). In 1996 the survival probablility dropped to 0.33 at 21 days post-release, and the final rowi in the cohort was censored due to a dropped transmitter, resulting in no further data after 27 days post-release (Figure 2.3).

The estimated survival rate during the critical period differed significantly among years. At 90 days post-release the variability in survival probability ranged from 1.00 (1999, 2006, 2007 and 2008), to 0.33 in 1996 (Figure 2.3), (Kaplan-Meier analysis χ^2=44.74, df=12, *P<0.01*).

Release season

Of the 149 rowi released between 1996 and 2011, 90 were released in Spring (1st September to 30th November), 50 in Summer (1st December to 28th February), three in Autumn (1st March to 31st May), and six in Winter (1st June to 31st August) (Table 2.1). Survival probability following the critical period varied significantly among seasons with a clear difference between autumn and winter compared to summer and spring releases (Figure 2.4). Survival probability at 90 days post-release was 0.821 (n=90) following release in Spring, 0.918 (n=50) following releases in Summer, 0.333 (n=3) following releases in Autumn and 0.167 (n=6) following releases in Winter, (Kaplan-Meier analysis χ^2=35.33, df=3, *P<0.001*).

Sex

At 90 days post-release the survival probability was 0.89 for males (n=44), and 0.932 for females (n=44), which is not a significant difference (Kaplan-Meier analysis χ^2=0.50, df=1, *P*=0.479). This suggests sex had no effect on survival during the critical period.

Release group size

Release group size varied within and between years. The survival probability at 90 days post-release was highest for birds released in groups of five, with no mortalities recorded giving a survival probability of 1 (Figure 2.5). The survival probability dropped to 0.92 for groups of six, 0.86 for groups of eight, 0.85 for groups of 14, and 0.85 for groups of four. The survival probability of birds released in groups of three, two or individuals was 0.64, 0.70 and 0.52 respectively. The Kaplan-Meier graph (Figure 2.5), showed two distinct clusters of group size survival probabilities at 90 days post-release, with individuals, twos and threes in the lowest cluster, fours, eights, fourteens, fives and sixes in the top cluster with the highest survival probability. This led me to re-categorize release groups for the 2009, 2010 and 2011 experimental releases, and investigate differences between small (where group size was one to three birds), and large groups (with four plus rowi).

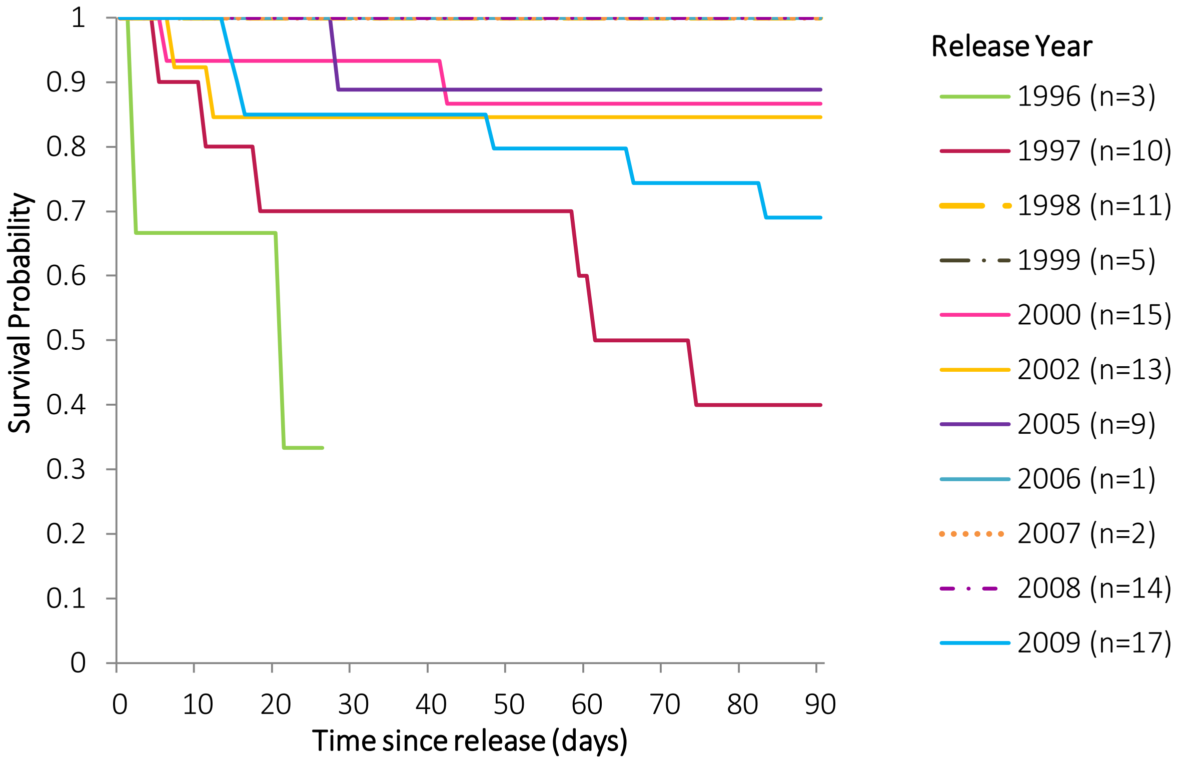

Figure 2.3. Estimated rowi survival probabilities following release (1996 to 2011). Year has a significant effect on survival probability. In 1998, 1999, 2006, 2007, and 2008 the survival probability remained at 1 throughout the critical period.

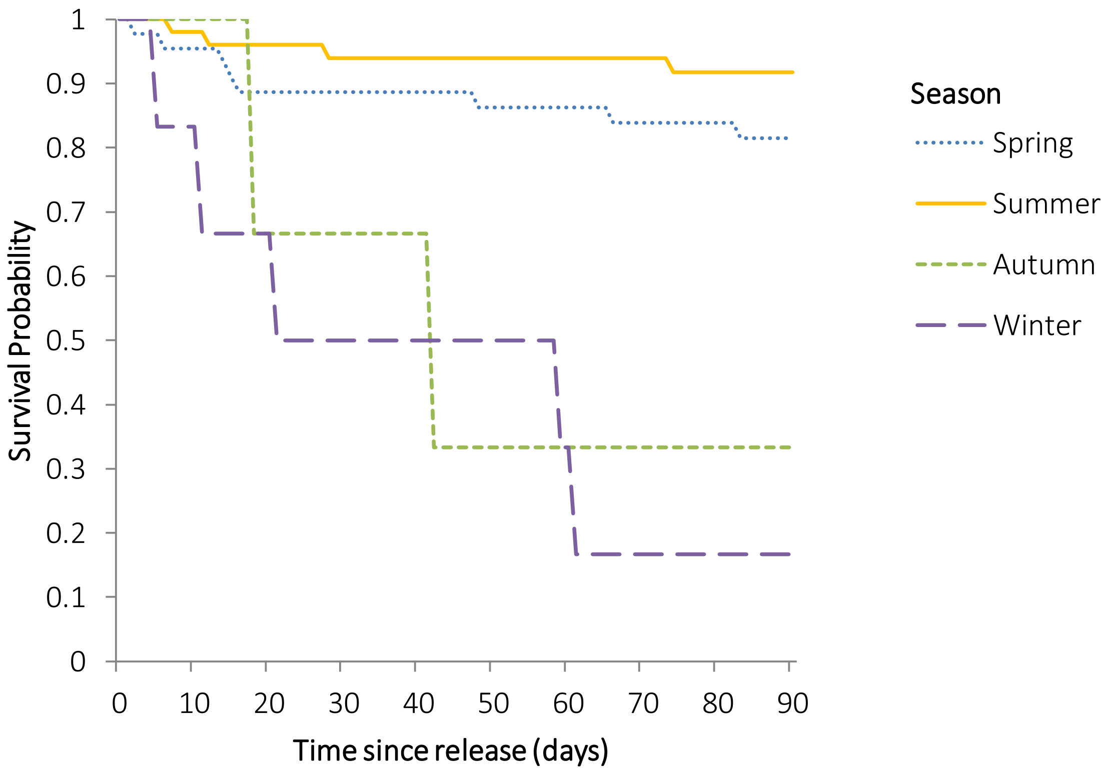

Figure 2.4. Estimated survival rate following release for release seasons (Spring (n=90), Summer (n= 50), Autumn (n= 3), and Winter (n=6)), showing a clear difference between Winter and Autumn compared to Spring and Summer. Spring and Summer had a significantly higher survival rate than Autumn and Winter.

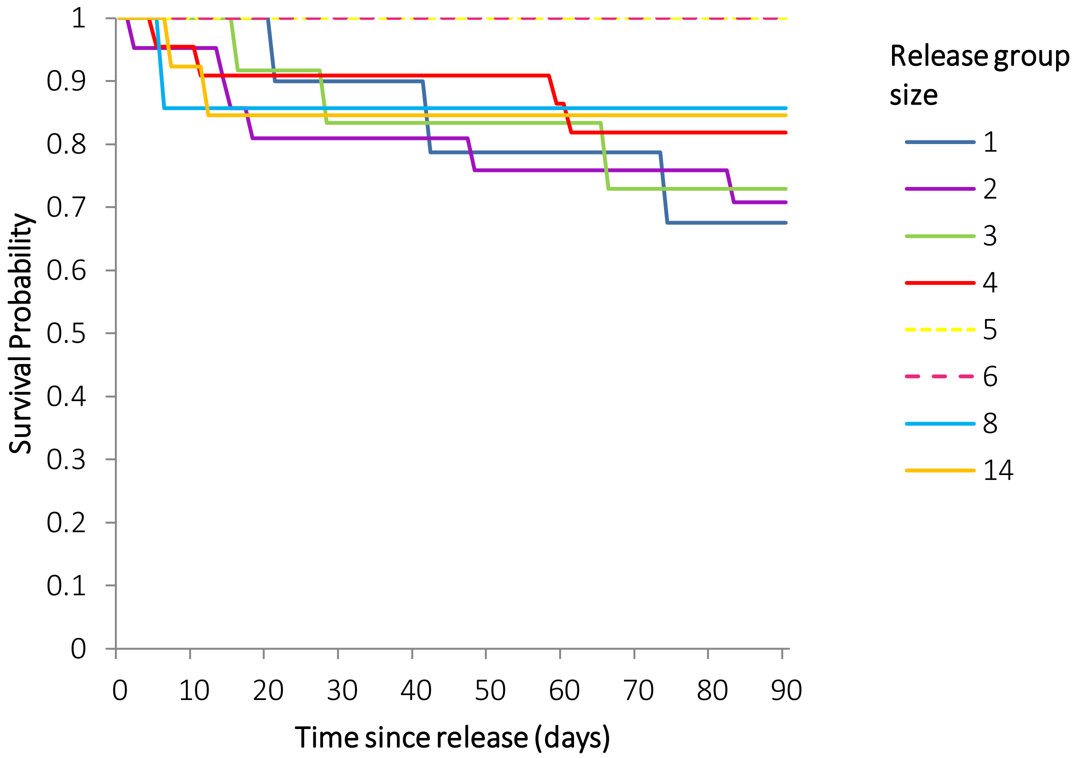

Figure 2.5. Estimated survival rate following release for group sizes 1 (n=10), 2 (n=26), 3 (n=12), 4 (n=40), 5 (n=14), 6 (n=27), 8 (n=7), 14 (n=13). While the graph shows a trend of lower estimated survival probability for individuals and small groups with greater survival probability for larger groups, the overall effect of group size on survival estimate was not significant.

Cox proportional hazards.

I constructed a series of eight candidate models based on the elements of release protocol that were found with the Kaplan-Meier analysis to have possible significant effects on post-release survival probability: year of release, season of release, and small or large release group. All models included group ID as a random effect to account for any untested homogeneity within release groups and to therefore prevent pseudo-replication. I ran a Cox proportional hazards analysis of the models to investigate the relative effects of each covariate, and ranked them by lowest AIC_C. The results of the Cox proportional hazards must be interpreted with caution since the variables throughout the investigation were not fully crossed. The most parsimonious model, M4, describes survival estimate as a factor of release season and small or large group (Table 2.2). The model including release year in addition to release season and group size, M7, is a competing model with a delta AICc of 1.81, however M4 has 2.46 more support than M7 (evidence ratio 0.69/0.28). This would suggest there may also be an effect of year, however since release group sizes were not crossed across all years, the year effect may be driven instead by mainly small groups being released in the early years. Unfortunately it was not possible to examine these interaction effects since the sample sizes were too small.

Table 2.2. Candidate models used to evaluate factors affecting survival estimates of released rowi during critical period, ranked by most parsimonious. Table includes number of parameters (K), Akaike Information Criterion corrected for small sample size (AICc), delta AICc (ΔAICc), Akaike weights (AIC_CWt), and log-likelihoods (LL). The highest ranking model includes season and release group size as predictors of post-release survival probability in rowi.

Candidate Model ID	Candidate Model	K	AICc	ΔAICc	AIC_CWt	LL
M4	Season + Small or large group	11	240.0	0.00	0.69	-107.91
M7	Season + Small or large group + Year	12	241.8	1.81	0.28	-107.93
M1	Season	13	247.6	7.85	0.02	-109.15
M6	Year + Small or large group	16	248.4	8.46	0.01	-106.39
M5	Season + Year	14	249.1	9.17	0.01	-109.26
M2	Small or large group	17	250.3	10.31	0.00	-106.16
M3	Year	17	254.3	14.34	0.00	-107.38
M8	Null	18	255.4	15.39	0.00	-107.37

Experimental releases

Year of release

In 2009, 2010 and 2011 the number of rowi released were 17, 34, and 15 respectively. In 2009, six (35.3%) birds died within the 90 day critical period following release. In 2010, eight (22.9%) died within the critical period, and in 2011 no birds died within the critical period. The survival probability at 90 days was 0.67 for birds released in 2009, 0.77 for those released in 2010, and 1.00 for those released in 2011 (Figure 2.6). The difference between these survival probabilities was not significant (Kaplan-Meier analysis, χ^2=5.901, df=2, *P*=0.052). This finding should be interpreted with caution since the range of variables being tested were not fully crossed across all years of the experiment. Therefore it was not possible to account for any potentially confounding interaction effects in the analysis of year effects, nor was it possible to account for any potential effect of release year in any of the analyses of other variables.

Release group size

Rowi were released in a variety of group sizes that were grouped into small groups (one, two or three birds at one release site) or large groups (four or more birds at a release site).

Between 2009 and 2011, 21 rowi were released in small groups, and 45 were released in large release groups. Ten of the rowi in small groups (45.46%) died within the critical period, and four of the large release group rowi (8.89%) died within the critical period. This gave a significant difference in survival probability at 90 days post-release: 0.55 for those in small release groups, and 0.91 for rowi released in large groups (Figure 2.7) (Kaplan-Meier analysis χ2=13.380, df=1, *P* = 0.000). These results may be confounded due to the fact that all of the release groups in the post-1080 predator control treatment were large groups (Figure 2.1), and that large and small groups occurred in both North and South Ōkārito pre 1080, but in unequal proportions. To discount the potential effect of the 1080 treatment, I analysed the effect of group size using only the pre 1080 data. There were 21 rowi released in small groups and 30 in large groups pre 1080. The survival probability at 90 days was still significantly different: 0.545 and 0.867 for small and large groups respectively (Figure 2.8, Kaplan-Meier analysis χ2=7.208, df=1, *P* = 0.007). Additionally, to account for the possible confounding effects of release site, I also conducted a separate analysis of only the pre 1080 release group further separated down into only pre-1080 North Ōkārito releases, and only pre-1080 South Ōkārito releases. Prior to the 1080 operation in North Ōkārito, there were 9 rowi released in small groups and 10 rowi released in large groups. The difference in survival probabilities was not statistically significant (Figure 2.9, Kaplan-Meier analysis χ2=1.054, df=1, *P* = 0.305). In South Ōkārito prior to 1080, there were 12 rowi released in small groups and 20 rowi released in large groups, with survival at 90 days 0.5 and 0.9 respectively. This difference is statistically significant (Figure 2.10, Kaplan-Meier analysis χ2=6.940, df=1, *P* = 0.008). Due to the variables not being fully crossed throughout the three years of the experiment, it was not possible to account for the potentially confounding effects of year of release in this analysis.

Conspecific density

I released a total of 66 rowi into the two experimental release sites with different conspecific densities, North Ōkārito with no existing rowi population prior to 2010 (n=34), and South Ōkārito with an approximate density of one rowi per 28 ha (n=32), over three successive years, 2009 to 2011 (Figure 2.1). In North Ōkārito, six rowi (17.1%) died within the critical period, compared to eight rowi (25.0 %) in South Ōkārito. The survival probability at 90 days post-release was not significantly different between sites: 0.829 in North Ōkārito and 0.75 in South Ōkārito (Figure 2.11, Kaplan-Meier analysis $\chi2=0.585$, df=1, $P=0.444$). However, the release group sizes across the two sites also differed, as did the occurrence of a 1080 application. To disentangle the possible confounding effects of group size and 1080 from the possible effects of release site, I compared releases of rowi only prior to the 1080 treatment, and only in small release groups across the two sites, and found no significant difference between releases of small release groups prior to 1080 in North (n=9) and South Ōkārito (n=12), (Figure 2.12,Kaplan-Meier analysis $\chi2=0.228$, df=1, $P = 0.633$). There was also no significant difference between large groups pre-1080 in North Ōkārito (n=10), and large groups pre-1080 in South Ōkārito (n=20), (Figure 2.13, Kaplan-Meier analysis $\chi2=0.567$, df=1, $P = 0.452$).

1080 predator control operation

A 1080 predator control operation took place in 2011, prior to the release of rowi that year. This resulted in a sample size of 52 rowi released pre 1080 (in 2009 and 2010), and 15 released post 1080 (in 2011) (Figure 2.1). Of the pre 1080 released rowi, 14 (26.93%) died within the 90 day critical period, and of the post 1080 released rowi, none (0%) died within the critical period. This difference was statistically significant (Figure 2.14, Kaplan-Meier analysis $\chi2=4.654$, df=1, $P=0.031$), and may indicate a positive impact of 1080 on post-release survival. However, the post 1080 sample consisted of only large groups (Figure 2.1), since evidence to this point suggested group size was influencing survival, and working with this critically endangered bird in an adaptive management framework therefore led to the decision to act on this evidence and release only large groups. To take into account the potentially confounding effects of group size within the analysis of the effect of 1080, a second analysis was undertaken with data from only large groups in North Ōkārito pre and post 1080, compared with a Kaplan-Meier analysis. In North Ōkārito pre 1080, four individuals from 30 (13.3%) in the large release groups died. Following 1080 no individuals (0.0%) of the 15 released in large groups died. The Kaplan Meier analysis (Figure 2.15) showed this to be a non-significant difference in the proportion of mortality pre and post 1080 ($\chi2=3.163$, df=1, $P=0.075$).

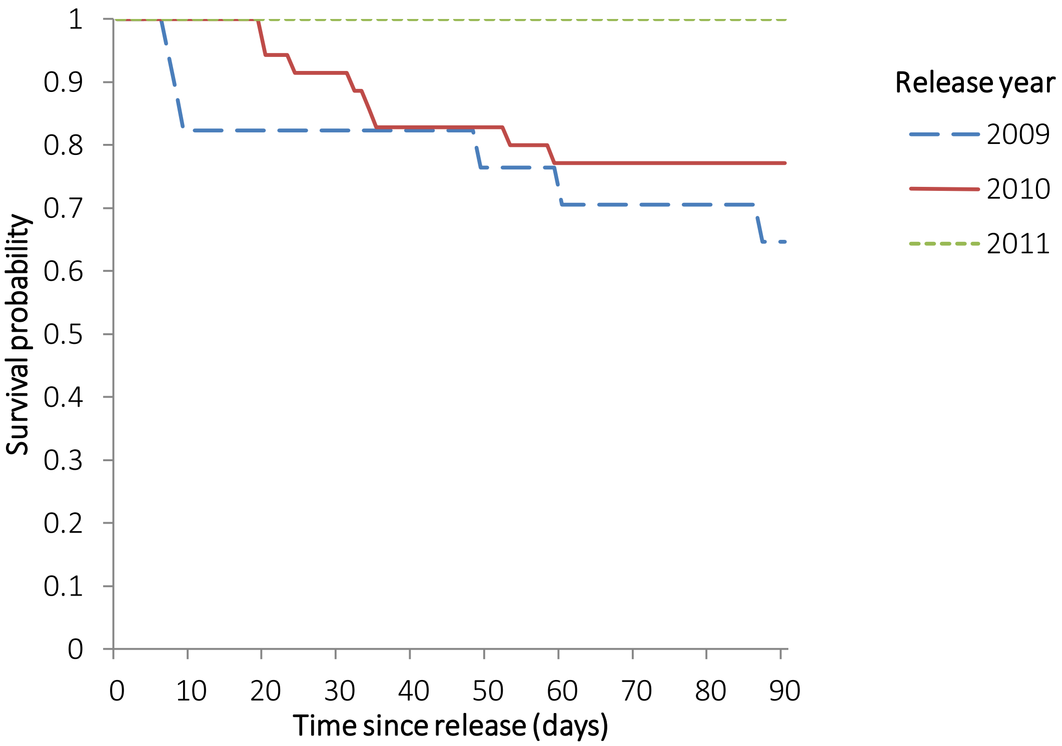

Figure 2.6. Estimated survival rate of rowi following reintroduction over three years: 2009 (n=17), 2010 (n=35), 2011 (n=15). While there appeared to be a trend of higher survival in 2011, this difference was not significant, suggesting the release year did not have an effect on rowi success. The fact that a predator control experiment took place between the 2010 and 2011 releases, along with the fact that in 2011 all releases occurred in large groups, may explain the difference in apparent estimated survival between 2009/2010 and 2011.

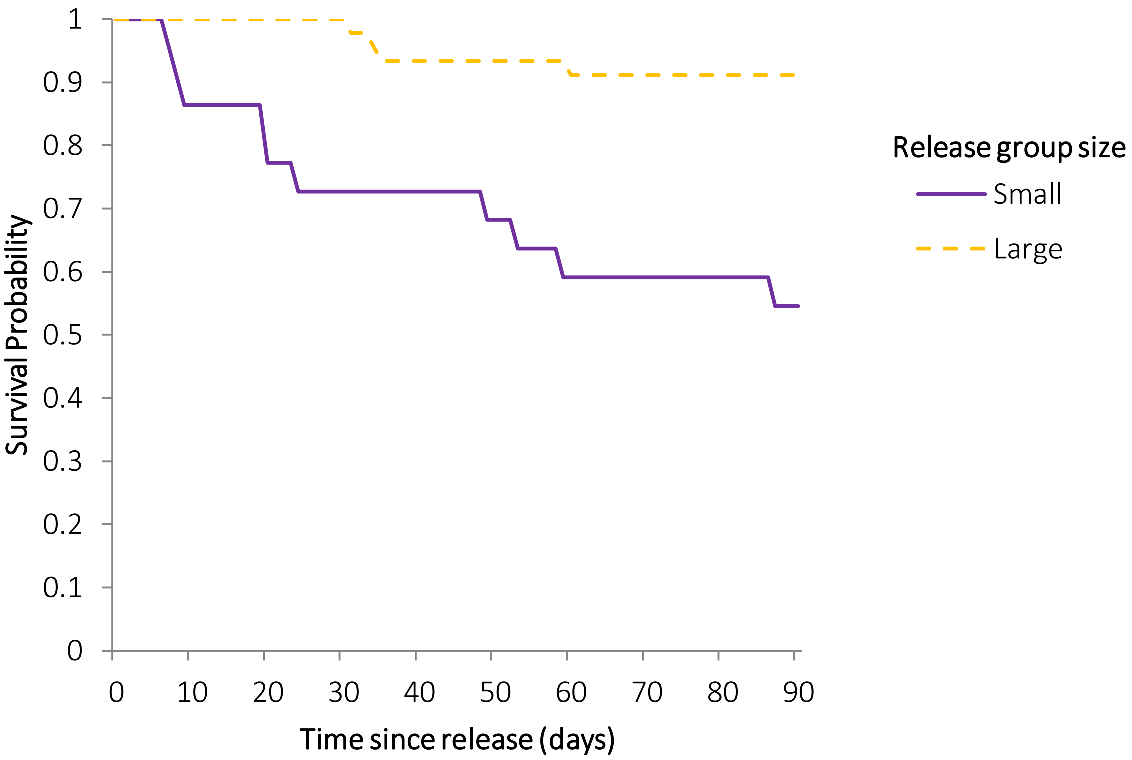

Figure 2.7. Survival estimates were significantly different for rowi released in small (n=22) and large (n=45) groups in 2009, 2010 and 2011.

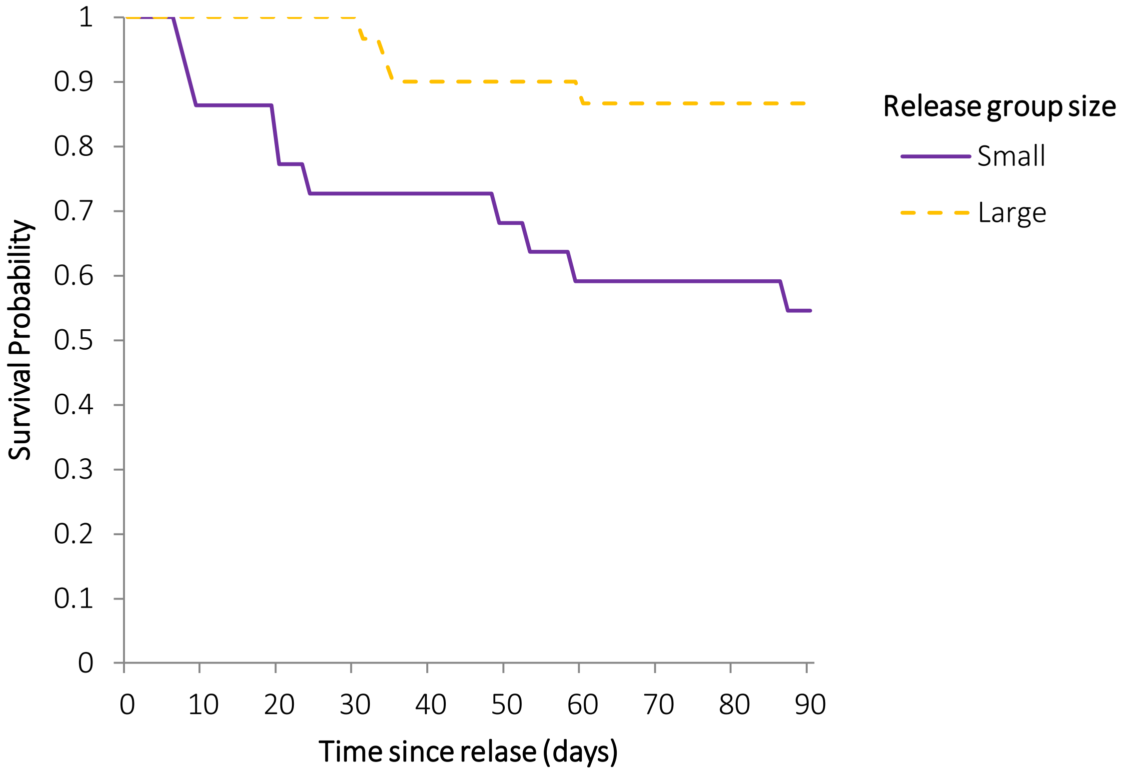

Figure 2.8. Survival estimates for rowi released in small (n=22) or large (n=30) groups from the pre 1080 release years 2009 and 2010 only. This showed that without the effect of predator control, group size remained having a statistically significant effect on survival estimate.

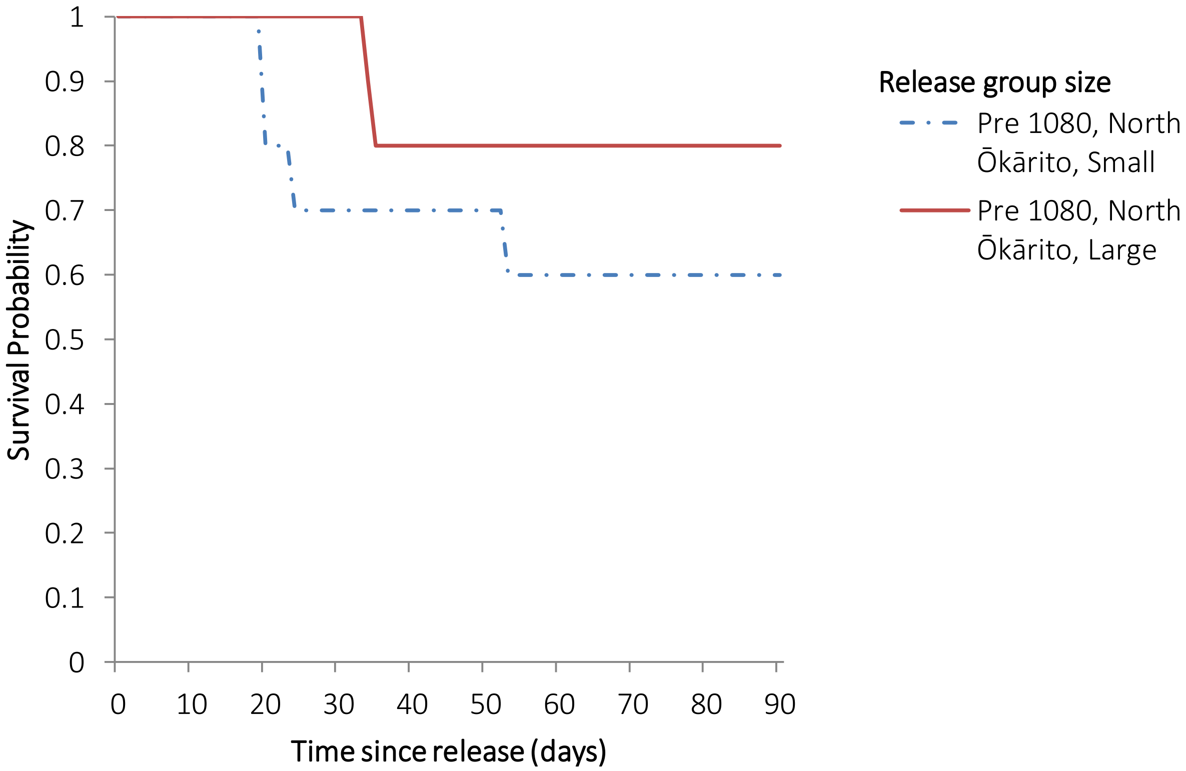

Figure 2.9. Survival estimates of rowi released in North Ōkārito prior to 1080 in different size groups, small (n=9) and large (n=10) were not significantly different (p=0.305), suggesting that in North Ōkārito, there was not any effect of release group size on post release survival during the critical period.

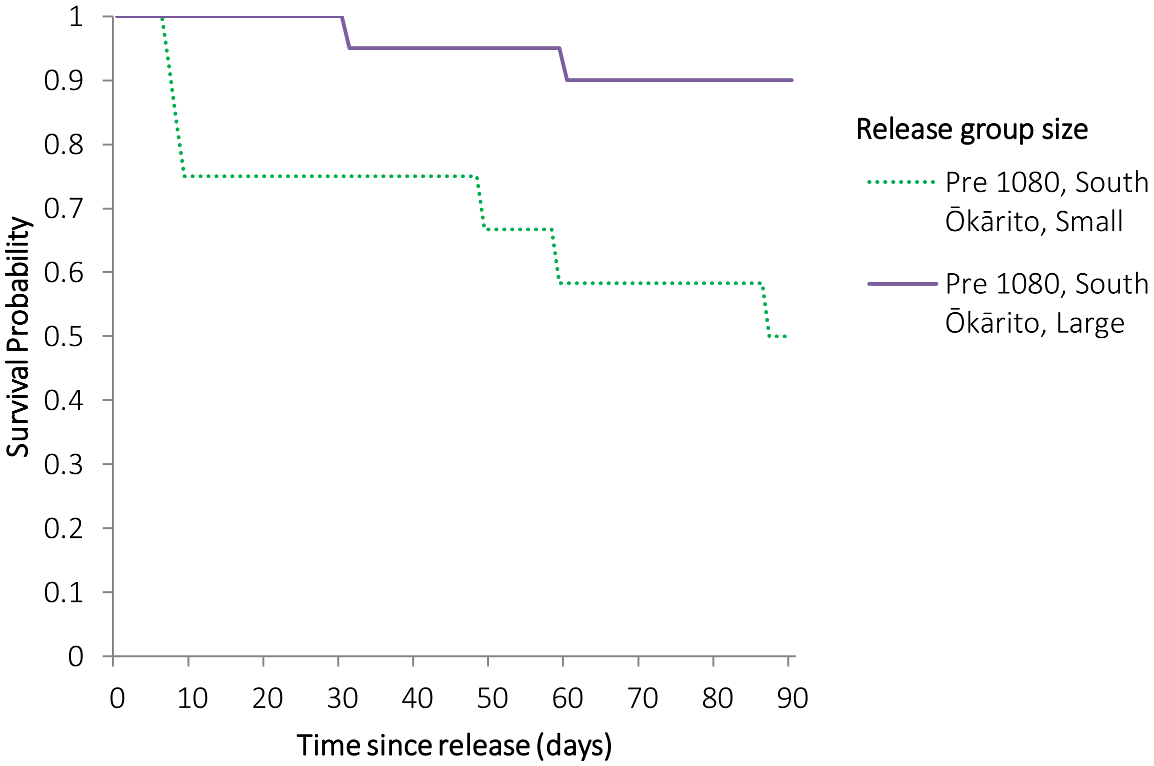

Figure 2.10. Survival estimates of rowi released in South Ōkārito prior to 1080 in different size groups, small (n=12) and large (n=20) were significantly different (p=0.008), suggesting that in South Ōkārito, there was an effect of release group size on post release survival during the critical period.

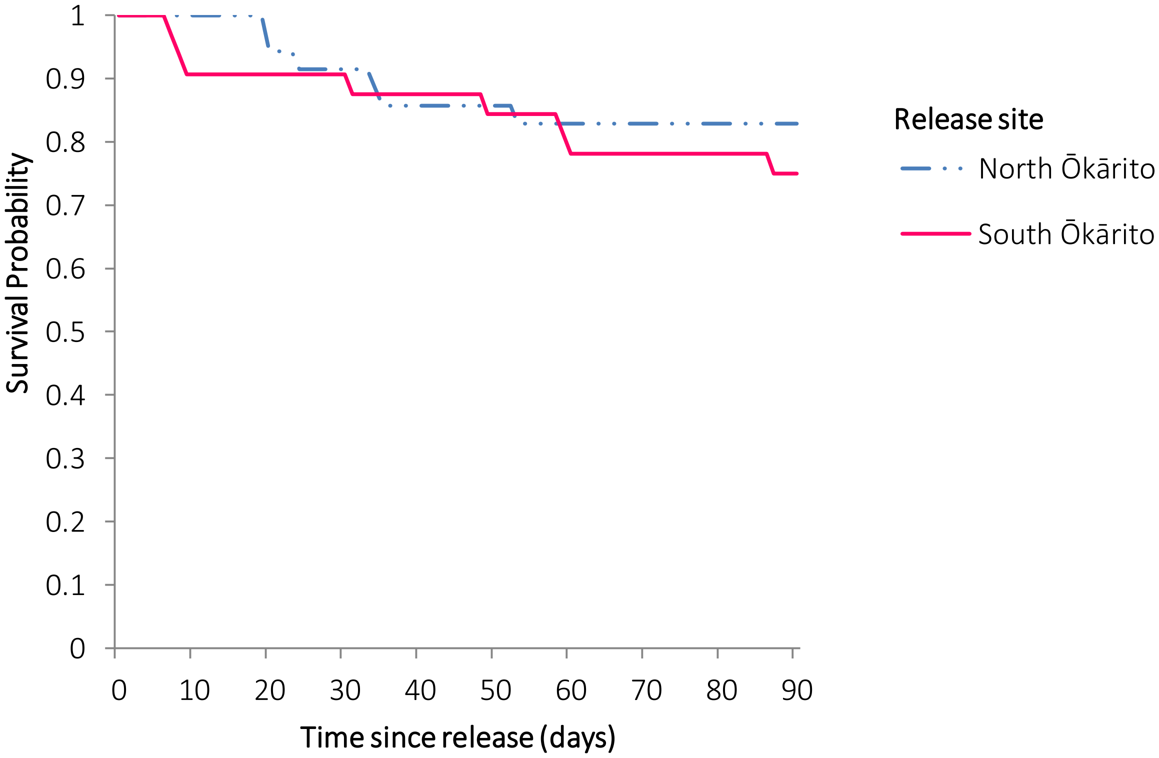

Figure 2.11. Survival estimates of rowi released into different sites, North Ōkārito (n=35) and South Ōkārito (n=32) were not significantly different, suggesting any differences between the sites, including conspecific density, did not have an effect on post release survival during the critical period.

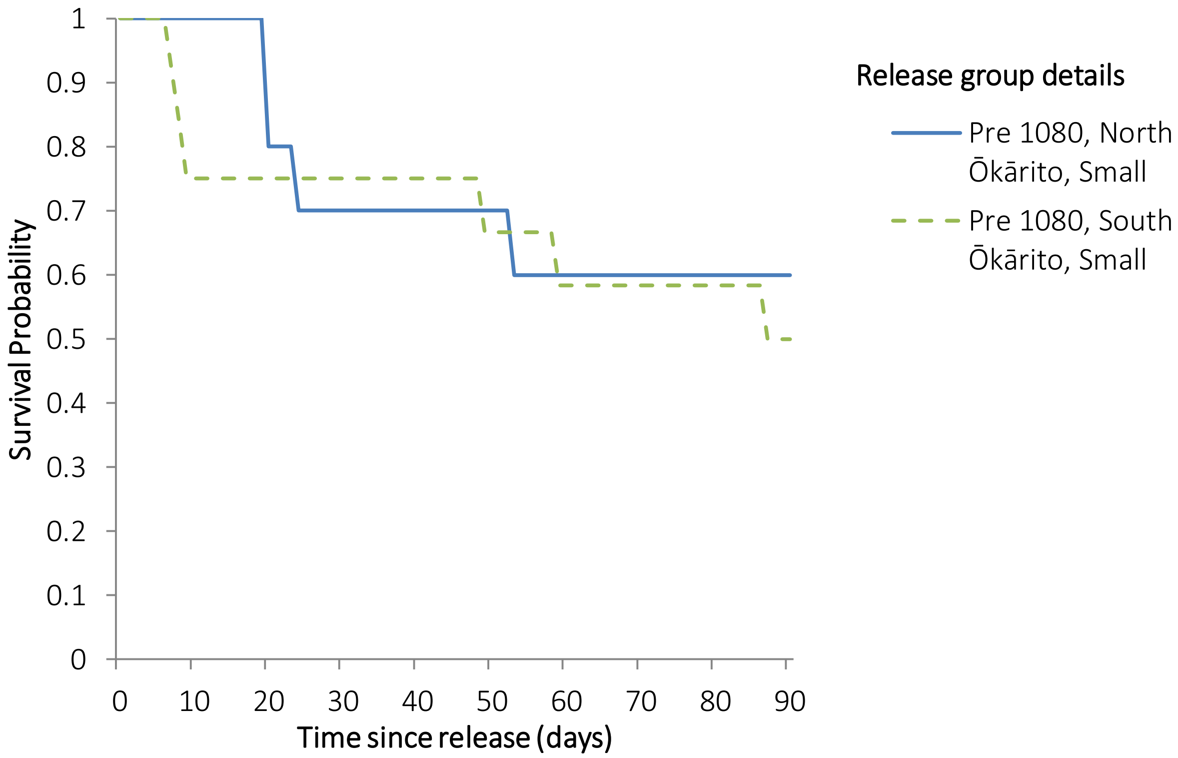

Figure 2.12. Survival estimates of rowi released only in small groups prior to 1080 into different sites, North Ōkārito (n=9) and South Ōkārito (n=12) were not significantly different (p=0.633), suggesting any differences between the sites, including conspecific density, did not have an effect on post release survival during the critical period.

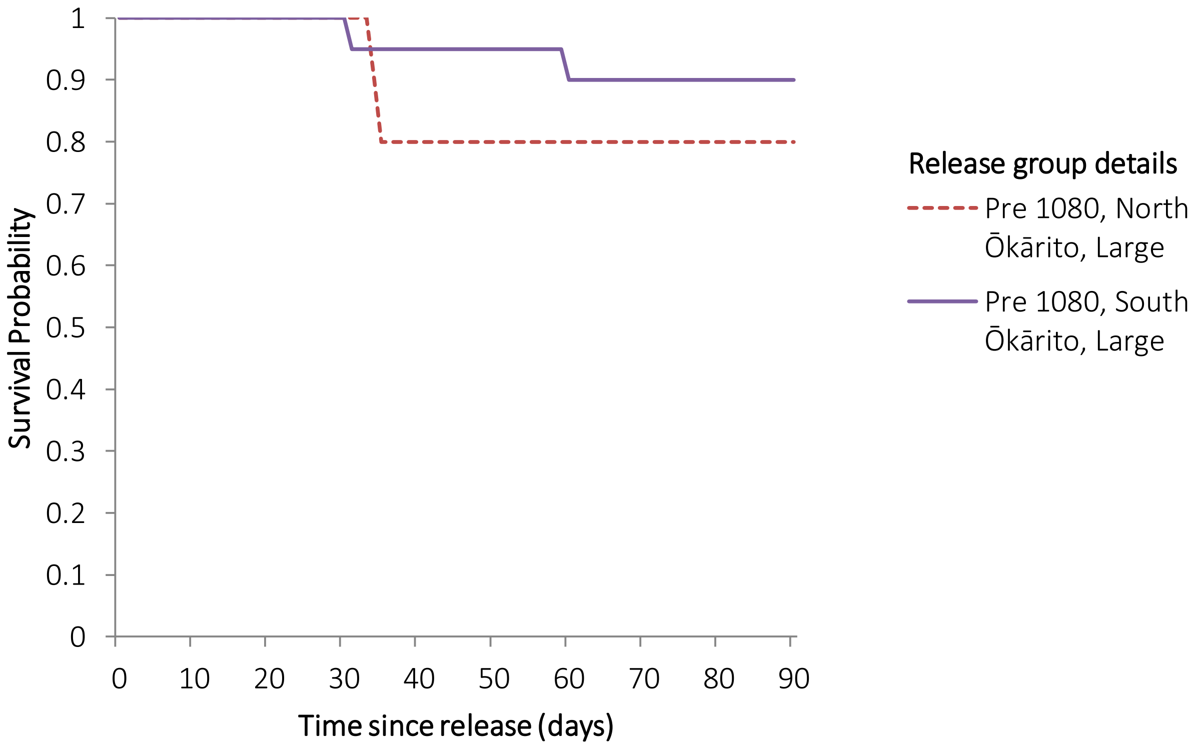

Figure 2.13. Survival estimates of rowi released in large groups prior to 1080 into different sites, North Ōkārito (n=10) and South Ōkārito (n=20) were not significantly different (p=0.452), suggesting any differences between the sites, including conspecific density, did not have an effect on post release survival during the critical period.

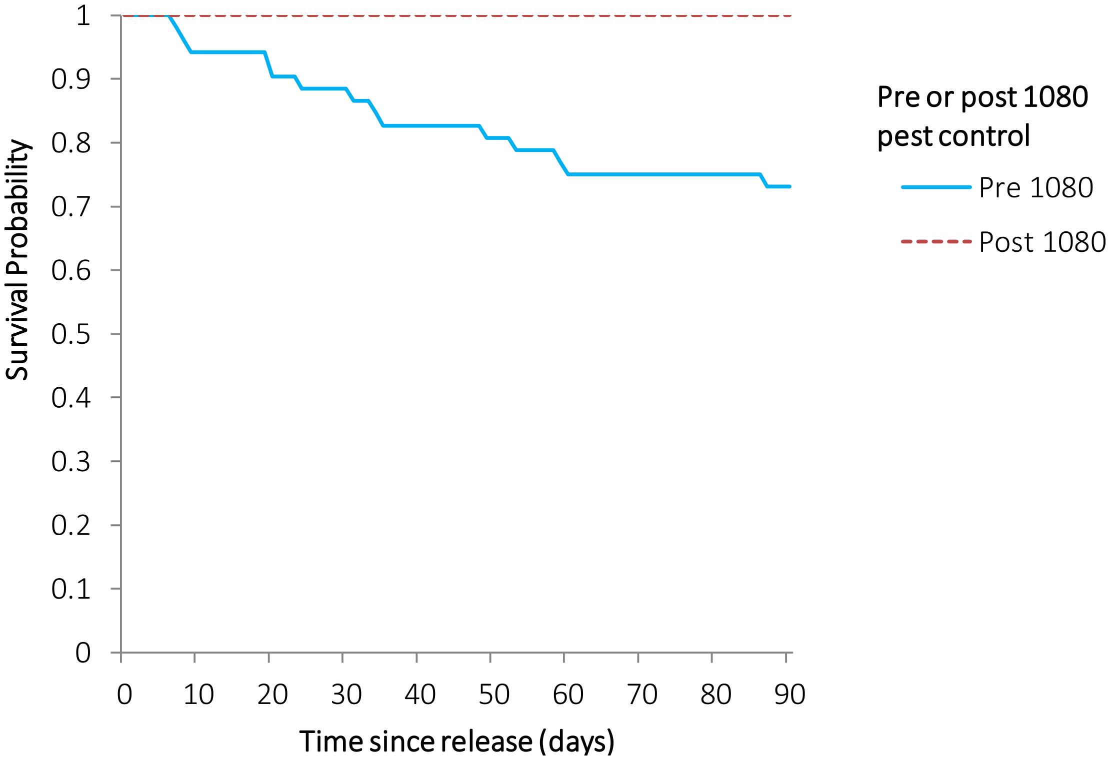

Figure 2.14. Survival estimates of rowi released pre (n=52) and post (n=15) predator control operation. There was a significant difference in the estimated survival during the critical period, suggesting predator control may have had an effect on the success of rowi releases.

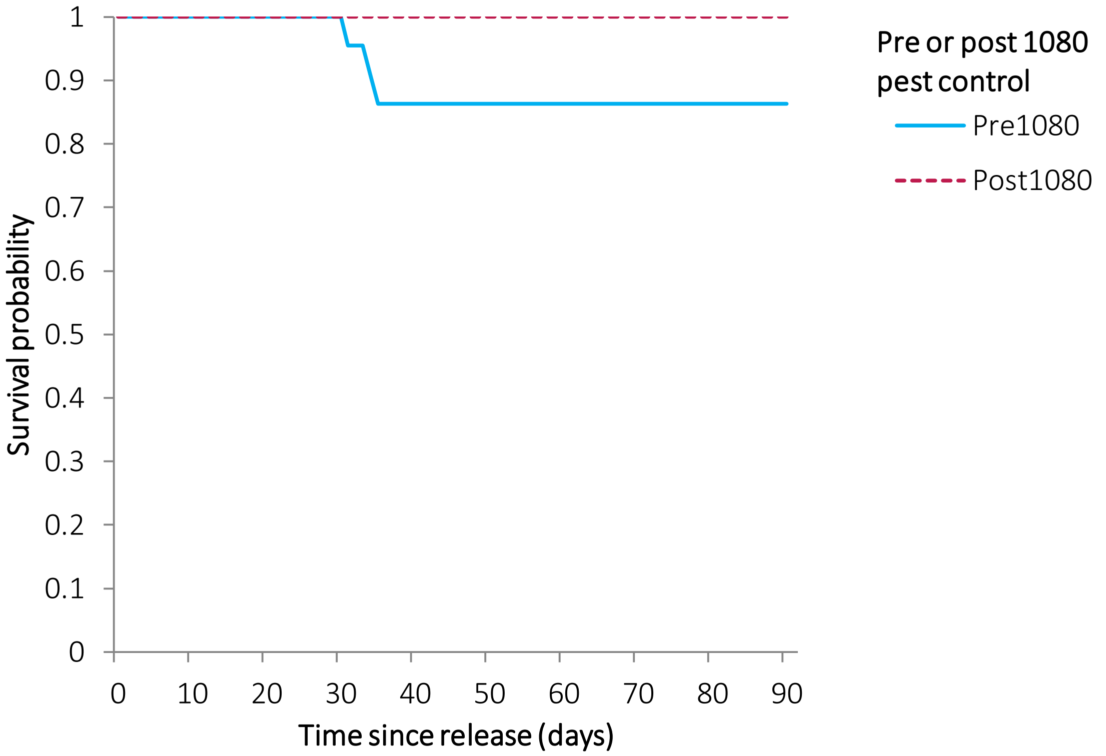

Figure 2.15. Survival estimates of rowi released in large groups only, in North Ōkārito pre (n=10) and post (n=14) predator control operation. There was no significant difference in the estimated survival during the critical period, suggesting that when group size was controlled for, predator control did not have a significant impact on post release survival. This highlights the fact that group size may have confounded the results in Figure 2.10.

Cox proportional hazards with mixed effects

I constructed a series of 10 candidate models to investigate the relative effects on survival probability of the following variables: year of release, small or large release group, conspecific density at release site and pre or post 1080. I ran a Cox proportional hazards analysis of the models and ranked them by lowest AICc (Table 2.3). To account for potential pseudo-replication within release groups, all models included group ID as a random effect term. The results of this test must be interpreted with caution as the experimental variables were not fully crossed, and the sample size was too small to allow consideration of interaction effects. The most parsimonious model described survival probability as a factor of group size. This suggests that large release groups have higher survival than small release groups. The second most parsimonious model, which had a ΔAICc of 0.14 and so can be considered a competing model, included group size and pre or post 1080. This would suggest that large groups released after a 1080 operation had a significantly higher survival probability than those released in small groups prior to a 1080 operation.

Table 2.3. Candidate models used to evaluate factors affecting survival estimates of released rowi during critical period, ranked by most parsimonious. Table includes number of parameters (K), Akaike Information Criterion corrected for small sample size (AICc), delta AICc (ΔAICc), Akaike weights (AIC_CWt), and log-likelihoods (LL). All models included group ID as a random effect to account for pseudo-replication within release groups.

Model	K	AICc	ΔAICc	AICcWt	LL
Group size	3	108.1	0.00	0.343	-51.51
Group size + Pre or post 1080	4	108.3	0.14	0.319	-49.93
Pre or post 1080	3	110.4	2.27	0.110	-52.65
Group size + site	4	111.0	2.86	0.082	-51.29
Group size + year	5	112.0	3.88	0.049	-49.78
Year	4	112.6	4.49	0.036	-52.10
Null	2	113.5	5.42	0.023	-55.60
Pre or post 1080 + site	4	113.7	5.58	0.021	-52.65
Site	3	115.5	7.34	0.009	-55.19
Site + year	5	115.8	7.71	0.007	-51.69

2.4 Discussion

My results show that, of the factors investigated, release group size is most likely to have a significant effect on post-release survival of rowi, particularly when releases are conducted in areas of high existing population density, and mortality may be further reduced when large release groups are coupled with a reduction in the density of predators and competitors via a landscape-scale application of 1080.

2.4.1 Data limitations

Data from the historic database was limited by inconsistent collection methodology and recording methods, having been collected by multiple persons over a span of many years, long before the beginning of this study. Results using this data therefore highlight patterns within the investigated factors, rather than providing conclusive experimental evidence of the impacts of various factors. Patterns observed within the analysis of the historic data provided the start point for experimental investigation undertaken. Unfortunately several factors limited the experimental design for the 2009 to 2011 releases, including the number of rowi available for release each year, the number of suitable release sites which were identified each year, and the number of trained kiwi handlers available to undertake concurrent releases. This led to the experimental design not being fully crossed across all variables, which makes drawing firm conclusions on individual effects impossible. In particular it was not possible to isolate the effects of release year from the effects of the 1080 application, since this only occurred in one release year. Instead of firm conclusions, the experimental investigation highlights patterns of factors likely to be affecting translocation success. These patterns provide a good starting point for further investigation, and illuminate areas for future research to focus, including looking into interaction effects of variables tested here, an extended analysis of effects of release group size and conspecific density on subsequent survival and longer term impacts on rowi behaviour and breeding success, plus further investigation of the impact of 1080 on post release survival of rowi.

2.4.2 Year effect

Release year appears to have had an effect on survival probability in the analysis of the full dataset (Figure 2.3), and showed a non-significant trend in the experimental data analysis (Figure 2.6). However this may have been an effect of another unmeasured covariate that also varied by year. In the historic database analysis, the season during which each group of birds was released also varied by year, meaning that the year effect may instead of been an artefact of a seasonal effect. In the experimental analysis, the 1080 predator control operation only occurred in 2011, and all birds released in 2011 were released in large groups, meaning the year effect that showed a difference in survival probabilities for released rowi between 2011 compared to 2009 and 2010, may be an artefact of the 1080 operation and release group size. The Cox proportional hazards analysis (Table 2.2 and Table 2.3), leads me to believe this is the case, since in the full dataset analysis the model containing year alone was ranked below the null model and in experimental data analysis it was only slightly above the null model.

2.4.3 Seasonal effects

Effect of season on survival following release was shown to be significant in the Kaplan-Meier analysis and the Cox proportional hazards analysis of the full dataset. The most parsimonious model contained season in combination with group size. Seasonal effects may be indicative of a range of factors at work. Average temperature, rainfall, and food availability are all likely to be affected by changes in season, and may all have had an effect on the survival of a newly released bird. However, the earliest release years, where winter and autumn releases occurred, also had higher numbers of smaller release groups, which may confound the historic analysis results of both seasonal and group size effects.

By 1997 it had been noted by rowi conservation managers that a pattern of low survival occurred with releases in autumn and winter. As a result of this, the management practice was altered so that in all releases after 1998, efforts were made to conduct releases in Spring or Summer only. This happened on all occasions except one release in Winter 2002. Since management practice has now altered to only conduct releases in Spring and Summer, I deemed it unnecessary to investigate further the exact climatic and mechanistic cause of the seasonal effect. I conducted all of the experimental releases in spring, and so no experimental data were available on seasonal effects.

2.4.4 Sex effects

Sex of released birds had no effect on post-release survival probability. This was unsurprising, since at the time of release, both male and female rowi were sexually monomorphic, meaning there was no inherent vulnerability of either sex compared to the other. Many other studies also find no effect of sex on the survival of animals post-release (e.g., Vancouver Island marmots (*Marmota vancouverensis),* brown treecreepers (*Climacteris picumnus*), (Aaltonen et al., 2009; Bennett et al., 2012)), although there are some exceptions to this (Campbell-Thompson et al., 2012; Heurich et al., 2012). Some authors suggests that the presumably unsettling nature of a release may in fact mask any inherent effect of sex on survival rates that might be apparent in other circumstances (Biggins et al., 1998).

2.4.5 Release group size

Release group size was shown to have a significant effect on survival in both the analysis of the full dataset and the experimental data analysis, with small groups having significantly lower survival probability at the end of the critical period compared to large release groups. When accounting for the uncrossed variables, analysis of only pre 1080 releases within a single release site (either North or South Ōkārito), reveals that the effect of group size is not evident within North Ōkārito, but is clear in South Ōkārito, where the existing population density is high.

Habitat-selection theory predicts that individuals of territorial species will thrive at lower densities due to density dependent fitness losses at higher rates of assemblage (Fretwell & Lucas Jr, 1969). However, Darwin noted in 1859, that there are occasions where large numbers of a species, relative to its enemies, are essential for its preservation (Darwin, 1859). He wrote about this in the context of wheat seed prevalence in relation to predation by mice. The idea that a minimum number within a cohort must exist for the group to persevere, or that fitness can be negatively affected by low density, is one which has been expanded upon greatly by many other authors since, with Warder Clyde Allee being one of the most influential. Allee (1932) described many situations where, contrary to habitat-selection theory, fitness proved to be positively density dependant. While Allee did not provide a concise definition of the phenomenon he was describing, “Allee effects” have been defined as “A positive relationship between any component of individual fitness and either numbers or density of conspecifics” (Stephens et al., 1999). The mechanisms that drive such Allee effects are diverse, ranging from predation dilution as in the wheat seed case described by Darwin (1859), through to ability to find a mate due to low density or skewed sex ratio (Molnár et al., 2008). Component Allee effects describe situations where a measurable component of fitness (e.g., survival), is higher in a larger aggregation unit such as social group or population (Somers et al., 2008; Stephens, 1999). If we consider the rowi release groups as a cohort or social group created by the release process, I propose that the results of this study, where large release group had a positive effect on post-release survival, may be a type of component Allee effect.

Release group size has been shown on many occasions to have effects on the outcome of translocations (Calvete & Estrada, 2004; Kingsley et al., 2012; Mateju et al., 2012; McCallum et al., 1995). The effect of larger group sizes is often associated with a dilution of predation risk, although in the case of European wild rabbits, large numbers served as an attractant to predators, resulting in a higher predation rate (Calvete & Estrada, 2004). In the case of rowi releases, where predation risk had been lessened by only releasing birds over 1.2 kg, it is unlikely that predation dilution is the mechanism driving positive density dependence. Larger release groups may result in more opportunity for social learning, including beneficial behaviours such as social cueing of areas with high food resources or suitable shelter (Chapman et al., 2008). In areas with high existing population density, such benefits are likely amplified, as demonstrated by the apparent difference in impact of release group size on survival between North and South Ōkārito.

In addition, a number of studies have demonstrated that early social environment and experiences can have profound and long lasting effects on the ontogeny of behaviour of birds and mammals prior to translocation for conservation (Hansen & Slagsvold, 2004). Particularly important effects may include those relating to dominance, (Hansen and Slagsvold 2004), and social learning ability (Chapman et al 2008). In studies of captive reared Takahē (*Porphyrio hochstetteri)*, rearing in the absence of adults may result in the sub-dominance of captive reared individuals in comparison to wild reared individuals (Maxwell and Jamieson 1997).

Placement of juvenile rowi on a predator free island, with a high density of conspecifics, zero territorial resident birds, and high resource availability may lead to an alteration in the social behaviour and conspecific tolerance of ONE rowi compared to wild rowi. The Ōkārito sanctuary has a density of one bird per 28 ha. The crèche island of Motuara has a higher density of birds, usually around 30 to 40 rowi on 59 hectares giving approximately one bird per 1.69 ha, and also has more abundant food resources than Ōkārito (R. Colbourne, pers. comm., 2011). Juvenile birds that would naturally associate exclusively with their parents are placed into a situation on the crèche island where the detrimental effects of increased sociality are low. These birds are not yet sexually mature, and so there is no competition for mates. There is also no competition for resources since artificial burrows are provided and the island has an abundant supply of invertebrates for food. The benefits of association with conspecifics may be high; added warmth by burrow sharing and opportunity for social learning regarding burrow sites and good foraging areas. The aggregation of the majority of artificial burrows in two small areas on Motuara Island may exacerbate this phenomenon of increased social tolerance. It is more common than not on Motuara Island to find multiple juvenile birds sharing one artificial burrow, with the record being 14 rowi squeezed into a 50 cm by 50 cm box (pers. obs. and A. Colombus pers. comm., 2011), despite other burrows being available. I suggest that this range of factors results in higher social tolerance of ONE rowi, which may continue once released back into Ōkārito. This social tolerance and history of successful social learning while on Motuara Island, along with sudden decrease in resource availability when they are relocated to Ōkārito, may lead translocated rowi to seek out conspecifics upon release. There has been evidence from other studies that newcomers from a release may be attracted rather than repelled by the presence on resident conspecifics (Muller et al., 1997). For rowi released in smaller release groups, this social attraction may result in a higher chance of encountering an aggressive territorial bird, whereas those birds released in a larger group are more able to associate with a tolerant conspecific and not therefore seek interaction with resident birds. This suggestion is in line with studies of translocations of social animals, which have demonstrated that familiarity with release counterparts can lead to a reduction in panic response and hence reduced dispersal distances(Mateju et al., 2012), thus increasing survival due to reduced risk of encountering aggressive unfamiliar individuals (Shier, 2006). Stress is another important consideration in translocation projects and may influence survival by interfering with processes involved in behavioural decision making and other cognitive abilities such as remembering the location of high resource areas (Teixeira et al., 2007). It is possible that birds released in larger groups experienced lower levels of stress than those in small groups due to the presence of familiar conspecifics, and this may in turn have affected the survival probability.

I therefore suggest that increased social tolerance and prior experience of successful conspecific cueing, coupled with reduction in post-release stress response among rowi released in larger groups are the most likely mechanisms driving the density dependent effect observed in the release groups. Further research is required to investigate these possible mechanisms further.

2.4.6 Conspecific density

It appears that the density of conspecifics did not have an effect on the survival probability of rowi, with birds released into the high density South Ōkārito having a similar survival probability as those released into the low density North Ōkārito. While presence of a high density of conspecifics did not appear to affect post-release survival within the critical period, this does not rule out that possibility that South Ōkārito may be close to carrying capacity, as the resource requirement for successful reproduction, long term population persistence and growth will be far greater than that for survival. With continued monitoring of the rowi released into both North and South Ōkārito, it will be possible to investigate whether the conspecific density may be limiting the reproduction rate in South Ōkārito, or if perhaps another factor, such as a predominantly geriatric population, may be the cause of the low fecundity.

2.4.7 Predator control

The 1080 predator control operation appeared to show a non-significant trend towards increasing the survival probability of released rowi when combined with large release groups. The Kaplan-Meier analysis including all experimental data showed that there was a significant difference between pre and post 1080 survival probabilities, but this does not take into consideration the fact that all of the post 1080 releases took place with large release groups. When this discrepancy is accounted for, the difference in survival between pre and post 1080 was not significant, but signals a trend. The Cox proportional hazards model accounted for this, and showed that a model containing pre or post 1080 alone does not explain a significant proportion of the variance in results observed. The model with only pre or post 1080 was given a ΔAIC_C of 2.27, so I did not consider it a competing model. The 1080 predator control appears to further increase the survival probability of those rowi released in large groups.

This research has demonstrated that several elements of the translocation procedure are likely to be playing an important part in determining the success of rowi translocations. I have shown that the critical period following release is 90 days, and that release group size and predator and competitor density are the most probable factors associated with post-release survival of rowi within this time. Further research in Chapters 3 to 6 will focus on analyses of habitat selection, dispersal and interactions following release to identify the mechanisms driving these effects. Additional research is required to disentangle further the effects of individual variables tested here, along with interaction effects. Of particular value would be an expanded analysis of release group size effects on post release survival, to identify a precise optimal group size.

3 Quantifying rowi habitat quality in Ōkārito forest

3.1 Introduction

Understanding habitat composition and quality is important for conservation management as it can drive decisions such as selecting the optimal location for translocations or number of individuals able to be released in reintroductions within finite areas such as reserves, protected areas or islands. In both terrestrial and marine environments direct observation and sampling of elements that would be used in assessing habitat quality such as biodiversity, or species biomass, densities, abundance, or presence, are expensive and time consuming (Dunn & Halpin, 2009; Gollan et al., 2009; Mannocci et al., 2013; Yeung et al., 2013). However, since ecosystem composition and function is driven by habitat structure, it is possible to use this as a proxy (Meager et al., 2011). In a variety of conservation management scenarios, such as restoration planning, targeting habitat protection or allocation of protective status, it is beneficial to use surrogates in models that can then be used to relate either a species distribution, abundance or biomass at known locations to data on readily obtainable information on spatial and environmental characteristics (Elith & Leathwick, 2009; Gollan et al., 2009). For example, hard bottom habitats support high levels of biodiversity and are therefore frequently used as a proxy for spatial planning in marine areas (Dunn & Halpin, 2009), and it is expected that soil-based parameters can make useful surrogates for terrestrial invertebrate biomass (Gollan et al., 2009).

Habitat quality can be defined as the ability of an area to provide conditions necessary for individual and population persistence (Hall et al., 1997). While a range of factors will contribute to overall habitat quality relevant to any given species, one major factor in describing the quality of a site for any organism is the relative availability of resources to meet energetic requirements, such as sunlight for plants and food for animals. Food availability has been shown to affect the breeding success of a range of species (e.g. African penguins (*Spheniscus demersus)* (Crawford et al., 2006), eagle owl (*Bubo bubo*), (Penteriani et al., 2002), song sparrow (*Melospiza melodi*) (Arcese & Smith, 1988), and little owls (*Athene noctua*))(Perrig et al., 2014)), and can affect whether birds even attempt to breed or not (Drent & Daan, 1980), therefore relating food supply to population performance. Other factors important in habitat quality include mate availability, suitable breeding sites, seed or egg deposition sites, sleeping sites, refugia from predators and accessibility of resources (Johnson, 2007).

For species that rely on the abundance of a prey species to meet energetic requirements, it can be a time consuming process to evaluate the relative habitat quality as described by resource availability, especially if the scale at which the prey species is relevant is large, or the prey are not easily observed with visual surveying (Mannocci et al., 2013; Yeung et al., 2013). Such is the case for invertebrate prey, which are the main source of energy for a range of species, including all species of kiwi (Holzapfel et al., 2008). Examples of using easily measured environmental variables to evaluate invertebrate prey abundance in relation to habitat quality include measuring the abundance of molehills as a proxy for earthworm abundance when considering the habitat quality of foraging sites of golden plover (*Pluvialis apricaria*) (Whittingham et al., 2000), and the use of a a Normalized Difference Vegetation Index to estimate grasshopper abundance when investigating habitat quality of Montagu's harriers (*Circus pygargus*) (Trierweiler et al., 2013).

When producing models of surrogates for a target species, variables included must be of ecological relevance to that species (Elith & Leathwick, 2009; Guisan & Zimmermann, 2000; Meager et al., 2011). There are a vast range of environmental variables that impact invertebrate density, abundance and biomass. Invertebrate body size and abundance, and hence overall species biomass, are likely to be affected by both microclimate and components of habitat structure (Meager et al., 2011). Soil properties such as hardness and texture influence arthropod assemblages (Bestelmeyer & Wiens, 2001), as does the chemical composition of soil, specifically carbon, phosphorus and potassium levels, along with pH (Oliver et al., 2005). For example, enchytraeid and nematode density and biomass is positively correlated with soil phosphorus/carbon and nitrogen/phosphorus ratios (Vonk & Mulder, 2013). Earthworm density and biomass is negatively correlated with soil pH (Václav et al., 2009), whereas snail abundance is positively correlated with soil pH (Kappes et al., 2006). Soil moisture and temperature can affect different microorganisms in different ways (Kamin, 2010). In some species such as grasshoppers, most essential activities are thermally influenced and behaviours including locomotion and oviposition are directly temperature related. For these species, while thermoregulation can play a part in mediating body temperatures, the ambient environmental temperature plays a large role in affecting activity patterns (Gilman et al., 2008; Whitman, 1988).

The vegetation composition in an environment is influenced by soil and topographic properties (Kappes et al., 2006; Rubino & McCarthy, 2003). In turn, the vegetation composition and forest productivity directly influences soil composition and invertebrate biomass, with the productivity of soil invertebrates enhanced by soil fertility (Cole et al., 2005; Mulder et al., 2009; Seagle & Sturtevant, 2005). Temperature, rainfall and solar radiation rates are often correlated with changes in elevation at a site (Elith & Leathwick, 2009). The aspect of a site is related to the amount of solar radiation, exposure to wind current and microclimate (Kappes et al., 2006). Slope gradient can affect the vegetation composition, as microsite conditions co-vary with topographic gradient (Rubino & McCarthy, 2003). Aspect, slope, and elevation are therefore not directly influencing factors, but work as distal factors, which in turn can have a large influence on vegetation and hence invertebrate assemblages, and are predictors of soil productivity in oak forests (Trimble, 1964). Further evidence of this link between topography and invertebrate biomass is shown by the positive correlation between invertebrate productivity and spatial variation caused by topographic changes in slope, aspect, and elevation (Seagle & Sturtevant, 2005).

The scale at which habitat variables are measured compared to the scale at which the habitat affects the population of a study species is a further consideration when selecting variables for inclusion in a model (Maurer, 1986). Habitat variables that affect micro fauna such as protozoa may be as small as millimetres, whereas habitat variables affecting the density or abundance of macro organisms such as crustacea and gastropods may be on a scale of tens of metres (Giller, 1996).

I set out to investigate the predictors of habitat quality throughout the range of a flightless territorial bird. I aimed to quantify the variables and identify a model that could predict the invertebrate density throughout the habitat of rowi (*Apteryx rowi*). Rowi are a critically endangered species of kiwi (Hitchmough, 2002), that rely on soil and litter invertebrates as a food resource (Holzapfel et al., 2008). Rowi are found only in Ōkārito forest within the 98000 ha South Westland National Park, situated between Hokitika and Fox Glacier on the

West Coast of the South Island of New Zealand (Colbourne et al., 2005; DOC, 2004), and are threatened by predation of eggs and chicks by introduced mammalian predators, in particular stoats (*Mustela erminae*) (McLennan et al., 1996). From 1992 to 2010, the entire range of rowi was encompassed by the South Ōkārito area, at a density of approximately one kiwi per 28 ha. Conservation management of rowi currently involves threat mitigation through the intensive egg collection and translocation process known as Operation Nest Egg (ONE) (Colbourne et al., 2005). In 2010 and 2011 I undertook experimental releases in both South Ōkārito and North Ōkārito as part of a larger investigation into factors affecting translocation success. Prior to the experimental release there had been no rowi present in North Ōkārito since the 1980s. Translocation success may be affected by the quality of habitat at release sites and where home ranges are established. I investigated biomass of invertebrates in rowi habitat and analysed corresponding abiotic habitat variables to establish a predictive model for relative invertebrate biomass as a proxy for habitat quality across the rowi range.

While precise dietary analysis for rowi has not been conducted, analysis of prey of other kiwi species has been shown to include a range of invertebrates with dietary composition thought to vary with local invertebrate availability rather than an ability of kiwi to preferentially select specific prey species (Reid et al., 1982). The gizzard contents of 50 North Island Brown kiwi (*Apteryx Australis Mantelii*) corresponded to local prey availability, with a wide variety of invertebrates present. Annelid worms, cicada nymphs (*Amphisalta*) and melolonthids (*Odontria*) were most abundant both within gizzards and in the environment (Reid et al., 1982). Ground wetas, cicada nymphs, fly larvae, adult and larval beetles, moth larvae and some adults, spiders, a few amphipods, and earthworms are found in Little Spotted kiwi diets (J. N. Jolly & R. G. Ordish pers. comm. in (Moeed & Meads, 1987)), with Scaribidea beetles and their larvae the most common prey of Little Spotted kiwi on Kapiti Island (Colbourne et al., 1990). The four invertebrate groups contributing most soft tissue dry matter to faecal samples of Stuart Island tokoeka (*A. australis*), were Lepidoptera (36%), Coleoptera (21%), Arachnida (19%) and Hemiptera (10%) (Colbourne & Powlesland, 1988). Invertebrate biomass was chosen as the most appropriate variable of habitat quality to measure, since energy flow through trophic levels is inextricably linked to body mass, and biomass is a better indicator than abundance or density of the functionality of a species (or in this case a group of species) within an ecosystem (Saint-Germain et al., 2007). Kiwi selectively feed on invertebrates with a body length 8mm or greater, and so only invertebrates meeting this requirement were included in analyses in this study (Colbourne et al., 1990).

3.2 Methods

3.2.1 Study site

Ōkārito is a cold temperate lowland costal wetland forest ecosystem ranging from sea level to 520 m.a.s.l. (Christie et al., 2006). The topography of Ōkārito is rugged and varied, with a combination of flat areas, undulating slopes and ridges (Christie et al., 2006). South Ōkārito is largely unmodified native podocarp-hardwood forest (Murphy et al., 2008). The predominant canopy vegetation is rimu (*Dacrydium cupressinum*), miro (*Prumnopitys ferruginea*), and southern rātā (*Meterosideros umbellata*) , with a subcanopy of quintinia (*Quintinia acutifolia*) and kāmahi (*Weinmannia racemosa*) (Rickard, 1996; Warburton et al., 1992). North Ōkārito was similar in vegetation structure and composition and topography to South Ōkārito until it was selectively logged at 25% of total merchantable volume in the 1970s and 1980s, resulting in a series of logging tracks throughout the area, and regenerating vegetation (Pearce & Griffiths, 1980; Piskaut, 2000).

3.2.2 Habitat sampling

Habitat sampling took place during May 2010 (South Ōkārito), and May and July 2012 (North and South Ōkārito). Plot locations were generated using the random points function in ArcGIS, with a minimum inter-plot distance of 200 m. In 2010, 15 random points were generated within the boundary of the entire South Ōkārito kiwi sanctuary and these plots sampled (Figure 3.1). In 2012, 20 North Ōkārito plots and 10 South Ōkārito plots were randomly generated. The range available for plots to be generated in for 2012 was restricted to areas that were able to be accessed within a day by creating polygons of accessible areas using ArcGIS and generating random points within these using the random points function (Figure 3.1). Due to logistic limitations, 19 of the 20 plots in North Ōkārito and seven of the 10 plots in South Ōkārito were sampled (Figure 3.1). Plots were located using handheld Global Positioning System (GPS) devices (Garmin USA Ltd), with an accuracy of ±10 m. The grid reference of the plot was taken as the southernmost point of the plot, at 0 m on a 20 m straight line transect with a due north heading. Pitfall traps were placed at 5 m intervals along the 20 m transect. Pitfall traps were constructed using standardised plastic cups sunk into the ground, with the rim flush with the soil level, containing Gault's solution (50 g sodium chloride, 10 g chloral hydrate, 10 g potassium nitrate, 1000 ml water) (Walker & Crosby, 1988). Pitfall traps were protected from rain by a plastic plate placed 5 cm above the rim of the cup, and supported on three pieces of garden wire pushed into the ground. Pitfall traps were left in place for five nights, the contents collected and analysed in the lab. Though the most widely used technique in sampling litter-dwelling invertebrate assemblages since the 1930's, pitfall traps are often criticised as a sampling method (Spence & Niemelä, 1994). A range of factors other than simply the abundance of invertebrates can influence catch rate (Duffield & Aebischer, 1994), including the vegetation surrounding the trap and activity of the species being sampled, and type of species being sampled (Greenslade, 1964). I chose to use pitfall traps as they offer a range of benefits: they are cost effective, allow the collection of many samples over a short timeframe, function in most weather conditions, collect both diurnal and nocturnal species (Duffield & Aebischer, 1994), and while they do not sample flying invertebrates, they do collect samples relevant to kiwi diets. Pitfall trap sampling however only provides samples partially relevant to kiwi diets, since kiwi also probe into the soil and extract invertebrates from beneath the leaf litter and soil surface. Such subterranean invertebrates may not be present in surface sampling via pitfall traps. It was decided however, that the surface level abundance and density of invertebrates would provide a suitable approximation of relative below ground invertebrate densities at the sampling points throughout the study area. I standardized the procedure throughout sampling in order to limit any effects of the sampling method on the species collected, and am confident that the use of pitfall traps was therefore an appropriate method and yielded reliable results in this study.

Specimens were recorded to order or, when possible, family, and body length from head to end of torso measured. Dry biomass of the collected invertebrates with a body length 8mm or greater was estimated using Rodgers, Hinds and Buschboms' (1975) equation that states:

$$W = 0.0305\ L^{2.62}$$

where (W) is dry biomass in milligrams and (L) is body length in millimetres. The total estimated dry biomass from each plot, comprising of five samples along the transect, was calculated and the value logarithmically transformed to homogenise variances and normalise residuals (Smith et al., 2006). The $\log_{10}$ values were then used to determine a relationship between the estimated plot biomass and topographical, physical and climatic characteristics of the plot through logistic regression modelling. Topographical factors were extracted from shape files of the study area (Land Information New Zealand), and a digital elevation model (DEM) (Landcare Research New Zealand Ltd) using the "Add surface information" and "Extract values to points" tool of ArcGIS (Table 3.1). Climatic conditions were obtained from the Cliflo database (National Institute of Water and Atmospheric Research), and originated from the closest possible monitoring station, located in Franz Josef Glacier (New Zealand Transverse Mercator grid reference 1371724 E, 5191782 N, elevation 155 m above mean sea level) (Table 3.1). Data on physical characteristics of the area were available from the Soil Fundamental Data Layers package from the New Zealand Land Resource Information System (Landcare Reasearch New Zealand Ltd) (Table 3.1).

Table 3.1. Descriptions of abiotic factors included as variables in the analysis of factors affecting invertebrate biomass in Ōkārito Forest. Measures of each soil related variable were extracted from a GIS layer of the Soil Fundamental Data Layers. Measures of weather conditions were taken from the Cliflo database, recorded in Franz Josef Glacier.

Variable and name in model	Continuous or categorical	Description	Reason for inclusion	Range	x̄ ± S.E.
Elevation	Continuous	Mean elevation of the plot site	Can have a large influence on vegetation and hence invertebrate assemblages, and is a predictor of soil productivity	3.64 m - 393.39 m	138.61 m ± 14.06 m
Slope gradient	Continuous	Max gradient of the plot site	As above	5° to 45°	14.27° ± 1.93°
Mean min temperature	Continuous	Mean of all minimum temperatures recorded over the pitfall trap sampling period	Ambient environmental temperature plays a large role in affecting activity patterns of many invertebrate, thus affecting the catch rate in pitfall traps	-0.42°C - 6.82°C	3.46°C ± 0.35°C
Total rainfall	Continuous	Total rainfall recorded over the pitfall trap sampling period	Rainfall also affects activity patterns of invertebrates and resulting catch rate in pitfall traps.	0.0 ml - 57.3 ml	16.06 ml ± 2.69 ml
Max phosphate retention (PRET_Max)	Continuous	Estimated as weighted averages for the upper part of the soil profile from 0–0.2 m depth, and expressed as a percentage	Affects invertebrate assemblages. Density and biomass of many invertebrate species is correlated with phosphate levels.	29.0 – 84.0%	44.12 % ± 3.51%
Gravel content (Gravel_Class)	Categorical	The percent of gravel in topsoil. Five categories, 0 - 4%, 5 - 14%, 15 - 34%, 35 - 69% and 70 - 100%	Affects vegetation assemblage which impacts invertebrate community.	0.0 - 4% - 15 - 34 %	
Phase (PHASE)	Categorical	The type of soil based on land topography, in three categories; A) flat land, B) hill, C) steep land	As above		

Variable and name in model	Continuous or categorical	Description	Reason for inclusion	Range	X̄ ± S.E.
Aspect (Aspect_Cat)	Categorical	The mean aspect of the site, split into five possible categories; A) -1 to 0 describes flat land with no aspect, B) Northerly, with bearing between 315° and 44°, C) Easterly, 45° to 134°, D) Southerly 135° to 224°, E) Westerly 225° to 314°	Influences the amount of solar radiation, exposure to wind current and microclimate, therefore affecting invertebrate assemblages.		
Potential rooting depth (PRD_CLASS)	Categorical	The minimum and maximum depths (in metres) to a layer in the soil that may impede root extension as described by potential rooting depth. Split into six categories; Very deep = 1.2 – 1.5, Deep = 0.9 – 119, Moderately deep = 0.6 – 0.89, Slightly deep = 0.45 – 0.59, Shallow = 0.25 – 0.44, Very shallow = 0.15 – 0.24	Impacts vegetation community composition which dictates invertebrate community.	Very shallow to very deep	
Min pH (PH_MIN)	Continuous	Minimum pH at a depth of 0.2 - 0.6m	pH is a well established correlate of differential soil processes and therefore impacts invertebrate assemblages.	4.5 - 5.5	4.75 ± 0.06
Macroporosity (Mpor_S_MAX)	Continuous	An expression of the air-filled porosity of the soil at 'field capacity'. Values are minimum values over the profile section of 0 – 0.6 m depth, and are expressed as a percentage of the soil volume	Air content of soil impacts the soil structure which influences the invertebrate community.	4.9 - 14.9%	8.31% ± 0.75%
Max carbon (CARBON_MAX)	Continuous	Maximum total carbon content at 0 - 0.2m , expressed as a percentage of the soil volume	Affects invertebrate biomass, e.g. enchytraeid and nematode density and biomass is positively correlated with soil phosphorus/carbon and nitrogen/phosphorus ratios .	3.9 % to 60 %	21.48% ± 3.11%

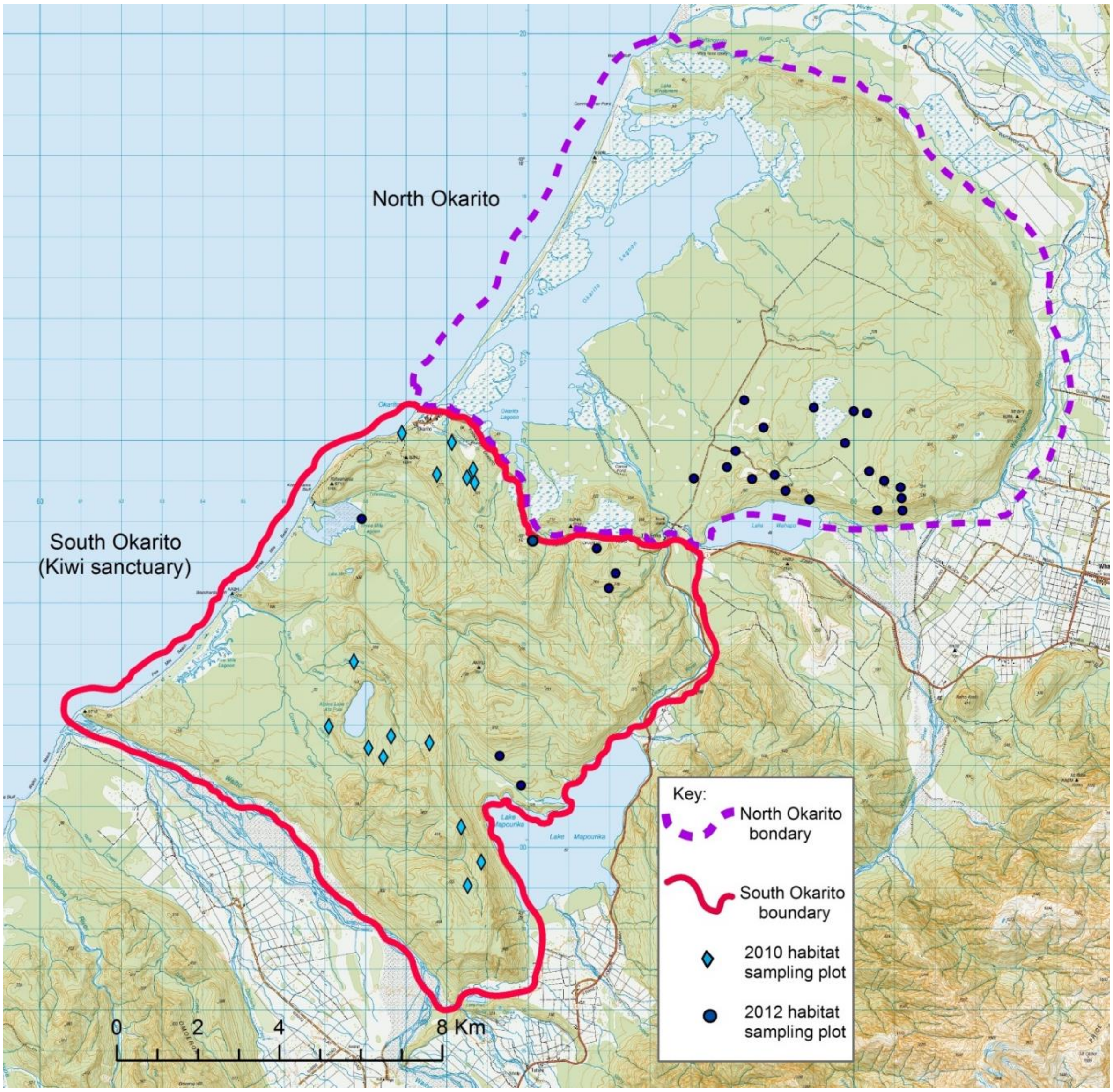

Figure 3.1. Map of North and South Ōkārito with locations of habitat sample plots. Five pitfall traps were placed at each plot location, 20 meters apart, and left for five nights before being collected and the contents analysed in the laboratory.

3.2.3 Data analysis

Data analyses were conducted in R version 2.15.2, using package MASS. The maximum Spearman rank correlation (rS) allowed between predictor variables was 0.7 (Fielding & Haworth, 1995), as strong correlations between predictor variables will lead to abnormally high standard errors and coefficients (Neter et al., 1989; Strauss & Biedermann, 2005). None of the variables included in these analyses had greater Spearman rank correlation than 0.49. I constructed a full linear model with invertebrate biomass as the dependant variable, and included all of the independent variables being analysed for predictive ability (Table 3.1). Since the number of independent variables was large (n=12), it was not feasible to do a comparison of a full set of candidate models (Statzner et al., 2008). Instead I performed a stepwise deletion of variables from the full model in both directions using MASS function stepAIC, with lowest Akaike's Information Criterion (AIC) (Burnham & Anderson, 2002) for model selection. This method has previously been used successfully in a variety of studies, including to predict invertebrate variance based on habitat variables (Elith & Leathwick, 2009; Hanson et al., 2009), to predict the impact of patch variables on species occupancy (Prugh et al., 2008), and to predict the abundance of vascular plants, marsupial and small reptile species (Pearce & Ferrier, 2001). While Bayesian alternatives are available and may be beneficial in situations with potential spatial autocorrelation (Latimer et al., 2006), this study worked on small scale variables over a large sampling area. In these circumstances spatial autocorrelation is not considered a concern (Guisan & Zimmermann, 2000). The final model was tested for accuracy, and data explored for outliers or influential cases looking at standardized model residuals, leverage, Cook's distance and covariance ratios. The model was also evaluated for predictive performance using the Spearman correlation, looking at the level of rank agreement, rather than absolute agreement since the estimated biomass measures were considered as relative estimates, rather than true counts (Pearce & Ferrier, 2001).

3.2.4 GIS mapping of Ōkārito habitat quality

A Geographic Information Systems (GIS) map was constructed containing a DEM of the Ōkārito area (Landcare Research New Zealand Ltd) and the relevant Soil Fundamental Data (SFD) layer from the New Zealand Land Resource Information System (Landcare Reasearch New Zealand Ltd). A 100 m x 100 m grid layer was applied over the top of the DEM and

SFD layers using the fishnet function in the Data Management Toolbox of ArcGIS. The fishnet layer was intersected with the SFD layer, to create a new layer containing polygons of maximum 100 m x 100 m containing the data from the SFD. Mean elevation, slope and aspect data for each polygon was extracted from the DEM layer to the intersected fishnet layer. The aspect data were converted into a categorical variable using the reclassify tool and categories described in Table 3.1. Once the final model had been selected, the mean value of minimum pH, the aspect category and phase category, along with a standardised 16 mm rainfall for all polygons (the mean value of rainfall during the sampling periods), was placed into the predictive model formula for each polygon. This produced an estimated relative biomass value for each polygon. The original biomass data from plot locations was analysed to find the mean and standard error of sampled biomass. These values were used to create categories of low, medium and high biomass, where the medium habitat quality included all values within one standard error of the mean, low includes all values below this and high included all values above this. Using this categorisation, a colour coded visual representation of relative estimated habitat quality was produced. Means are presented ± standard error unless otherwise stated.

3.3 Results

Over 600 invertebrates were collected in the pitfall traps, catalogued and measured. Of these, a total of 191 met the criteria of body length greater than 8 mm, were included in analyses, and will be described here. The most abundant and widespread invertebrates were Talitridae (landhoppers), occurring in 25 of the 41 plots (61%), with a total of 65 individuals recorded. Landhopper body lengths included in the analysis ranged from 8 mm to 20 mm, with a mean of 10.75 mm ± 0.37 mm, and accounted for 24.22% of the total sampled biomass (Table 3.2). Sixty two individual Ground wētā (*Hemiandrus spp.)* were found over 23 of the 45 plots, (51%). Ground wētā body length in the analysis ranged from 8 mm to 29 mm with a mean length of 17.47 mm ± 0.72 mm, and accounted for 67.84% of the total biomass sampled (Table 3.2). The plots with highest biomass were characterised by high overall body lengths of landhopper, and ground wētā. The plots with the lowest biomass had no invertebrates over 8 mm body length, and of those with at least some invertebrates greater than 8 mm but low biomass, landhoppers, ground wētā and beetles were almost completely absent.

The biomass within plots ranged from 0.00g to 68.78 g. The overall mean biomass in plots was 5.14 g ± 1.78 g. There was no significant difference in the mean between plots sampled in 2010 and 2012 (7.68 g ± 4.46 g and 3.68 g ± 1.23 g respectively, t-test; t=1.071, df=39, P=0.291), or between plots in North or South Ōkārito (4.22 g ± 1.64 g and 5.94 g ± 3.07 g respectively, t-test; t=-0.473, df=39, P=0.639) (Figure 3.2).

The model selected to predict invertebrate biomass, included the variables minimum pH, cumulative rain, aspect and phase class (Table 3.3). The adjusted r^2 of the chosen model was 0.51, meaning the model describes 51% of the invertebrate biomass variation. The coefficients of this model are shown in Table 7, giving the predictive formula;

$$\text{Estimated } \log_{10} \text{ biomass} = 18.83746 + (-3.36297 \times \text{pH min}) + (0.027017 \times \text{cumulative rain}) + (-1.25847 \times \text{Aspect cat B*}) + (-1.90969 \times \text{Aspect cat C*}) + (0.484933 \times \text{Aspect cat D*}) + (-1.43382 \times \text{Aspect cat E*}) + (-0.6649 \times \text{Phase B*}) + (2.636056 \times \text{Phase C*})$$

*(see Table 3.1 for description of categories)

Two of 41 cases (4.87%) in the model had standardized residuals outside ± 2, which is within the 5.00% expected for an ordinary sample. The Cook's distances of these cases were 0.184 and 0.157, well below the value of 1, which would indicate these cases were outliers having an effect on the model (Cook & Weisberg, 1982). Average leverages were 0.256 and 0.199, with covariance ratios of 0.414 and 0.288, further suggesting the cases do not have any undue effect on the model (Field et al., 2013). Overall these diagnostic statistics suggest the model is reliable and not unduly influenced by any cases. The Spearman correlation between the actual biomass from pitfall traps and estimated biomass predicted for pitfall locations using the model gave a correlation coefficient of 0.59, which was significant ($P > 0.05$).

The mean of the biomass from plots was 5.14 g, with a standard deviation of 1.15 g. This gave habitat quality categories of low=0 g to 3.99 g, medium=4.0 g to 6.29 g, and high=6.3 g and above. These categories were applied to values of estimated biomass calculated for all intersected fishnet polygons, producing a visualisation of relative invertebrate biomass (Figure 3.3).

Table 3.2. Summary of invertebrates within pitfall traps collected over five nights from a total of 41 plot locations sampled in 2010 in South Ōkārito and in 2012 in North and South Ōkārito.

Invertebrate	No of individuals recorded	Frequency in plots (%)	Mean body length (mm)	SE mean body length	Overall dry biomass (g)	Percent of total biomass
All <8mm body length	>400	100.00	3.26	0.11	>264.45	Not included
Landhoppers (Talitridae)	65	60.98	10.75	0.37	86.79	22.01
Ground wētā (*Hemiandrus spp.)*	62	56.10	17.47	0.72	272.29	69.04
Beetle (Carabidae)	26	41.46	16.36	0.56	32.65	8.28
Spider (Arachnid)	15	29.27	11.00	0.96	2.37	0.60
Beetle (Carabidae) larvae	4	9.76	16.5	2.87	0.18	0.05
Centipede (Chilopoda)	3	7.32	18.00	4.00	0.09	0.02
Unknown Larvae	3	2.44	13.67	2.67	0.00	0.00
Caterpillar (Lepidoptera larvae)	2	4.88	15.00	2.00	0.02	0.01
Earwig (Dermaptera)	2	4.88	10.5	1.50	0.01	0.00
Earthworm (Haplotaxida)	2	4.88	9.00	1.00	0.01	0.00
Millepede (Diplopoda)	1	2.44	11.5	2.50	0.00	0.00
Grasshopper (Caelifera)	1	2.44	12.00		0.00	0.00
Cricket (Gryillidae)	1	2.44	11.00		0.00	0.00
Woodlouse (Oniscidea)	1	2.44	10.00		0.00	0.00
Pill millipede (Sphaerotheridae)	1	2.44	9.00		0.00	0.00
Fly (Diptera)	1	2.44	8.00		0.00	0.00

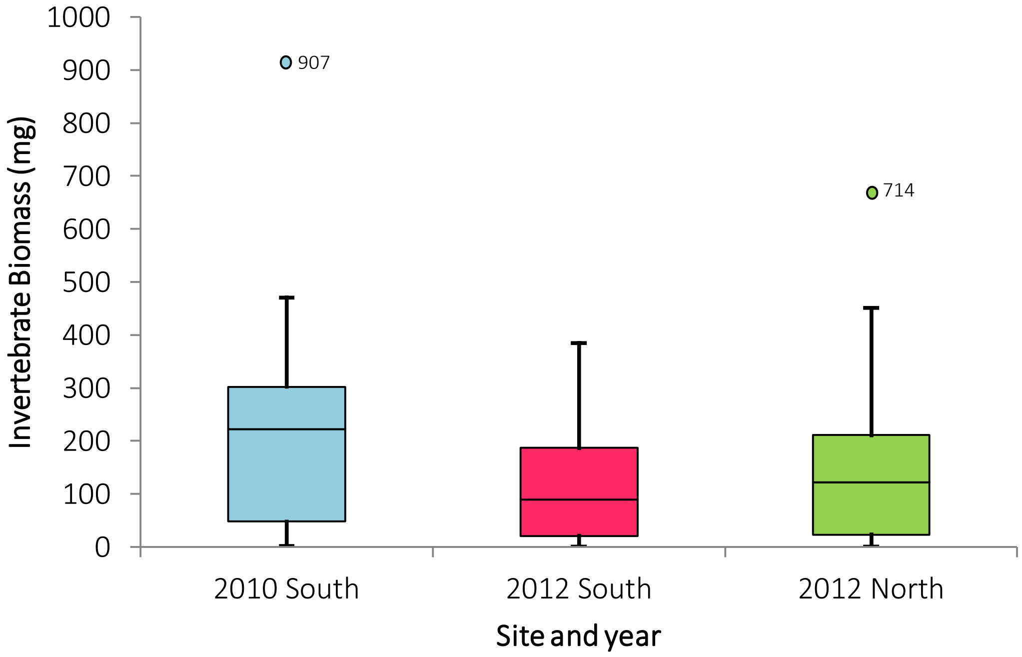

Figure 3.2. Total dry biomass for each plot shown by sampling location and year. The highest biomass was in South Ōkārito in 2010, and all three sets of data have several plots with zero biomass recorded. There was no significant difference between the mean biomass over the plot sites or plot years. Boxes show the upper and lower quartiles, divided by the median, with whiskers showing minimum and maximum values, and outliers as dots, labelled with their values.

Table 3.3. Summary of top five models (those with ΔAIC under 17) for predicting invertebrate biomass in Ōkārito forest. Table includes number of parameters (K), Akaike Information Criterion corrected for small sample size (AICc), delta AICc (ΔAICc), Akaike weights (AIC_CWt), cumulative Akaike weights (ω), and log-likelihoods (LL).

Variables	K	AICc	ΔAICc	AICcWt	ω	LL
pH min + Cumulative rain + Aspect + Phase	10	128.66	0	0.94	0.94	-50.66
pH min + PRD + Cumulative rain + Aspect + Phase	13	135.61	6.95	0.03	0.97	-48.07
pH min + PRD + Cumulative rain + Aspect + Max Slope + Phase	14	139.52	10.85	0	1	-47.68
pH min + PRD + Cumulative rain + Aspect + Max Slope + Phase + Mean min Temp + Aspect + Max Slope + Phase	15	144.33	15.67	0	1	-47.56
Elevation + pH min + PRD + Cumulative rain + Mean min Temp + Aspect + Max Slope + Phase	16	149.72	21.06	0	1	47.53

Table 3.4. Coefficients from the chosen best model describing habitat variables that can be used to predict estimated invertebrate biomass.

Variable	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	18.84	4.56	4.13	0.00024
pH_MIN	-3.36	0.97	-3.45	0.00159
Cumulative_rain	0.03	0.01	2.78	0.00905
Aspect_CatB	-1.26	0.47	-2.67	0.01189
Aspect_CatC	-1.91	0.57	-3.36	0.00204
Aspect_CatD	0.48	0.53	0.92	0.36636
Aspect_CatE	-1.43	0.47	-3.03	0.00476
PHASEb	-0.66	0.45	-1.47	0.15095
PHASEc	2.64	0.99	2.65	0.01229

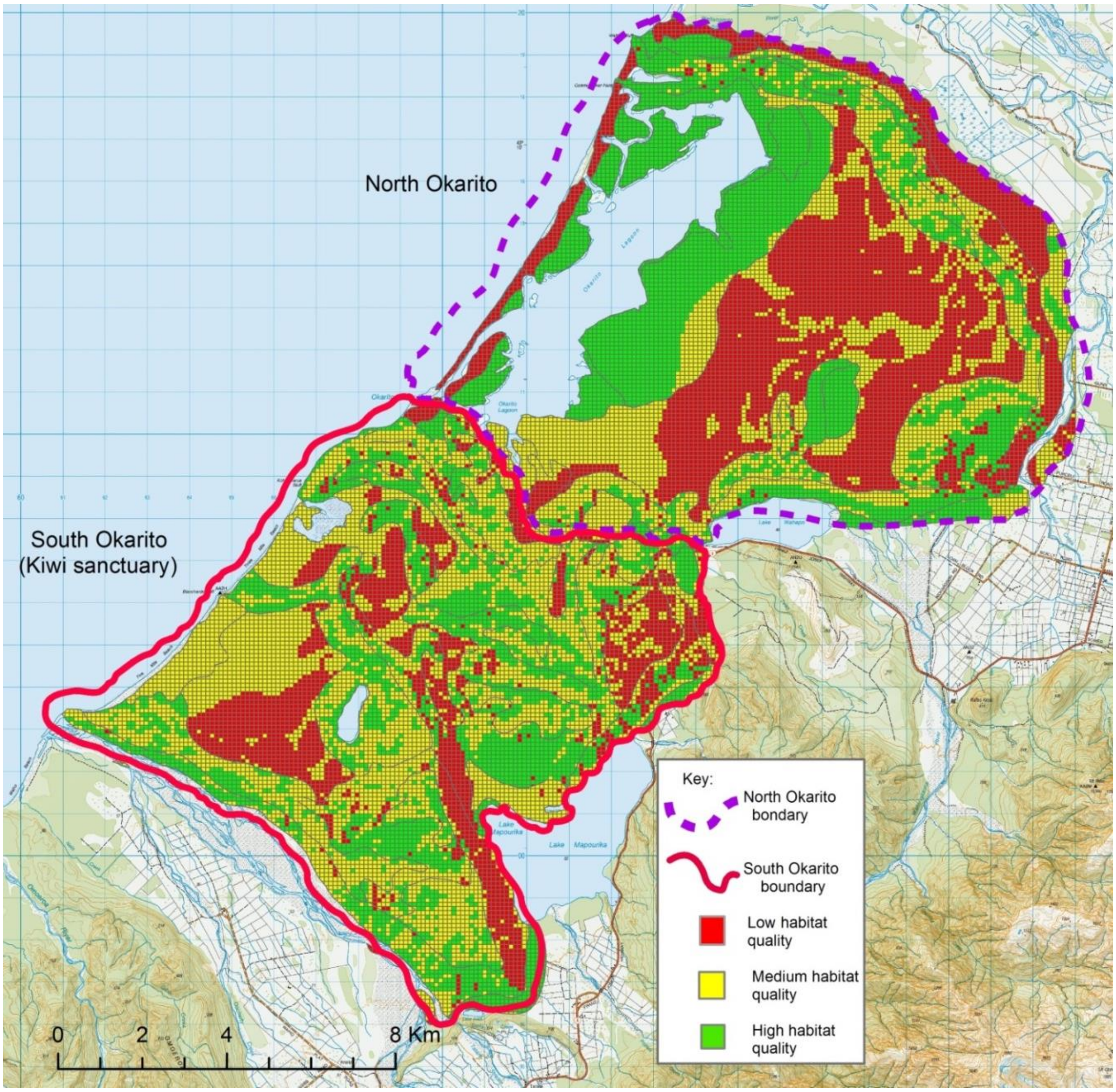

Figure 3.3. Map of the study site with relative habitat quality shown. Low (0 g to 3.99 g), medium (4.0 g to 6.29 g), and high (6.3 g and above) quality is based on mean estimated invertebrate biomass calculated for each polygon using predictive formula including values of mean maximum pH, aspect category, phase category and standardised value of rainfall.

3.4 Discussion

Overall the model selected is highly relevant to investigating invertebrate ecology, and appears to provide a convincing representative model of rowi habitat throughout the Ōkārito area. The model accuracy was considered reasonable, with only 4.87% standardised residuals outside the ± 2 range and Cook's distances, average leverages and covariance ratios for the two potentially outlying cases all within acceptable limits. Therefore the sample appears to conform to what I would expect for a fairly accurate model (Field et al., 2013).

Landhoppers appeared in 60.98% of plots sampled, and accounted for 24.22% of the total calculated biomass. Leaf litter arthropods such as landhoppers have a fundamentally patchy distribution (Richardson, 1992), and spatial variability in detection during this study likely reflects this. The presence or absence of landhoppers has been attributed to variation in microclimate, with different species holding niches of differing temperature and moisture regions (Richardson, 1990). Within species distributions, variations in moisture content and temperature of sand have been found to illicit burrowing and surface migration responses to cope in sand and soil dwelling species (Richardson, 1992; Tsubokura et al., 1997), with downward retreat into deeper soil during drier periods common, and upward migration out of leaf litter into moss and under tree bark observed in extremely wet conditions (Hurley, 1968). Individual landhoppers have been known to travel 25 to 35 meters across the surface in a night (Hurley, 1968). The variation recorded in presence of landhoppers throughout the pitfall traps in this study may be due to a combination of climatic and microclimate factors, that are affected by environmental variables such as vegetation composition, slope aspect and rainfall (Richardson, 1990).

Ground wētā were found in 56.10% of sampled plots, and accounted for 67.84% of total calculated biomass. In contrast to the dependence of landhoppers on climatic variables, ground wētā distributions have been linked to the depth of friable soil, with wētā most abundant where soil available for burrowing was deepest, which corresponds to potential rooting depth (PRD) in this study (Van Wyngaarden, 1995). Wētā activity has been linked with the lunar cycle, with highest activity recorded on darkest nights during the phase around a new moon, an activity pattern attributed to predator avoidance (Van

Wyngaarden, 1995). Lunar cycles have been attributed to fluctuations in movement, foraging success and reproductive behaviour in a range of invertebrate species (Anderson, 1966; Kronfeld-Schor et al., 2013). It is possible that the variation in lunar stage may have affected the presence and abundance of wētā in pitfall traps, however, the timescale of sampling (five nights), means that variation in lunar illumination within samples may be large, and may also have been confounded by other variables such as cloud cover. Therefore, it was not possible to assess the impact of lunar stage on collected invertebrate biomass within this study, but I suggest it is an important area for further investigation.

Overall, the main factors likely to have affected the presence and abundance of invertebrates with greater than 8 mm body length in pitfall traps were the variables included in the chosen predictive model. These were minimum pH, cumulative rain, aspect and phase class. It is important to evaluate the chosen model within the context of invertebrate ecology (Wiersma, 2011). The minimum pH at each plot is biologically relevant to invertebrate biomass and has both proximal and distal impacts on invertebrate assemblages. The model estimate of the slope for pH is -3.36, which indicates a negative relationship between minimum pH and estimated Invertebrate biomass. Ōkārito forest has a high density of rimu, which is known to cause highly acidic soils (Adams & Norton, 1991; Burns, 1931). The invertebrate assemblages present at Ōkārito are likely to be dominated by species that have evolved tolerance for very acidic soil, and so a negative correlation of invertebrate biomass with pH is not surprising. The acidity of soil has a strong impact on its nutrient mobility, absorption and precipitation, which in turn are linked to the distribution of biomass across body-size classes of all occurring soil invertebrates (Mulder & Elser, 2009). Soil pH also affects vegetation composition, which in turn affects nutrient availability and therefore invertebrate assemblages in the soil (McEwan et al., 2005).

Rainfall had a positive relationship with invertebrate biomass (Table 3.4). Ōkārito has a mean annual rainfall of 3231.1 mm (based on data from 1981 to 2010, Cliflo database), and so invertebrates present in the ecosystem are likely to be well adapted to rainfall events. A study of carabid beetles (*Pterostichus melanarius*) found activity was decreased by dry spells, and increased following rainfall events (Thomas et al., 1998). Landhopper catch rate has also been positively linked with rainfall in a previous study (Scapini et al., 1992).

Different soil types as described by different phase categories are likely to support different assemblages of both plants and invertebrates due to the different soil structure and chemical composition in each. The effect of flat land with no aspect (category A), on invertebrate biomass is included in the model intercept. Relative to flat land, southerly facing land (aspect category D), has positive relationship with invertebrate biomass (Table 3.4), while northerly, easterly and westerly facing land has a negative relationship with invertebrate biomass. The aspect of a slope dictates its climatic situation (Kappes et al., 2006), and plays a large role in influencing moisture availability and daily insolation, which in turn leads to variability in vegetation composition and structure, as well as variation in chemical characteristics among slopes with different aspects (Kappes et al., 2006; McCarthy et al., 2001; Rubino & McCarthy, 2003).

The model has clear limitations. It only addresses one area of habitat quality relating to food, while many other aspects including suitability of burrow sites and proximity to potential mates are also likely important for rowi habitat. In addition, the selected model described around only 51% of invertebrate biomass variation, the remaining 49% of variation was unaccounted for, indicating future work should investigate further factors that could be incorporated into the predictive model.

The map produced for variation in habitat quality throughout the Ōkārito area (Figure 3.3) used grid squares of a maximum of 0.1 km x 0.1 km. Wild rowi home ranges had a mean size of 1.06 km^2, and rowi that were raised through Operation Nest Egg had a mean home range of 3.35 km^2 (Chapter 5). Therefore, the scale of the habitat quality assessment used when producing this map of Ōkārito habitat quality was considered appropriate for use in a study of rowi habitat selection. Inferences regarding habitat quality can be drawn from this map and its associated GIS layers, and these results of relative habitat quality throughout the range can be applied to questions regarding habitat use by rowi. This map could be used to investigate the selection of habitat quality within home ranges of reintroduced rowi, as well as to investigate the effects of release site habitat quality on translocation success. While a good representation of habitat quality as described by food availability, since other factors also affect habitat quality, it is important to consider the limitations of this map when using it. It would be unwise to draw and firm conclusions about rowi habitat using this map alone, since it is possible that habitat quality could be affected by another limiting factor which may impact population performance, such as number of suitable burrow sites or availability of mates. Future research into how other variables affect habitat quality for rowi is recommended.

4 Investigation of factors affecting dispersal and association rates of reintroduced rowi

4.1 Introduction

Reintroduction attempts often fail to meet their goals or to optimise success due to sub optimal release protocols, created without an understanding of mechanisms occurring as a result of the release protocol (Bernardo et al., 2011; Fischer & Lindenmayer, 2000; Hardman & Moro, 2006; Ryckman et al., 2010). Elements of the release process can affect the behaviour of animals following release and, in turn, can impact on demographic and spatial characteristics of the population and long term success of the reintroduction (Ryckman et al., 2010). To maximise conservation success, it is essential to identify factors causing reintroduction failure and potential solutions (Buner et al., 2011; Green et al., 2005; Mihoub et al., 2011), yet factors influencing this are rarely empirically tested (Hardman & Moro, 2006; Moorhouse et al., 2009). Post-release monitoring can provide valuable insight into factors affecting release success (Pierre, 1999), but experimental testing of hypotheses relating to parameters producing reintroduction success are more beneficial than post-hoc analyses of data collected through monitoring (Armstrong & Seddon, 2008).

A more complete understanding of how elements of the release procedure affect post-release movement and associations of released individuals, and subsequent impacts on survival, can lead to improvements in reintroductions (Armstrong et al., 1999; Yott et al., 2011). Post-release dispersal has a large influence over short term survival, future vital rates (survival, reproduction, home range establishment, etc.) and demographic structure of a population as it results in shuffling genes across the social and physical landscape (Di Fiore et al., 2009; Dzialak et al., 2005; Gouar et al., 2008; Ryckman et al., 2010). Translocated animals often wander prior to finding suitable habitat and settling in to a home range (HR) following release (Costello, 2010; Spencer, 2012; Wolf et al., 2009). These movements do not always correspond to natal or juvenile dispersal (Van Heezik et al., 2009), with released animals sometimes becoming more vagrant than wild conspecifics (Champagnon et al., 2012). Benefits of natal dispersal consist of minimising negative consequences of remaining in the natal area, such as mate competition, inbreeding and resource competition (Matthysen, 2012; Petersburg et al., 2000). However, dispersal away from a carefully selected release site can undermine the objectives of the reintroduction and may prevent successful population re-establishment as animals may move away from potential mates and suitable habitat (Skjelseth et al., 2007; Van Heezik et al., 2009; Yott et al., 2011). The process of dispersal itself may also increase the risk that released animals face as they traverse unfamiliar habitat without knowledge of resource availability, predation risks or refuge sites (Devillard & Bray, 2009; Di Fiore et al., 2009). Increased mortality during the period immediately following release has long been attributed to the behavioural responses of individuals, therefore understanding movement patterns and the factors that drive them are essential for increasing reintroduction success (Ryckman et al., 2010; Skjelseth et al., 2007; Yott et al., 2011).

Dispersal is driven by a range of factors, including environmental effects and individual characteristics of the animal (Matthysen, 2012). While dispersal is often thought of as a sex specific trait, for some species dispersal strategies of both sexes may be affected by local ecological and social conditions (Wikberg et al., 2012). Age of released individuals may influence dispersal distance, as demonstrated by reintroductions of elk (*Cervus elaphus*), which had higher dispersal distances when released animals were adults compared to juveniles (Ryckman et al., 2010; Yott et al., 2011) and Griffon vultures (*Gyps fulvus*), which have lower dispersal rates when adults are released compared with juveniles (Gouar et al., 2008). In an investigation of factors affecting reintroduction success of water voles (*Arvicola terrestris*), Moorhouse et al (2009) found sex and release site vegetation abundance significantly influenced dispersal distance. Male voles travelled double the mean dispersal distance as females, and those voles released in poor quality habitat ranged further and had lower survival than those released in good quality habitat. The increase in dispersal distance from poor quality release sites was attributed to individuals searching for a better quality home range (Moorhouse et al., 2009). The release of un-fostered juvenile grey partridges (*Perdix perdix*) had the effect of increasing dispersal distance and reducing survival following release compared with releasing juveniles that had been fostered onto wild adults with failed nests (Buner et al., 2011). Lower release population densities increased dispersal rates for grey partridges compared to those released at high densities, which was attributed to birds in low density populations moving further to find mates (Buner et al., 2011). Familiarity with release conspecifics had significant effects on the post-release dispersal of Stephens kangaroo rats (*Dipodomys stephensi*), with familiar release cohorts dispersing shorter distances and having increased survival and higher reproductive rates than unfamiliar release cohorts (Shier & Swaisgood, 2012). Habitat quality may affect dispersal decisions, with individuals released in lower quality habitat forced to disperse further to locate better quality areas for establishing a home range (Bennett et al., 2012; Enfjall & Leimar, 2009). Natal habitat preference induction (NHPI), where an animal selects habitat based upon stimuli comparable to those experienced during its natal period, may also occur following translocation (Stamps & Swaisgood, 2007), with favourable experiences during the natal period increasing the likelihood of NHIP occurring (Stamps et al., 2009).

In addition to dispersal, the rate a released individual associates with conspecifics may influence their post-release survival by increasing fitness and buffering against stress (Abeyesinghe et al., 2013; Pinter-Wollman, 2009). Association may provide added benefits in a novel environment which outweigh the cost of increased competition (Pinter-Wollman, 2009). Social learning and cueing from conspecifics through association can confer benefits via rapid knowledge acquisition about a novel environment (Pinter-Wollman, 2009). Association with conspecifics may also reduce predation risk (Isbell et al., 1990), and prevent or reduce aggression from unfamiliar residents (Connor, 2007; Jack & Fedigan, 2004). African elephants (*Loxodonta africana*) which have more association with conspecifics immediately following release have higher body condition indices than less associated individuals (Pinter-Wollman, 2009). Association can be investigated for species that are difficult to observe directly using proximity as a proxy for interactions (Whitehead & Dufault, 1999). Pairwise association indices such as twice weight (TWI) and half weight indices (HWI) give estimates of the proportion of time pairs of individuals (dyads) are associating together (Carter et al., 2009). TWI gives a measure of the strength of associations between a dyad, between 0 and 1, where 0 signifies no association within the dyad, and 1 means the dyad was always associated. It takes the number of occurrences of association relative to the number of times each individual was observed within the focal period but not associating. The TWI corrects for any bias that occurs due to individuals of a dyad being more likely to be found when associating than when not associating (Arnold & Whiten, 2001).

4.1.1 Rowi translocation management model

Rowi (*Apteryx rowi)* are a species of kiwi, flightless ratites endemic to New Zealand (Holzapfel et al., 2008). Historically, the rowi range extended from north of the Haast Pass on the South Island, through to the lower North Island and as far north as Hawkes Bay (Holzapfel et al., 2008; Shepherd & Lambert, 2008). This distribution was greatly reduced following the arrival of Europeans and the predator species they introduced (Holzapfel et al., 2008). Predation of chicks by introduced stoats is cited as the main cause of decline for rowi (Colbourne et al., 2005). By the late 1800s rowi were found only on the West Coast of the South Island, and by the 1990s, the entire range was thought to be encompassed by the 10000 ha South Ōkārito forest area (DOC, 2006; Holzapfel et al., 2008) (Figure 1.1). Rowi are now listed as nationally critical, with the population dropping as low as 150 in the 1990s, and reaching an estimated 300 by 2008 as a result of intensive management practices (Hitchmough, 2002; Robertson, 2003). In 2000, South Ōkārito was designated as one of five national kiwi sanctuaries. This does not mean the area is enclosed by fencing; rather the area is afforded extra legislative protection (exclusion of dogs), and funding from both the New Zealand government and corporate sponsorship through "Kiwis for Kiwi" (formerly the "BNZ Save the Kiwi Trust") (Robertson, 2004).

The main management process for rowi involves mitigating the threat from stoats (*Mustela erminae*). When rowi reach at least 1.2 kg they are less vulnerable to predation, and the management program known as Operation Nest Egg (ONE) is built around this fact (Colbourne et al., 2005). ONE involves monitoring breeding adults with leg mounted transmitters, removal of their eggs from the forest, hatching eggs in captivity, rearing chicks on a predator free island and translocation of juveniles back to the source population once they have reached at least 1.2 kg. Rowi lend themselves to this management approach as they are semi-precocious upon hatching, and wild chicks leave the nest to forage independently within one week of hatching (Colbourne et al., 2005).

The ONE process provides a valuable opportunity to investigate a range of areas of rowi ecology including factors affecting reintroduction success. For example, mortality is higher in the first 90 days post-release (henceforth referred to as the critical period) than after 90 days (see Chapter 2), and the size of release group affects survival during this critical period. Birds released in groups of three or less (small groups) having significantly lower survival than those released in groups of four or more (large groups) (see Chapter 2).

4.1.2 Study Aims

By monitoring rowi in the initial stages following release, I aimed to identify factors leading to success or failures in rowi reintroductions. Specifically, I asked: Do release group size, conspecific density, release location habitat quality or sex significantly affect the maximum dispersal distances or association rates respectively, of rowi during the critical period following release? If birds from small and large release groups disperse significantly different distances or have significantly different levels of association this would provide a possible mechanism for different survival rates for these group sizes.

4.2 Methods

In order to investigate the mechanisms driving the variation in survival of different release group sizes, I investigated effects of release group size and the interaction with other variables (habitat quality at the release location, sex and resident conspecific density), on the dispersal and association of rowi following release. Throughout this study release site refers to either North or South Ōkārito, and release location refers to the specific point within North or South Ōkārito where the rowi were released. Habitat quality at release location was measured using relative invertebrate biomass as a proxy, which was estimated using a predictive model based on measures of habitat variables extracted for each point from an ArcGIS layer (see Chapter 3). Rowi feed predominantly on soil and litter invertebrates, as well as some fruit (Holzapfel et al., 2008). Invertebrate biomass was therefore chosen as the most appropriate variable of habitat quality to measure, since energy flow through trophic levels is inextricably linked to body mass, and biomass is a better indicator than abundance or density of the functionality of a species (or in this case group of species) within an ecosystem (Saint-Germain et al., 2007).

In this study I examine the movement between the release location and subsequent spatial fixes, measured as the linear distance between fixes (Bernardo et al., 2011; Moorhouse et al., 2009; Ryckman et al., 2010). I acknowledge that linear distances underrepresent the distance covered between the initial and final fix, but instead represent the end result of the movement (Lawes et al., 2013). As part of a wider investigation into rowi ecology and the factors influencing reintroduction success I experimentally manipulated a range of release variables during reintroductions in South Ōkārito in 2009, and in both South and North Ōkārito in 2010 and 2011 (Figure 1.1) (see Chapter 2). Prior to the 2010 release there were not thought to be any rowi in North Ōkārito. The suitability of North Ōkārito as a rowi release site was assessed by Rogan Colbourne, Kiwi scientist with the Department of Conservation, in 2010. South Ōkārito has always been assumed to be a suitable release site due to the existing presence of rowi, which are present at a density of around one rowi per 28 ha.

Ōkārito forest is in the 98000 ha South Westland National Park, situated between Hokitika and Fox Glacier on the West Coast of the South Island of New Zealand, (Colbourne et al., 2005; DOC, 2004) (Figure 1.1). Ōkārito forest is a cold temperate lowland costal wetland forest ecosystem ranging from sea level to 520 m.a.s.l. (Christie et al., 2006). South Ōkārito is largely unmodified native podocarp-hardwood forest (Murphy et al., 2008). North Ōkārito was selectively logged at 25% of total merchantable volume in the 1970’s and 1980s, resulting in a series of logging tracks throughout the area, and regenerating vegetation (Pearce & Griffiths, 1980; Piskaut, 2000).

Prior to releases in 2009, 2010 and 2011, 66 rowi were fitted with individually identifying VHF transmitters in order to relocate them. Transmitters were attached following guidelines set out in the Kiwi Best Practice Manual (Robertson & Coulbourne, 2003), and have a battery life of approximately 12 to 15 months (Keye et al., 2011; Robertson & Coulbourne, 2003). Transmitters monitor activity rates and were able to detect a drop in activity indicating either the transmitter had fallen off (dropped), or the bird had died, and would omit a specific pulse rate to indicate this had happened. Ground based monitoring was conducted using a hand held TR4 receiver (Telonics^{TM}) and Sika receivers (Biotrack ltd), along with three-element folding Yagi antennas (Sirtrack Ltd). Following release, signals of rowi were checked on average once a week, and relocations (fixes) were scheduled at four weeks and three months post-release. If a signal indicated that a rowi was deceased or had dropped a transmitter, the signal was tracked and the final location, either of the transmitter when dropped or dead bird was included as a location fix in the dataset. A beacon study was conducted to verify the suitability of triangulation for obtaining fixes of locations in North Ōkārito (see Appendix 1). Triangulations were then used to provide additional fixes for rowi in North Ōkārito.

Distances of fixes from the release location were calculated using the program Geospatial Modelling Environment's point distance tool (Bayer 2012), which measures the straight line between points. For initial investigation of the influence of release group size, sex and release site (North or South Ōkārito), I conducted a series of nested ANOVAs, with group ID as a nested factor to account for repeated measures from within release groups. To investigate factors influencing maximum dispersal distance following release, linear mixed-effects models fitted by maximum likelihood were used in an interactive forward stepwise selection process (Statzner et al., 2008). I used two criteria to assess improvement in the model; decrease in the AIC (Burnham & Anderson, 2002) and partial P value with P=0.05 as the threshold for inclusion of predictor variables and interactions (Sauerbrei et al., 2007). Explanatory variables included as linear terms in the models were; release group size (small or large), release site (North or South Ōkārito), sex, and estimated biomass at release location (Chapter 3). Interaction effects of each combination of these four variables were also included. Release group ID was included when necessary to account for repeated measures (Pinheiro & Bates, 2000). In addition, the estimated biomass across North and South Ōkārito were compared using a non-parametric Kruskal Wallis test as variance was unequal.

It was not possible to accurately assess association rates in South Ōkārito due to the presence of unmonitored birds so association rates were calculated between dyads of North Ōkārito birds only (n=34). As in other studies of associations (Garroway & Broders, 2007), it was not possible to observe rowi associations directly. Therefore, association was considered to be fixes occurring within 1.5 km of one another within a 48 h period. This was because rowi are able to hear the call of one another over about 1.5 km (Rogan Coulbourne pers. comm. 2010), and it was assumed that a rowi within 1.5 km would be aware of the presence of each other even after a 48 h time lag due to the frequency of scent marking. Associations were considered for dyads made up of a focal bird and any other bird the focal bird associated with throughout the focal bird's critical period following release. It was possible that the second bird in the dyad was outside its critical period, e.g., if a 2011 bird (2011A) within its critical period, associated with a bird from the 2010 release (2010B), this created an entry for association just for the focal bird 2011A with 2010B, but not the dyad focal bird 2010B with 2011A. In 2010 there were 19 birds released, with the possibility of associating with each of the other 18 birds giving a possible 342 dyads. In 2011 there were a further 15 birds released, each with the possibility of associating with the other 14 rowi released that year and the 11 still alive from the year before, giving 375 possible dyads. In total there were 717 possible dyads. Of the 34 birds included in the analysis, nine were from small release groups and 25 were from large release groups. Twice weight indices (TWI) of association were calculated for all possible dyads. In Ōkārito the terrain is so diverse that if a bird is located in one location there is a higher chance of picking up a signal for other rowi it is associating with, compared to if the second rowi were at a random location within the rest of the forest. This index is non-parametric and was chosen due to the data not meeting assumptions of independence of samples required for parametric tests. Twice weight indices (TWI) of association were calculated using the formula;

$$I_{AB} = \frac{S_{AB}}{(S_A + S_B - S_{AB})}$$

Where I_{AB} is the TWI, S_{AB} is the number of observations with A and B interacting, S_A is the total number of observations of A, S_B is the total number of observations of B.

Differences between the TWI coefficients of association for birds in large compared with small release groups and male compared with female were compared in R using a nested ANOVA to account for repeated observations from all birds. The relationship between the estimated release location biomass for each bird and its mean TWI value was also assessed to investigate any correlation between release location biomass and association rates.

Of the 717 possible dyads, 112 were female – female, 174 male – male, 161 female – male and 148 male – female and 97 with at least one member of unknown sex which were omitted from the analyses. TWI values were split into four categories of increasing levels of association, 0 to 0.24, 0.25 to 0.49, 0.5 to 0.74 and 0.75 to 1, which describe low to no, low to medium, medium and high association rates respectively. The percent of dyads of each sex composition (female – female, male – female, female – male or male - female), occurring within each TWI association coefficient category was assessed.

4.3 Results

4.3.1 Dispersal

Data were collected on 54 of the 66 released rowi during the critical periods following 2009, 2010 and 2011 experimental releases. The remaining 12 rowi were not able to be found during the critical period. One hundred fixes of rowi were recorded (n=54), within the critical period, at between two and 87 days following release. On average, the 54 rowi were relocated twice within the critical period, with number of fixes ranging from one (n=29) to six (n=1) relocations. Sample sizes this small result in limited power of inference, yet still provide some evidence of underlying behavioural patterns. The range of dispersal distances from the release location was from 14.76 m through to 3648.17 m, which were recorded at 20 and 25 days post-release respectively. The mean maximum dispersal distances during the critical period of rowi released in small groups was 1402.25 m and for large groups it was 1340.20 m, which is not a significant difference (nested ANOVA, F=0.007, df=1, P=0.93304). The mean maximum dispersal distance for females was 1282.67 m and for males it was 1281.80 m, which is not a significant difference (nested ANOVA F=0.00, df=1, P=0.99725). Rowi released in North Ōkārito had a mean maximum dispersal distance of 1053.62 m, and those released in South Ōkārito had a significantly higher mean maximum dispersal distance of 1923.64 m (nested ANOVA F= 25.254, df=1, P<0.001). In a further investigation of factors affecting maximum dispersal distance, the most parsimonious linear mixed effects models fitted by maximum likelihood with release group ID as a random variable, included the variables release site (North or South Ōkārito), and the interaction between release site (North or South Ōkārito) and estimated biomass at the release location (Table 4.1). Relative release location biomasses in North Ōkārito varied from 22.77 mg to 13689.38 mg, and in South Ōkārito ranged from 7.61 mg to 618.30 mg, with means of 4307.53 mg ± 1959.02 mg and 133.24 mg ± 83.08 mg respectively, and no significant difference was found (Kruskal Wallis test, P=0.80). When examining the interaction effects between North or South Ōkārito and the estimated biomass at the release location, it is clear that release location biomass does not significantly predict dispersal at either site (P=0.14 in North Ōkārito, P=0.25 in South

Ōkārito), but the negative gradient of the slope predicting the effect of it in South (-12.62) was larger than in North (-2.09). Rowi released at location with higher biomass dispersed shorter distances, and this pattern was stronger in South Ōkārito than in North Ōkārito.

Table 4.1. Summary of the top models (with ΔAIC <6) describing maximum distance dispersed from release location by rowi within 90 days of release. The three top models have competing ΔAIC values (≤2). Variables included in the candidate models included release site (North or South Ōkārito), sex, release group size (small or large) and estimated biomass at release site (estimated using a predictive model and values of habitat variables extracted from an ArcGIS layer of the site). Interaction effects of each combination of these five variables were also included. Release group ID was included to account for repeated measures.

Variables	K	AIC	ΔAIC	LL
Site + Site:Release location estimated biomass	3	692.362	0	-341.181
Site + Release location estimated biomass:Group size	3	692.4787	0.1167	-341.239
Site + Release location estimated biomass	3	693.3751	1.0131	-341.688
Site	2	695.3731	3.0111	-343.687

4.3.2 Association

The number of fixes collected for each North Ōkārito rowi (n=34) within the critical period following release ranged from one (n=13) to four (n=2), with a mean of two. Of the 717 possible dyads, 104 met the criteria for displaying association. These 104 dyads included 30 of the 34 birds in the sample. Four birds were never recorded within 1.5 km and 48 hours of another bird. All four of these birds were only located once during their critical period. Eighteen pairs of dyads had two occurrences of association giving a total of 122 occurrences of association. In the 30 birds displaying association, six were from small release groups and 24 were from large release groups. Of the 717 possible dyads, 162 focal birds were from small groups and 555 were from large groups. Of the 162 small group focal birds, 12 (7.4%) were included in the 104 dyads displaying association. Of the 555 large group focal birds, 92 (16.6%) contributed to the 104 dyads displaying association. Individuals from large groups had a higher mean number of location fixes than those from small groups, 1.33 compared to 3.84 respectively, which is a significant difference (t-test t=-3.232, df=32, P<0.013). When considering the coefficient of association produced using the TWI, there was no significant effect of group size on rate of association; mean small group TWI was 0.0267 and mean large group TWI was 0.042 (nested ANOVA f=2.19, df=1, P=0.14).

The sex of the focal bird also had no significant impact on the TWI association coefficient, which was 0.05 for females and 0.03 for males (nested ANOVA F=2.331 df=1, P=0.13). There was no significant correlation between the biomass at release locations and the coefficient of association of released birds (Spearman rank correlation, r_s =-0.035, P=0.32). Examination of the percent of dyads from each category of sex composition within each of the categories of association indices showed that Female – Female dyads have the highest percent within the low to medium (0.25-0.49), medium (0.5 - 0.74) and high (0.75 - 1) association rate categories (Figure 4.1). The difference between the mean association rates for different categories of sex composition of dyads is statistically significant (nested ANOVA, F=6.336, df=1, P= 0.01211 (Figure 44.2)).

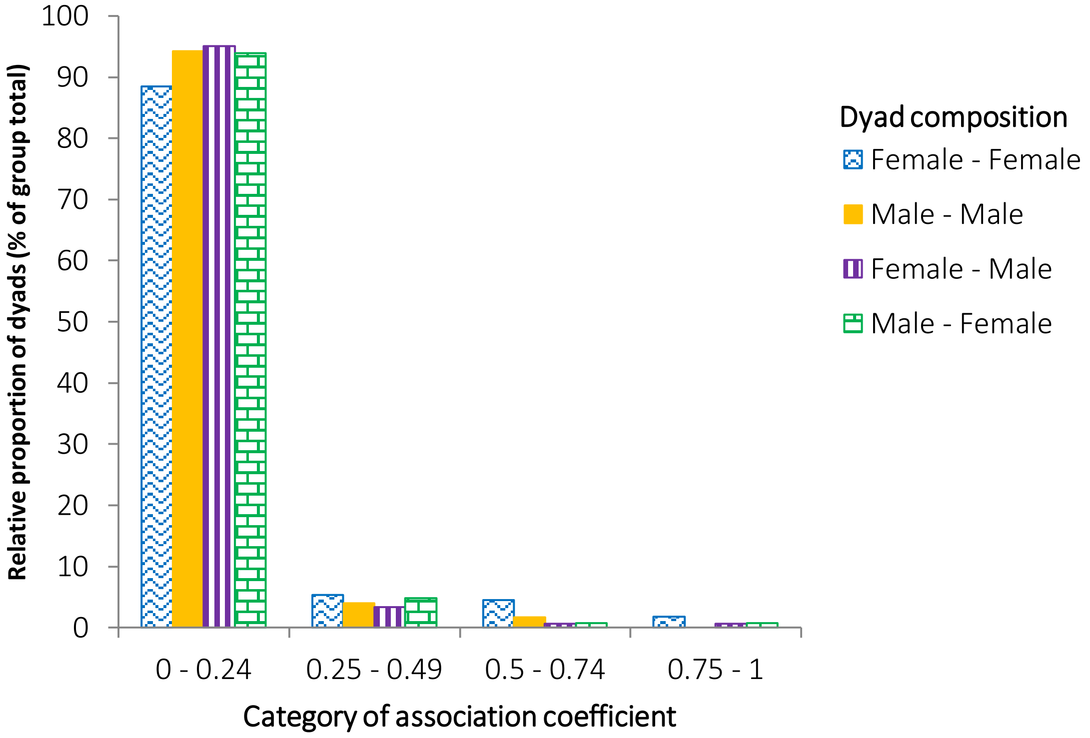

Figure 4.1. Percent of total dyads from each sex category divided by categories of TWI association coefficient. Female – Female dyads have the lowest proportion within the low rate of association category and highest proportion in the high rate of association category, while Male – Male dyads do not appear at all in the high rate of association category.

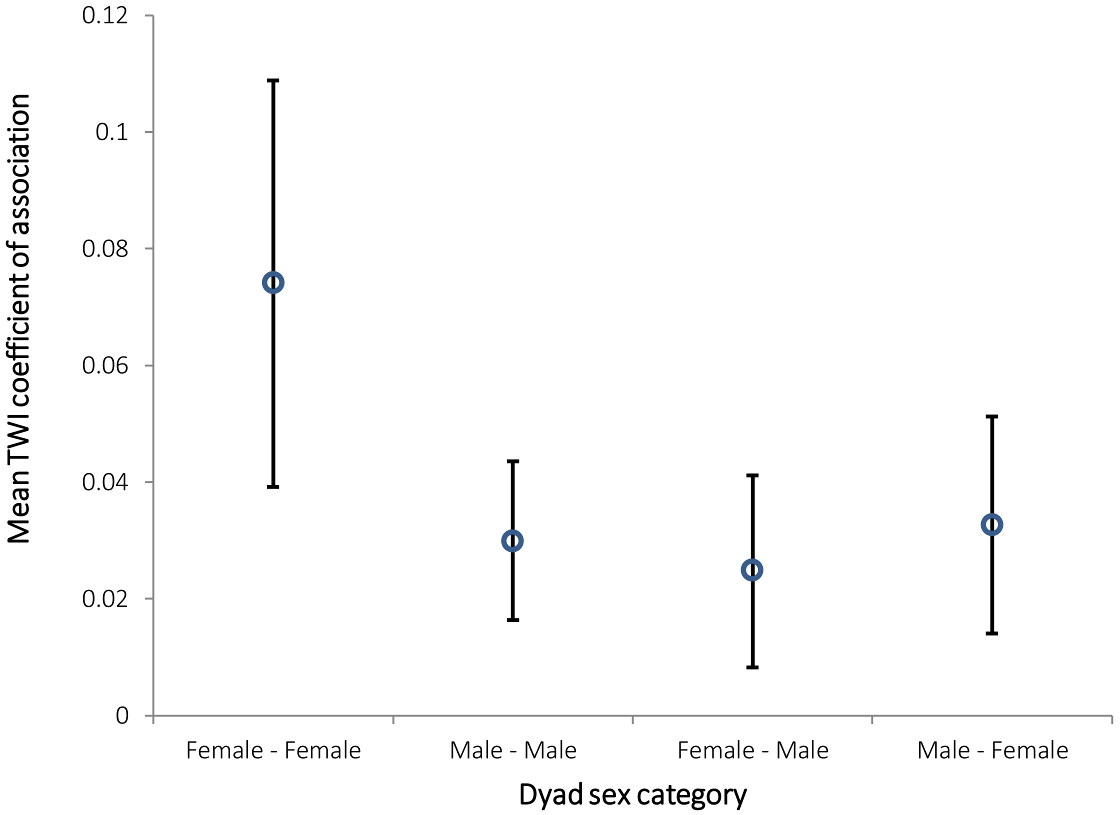

Figure 4.2. Mean Twice Weight Index (TWI) association coefficient for various sex compositions of dyads with 95% confidence intervals. Female – Female dyads have the highest mean TWI association co-efficient, meaning they displayed highest rates of association. Female – Male dyads showed the lowest mean rate of association, meaning that the number of times female - male dyads were seen together, relative to the number of time each member of the dyads were seen within the sampling period, was lowest for this sex category. The difference in rate of association between these groups is statistically significant.

4.4 Discussion

Detection rates of rowi within the critical period were low, meaning the power of dispersal and association analysis was severely limited, and robust conclusions cannot be drawn. The restrictions imposed by the terrain and vegetation mean that it was not possible to use GPS trackers on the birds, and that fixes from the VHF transmitters were frequently hard to find due to the rugged terrain. As a result, there were a number of birds for whom no fixes could be obtained during the critical period, although they were located alive after the end of this period. The number of fixes collected for the birds that were included was smaller than ideal due to time and resource restrictions throughout data collection. However several patterns were evident within the data, which led to several key observations:

Neither maximum dispersal distances nor rates of association within the critical period were affected by the release group size of rowi. Maximum dispersal distance was affected by the release site (North or South Ōkārito), and the interaction of release site and the estimated invertebrate biomass at the release location. The habitat quality as described by mean estimated biomass for release locations in North Ōkārito was higher than in South Ōkārito, but the difference was not found to be statistically significant, so any difference between the dispersal or association of birds released at the two sites must also be influenced by other variables. Birds released in North Ōkārito dispersed shorter maximum distances than those released in South Ōkārito. Rate of association was only investigated in North Ōkārito due to the presence of unmonitored wild rowi in South Ōkārito that may confound any investigation of association rates, and while neither biomass at release location nor sex of the focal bird had any significant effects on the association rate of dyads, I did find that female-female dyads had a significantly higher rate of association than any other sex category.

The difference in dispersal distance between North and South Ōkārito, and the differing rate of response to estimated invertebrate biomass at release location between the two sites may reflect a response to the difference densities of resident conspecifics at the two sites. South Ōkārito has a density of around one rowi per 28 ha, whereas North Ōkārito had no resident conspecifics that could be detected prior to the first experimental release for this study in 2010. Rowi have been known to display extreme territorial behaviour (Holzapfel et al., 2008), to the point of inflicting death on rowi released during the first few years of ONE (Colbourne et al., 2005). While every effort is now made to ensure ONE rowi are not released inside the territory of resident rowi, it may be the case that following release they wander into territories that are being defended, and are chased out, sending them further away from the release location as they attempt to escape hostile residents. Also, the higher density of residents currently occupying much of the high quality habitat in South Ōkārito may result in the need to disperse further from the release location in search of suitable unoccupied habitat than if the resident birds were not present. The presence of conspecifics has influenced the behaviour and decision making of released individuals in previous studies of birds and mammals (Bernardo, 2012; Stoen et al., 2009). An examination of the behaviour of captive bred red-billed currassow *(Crax blumenbachii)* following release found that upon release of a second cohort, birds released in the first cohort had a tendency to leave the area they had occupied up to that point and select other previously unoccupied areas, although the study was unable to distinguish precisely what factor led to this movement (Bernardo, 2012). White rhinoceroses (*Ceratotherium simum*) dispersed further following release as the density of the release site population increased (Stoen et al., 2009). The most parsimonious model to explain dispersal distance included interaction between release location biomass and site (North or South Ōkārito), that may also reflect the fact that in South Ōkārito much of the suitable kiwi habitat is already occupied. The pattern of decrease in dispersal distance as release location biomass increased was more pronounced in South Ōkārito than North. This may reflect the fact that due to the relative scarcity of unoccupied habitat in South Ōkārito, rowi released in higher quality habitat in South Ōkārito were less able to improve upon their resource availability at their release location by finding more productive unoccupied areas than those in North Ōkārito, and therefore may have stayed closer to the release location. Habitat quality of patches significantly influences dispersal decisions in a range of species, with dispersal distances generally being reduced with increasing patch habitat quality. Both prarie voles (*Microtus ochrogaster*) and water voles show significantly less dispersal from high quality patches than from lower quality patches (Lin et al., 2006; Moorhouse et al., 2009). In the case of water voles, it was also shown that those released in higher quality areas were less likely to experience mortality, although a causal relationship between habitat quality, dispersal and survival was unable to be established (Moorhouse et al., 2009).

Female-female dyads within this study had a significantly higher rate of association than any other sex category. Associations within a dyad do not necessarily mean that the individuals are behaving favourably towards one another. The rate of association between females may reflect benefits of conspecific cueing and social learning, or aggressive interactions or attempts by one female to chase the other female away. Like all species of kiwi, rowi females are larger than male counterparts (Robertson & Coulbourne, 2003). Reverse sex dimorphism occurs in several species of bird, facilitates female dominance, and is thought to have evolved as a result of sexual selection (Heinsohn et al., 2005; Mueller, 1990). Female rowi are generally more aggressive than males when being handled (pers. obs.), and may be more aggressive to one another than any other combination of sexes in dyads. It is also possible that the associations occurred through random or passive independent attraction to the same area, perhaps towards an area of high resources or because of site fidelity, rather than as a result of a conscious decision to affiliate with another individual (Newton-Fisher, 1999). The association of dusky dolphins (*Lagenorhynchus obscurus*) is primarily driven by foraging tactics, with large groups associating essentially as a by-product of the benefits afforded when foraging in large groups (Pearson, 2009). The associations of Ugandan female chimpanzee were found to be a consequence of individual behaviour and range overlap rather than a correlate of cooperation as is found in males (Gilby & Wrangham, 2008). Without more detailed analyses of factors driving associations, and also the types of interactions, if any, that occur during associations, precise reflection on the reason for association is not possible. This is certainly one area where future research involving new technology, such as proximity and biometric loggers that can record combinations of behaviour and physiological factors including locomotion, heart rate and hormone levels (Cesarovic et al., 2011; Rieux, 2008), could shed further light on the mechanisms and impacts of post-release association.

No relationship could be established between release group size and dispersal distance or association rates, which may result from a range of factors. It is highly likely that the sample size and monitoring regime used in this study were insufficient to detect any such effects. It is also possible that release group size does not have any effect on these behaviours. A larger experiment with more on the ground support may illuminate further relationships between group size and post-release behaviour. Additionally, proximity loggers would be a reliable way to gather far more accurate and a greater quantity of data on association rates and social behaviour following release. Sometimes referred to as “reality mining”, this method uses cutting edge technology to employ animal borne equipment that can monitor and record the activities and social interactions of whole populations down to temporal scales as small as seconds (Krause et al., 2013). Proximity loggers have been successfully used in many recent studies (Cross et al., 2013; Meise et al., 2013; Rutz et al., 2012), including to investigate dyadic interactions in two populations of rabbits (*Oryctolagus cuniculus*) in Australia to demonstrate that individual behaviour was more important than habitat quality in determining social network structure in the study populations (Marsh et al., 2011), on wire-tailed manakins (*Pipra filicaud*) to characterise variations in the behaviour of this lekking species (Ryder et al., 2012), and in a study on brushtail possums (*Trichosurus Vulpecula*), which found that most occasions of contact between individuals were related to breeding behaviour (Ji et al., 2005).

This study set out to investigate the elements of translocation procedures that affect dispersal and association behaviour following translocation. The study was conducted on translocated rowi, with particular emphasis on the effects of release group size. Release group size has been shown to be likely to affect post-release survival in rowi, and identifying a difference in the dispersal or association behaviour of birds from small or large groups may help identify the mechanisms driving differing survival rates. The limited detection rate of rowi post-release meant that data was insufficient to draw any firm conclusions. Overall, there were no observed differences in dispersal distances or association rates for rowi released in different group sizes. It is possible that either some other element of post-release behaviour is affected by release group size, which then has a subsequent effect on survival, or that the study size and monitoring effort applied here was not sufficient to detect such an effect. Factors affecting rowi dispersal were the presence of conspecifics and habitat quality at release location. High quality release location and low density of conspecifics limits post-release dispersal. This knowledge can be used by conservation managers to plan future reintroductions, and will be especially useful in cases where it is desirable to encourage released individuals to remain in the release area, as this will be achievable through manipulating release location habitat quality and resident conspecific density.

5 Conservation management affects home range behaviour of an endangered kiwi

5.1 Introduction

The home range (HR) of an animal determines the availability of food resources, mates and nest sites, and thus has fundamental consequences for ecological processes such as growth, reproduction and ultimately survival and fitness (Börger et al., 2008). Therefore HR behaviour, temporal movement dynamics and habitat selection cues are of central importance to population and behavioural ecology, and are important areas of consideration for conservation managers (Spencer, 2012; Villegas-Ríos et al., 2013). Reserve areas must be large enough and of high enough quality habitat to meet conservation goals such as long term persistence through self-sustaining populations (Basse & McLennan, 2003). Management decisions regarding the protection or restoration of adequate amounts of habitat must be based on empirical evidence (Corriale et al., 2013). Reintroduction attempts have in the past been unsuccessful due to incomplete understanding of HR behaviour (Bennett et al., 2013; Germano & Bishop, 2009; Linklater & Swaisgood, 2008; Short et al., 1992), and often reserves sizes designated for species conservation lack empirical testing (Villegas-Ríos et al., 2013).

HRs are structured by benefits gained through resources, constraints such as resource depletion by competitors, and are limited by the cost of resource acquisition and maintenance (Corriale et al., 2013; Mitchell & Powell, 2012). Home range behaviours and patterns also directly influence the spatial distribution of animal populations, and consequently have impacts at the population level (Moorcroft, 2012; Wang & Grimm, 2007). It is essential for effective species conservation that accurate estimations of home range size exist, and factors that underlie home range size and the behavioural basis of habitat selection are understood (Van Moorter et al., 2013). Understanding the effects of reintroductions on movement, habitat selection and HR behaviour is important for ensuring maximum conservation output from management practices. Translocated animals often wander prior to finding suitable habitat and settling in to a HR following release (Costello, 2010; Spencer, 2012; Wolf et al., 2009). These movements do not always correspond to natal or juvenile dispersal (Van Heezik et al., 2009), with released animals sometimes becoming more vagrant than wild conspecifics (Champagnon et al., 2012). The time it takes for an animal to display site fidelity following reintroduction can highlight the availability or suitability of habitat within the reintroduction environment. The movement behaviour and habitat selection of an individual during this period prior to HR formation can illuminate mechanisms driving HR behaviour. I have defined the space an animal uses during this time prior to HR formation as their area of habitation (AoH). The size and habitat quality within this AoH can be analysed in a similar way to HR.

5.1.1 Concepts of home range and site fidelity

While Darwin remarked in 1859 that "…most animals and plants keep to their proper home" , the first definition of home range was put forward by Burt (1943), and has since developed to become considered a concept, rather than an entity (Morris, 1988). Home range differs from the concept of territory in that a HR is defined or estimated without reference to exclusivity, or behaviours such as advertisement of presence, or defence from, or reaction to intrusion by conspecifics (Brown & Gordon, 1970). Home ranges are not static but can vary within individuals over time (Powell & Mitchell, 2012). Munger (1984) defined HR as site fidelity through limited, non-random movement over a landscape where the area used by an animal is significantly smaller than the area that would be covered if an animal was moving randomly through the landscape (Munger, 1984; Spencer et al., 1990). Thus site fidelity provides a quantitative measure of HR (Cameron, 1995; Danielson & Swihart, 1987; Spencer et al., 1990). Site fidelity has been measured in a variety of ways, including the occurrence of minimum convex polygon (MCP) centroids within a certain distance of one another over subsequent years, a minimum percent overlap of total accumulated HR within each year of the study, and the assessment of location fix movement pathways in comparison to a randomly walk pathway, where a significant difference between the mean squared displacement of the two indicates site fidelity (Börger et al., 2008; Brown, 1992; Kernohan et al., 2001; Pérez-García et al., 2013; Spencer et al., 1990).

Cognitive aspects of movement processes, including understanding processes of learning and memory, sensory perception, prioritisation within space-use decisions and prior experience are increasingly being incorporated into home range theory (Avgar et al., 2013; Börger et al., 2008; Fagan et al., 2013; Fletcher, 2007; Powell & Mitchell, 2012; Recio &

Seddon, 2013; Spencer, 2012; Van Moorter et al., 2009), expanding the definition of HR to include an area that an animal regularly uses and about which it keeps up to date information stored in its cognitive map (Powell & Mitchell, 2012; Spencer, 2012). The inclusion of cognition as a consideration is viewed as essential to providing a complete picture of movement behaviour (Fagan et al., 2013; Moorcroft, 2012; Powell & Mitchell, 2012), and is evident in recent theoretical and computational studies of movement behaviour. Van Moorter et al (2013) produced a general mechanistic model of stable HR formation based on a biased correlated random walk informed by a two part memory system that provides the individual the ability to both avoid recently visited patches and store a preference for certain feeding patches. Spencer (2012) recently demonstrated, using simple deterministic models, how an individual's expectations about resource availability drive diverse movement patterns that influence HR formation. Yet while there are many examples of theoretical explorations of cognitive mechanisms driving HR behaviour, empirical studies are rare (Avgar et al., 2013). Studies that consider cognition tend to focus exclusively on the animal's ability for spatial mapping and memory of spatial features (e.g. relative locations of resources, reference points and topographical barriers (Powell & Mitchell, 2012; Recio & Seddon, 2013; Wolf et al., 2009), although see Recio & Seddon (2013) for an example of a home range study of feral cats (*Felis catus*) including social factors. There is vast scope for increasing understanding in this area through expansion of studies to include broader cognitive concepts such as conspecific attraction and social learning (Börger et al., 2008; Fagan et al., 2013). Animals arriving in novel environments, either through dispersal or translocation lack spatial memory of the new site (Berger-Tal & Avgar, 2012). In such situations, movement behaviour must be guided by other mechanisms. Behavioural studies occurring as part of reintroduction attempts for conservation provide the opportunity to gather empirical evidence for the role of a variety of cognitive mechanisms in HR establishment, and have been proposed as one method for increasing understanding of how cognitive processes influence movement behaviour (Dzialak et al., 2005; Fagan et al., 2013; Spencer, 2012), yet such analyses are rare (Bernardo et al., 2011).

5.1.2 Home range estimation

The most appropriate method for estimating HR depends on the questions being addressed (Fieberg & Börger, 2012; Powell & Mitchell, 2012). It is essential to acknowledge that it is almost impossible to avoid intrinsic errors in data collection for home range analyses (Monterroso et al., 2013; Springer, 2003). Radio telemetry (RT) fixes only provide a subsample of all the locations of an animal within a sampling period, with researchers forced to assume that the collected data are representative of the animal's activities over the sampling period (Kernohan et al., 2001). Both RT and global positioning system (GPS) fixes have an associated positioning error and so are not 100% accurate (Gula & Theuerkauf, 2013; Rodgers, 2001; Withey et al., 2001). As a result, home range metrics reported are always estimates, which are limited models of reality at best (Powell & Mitchell, 2012; Springer, 2003).

Kernel Density Estimation (KDE) and Minimum Convex Polygons (MCP) are the most common methods used in HR analysis (Laver & Kelly, 2008). KDE provides a probabilistic and objective estimator of home range and is favoured by many authors because it is nonparametric, is insensitive to outliers, it is able to work with reasonable sample sizes, and it computes home ranges with multiple centres of activity (Kernohan et al., 2001; Laver & Kelly, 2008). However, others have suggested that several elements of the process, such as bandwidth, search radius and computational algorithms cannot be standardised among studies (Haines et al., 2006; Hemson et al., 2005; Kernohan et al., 2001; Laver & Kelly, 2008).

The sampling regime in HR studies is a contentious issue (Laver & Kelly, 2008). Both standardisation of sampling regime with a constant sampling interval (Börger et al., 2006), and randomised sampling conducted over a pre-defined period have been recommended (Kernohan et al., 2001; Otis & White, 1999). Within wildlife studies, a constant sampling interval is often impractical, and it is better to determine when sufficient samples have been collected such that further measurements no longer affect the measured parameters (Gula & Theuerkauf, 2013; Laver & Kelly, 2008). As sample size increases, HR size estimates tend to increase asymptotically, and insufficient fixes may lead to underestimation of HR (Bekoff & Mech, 1984; Odum & Kuenzler, 1955; Springer, 1982; Villegas-Ríos et al., 2013). Asymptotes of home ranges, that is the point at which an increase in sample size no longer leads to an increase in HR size, can be assessed to ensure an adequate number of fixes has been used in determining the HR area (Laver & Kelly, 2008). Methods to do this include calculating how many fixes provide a HR estimate of 95% of the full HR (Laver & Kelly, 2008), visually judging observation-area curves for slope discontinuity (Drygala & Zoller, 2013; Hyslop et al., 2014), or selecting the point at which the % change in an observation-area curve is less than a given percent for at least n successive fixes (Laver & Kelly, 2008), such as <5% change over five successive fixes (Laundré & Keller, 1984; Villegas-Ríos et al., 2013). HR's can change over time, with changes often reflecting changes in seasons or life stages. It is therefore important to consider the timeframe over which the HR is monitored, as monitoring to determine a seasonal HR, such as breeding season, would give different estimates, and require a different number of fixes than if the intentions of a study were to determine the annual or lifetime HR.

In addition, HR analysis often neglects to assess the difference between the planar HR, and the actual surface area of the HR resulting from the three dimensional topography (3D) of the site (Greenberg & McClintock, 2008). An HR estimated without consideration of topography is likely to underestimate the actual area (Monterroso et al., 2013), and a review of studies using both 3D and planar measurements found this underestimation can be as much as 23% (Grueter et al., 2008).

5.1.3 Rowi case study

Rowi (*Apteryx rowi)* are flightless ratites endemic to New Zealand (Holzapfel et al., 2008). Historically the rowi range extended from north of the Haast Pass on the South Island of New Zealand, through the lower North Island and as far north as Hawkes Bay (Holzapfel et al., 2008; Shepherd & Lambert, 2008). This area was greatly reduced following the arrival of Europeans and the predator species they introduced (Holzapfel et al., 2008). By the late 1800s, rowi were found only on the West Coast of the South Island, and by the 1990s, the entire range was thought to be encompassed by the 10000 ha South Ōkārito forest (DOC, 2006; Holzapfel et al., 2008). Rowi are now listed as "nationally critical", with the population dropping as low as 150 in the 1990s, and reaching an estimated 300 by 2008 as a result of intensive management practices (Hitchmough, 2002; Robertson, 2003). In 2000, South Ōkārito was designated as one of five national "kiwi sanctuaries" and afforded extra legislative protection (exclusion of dogs), and funding (Robertson, 2004).

Predation of chicks by introduced stoats is cited as the main cause of rowi decline (Colbourne et al., 2005). When rowi reach at least 1.2 kg they are less vulnerable to stoat predation, and the management program known as Operation Nest Egg (ONE) is built around this fact (Colbourne et al., 2005). ONE involves monitoring breeding adults with leg mounted transmitters, removing their eggs from the forest, hatching eggs in captivity, rearing chicks on a predator free island and reintroducing juveniles back to the source population once they have reached at least 1.2 kg. Rowi lend themselves well to this management approach as they are semi-precocious, and wild chicks leave the nest to forage independently within one week of hatching (Colbourne et al., 2005). The ONE programme provides a valuable opportunity to investigate a range of areas of rowi ecology plus factors affecting reintroduction success.

Currently, around 40% of adult rowi do not attempt to breed (Holzapfel et al., 2008), which may be due to South Ōkārito Kiwi Sanctuary being close to carrying capacity (H. Robertson, DOC, pers. comm. in Holzapfel et al (2008)). Despite the rowi population doubling between 1990 and 2011, the range of rowi has not expanded, perhaps due to social fencing and conspecific cueing, and the current density of rowi in South Ōkārito is estimated to be 1 bird per 28 ha (Holzapfel et al., 2008). Kiwi settled down quickly into normal ranging patterns after relocation (Potter, 1990), however this has never been empirically tested and assessment of the HR size of any taxa of wild kiwi are rare. Estimated HR for North Island brown kiwi (*Apteryx mantelii*) in Northland is 40.5 ha ± 5.1 S.E. (Potter, 1989), and for North Island brown kiwi in Hawkes Bay 14.6 to 40.3 ha (McLennan et al., 1986). Investigation into impacts of increasing on HR habitat quality or size or movement behaviour for either wild or ONE rowi is lacking, as is the time it takes for ONE rowi to demonstrate site fidelity following release. ONE birds wander initially while searching for suitable habitat, and so display increasing site fidelity over time since release as they settle in HRs. During this time I have defined the space they use as their area of habitation (AoH), and investigation into the size and quality of these areas along with investigating HR and HR settling behaviour will have two benefits: they will inform managers on the time to settle into a HR, and also the behaviour of rowi prior to settling. A long period of wandering and a large AoH may suggest that suitable habitat is hard to locate, which could be influenced by territorial resident birds or low resource availability. A short period from release to settling could indicate either an abundance of suitable habitat, inability to disperse from the release location due to social fencing, territorial resident birds, or preference for continued association with release conspecifics over habitat surveying behaviour. Understanding which of these occurs and why would allow management decisions that take advantage of these mechanisms to be made. For example, if low quality habitat at release site increases time to settling, and it was desirable to increase dispersal post-release to facilitate increased recruitment to the wild population rather than pairings occurring within the released individuals, it would be beneficial for releases to take place at low habitat quality areas.

Manipulation of ONE release procedures allows investigation of a range of theoretical concepts pertaining to movement behaviour and reintroduction success. As part of a wider investigation into rowi ecology and the factors influencing reintroduction success, I experimentally manipulated release variables during reintroductions in South Ōkārito in 2009, and in both South Ōkārito and North Ōkārito in 2010 and 2011 (Figure 6.1) (see Chapter 2). The variables manipulated included release group size, predator and competitor density via a 1080 (sodium flouroacetate) application and conspecific density at release area via the use of North Ōkārito as a new release location. Prior to the 2010 release, there was no evidence of any surviving wild rowi in North Ōkārito. The suitability of North Ōkārito as a rowi release area was assessed by the Department of Conservation in 2010. South Ōkārito has always been assumed to be a suitable release area due to the presence of existing rowi. South Ōkārito is largely unmodified native podocarp-hardwood forest (Murphy et al., 2008). North Ōkārito was similar, until it was selectively logged at 25% of total merchantable volume in the 1970s and 1980s, resulting in a series of logging tracks throughout the area, and regenerating vegetation (Pearce & Griffiths, 1980; Piskaut, 2000). A difference in the behaviour of rowi released in North and South Ōkārito would highlight a possible effect of the presence of conspecifics, whereas similar behaviour in both settings would suggest the influence of alternative mechanisms driving movement decisions and HR behaviour of ONE rowi. Any difference observed between ONE and wild rowi HRs could be caused by a variety of factors. Reintroductions sometimes lead to released animals being forced into lower quality habitat due to sub dominance to resident conspecifics. Dominant animals have superior competitive ability, allowing them to occupy high quality habitat while sub dominant individuals are forced into lower quality areas (Burns, 2005). A number of studies have demonstrated that early social environment and experiences can have profound long lasting effect on subsequent behaviour (Chapman et al., 2008; Hansen & Slagsvold, 2004; Harvey et al., 2002; Horwich, 1989). While in a novel environment, rowi may rely on previous experience, such as positive experiences of social learning for resource locations, and conspecific cueing for locating suitable habitat. This tactic has been observed in a range of species, including; collared flycatchers (*Ficedula albicollis*) (Doligez et al., 2002), Brewer's sparrows (*Spizella breweri breweri*) (Harrison et al., 2009), porcelain crabs *(Petrolisthes cinctipes)* (Donahue, 2006), northern wheatear (*Oenanthe oenanthe*) (Part et al., 2011), alpine ibex (*Capra ibex*) (Scillitani et al., 2013) and European rollers (*Coracias garrulous) (Václav et al., 2011)*. Investigating the AoH, HR and movement of reintroduced ONE rowi is both beneficial for rowi management practice, and provides exploration of general mechanistic processes driving HR behaviour in a novel environment.

I investigated AoH and HR of rowi. I specifically asked: 1) Do ONE rowi differ from wild rowi in their HR size and habitat quality? 2) What factors predict the size and habitat quality of the post-release AoH of ONE rowi? 3) Does time since release affect site fidelity and size of AoH of ONE rowi?

5.2 Methods

Wild rowi were located using specially trained kiwi tracking dogs or called in at night using audio playback of rowi calls. Once located, wild rowi were caught, banded and fitted with very high frequency (VHF) transmitters (Sirtrack Ltd.) in order to relocate them and identify egg laying/incubation. ONE rowi released into Ōkārito forest were also fitted with ID bands and VHF transmitters to allow relocation. Transmitters were attached following guidelines set out in the Kiwi Best Practice Manual (Robertson & Coulbourne, 2003) and had a battery life of approximately 12 to 15 months, and were systematically replaced on the same bird prior to the end of battery life (Keye et al., 2011; Robertson & Coulbourne, 2003). Ground based monitoring was conducted using a hand held TR4 receiver (Telonics^{TM}) with 3-element folding Yagi antennas (Sirtrack Ltd.). Monitoring effort and type of data collected varied over the course of rowi management. Information available for most birds included first location (capture site or release site), subsequent monitoring dates and recapture locations, dates of transmitter failures or removals, mortalities detected within the monitoring periods and detection of egg incubation behaviour as observed by intensive night time monitoring of burrows from 1996 to 2008 and then the use of activity logging transmitters from 2008 to present. Location fixes were recorded using either estimation using map and compass navigation techniques which had an accuracy of ±100m, or handheld GPS units with a maximum recorded error of ±100m. Triangulated locations of rowi were available from North Ōkārito for 2010 to 2012, after a beacon study had been conducted to assess the precision and accuracy of this method (Appendix 1). In this study site triangulation had a mean linear error of 331 m (n= 22, SD = 256). Estimate of the bearing bias as calculated from the mean difference in recorded azimuth and true azimuth from the station to the transmitter was 39° (n= 69, CI 95% = 13). The precision of the system within this study site, calculated as the standard deviation of the bearing bias was 54°.

Data were available on the repeated locations of 102 wild rowi that had been monitored in South Ōkārito as part of rowi conservation management and ONE between 1979 and 2012. Only those with at least 20 fixes were included in the analysis (n=68, see Table 9.1, Appendix 2). Some ONE birds were monitored for an initial period following release, had transmitters removed for a period, and were then re-caught using dogs or call playback at a later date, while others were monitored continuously from release until death, giving varying durations and intensities of monitoring effort over time. Only those ONE birds with at least twenty fixes following release were included in HR analyses, (n=20, see Table 9.2, Appendix 2). Only fixes from birds released in North and South Ōkārito during the experimental release years 2009, 2010 and 2011 were included in the investigation of effects of conspecific density on AoH size and habitat quality.

5.2.1 Analyses

In order to establish whether both wild and ONE rowi display significant levels of site fidelity, I compared whether the observed movement paths were significantly different from random (Crook, 2004), using the procedure of Munger (1984), as modified by Danielson and Swihart (1987), Spencer et al. (1990) and Crook (2004). I conducted analyses using Visual Basic macros written in Excel© 2000 (Microsoft, USA), ArcGIS, R and Geospatial Modelling Environment (GME) (Beyer, 2012), and specifically GME tools Path

Metrics and Correlated Random Walks (CRW). For each individual rowi, I created a Minimum Convex Polygon (MCP) using all available fixes, calculated the centroid of the MCP, and the Mean Squared Distance (MSD) from the centroid to each fix. I also calculated the distance between successive fixes (step length). Due to the large volume of data and the requirements of the program GME, all step lengths were allocated into bins of 0-50m, 51-100m then 100m bins up to 1000m, 500m bins from 1001m to 5000m, and 1000m bins from 5001m to 11000m, giving a total of 25 bins and (n) steps within each bin. These bin sizes were selected to keep the number of bins small enough for the program to deal with, while maintaining the fine scale detail from movements within the smaller ranges (0 to 1000m), where the majority of the fixes were located. The CRW tool was used to reproduce each movement path, randomising the order of the steps and assigning each a compass heading chosen randomly from the interval 1° to 360°, thereby generating a sequence of randomised movement vectors based upon the step lengths of the observed rowi movement path. To prevent generated fixes occurring in surrounding bodies of water, and also to reflect the restricted range that rowi currently occupy, I confined the random walks to a bounding polygon of the North and South Ōkārito rowi range in ArcGIS. The CRW procedure was repeated 100 times for each observed rowi and MSD of each fix calculated from the centroid of the MCP. I addition I assessed ONE rowi site fidelity over time. Fixes were separated into 12 month blocks running from 1 July through to 31 June to encompass one breeding season (July to February) and included individuals with at least three fixes within a year. A significant difference ($P<0.05$) between the MSD of observed movement path fixes and the CRW movement path fixes was taken as evidence of site fidelity and was tested using a Mann Whitney U test.

I further analysed the whether the number of fixes available were sufficient to provide an accurate representation of the HR. For each bird I calculated cumulative 95% MCP areas, adding fixes in random order since the inter-fix interval was variable, and observed whether an asymptote was reached in the observation-area curve. An asymptote was considered as <5% increase in area, for at least 12 successive additions of fixes. I chose to use the 95% MCP areas to assess asymptotic HR requirements as they provide a more conservative assesment than 95% KDE asymptote analysis.

Home range size was estimated for all rowi displaying site fidelity and showing asymptote of HR area-observation curve, using the Kernel Density Estimation (KDE) method using ArcGIS, R, GME and Excel, and specifically the Spatial Analyst KDE tool (ESRI 2011) in ArcGIS 10. This tool requires that you specify a cell size, search radius (equivalent to bandwidth or smoothing parameter in other programmes) and processing extent. When choosing these there is no apriori way to select the best values, and optimal selection will depend, amongst other things, on the biology, behaviour and distances typically moved by the species being investigated, as well as the size of the study area and the resolution of the spatial data (Kernohan et al., 2001; Kie, 2013). Through a trial and error process of testing different values iteratively and looking for values that produced biologically meaningful representations of HR, I selected a cell size of 10m, and a fixed search area of 370m^2, with a constant processing extent that covered the whole rowi range (Seaman & Powell, 1996). A 95% isopleth of each bird's KDE was selected to represent the estimated home range of rowi as recommended by Laver and Kelly (2008). This is the most commonly used measurement for home ranges using the KDE method and is thought provide an accurate representation of home range while excluding regions around fixes that are outliers caused by occasional sallies outside the home range (Gula & Theuerkauf, 2013; Laver & Kelly, 2008). The area of the estimated home range using both planar and 3D surface measurements were considered to investigate whether the rate of underestimation of surface occurring through planar estimations of undulating topography was the same for both ONE and wild rowi. A difference in the mean underestimation would suggest that ONE and wild rowi have HRs in areas of different topographic gradients. If ONE rowi select habitat that is characterised by steep, hilly terrain, while wild rowi preferentially occupy flat areas, or vice versa, a comparison of HR areas using a planar measurement would lead to a bias in the results, whereas if no preference is observed by either group, the planar areas will be suitable for comparison and used in the study to enable simple comparison with other studies and future research. A Digital Elevation Model (DEM) (data reproduced with the permission of Landcare Research New Zealand Limited), was used to produce a Triangulated Irregular Network (TIN) file of the study area, from which the 3D surface areas of the estimated home ranges could be calculated using ArcGIS 3D Analyst tools. Data were normally distributed, so t-tests were used to compare the mean HR areas of wild rowi and ONE rowi.

In addition to the analysis of HR based on all fixes from the monitoring period, a 95% KDE estimate of the AoH was also conducted using fixes from within a single year whenever an ONE rowi had displayed within-year site fidelity. If a bird had multiple years of within-year site fidelity, values were combined and the mean within-year value for each ONE rowi was included in analyses to avoid pseudoreplication.

The map of habitat quality throughout the rowi range in Chapter Three, based on estimated invertebrate biomass predicted by abiotic habitat variables, was overlaid with a layer of shapefiles containing all 95% KDE describing estimated HRs in ArcGIS. The Spatial Join tool was then used to extract the mean estimated invertebrate biomass for each bird's estimated HR, thus allowing comparison of relative HR habitat quality between wild and ONE rowi. All data were normally distributed. Mean habitat quality was compared using t-tests in R. If an ONE bird had multiple years of within-year site fidelity, estimated invertebrate biomass values were combined and the mean within-year biomass for each ONE rowi was included in analyses to avoid pseudoreplication.

I conducted experimental releases into both South and North Ōkārito to investigate the influence of conspecific density on ONE rowi AoH size and habitat quality. South Ōkārito had a high density of conspecifics (one rowi per 28 ha), while North Ōkārito had a low density (no evidence of presence since 1980s until the 2010 release). In 2009, 17 rowi were released into South Ōkārito, in 2010, 15 rowi were released into South Ōkārito and 19 in North Ōkārito. In 2011, 15 rowi were released into North Ōkārito. Releases took place in either small groups (two or three rowi) or large groups (four to six rowi), at each of 24 release locations throughout North and South Ōkārito. AoH size and mean estimated invertebrate biomass within the AoHs in North and South Ōkārito were compared respectively using t-tests. Linear mixed effects models fit using maximum likelihood were constructed and analysed in R using package nlme, to investigate which factors most influenced a) the estimated size of the AoH, and b) the estimated biomass within the AoH. Factors included in the candidate models of AoH size were: relative habitat quality at release site (continuous variable, mean dry biomass in mg), release group size (categorical variable, small or large), release site location conspecific density (categorical variable, South or North Ōkārito), habitat quality of AoH (continuous variable, mean dry biomass in mg). Factors included in the candidate models of AoH habitat quality were: habitat quality at release site (continuous variable, mean dry biomass in mg), release group size (categorical variable, small or large), release site location conspecific density (categorical variable, South or North Ōkārito), and AoH size (continuous variable, area in km^2). I included group ID as a random variable in all models to account for possible homogeneity in release groups and thus prevent pseudoreplication. I compiled a complete set of candidate models of all possible main effects permutations of variables, and ranked models based on Akaike's Information Criterion corrected for small sample size (AIC_c) (Burnham & Anderson, 2002). I considered models with a Δ AIC_C values ≤2 compared to the best model, as competing models (Price et al., 2010). I ran a goodness of fit test on the top model, calculating both the marginal and conditional R^2 using the function rsquared.glmm, to identify how much of variance is explained by the model, and specifically how much of that variance is explained by the fixed factors alone compared to that explained by both the fixed and random factors . Means are presented ± standard error unless otherwise stated.

5.3 Results

Of 40 wild rowi that had been monitored, the number of location fixes per bird varied from twenty to 270, with a mean of 52.6 (Table 5.1). The length of time wild birds were monitored ranged from 317 days to 10575 days, time between fixes varied from one day to 14 years, and the mean inter fix interval was 54 days (Table 5.1). The number of location fixes per ONE bird varied from twenty to 105, with a mean of 22 (Table 5.1). The length of time ONE birds were monitored for ranged from 12 days to 13.5 years and mean time monitored for was 1863 days. Time between fixes varied from one day to 2210 days, and the mean inter fix interval was 87 days (Table 5.1).

Table 5.1. Summary of monitoring data on wild and ONE rowi. The data summarised here was used to investigate HR behaviours, including habitat quality and HR size. Units of time given in days (d) if less than 365 days, years (yr) if over 365 days. ONE rowi have a shorter minimum, maximum and mean monitoring period, lower numbers of fixes, and higher inter-fix interval than wild rowi.

	Monitoring period			Number of fixes			Inter fix interval		
	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
Wild rowi (n= 40)	908 d	28.9 yr	10.36 yr	20	238	95	1 d	14 yr	54 d
ONE rowi (n=17)	122 d	13.5 yr	8.8 yr	20	105	50	1 d	6.05 yr	87 d

5.3.1 Do ONE rowi differ from wild rowi in their HR size and habitat quality?

Of 102 wild birds included in the site fidelity analysis, 98 demonstrate site fidelity throughout their history of being studied, and of these 40 also demonstrated an asymptote in their observation-area curve. Of the 68 ONE birds analysed, 52 demonstrated site fidelity over the whole duration of being studied, and 17 of these demonstrated an asymptote in their observation-area curve. The mean estimated HR of ONE rowi is significantly larger than that of wild rowi (t-test, t = 8.098, df=55, p-value = <0.001) (Table 5.2). The mean underestimation of HR area using planar compared to 3D area of ONE birds is higher than for wild birds (t-test, t = 7.513, df=55, p-value = 0.000). The mean estimated biomass in HRs of ONE birds with site fidelity over the full sampling period is significantly lower than in wild birds HR (t-test, t = -4.33, df=55, p-value = 0.039) (Figure 5.1).

Table 5.2. Summary of data on ONE and wild rowi HR estimated area and invertebrate biomass. Wild rowi have a significantly smaller mean home range (HR) with significantly higher mean estimated invertebrate biomass, than ONE rowi with full sampling period site fidelity. There is no significant difference in the mean size and estimated invertebrate biomass in HRs of wild rowi compared to ONE rowi with within-year site fidelity. The mean underestimation of HR area when using plainar compared to 3D analysis is not dissimilar between wild, ONE with full and ONE with within-year site fidelity.

Site fidelity period	x̄ planar HR area (km^2)	3D est. HR area (km^2)	Underestimated area - plainar vs 3D (%)			HR mean est. invertebrate biomass (mg)
			x̄	Min	Max	
Wild full (n=40)	1.06 ± 0.096	1.10 ± 0.099	4.16 ± 0.387	<0.000	11.46	201.69 ± 16.54
ONE full (n=17)	3.35 ± 0.37	3.50 ±0.390	4.41 ± 0.273	2.61	6.37	145.27 ± 11.78

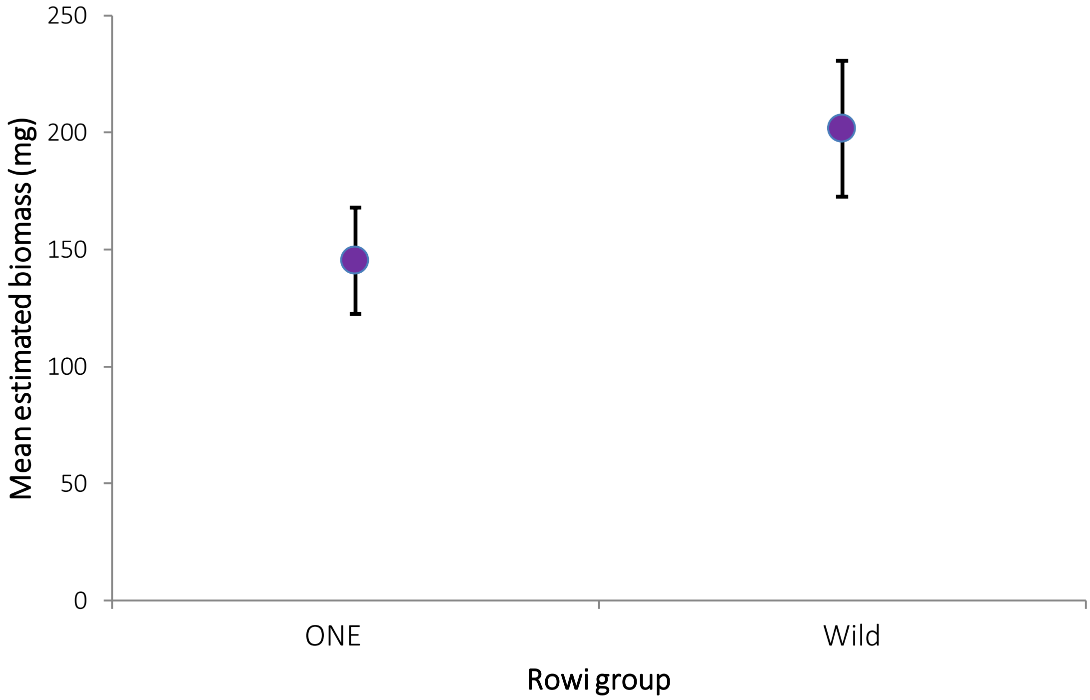

Figure 5.1. Mean estimated invertebrate biomass within HR of ONE and Wild rowi, and 95% confidence intervals. There is a significant difference between the estimated biomass within wild rowi HR compared to within ONE HR.

5.3.2 *What factors predict the size and habitat quality of an ONE rowi area of inhabitation*?

The difference in mean estimated area of inhabitation (AoH) of ONE rowi with site fidelity across the full sampling period in South versus North Ōkārito was not significant (South Ōkārito= 0.83 ± 0.07 km^2; North Ōkārito= 1.00 ± 0.11 km^2, t-test, t = 1.2464, df=27, p-value = 0.2233). The difference in mean estimated biomass of AoH of ONE rowi in South and North Ōkārito was not significant (South Ōkārito = 2835.15 ± 641.21 mg; North Ōkārito = 3121.79 ± 466.66 mg, t-test, t = 0.370, df=27, p-value = 0.714).

The model for ONE rowi AoH with lowest AICc contained release group size (Table 5.3). A goodness of fit test showed the top model explains 28% of the variation in the data. Of this, 23% is explained by the fixed factor (release group size), and 5% is explained by the random variables (group ID). As group size increases, home range area also generally increases although confidence intervals overlap (Figure 5.2). Models for AoH habitat quality provided no further explanation of variables affecting HR behaviour as no model was better than the null model. The only model with a competing delta AICc contained release group size (Table 5.3), but when tested for goodness of fit it was found this model explained just 3% of the variation seen in the data.

Table 5.3. Models for investigating effects of variables on a) home range (HR) size, and b) HR habitat quality. In model of AoH size, variables included were; release group size (small or large), release site location (North or South Ōkārito), release site estimated biomass and estimated biomass of HR. In the model of AoH habitat quality variables included were AoH size, release group size (small or large), release site location (North or South Ōkārito), and release site estimated biomass. Table includes number of parameters (K), Akaike Information Criterion corrected for small sample size (AICc), delta AICc (ΔAICc), AIC_c weights (AIC_c Weight), cumulative Akaike weights (ω), and log-likelihoods (LL). All models included release group ID as a random variable. Models with ΔAIC lower than 6 are shown, ordered by lowest AICc values.

Model a) Effects on AoH size

Model variables	K	AICc	Δ AICc	AICc Weight	ω	LL
Release group size	4	26.61	0	0.42	0.42	-8.47
Release group size + Release site biomass	5	29.05	2.44	0.12	0.54	-8.22
Release group size + Release site location	5	29.09	2.48	0.12	0.66	-8.24
Release group size + Est HR biomass	5	29.54	2.93	0.1	0.76	-8.46
Null	3	30.41	3.8	0.06	0.82	-11.73
Release group size + Release site biomass + Release area	6	31.11	4.5	0.04	0.87	-7.65
Release group size +Release site biomass + Est AoH biomass	6	32.24	5.63	0.02	0.89	-8.21
Release site location	4	32.25	5.64	0.02	0.92	-11.29
Release group size + Release site location + Est AoH biomass	6	32.26	5.65	0.02	0.94	-8.22

Model b) Effects on AoH habitat quality

Model variables	K	AICc	Δ AICc	AICc Weight	ω	LL
Null	3	530.32	0	0.36	0.36	-261.68
Release group size	4	532.25	1.93	0.14	0.49	-261.29
AoH area	4	532.78	2.46	0.1	0.6	-261.56
Release site	4	532.85	2.53	0.1	0.7	-261.59
Release site biomass	4	533	2.68	0.09	0.79	-261.67
Release group size + Release site location	5	534.81	4.49	0.04	0.83	-261.1
Release group size + AoH size	5	535.19	4.87	0.03	0.86	-261.29
Release site biomass + Release group size	5	535.2	4.87	0.03	0.89	-261.29
Release site location + AoH size	5	535.44	5.11	0.03	0.92	-261.41
Release site location + Release site biomass	5	535.65	5.32	0.02	0.95	-261.52
Release site biomass + AoH size	5	535.69	5.37	0.02	0.97	-261.54

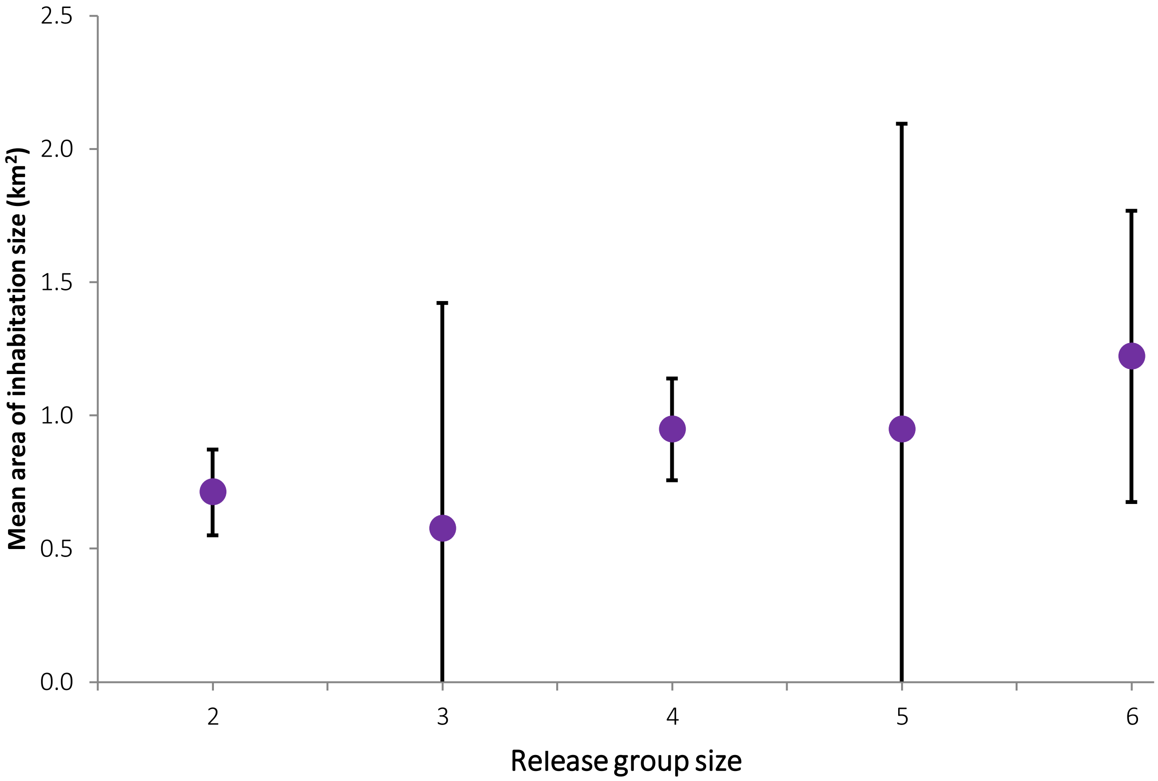

Figure 5.2. Area of inhabitation and 95% confidence intervals by release group size. As release group size increases, HR area follows a general pattern of increasing although there is a lot of overlap of confidence intervals.

5.3.3 Does time since release affect site fidelity and AOH size of ONE rowi?

There were 96 occasions of within-year site fidelity detected for ONE birds. These involved 48 birds of the 68 observed, 36 of which also show complete sampling period fidelity, and 12 of which do not. There is no clear pattern of increasing site fidelity within a breeding year over time following release (Figure 5.3). The number of rowi observed with at least three fixes within a year decreased over time since release, from 57 in the first year down to one in the 11th year after release (Figure 5.3). The percent of these birds displaying site fidelity does not follow any obvious pattern, with an initial rate of 66% in the first year, dropping to a low of 38% in the fourth year and then increasing to the highest proportion of 75% in the ninth year after release (Figure 5.4). The mean within-year HR size showed an initial steep decrease from 1.27 km^2 within one year after release down to 0.97 km^2 in the second year after release, followed by a continuing decline to 0.77 km^2 by four years post-release, when it then appears to plateau between 0.81 km^2 and 0.73 km^2 throughout the remaining years with sufficient data available to produce estimates (Figure 5.3)

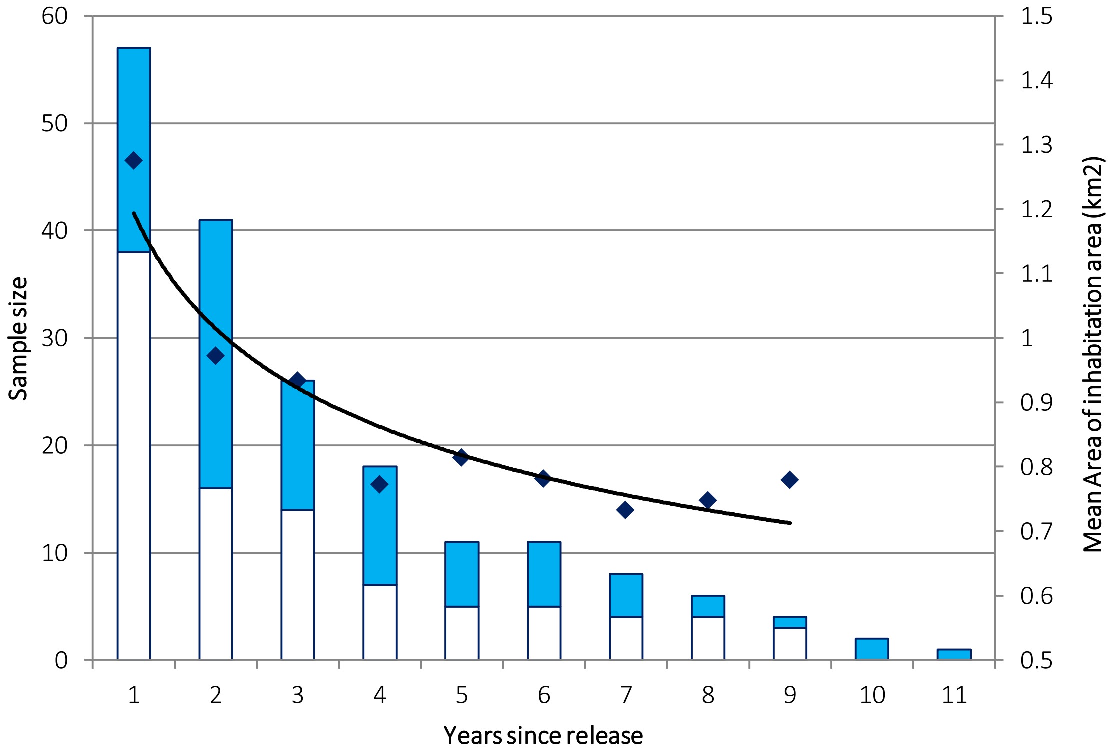

Figure 5.3. Total number of rowi with three or more fixes per year, divided into those that do (☐), and those that do not (🟦) display site fidelity, along with the mean AOH area (◆) of those that do display site fidelity, over time since release. The number of birds with at least three fixes within a year generally reduces over time since release. The mean AOH area drops for the first four years after release, when it then plateaus around 0.75 to 0.85 km^2. The black line show this general trend.

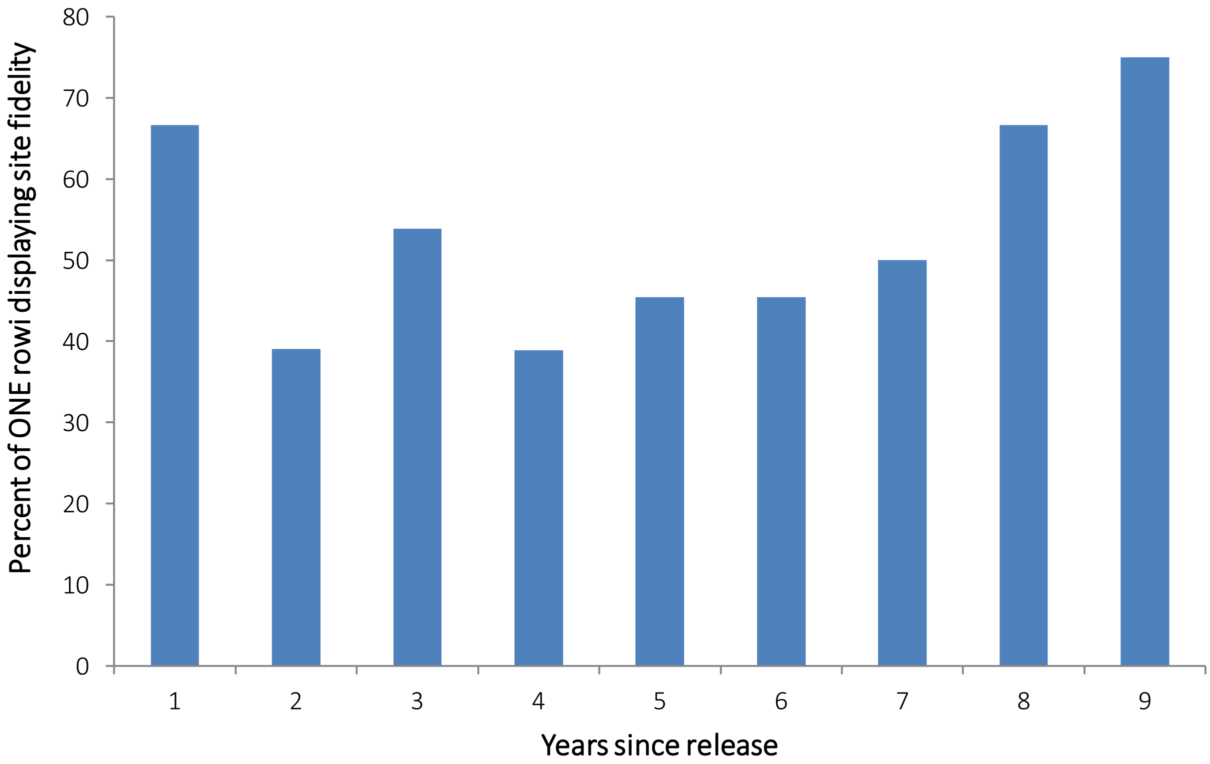

Figure 5.4. The percent of birds with three or more fixes within a year that display within-year site fidelity does not appear to increase over time since release. There is no pattern between the first and after release, but from the sixth year post release onwards, the proportion of rowi showing within-year site fidelity shows steady increase. This stage may correspond with the start of breeding behaviour.

5.4 Discussion

I found that ONE rowi have larger, lower quality HR's than wild rowi. Release group size was the only variable found to have a significant effect on ONE rowi HR size and habitat quality. There was no significant effect of conspecific density on HR habitat selection or size for ONE rowi, and ONE rowi did not show any clear pattern of change in site fidelity over time since release.

5.4.1 Do ONE rowi differ from wild rowi in their HR size and habitat quality?

The mean HR of ONE rowi was significantly larger than the mean wild rowi HR. However, within-year AoIs of ONE rowi were not significantly different from wild rowi HRs. Wild rowi hold HRs with significantly higher habitat quality, as demonstrated by estimated invertebrate biomass, than ONE rowi displaying site fidelity over both the full sampling period and within-year. For many species, food abundance is generally thought to have an inverse relationship with HR size (McLoughlin et al., 2000). This would appear to be partly the case for rowi, where ONE rowi with full sample period fidelity have both lower estimate invertebrate biomass and larger HRs than wild rowi and there are several possible explanations for this. The first is that ONE birds may be behaviourally subdominant to wild rowi and as a result are forced into suboptimal edge habitat, where a HR needs to be larger in order to meet the energetic requirements of the bird. Sub-dominant individuals are often out competed for high quality resources and habitat quality is often strongly correlated with dominance rank (Burns, 2005; Fox et al., 1981; King, 1973; Krebs, 1971; Miller et al., 2014). Captive breeding and rearing can lead to the selection of individuals displaying genetic and phenotypic traits best suited to captivity (Kleiman, 1980). Such traits include adaptability to high levels of human interaction, limited breeding opportunities, constraints on social interaction and restricted food types (Griffin et al., 2000; Harvey et al., 2002; McDougall et al., 2006). The long term result of this type of selection is often domestication of a species, accompanied by the loss of key behavioural traits and physiological features necessary for survival in the wild (O'Regan & Kitchener, 2005; Price, 1999). While the collection of eggs from the wild for ONE reduces the risk of this type of domestication occurring, rearing in a non-natural setting may select for those individuals best suited to the crèche environment on both a physiological and behavioural level. This could lead to sub-dominance of ONE compared with wild individuals reared in a parental territory.

Such alterations in dominance behaviour due to early rearing experience varying from that of wild individuals have been observed in many species including: bank voles (*Clethrionomys glareolus*) (Mathews et al., 2005), Hawaiian geese (*Branta sandvicensis*) (Marshall & Black, 1992), Chinook salmon (*Oncorhynchus tshawytscha)* (Pearsons et al., 2007), veiled chameleons (*Chamaeleo calyptratus)* (Ballen et al., 2014) and Takahē (*Porphyrio hochstetteri*) (Maxwell & Jamieson, 1997). Burns (2005) found the absence of resident animals led to translocated white footed mice (*Peromyscus leucopus*) selecting higher quality habitat than when residents were present. A study on sun bears (*Helarctos malayanus*) in Indonesia showed the death of released bears occurred after they were forced by dominant residents out of the forest and into unsuitable habitat (Fredriksson, 2005), and a translocation of black rhinos (*Diceros bicornis*) in Tanzania found two translocated individuals were pushed out of the monitored area of suitable habitat by a dominant bull (Fyumagwa & Nyahongo, 2010). There is also a phenomenon known as the prior-residence effect which may be occurring, where resident animals have an increased likelihood of winning in a competition for resources, or will go unchallenged, simply because they have current residency of an area (Kokko et al., 2006).

While the mechanism of sub-dominance resulting from early rearing environment has been shown to shape the HR behaviour in these examples, I suggest that this is not the case for rowi. In North Ōkārito, where there was no resident population prior to 2010, and very low densities after this, the released birds did not show any difference in HR selection to those released in South Ōkārito. Rowi released in the experimental years in North Ōkārito set up similar sized HRs of similar habitat quality (based on estimated relative invertebrate biomass), to those ONE rowi in South Ōkārito. This is despite higher quality habitat being available and unoccupied in North Ōkārito. Therefore the presence of resident conspecifics is unlikely to be driving the low quality habitat selection in rowi, and instead there may be other factors driving the behavioural movement response that leads to large low quality habitats being formed in both North and South Ōkārito.

The third explanation for the large home range observed in ONE rowi may be the age and life stage of these individuals, compared to that of the wild rowi in this study. There is little literature available on the age of first breeding for rowi, or in fact any species of kiwi in the wild (Robertson, 2004). A median age of first breeding has been estimated at 3.5 years for North Island brown kiwi (*Apteryx mantelii*), but this may be later in species such as rowi that have a tendency to remain in the parental territory for between two and five years (Robertson, 2004). One of the major limitations of this study is that for this nocturnal animal, only daytime location fixes were collected and analysed. This may result in an underrepresentation of locations, with fixes biased towards those areas suitable for nesting or roosting during the day (Kernohan et al., 2001). The nature of data collection for the wild rowi was such that it focused on those birds that were likely to be breeding. This skews the wild rowi data collection to those past the sub-adult phase, whereas data collection for ONE rowi included fixes obtained while release birds were still sub adults, not yet at the breeding stage of their life history. Adolescent animals may wander in search of a home range and during this time do not have what is considered a true home range (Burt, 1943). However the use of site fidelity as an indicator of home range infers that the random wanderings of an adolescent animal would be discounted from my analyses of HR. Instead of random wandering, it may be that the sub-adult stage animals have different energetic requirements to those making breeding attempts (Hawes, 1977). A larger HR prior to breeding may also be beneficial as it could increase the chances of encountering unpaired individuals of the opposite sex that are potential future mates.

A further explanation for the difference observed between wild rowi and ONE rowi HRs is the effect of prior experience on behaviour. HRs are thought to be representations of an animal’s exploitation of the information within its cognitive map (Spencer, 2012). Most descriptions and definitions of the cognitive map focus on spatial information, that is the encoding of geographic information via cognitive mapping abilities and spatial memory facilitated by the hippocampus (Powell & Mitchell, 2012). Translocation results in the spatial elements of the previous map having little use, but if other elements of memory are also important in behaviourally mediating movement activity, the impact of previous experiences may continue to have consequences. I therefore propose an additional thread to the theory of cognitive maps, in which the neurally encoded representation of an environment is augmented by the prior experience of an animal in relation to familiar individuals and social interactions. That is, not only do animals encode their geographic surroundings, but also their social landscape (Figure 5.5). Under this framework, ONE birds HR behaviour may also be influenced by prior experience, where resource acquisition and survival on the crèche island corresponded to maintaining a HR in close proximity to conspecifics (approx. density 1 bird/0.06 km^2). Often as many as 14 rowi were found sharing a burrow together on the crèche island (pers. obs.). This is very different from the natural setting of a juvenile and sub-adult rowi remaining in a parental territory that is fiercely defended from intrusions by other birds (Colbourne et al., 2005). The natural setting likely results in limited interaction with any individuals other than the immediate family group, whereas the setting of the crèche island provides an environment with adequate resources and insufficient competition that evokes increased social tolerance, which perhaps in turn offers benefits such as warmth and social cueing for good foraging patches. Furthermore this beneficial experience of social tolerance and close proximity could be the mechanism leading to HR selection of ONE birds in close proximity to one another, sharing resources rather than defending territories, which in turn leads to large HR areas to meet energetic requirements. It was not possible to investigate the level of HR overlap in either wild or ONE rowi as the data collection for each bird was temporally distinct, starting and finishing at different points in time, but this would be an interesting and important area for further investigation to understand how ONE might change behaviour.

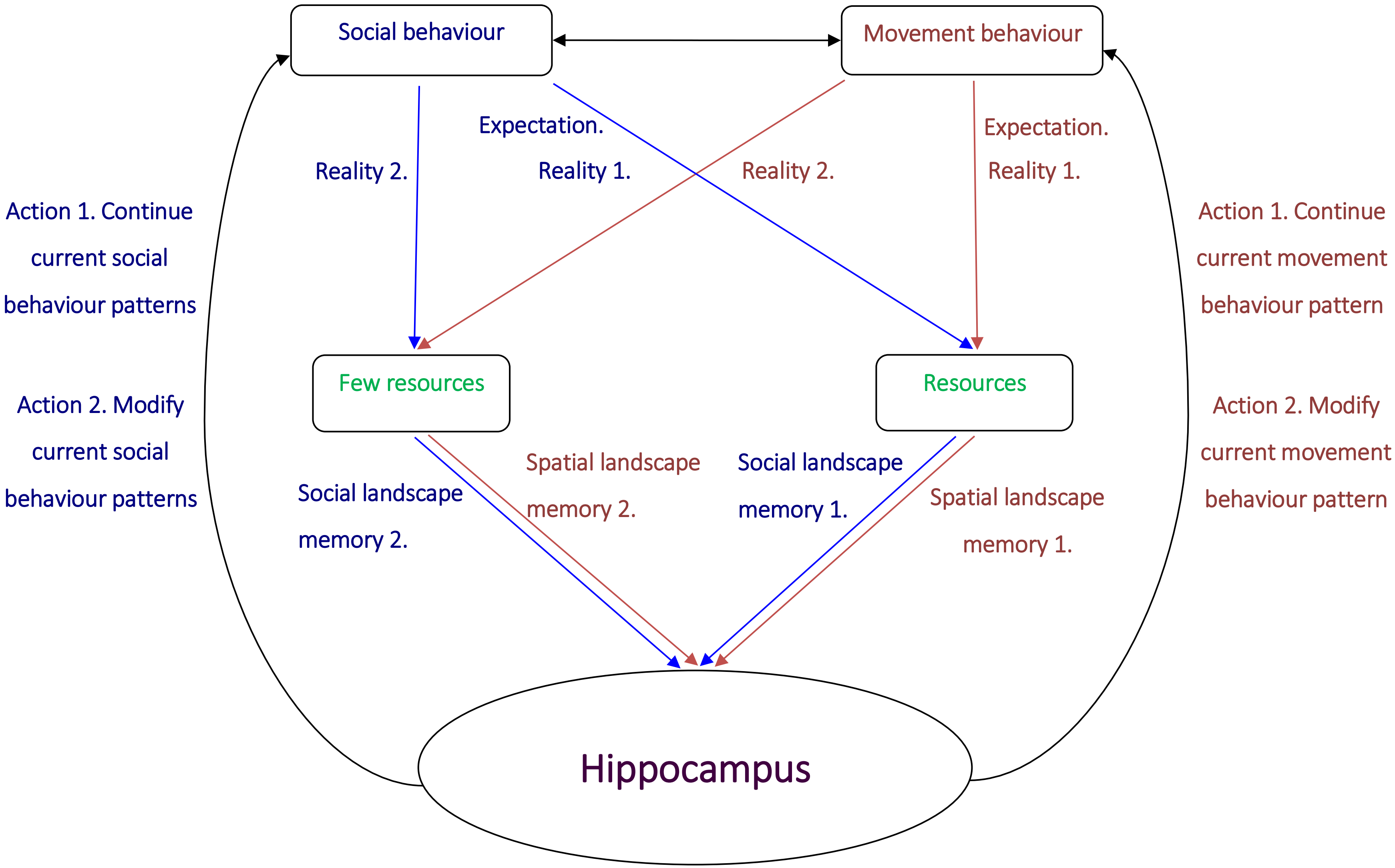

Figure 5.5. Diagram of expansion to current cognitive theory on HR behaviour and mapping. Information in red is included in current theory of cognitive maps, where expectations based on spatial knowledge motivates movement through a landscape, as described by Spencer (2012). Goal directed motivation leads to movement patterns based on expectations of sites and influenced by the internal state of the animal (hunger, thirst, fear etc.). In turn these movements lead to updated information and the formation of new memory, or bolstering of existing memory, which facilitates a feedback loop to the movement behaviours. Information in blue describes my addition to current theory, where social experience also contributed to expectancies about areas, and a similar feedback loop exists where productive social landscapes create memories that facilitate repetition of similar social behaviours.

5.4.2 What factors predict the size and habitat quality of an ONE rowi AoH?

The models that best described the area of a AoH, and also habitat quality of AoH included release group size. As group size increased, so did the AoH area and AoH habitat quality of individual ONE rowi. In a small release group, individual rowi may be more vulnerable to being forced into small areas of available habitat by more dominant resident conspecifics, whereas in a larger release group, if the ONE individuals are socially tolerant of one another, they may form a coalition whereby they hold a larger HRs of higher quality that overlap with one another and defended it from territorial wild conspecifics. It was not possible to document the level of territorial interactions between ONE and wild or within ONE rowi in this study, but this would be an interesting and informative area for future research to understand how ONE is affecting the social dynamics and spacing behaviour of rowi.

Rowi display long term site fidelity. Of the four wild birds for whom significant fidelity over the whole sampling period was not shown, three have one outlying fix that dramatically influence the locations of their centroids, and thus the mean squared distance of all real fixes from it. The fourth has a large number of fixes (n=20) over just four separate locations. This resulted in the step distance between many of the fixes being 0 m, and when simulated with the correlated random walks, it produced a cluster of simulated fixes not significantly dissimilar to the real fixes. These erroneous results demonstrate the limitations of this methodology, and highlight the need for a comprehensive understanding of the monitoring procedure implemented, and species behaviour when investigating home range behaviour.

5.4.3 Does time since release affect site fidelity and AoH size of ONE rowi?

There were no patterns to the acquisition of site fidelity over time in ONE rowi, but the size of within-year areas of habitation declined for the first four years, followed by a plateau at around 0.77 km^2. The lack of pattern in the site fidelity suggests that there may be several variables interacting to affect the movement behaviour of rowi post-release, which could include sex, release group size, annual variations in climate and subsequent resource availability, proximity of release site to resident conspecifics and reproductive status (whether the individual has formed a pair-bond or not). Many individuals had gaps in their monitoring where insufficient fixes were obtained to be able to estimate within-year site fidelity and AoI, so there was not sufficient data to investigate how the influence and interaction of such variables change over time, leading to different patterns among individuals. The pattern of decreasing AoI size over time to a plateau implies that different behaviour patterns or environmental requirements occur during the first few years compared to the later years following release. Factors affecting this may include a change in reproductive status leading to different habitat requirements, alteration in relative dominance within the social landscape leading to the ability to hold better quality habitat, or simply a change in the location where the bird has its AoH, having had the chance to prospect for and select the best quality available habitat over the preceding years, or a combination of those factors. Additionally, if prior social landscape does influence behaviour and movement decisions following translocation, this behaviour and the corresponding movement activity may continue until memory decay occurs or new memories and expectations are formed based on recent experience (Spencer, 2012). The pattern observed here may reflect the decay of former expectations regarding social landscape and resource availability, which would persist until the incomplete information regarding the geographic component of the habitat is integrated into their cognitive map. The amount of time this takes would depend on the severity of effects of continuing the previous behaviour patterns, and may be influenced by other physiological changes such as breeding status.

5.4.4 Inferences and limitations

When using KDEs to estimate home range, long duration studies may be necessary to accurately characterize long-term space use, especially in cases where location data may be highly correlated (Fieberg, 2007). This study included data collected over a 21 year period. There is no definitive estimate of rowi lifespan, and estimates in the literature range from 40 to 100 years. I suggest the evidence presented here provided a sufficient timeframe to be able to draw conclusions on the lifetime home range behaviour of wild rowi.

The number of location fixes is often thought to be the most important factor when estimating home range, more so than maintaining a statistically independent time interval between sampling occasions (Kernohan et al., 2001; Swihart & Slade, 1997). Meeting requirements of independence or asymptotic requirements while not addressing adequate representation over the temporal scale can also lead to biases in home range estimates (Fieberg, 2007; Laver & Kelly, 2008; Otis & White, 1999). If an effect of sample size were present, increasing the number of fixes by extending duration of the sampling period (as opposed to increasing sampling intensity), would likely lead to larger HR estimates (Fieberg, 2007; Springer, 1982). I therefore decided to include data on only those birds that displayed site fidelity and reached asymptote in the analysis of HR size and treat HR sizes reported here as conservative estimates of rowi HR. Even with this consideration in mind, the rowi HR reported here were larger than that reported for any other species of kiwi, which could imply that Ōkārito had low resource availability in general, or that rowi had a higher resource requirement than other kiwi species.

5.4.5 Implications and areas for further research

Resource limitations within a habitat for reintroduced or restocked are often overlooked, and the question of whether wild populations are pushed beyond their carrying capacity by releases is rarely addressed (Champagnon et al., 2012). This study therefore demonstrates the continuing need to assess the carrying capacity of South Ōkārito, and the benefit of exploring North Ōkārito as a release site location for rowi. I recommend that investigation into the benefit of expanding of ONE into North Ōkārito, or other suitable sites within the historic range, on a permanent basis continues. If North Ōkārito is maintained as an extension to the current rowi sanctuary, the cost of any future pest control operations increases dramatically compared to maintain the whole Ōkārito population within South Ōkārito. For this reason there must be solid evidence that North Ōkārito offers benefits to the long term viability of the rowi population before further releases occur there. In particular, the impact of population density on reproductive success of rowi released during this study should be compared across North and South Ōkārito.

In addition to documenting the first estimates of rowi HR size, habitat selection and the impact of ONE on these, this study has led to an expansion of current HR theory, highlighting a previously undescribed potential mechanism driving HR behaviour, namely the incorporation of prior social landscape into the cognitive map. This is an important area of consideration, especially for conservation translocation practices that alter early rearing conditions. If confirmed, alterations in behaviour as a result of this mechanism could have serious negative long term consequences for the outcome of translocations, potentially leading to the formation of ecological traps. I would recommend further research focus on the impact of social landscape on the cognitive map and HR selection following translocation.

6 Summary and concluding discussion on factors affecting translocation success

Translocations are a key component of many conservation programmes, and are increasingly being used, yet a great many fail to achieve their goals or optimise conservation outcomes (Fischer & Lindenmayer, 2000; Mathews et al., 2005). The overarching aim of this study was to expand the current knowledge on factors influencing translocation success in order to improve conservation outcomes. I achieved this by providing new evidence and knowledge of behavioural mechanisms driving translocation success. I used rowi (*Apteryx rowi*) as a model of translocation management and investigated impacts of current conservation management practices on rowi behaviour and translocation success, using a series of behavioural studies. This thesis includes the most detailed study to date study on factors affecting translocation success of rowi and the first study of rowi home range behaviour, and provides new knowledge applicable to other conservation translocations and relevant to the wider literature on translocation success. Release season and release group size were found to be likely to influence post-release survival, with highest survival in spring, and for large release groups of four or more birds per release site. Maximum dispersal distance was affected by the release site (North or South Ōkārito), and the interaction of release site and the estimated invertebrate biomass at the release location. Translocated rowi had larger, lower quality home ranges than wild rowi. The effects of early rearing experience are proposed as a key factor influencing the behaviour of translocated rowi.

6.1 Review of results

6.1.1 Release group size affects post-release survival of rowi (*Apteryx rowi*)

In Chapter 2 I investigated elements of the release protocol that have an effect on the success of rowi reintroductions, with the aim of analysing and maximising the efficiency of rowi conservation management. Highlighting the particular elements of the procedures that affect behaviours and influence the outcome of translocation enables these areas to be targeted for modification in order to create the most effective management practice with optimal results, and contributes to the wider literature on translocation success. I used a combination of analyses of data from an historic database and a series of experimental releases and intensive post-release monitoring to measure reintroduction success as survival following release. I found the critical period of increased mortality following release was 90 days for rowi. I then went on to investigate which elements of the release affected survival during this critical period. The historic data analysed was collected over many years with inconsistent methodology and it is important to note that it was not possible to fully separate the effects of the variables investigated. Patterns in the historic data suggested that season may have a significant influence on post-release survival. Spring and Summer releases led to significantly higher post-release survival than Winter or Autumn releases, however releases which occurred in Autumn and Winter also involved small release groups, which may have influenced this result. The sex of release individuals did not have any effect on post-release survival. Flaws in the design of the experimental releases occurred due to a range of circumstances outside of the control of this study. As a result the range of variables tested were not fully crossed across all years of the experiment. Therefore it was not possible to account for any potentially confounding interaction effects in the analysis of year effects, nor was it possible to account for any potential effect of release year in the analyses of other variables. Subsequently, results presented here highlight patterns of likely effects of variables on translocation success, and provide a good starting point for future research, but are not conclusive evidence of effects. The existing population density of release site appeared to have no effect on post-release survival: rowi released in North Ōkārito which had no identifiable population of rowi prior to the 2010 experimental release, had a similar survival probability to those released in South Ōkārito with a population density of approximately one rowi per 28 ha. Rowi released in groups of three or less had significantly lower survival than those released in groups of four or more. The occurrence of a 1080 predator control operation appeared to show a non-significant trend towards increasing the survival probability of released rowi when combined with large release groups. The use of 1080 operation alone resulted in a non-significant positive effect on rowi survival.

6.1.2 Quantifying rowi habitat quality in Ōkārito forest

In Chapter 3 I investigated biomass of invertebrates in rowi habitat and analysed corresponding habitat variables to establish a predictive model for relative invertebrate biomass as a proxy for habitat quality across the rowi range. Habitat sampling showed no significant difference between mean invertebrate biomass collected in North compared to South Ōkārito, or in 2010 compared to 2012. Factors found to influence invertebrate biomass were: cumulative rainfall, minimum pH, aspect and soil type based on land topography. These variables were biologically relevant to the biomass of invertebrates. The variables selected provided a reasonably accurate model, accounting for 51% of the variation in invertebrate biomass and therefore the GIS layer produced using the model was considered a representative depiction of invertebrate biomass throughout Ōkārito.

I used the predictive model to produce a GIS layer and map of relative habitat quality throughout the study area, which I employed in subsequent chapters to address questions regarding the selection of habitat quality within home ranges of reintroduced rowi, as well as to investigate the effects of release site habitat quality on translocation success. It should be noted that food availability is just one aspect that drives habitat quality, therefore the ability to draw robust conclusions using the food based habitat quality map alone is limited. Further work to identify additional elements of the environment which impact habitat quality for rowi is recommended.

6.1.3 Investigation of factors affecting dispersal and association rates of reintroduced rowi

In Chapter 4, I investigated impacts of release strategy variables on dispersal distance and association rates following release. Variables included were sex of released rowi, release group size, release location (North or South Ōkārito) and habitat quality at release location (where release location refers to the specific point of release within the release site). Post release detection rates were low, undermining the ability to draw robust conclusions from the data. I found no significant difference between the maximum dispersal distances of rowi released in small compared with large release groups. Release site had an effect on maximum dispersal distance following release, with rowi released in South Ōkārito dispersing significantly further than those released in North Ōkārito. The most parsimonious linear mixed effects model used to describe factors affecting maximum dispersal distance included release site (North or South Ōkārito), the interaction between release site (North or South Ōkārito), and estimated biomass at the release location, with release group ID as a random variable. There was no significant difference between the rate of association of rowi released in small release groups compared with those released in large release groups. Those in large release groups did have a higher mean number of location fixes than those from small release groups. The sex composition of dyads had a significant effect on the rate of association between release rowi, with female-female dyads having the highest association rates, and female – male dyads the lowest.

6.1.4 Conservation management affects home range behaviour of an endangered kiwi

Chapter 5 investigated factors affecting rowi home range, particularly those related to the operation nest egg (ONE) programme. I identified factors that influenced rowi movement behaviour and spatial ecology following translocation and proposed a new branch to the theory of home range behaviour and cognitive mapping. ONE rowi had significantly larger and lower quality home ranges than wild conspecifics. I investigated the size and quality of the area of habitation (AoH) of rowi following release and prior to HR formation. The only variable included in the most parsimonious predictive model of size of an ONE rowi area of habitation (AoH) was release group size, with rowi released in larger groups generally having larger AoHs. In the predictive model of rowi area of habitation habitat quality, release group size was again the only variable included. As release group size increased, so did the area and habitat quality of individual ONE rowi area of habitation. There was no clear pattern of changing site fidelity over time since release, however the size of within-year AoHs declined for the first four years, followed by a plateau at around 0.77 km^2.

6.2 Discussion

Management practices can benefit from increased knowledge and understanding of the impact of translocation practices on post-release behaviour. Protocols can be modified to use elements that affect behavioural mechanisms. In this way post-release behaviour could be manipulated to produce outcomes favourable to the long term goals of the conservation management, or at least to prevent the continuation of processes that are detrimental to the long term population viability of the species. One widely used technique that demonstrates this is acoustic anchoring, where if the translocated species is known to employ conspecific cueing to assess habitat suitability, it is possible to take advantage of this (Ahlering et al., 2006; Bradley et al., 2011; Kress, 1983). Playback of calls or placement of dummies can be used to anchor the translocated individuals to the chosen release site, thus preventing dispersal that might reduce the likelihood of successful population establishment (Arnold et al., 2011; Molles et al., 2008).

This study has shown that it may be possible to manipulate release group size to improve post-release survival. It was not possible to identify the mechanism driving this, although impacts on dispersal distance and association rates were not shown to be related to release group size in this study. However the sample size and length of the observations period may not have been sufficient to pick up such an effect and further investigation into causes of differential survival rates for different release group sizes is recommended. Release group size also appears to have impacts on home range size and habitat quality. Further research is required to identify the mechanisms leading to this effect. The identification of release group size as a key variable nonetheless has significant impact for rowi management, and is also relevant to other species managed through translocations.

This study identified possible post-release effects that would indicate that the early rearing conditions of ONE have multi-faceted impacts on post-release behaviour. This provides further evidence that management practices can affect the behaviour of animals born or raised in non-natural conditions for conservation, which is an area of concern in current management of rowi and other species (Kraaijeveld-Smit et al., 2006; Salvanes et al., 2013; Snyder et al., 1996; Snyder et al., 2003), as the long term effects of such behaviour changes often remain unknown (Colbourne et al., 2005; Snyder et al., 2003). In cases where long term effects of non-natural rearing conditions have been studied, the outcome is often a negative effect on the social and behavioural competency of animals (Snyder et al., 2003). Species evolve phenotypic traits in response to the requirements of their environment, altering these therefore has the potential to have severe negative impacts on long term population viability, thus undermining the benefits of undertaking the conservation management. Raising animals in non-natural settings can have impacts at an individual level, such as maladaptation in foraging behaviour, e.g. black footed ferrets, (*Mustela nigripes)* (Biggins et al., 1999), unsuitable predator responses, e.g. Siberian polecats (*Mustela eversmanni*) (Miller et al., 1990) and quokka (*Setonix brachyurus*) (Short et al., 1992), or unsuccessful offspring care , e.g. chimpanzees (*Pan troglodytes*) (Brent et al., 1996). In addition, rearing in the absence of source population conspecifics may lead to population level divergence between the source and backup population, such as cultural variation or local song diversity (Laiolo, 2010; Laiolo & Jovani, 2007; Valderrama et al., 2013). These types of changes caused by the translocation process are less immediately obvious than individual level effects, but may have long term impacts on the success of the translocation. A study on North Island kōkako (*Callaeas wilsoni*) translocations found post-release assortative pairing (like with like), that is, birds demonstrated a preference for mates from the same source population exhibiting similar vocal dialects (Bradley et al., 2013), a phenomenon that can hinder the genetic rescue of populations. Wild rowi at Ōkārito are asocial and highly territorial, while ONE rowi on Motuara Island are socially tolerant. Back-up insurance populations of ONE rowi are being formed on offshore islands to safeguard the species from catastrophic stochastic events such as disease or severe predation events (e.g. stray dogs have caused localised extinctions in other kiwi species (Pierce & Sporle, 1997)). Currently, one population comprising of 20 ONE rowi translocated directly from Motuara Island has been formed on Mana Island, off the west coast of the North Island, with other populations planned. Management plans state that any rowi chicks hatched on Mana Island will be transferred back to Ōkārito. It is important to ensure that translocated individuals being used in population augmentation possess cultural norms of the natives, whether these cultures be ecologically adaptive to the environment or socially adaptive (Whitehead, 2010). Assortative pairing within ONE rowi or delayed pairing due to social and cultural incompatibility would reduce the conservation benefits of ONE. For this reason, it is important to ensure that the long term consequences of translocation processes continue to be monitored.

Current theory on cognitive mapping and home range behaviour focuses on spatial mapping and memory of resource locations (Spencer, 2012). Situations where the release environment is novel, as with translocations, provide the opportunity to investigate the underpinning mechanisms of home range and movement behaviour beyond the current theoretical foundations of spatial memory and cognitive mapping. By monitoring the home range behaviour resulting from the translocation of rowi held in a non-natural social situation, this research has highlighted the potential impact of prior social experience and social memory on cognitive mapping and home range establishment. I theorise that while knowledge of the physical landscape is lacking, memory of social landscapes and familiar individuals may be relied upon during movement decisions. This innovative approach has potential to be a particularly valuable expansion to current home range/cognitive mapping theory, and warrants further exploration. The inclusion of prior social experience in the cognitive processes determining home range behaviour would further highlight the importance of the consideration of impacts of early rearing environment on animals reared in non-natural situations for conservation.

6.3 Management recommendations

Action 8.1 in the 2008 Kiwi Recovery Plan (2008 – 2018) specifies that while Operation Nest Egg procedure is recommended to be increased, monitoring the effects of this on both population structure and behaviour throughout the term of the plan is essential. I agree that monitoring population structure and impacts of ONE on behaviour is essential, and should be ongoing. In addition, I propose the following management recommendations:

- Rowi releases should take place in groups of four or more birds at a single release location. This may help ensure maximum survival of released rowi.
- Additional work should be undertaken to address the uncertainties remaining from this study and allow firm conclusions to be drawn on the impact of release group size on post release survival of rowi.
- Data should continue to be collected on the release group demographics and survival of released rowi, and optimal group size reassessed accordingly.
- The survival of released birds should be monitored at least up to 90 days post-release. This is the critical period for rowi and the period on which further analysis of release group success relative to initial survival should be based.
- New populations of rowi being founded on predator free islands should include a mix of ONE and wild rowi to minimise the risk of creating behaviourally divergent and incompatible populations.

- Any rowi hatched in new populations on predator free islands should remain on the island until they naturally disperse from their parental territory, at which point they can remain on the island or be translocated to Ōkārito or other sites as required by the current management plan. This will help to reduce any long term negative effects of non-natural early rearing conditions permeating throughout the populations of rowi.
- The breeding success of rowi in North Ōkārito should be monitored closely until at least 2024, which would provide five years of breeding data beyond the current mean time to breeding following release. This will allow comparison with the South Ōkārito population that will shed light on whether South Ōkārito is at or close to carrying capacity and whether future reintroductions should occur into North Ōkārito instead of only South Ōkārito.
- Further investigation into the carrying capacity and habitat quality of both South and North Ōkārito, and in any regions of former rowi habitat where reestablishment may be possible, is recommended. Despite the continued presence of rowi at Ōkārito, there may be more productive, higher quality habitat areas available for rowi conservation elsewhere in their former range.
- Information from genetic analyses of the rowi population (which are currently underway) should be incorporated into future rowi conservation planning to ensure good genetic representation of rowi throughout ONE, management of relatedness of individuals within release groups and reduction of inbreeding risks in populations. Inclusion of genetic factors in analyses of post-release survival and behaviour may provide further information on potential mechanisms with impacts on translocation success.

6.4 Recommendations for future research

My work has highlighted a number of avenues for further research with both theoretical and conservation implications in relation to behavioural mechanisms and translocation success. Specifically, I recommend future research addresses the following questions:

1) What is the optimal size of a release group for rowi?

In this thesis I experimentally tested the effects of varying release group sizes between small (two or three birds in a group), and large (four to six birds in a group). The separation of group sizes between three and four birds in a release group was based on results of the analysis of historic ONE data (Chapter 2). In the experiments I chose to include group sizes with a maximum of six birds, and to condense the groups into small or large due to the limitations of available rowi and the need to have a large enough sample sizes for results to be meaningful. Unfortunately there remains uncertainty from the results as variables were not fully crossed and therefore their effects were not able to be fully disentangled. To address this, it would be prudent to continue to conduct releases over a range of group sizes of four and more, and include data collection on other group demographics (for example, sex ratio, physiological morphometrics of release birds, genetic data on relatedness/inbreeding coefficients of individuals). Analysis of the survival of rowi in specific group sizes will help to identify the optimal group size and compositions.

2) What is the mechanism that leads to higher survival for rowi released in large compared to small release groups?

In Chapter 2, I suggest that increased social tolerance and prior experience of successful conspecific cueing, coupled with reduction in post-release stress response among rowi released in larger groups are the most likely mechanisms causing the density-dependent effect seen in the release groups. Further research is required to investigate this and other possible mechanisms leading to improved survival of large release groups. Understanding the cause of higher survival in large release groups will enable managers to manipulate the release strategy to ensure optimal results, particularly since release group size may also affect home range or habitat selection behaviour.

3) What effect does level of familiarity with release conspecifics have on release group success and home range behaviour?

Other studies have shown that familiarity with release conspecifics can reduce stress and lower the post-release dispersal response, leading to higher survival (Shier & Swaisgood, 2012). To date there has been no record of which part of Motuara Island birds are collected from prior to their translocation to Ōkārito, nor any genetic data on relatedness of ONE individuals. Data collection of the location and proximity to other birds, along with an experimental test of how varying levels of familiarity (i.e. all collected from the same burrow box/neighbouring boxes vs. collected from different ends of the island), and relatedness, would allow analyses of how these factors affect post-release survival, home range behaviour and fitness.

4) What factors influence association rates among ONE birds and between ONE and wild rowi?

Understanding the dynamics of interactions among ONE rowi and between ONE and wild rowi could lead to improvements in management techniques in order to maximise recruitment of ONE rowi into the breeding population. I suggest that as technology improves and becomes more affordable, proximity loggers inside rowi transmitters would provide a wealth of knowledge and allow far more complex understanding of rowi social behaviour. The effects of management techniques on post-release association and interaction rates could provide knowledge on mechanisms that it may be possible to manipulate in order to increase ONE-wild rowi pairings.

5) How does resource availability, in particular invertebrate density, on Motuara compare with Ōkārito? And how does Ōkārito compare with other areas of the rowi former range, and current ranges of other kiwi species?

To date there has been no quantifiable study published of relative habitat quality at Ōkārito compared with Motuara or any other rowi sites (Bluemine Island, Allports Island and Mana Island), or areas of their former range, or ranges of other kiwi species. An investigation into resource availability relative to other sites, and a comparison with sites where other kiwi species are present, would provide evidence for what mechanisms drive the current social organisation of rowi. A comparison with Motuara Island, the crèche island where ONE rowi are currently reared, would provide evidence of resource availability which may be leading to the variation in spatial organisation of rowi at the two sites.

6) Does the size and habitat quality of ONE rowi impact on their reproductive success? What other variables influence reproductive success or failure in ONE and wild rowi?

In Chapter 5, I found that ONE rowi had larger, lower quality home ranges than wild rowi. The impact of this on breeding behaviour and reproductive success is fundamental in establishing the long term impacts of ONE on the Ōkārito rowi population viability. In combination with ongoing analysis of breeding success of rowi released into North Ōkārito, and incorporation of genetic analysis of ONE rowi and the whole rowi population, analyses of the factors affecting breeding success are essential to ensuring the future success of the rowi.

7) How does prior social experience affect home range behaviour? Is the social landscape a valid aspect of the cognitive map?

This area of theory will require some innovative experimental approaches to explore. I suggest that it would be possible to manipulate translocations so that post-release home range behaviour of individuals with experience of a natural early rearing social situation (i.e., island born rowi) could be compared to that of rowi which have experienced the non-natural ONE process of early rearing on a crèche island with same age conspecifics.

6.5 Summary

In conclusion, translocations can be an effective conservation tool, and ONE has proven successful at increasing rowi numbers, but as with any conservation management process, comprehensive monitoring must be undertaken, and followed up by ongoing analysis of processes and techniques to ensure that it is being conducted in the most efficient and effective way possible. There remains much to learn about the behavioural mechanisms affecting translocation success and this study has shown the application of behavioural studies within conservation monitoring can provide insight into this. In particular, the findings from this study underscore the need for careful consideration of the impact of early rearing environment on mechanisms affecting the success of translocations, an area which is often overlooked by conservation managers.

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8 Appendix 1 : Quantifying triangulation errors

8.1 Introduction

Triangulation of very high frequency (VHF) radio telemetry signals provides conservation researches with a valuable tool for estimating the location of multiple animals at relatively low cost (Girard et al., 2006). Triangulating signals is often preferential to tracking in close to an animal to confirm its location, as it reduces observer effects by eliminating disturbance to the animal, and greatly reduces the amount of walking involved, thus increasing monitoring efficiency (Mech & Barber, 2002). To conduct triangulations, signal taking "stations" are selected at appropriate sites around the study area, where telemetry signals can be listened to and the bearing and strength recorded. Stations can be in fixed locations or random sites chosen whenever a signal is heard, as long as the exact location of the "station" is recorded along with the signal information (White & Garrott, 1990). Multiple signals for an individual taken from separate stations can then be plotted onto a map of the study area, either by hand or using a programme such as LOCATE III (Pacer Computing), or Location Of A Signal (LOAS), (Ecological Software Solutions), to produce an estimate of the animal's location based on the convergence point of the signals.

Triangulation does not provide an exact location, only an estimate of the true position of the animal, since triangulations are affected by sampling errors and bias (Millspaugh & Marzluff, 2001). Due to the nature of radio signals, interference from vegetation or terrain is common, and signal bounce can be caused by slopes, bluffs and large bodies of water (Lee et al., 1985). The effect of these types of sampling errors must be taken into consideration, and the amount of error quantified to allow a decision on whether triangulation is a suitable tool for use in any given environment, and this quantification of accuracy and precision should be reported within the study (Lee et al., 1985; Saltz, 1994; Withey et al., 2001; Zimmerman, 1990). Precision of a triangulation system describes how consistent the results of triangulation are using the chosen method. This is reported as the standard deviation of bearing errors, where bearing error is the difference between the estimated bearing and the true bearing (Saltz, 1994; Withey et al., 2001; Zimmerman, 1990). Accuracy of the system measures how close the triangulated location estimate is to the actual location of the transmitter. This is reported as the mean linear error between the actual and reported location (Withey et al., 2001). Many studies do not report the error and variability associated with their results, and of those that do report accuracy and precision of their system, many fail to report the method used to calculate it (Bartolommei et al., 2012; Saltz, 1994).

This paper outlines the methods and findings of an investigation into the suitability of triangulation as a technique for estimating kiwi (*Apteryx spp.)* locations as part of a larger study on the rarest species of kiwi, rowi (*A. rowi*). I chose to triangulate radio telemetry signals in order to increase the amount of data collected in a short time frame and reduce any observer effects on the study animals. I conducted a beacon study in the study site to quantify the error of telemetry triangulations and to ensure that triangulation was a suitable technique for use in the study area. Since rowi are nocturnal, it was possible to take multiple azimuths for an individual animal over the course of a single day, to provide an estimate of its resting location, rather than needing to reduce the timeframe for getting signals due to animal movement. Following the advice of Withey et al (2001), I will provide measurements of both the precision and accuracy of triangulations within the field site. The level of error acceptable within any study will depend on the scale relevant to the study species and study aims. In the case of rowi and this study, wild rowi home ranges have a mean size of 0.99 km^2 and ONE rowi have a mean home range of 2.35 km^2 (Chapter 6), and conspecific associations are being considered within a 1.5 km distance (Chapter 5), so it was decided that error ellipses less than 0.25 km^2 would be an acceptable level of accuracy.

8.2 Methods

Study area

This study took place in the North Ōkārito area of the Westland Tai Poutini National Park, New Zealand. The topography of the area comprised a range of low lying forest and swamps, sloping hills and ridgelines with several high points ranging from 134 m to 347 m elevation. Vegetation in the area was mainly podocarp rātā forest. The area was selectively logged in the past, resulting in a series of logging tracks throughout the site, and regenerating vegetation. The forest is historic rowi habitat, that borders on the range of the current extant rowi population. Thirty five rowi were released into this area between 2010 and 2011 as part of a wider study into current kiwi management practices (Chapter 2).

I conducted a combination of a standard beacon study (White & Garrott, 1990), with test transmitters at known locations, and a modified beacon study (Millspaugh & Marzluff, 2001) using fixes of rowi gained through telemetry and triangulation compared with locations of the same rowi on the same day, found by homing. Seventeen transmitters (Sirtrack Ltd) were placed throughout the study site by a field assistant at locations selected to represent the range of possible locations of rowi within the area. Locations included a range of elevations, aspects and habitat types ranging from swamps to slopes and ridgelines. Transmitters were placed between approximately 2cm and 8cm above the ground to represent the position of a transmitter on a resting kiwi's leg. The locations of transmitters were recorded using a handheld Garmin GPSMAP 62s Global Positioning System (GPS) unit (Garmin International Inc.) and not disclosed to the observer.

The observer took bearings of the transmitters in a replication of the conditions that would occur during the rowi triangulation study. Azimuths from the station to the transmitter were taken from multiple stations throughout the study site using a Yagi antenna (Sirtrack Ltd) and a Sika receiver (Biotrack Ltd). The locations of the listening stations were recorded using a handheld Garmin GPSMAP 62s GPS unit. Bearings were taken from as many stations as possible. Azimuths and station coordinates were entered into the program LOCATE III (Pacer Computing). Haskell and Ballard (2007) found that the subjective ranking of confidence in accuracy of a signal was correlated with bearing error. Therefore the observer also recorded a subjective confidence in the signal on a scale of one to five, where one meant the observer was certain the signal is coming from the direction of the bearing taken, and five meant the signal could hardly be heard or was equally loud in multiple directions, and deciding the exact direction was barely possible. When inputting the bearings into LOCATE III, if a situation arose where multiple bearings had been taken for a transmitter, but one or more of these bearings caused the programme to be unable to triangulate the location due to widely diverging bearings, these subjective observations were used to help decide which signals to discount from the triangulation.

LOCATE III calculated an estimated triangulated location for each transmitter based on the data entered. Results from the beacons study were combined with results of the modified beacon study of rowi locations to provide a larger sample (n=22) of triangulated locations and corresponding known locations for estimating error. Estimates of the linear error were calculated using the distance between triangulated locations and actual locations, and an estimate of the bearing bias was calculated using the mean difference in recorded azimuth and true azimuth from the station to the transmitter. The standard deviation of the bearing bias is the bearing error.

8.3 Results

Estimates of the mean linear error, calculated using the distance between triangulated locations and actual locations was 331 m (n= 22, SD = 256). Estimate of the bearing bias as calculated from the mean difference in recorded azimuth and true azimuth from the station to the transmitter was 39° (n= 69, CI 95% = 13). The precision of the system within this study site, calculated as the standard deviation of the bearing bias was 54°.

Distance between station and transmitter was significantly negatively correlated with location error, (r=-0.262, n=69, p=0.03 Pearson's correlation two tailed) (Figure 4.1). As distance between the station and the transmitter increased, bearing precision significantly increased.

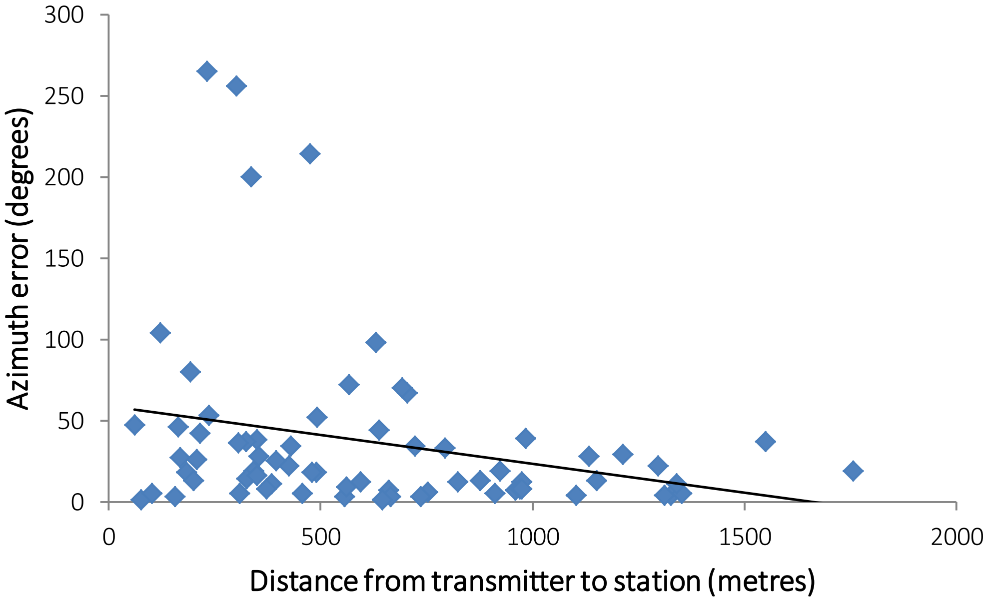

Figure 4.1. Azimuth error over increasing distance from transmitter to station. There was a significant negative relationship between error and distance, meaning that as distance between transmitter and station increases, azimuth error decreased. Black line is a trend line.

8.4 Discussion

Having assessed the suitability of the North Ōkārito site for radio telemetry triangulations, I found the errors associated with this technique in the site to be within acceptable levels for the purposes of investigating rowi movement behaviour. The negative correlation between distance from transmitter to station and location estimate error was contrary to the findings of other similar studies (Bartolommei et al., 2012; Springer, 1979). This was likely to have occurred because high points happened to be predominantly spaced around the edge of the study area. Therefore, the increasing distance from the transmitters meant the station was more likely to be on a high point within the study area, and the signal bounce from the transmitter to this point may have been reduced by the elevation of the station. This is an important finding since guidelines given by other studies suggest making efforts to minimise the distance from the subject to the station, which if followed in this study, would result in less accurate location estimates. These findings emphasise the need for every study site where radio telemetry triangulations are being used to conduct a beacon study to assess site suitability and limitations, or at least measures of error, accuracy and precision.

Management implications

Based on these findings, triangulations of transmitter signals will be used to gather data on rowi locations in North Ōkārito in future studies. The bearing error measurement calculated from the beacon study will be used in a Maximum Likelihood Estimator (MLE) function of the programme LOCATE III to create error ellipses for subsequent triangulations within the study site. The smaller the error ellipse, the more confidence can be assigned to the estimated location. In order to reduce the impact of telemetry error on study accuracy, future studies on rowi at this site should only include fixes calculated to have an error ellipse of less than 250,000m^2.

9 Appendix 2 : Summary of data used in spatial ecology and home range analysis

Table 9.1 Summary of data from Wild rowi used to calculate home range metrics.

ID number	Name	No. of fixes	Total days monitored	Max days between fixes	Mean days between fixes	No. of fixes to reach asymptote	P value of site fidelity displayed	Area of HR[a].	3D area of HR[a].	Est Biomass of HR[a].
24	Colin	206	10575	5129	51.35	58	<0.005	0.733	0.767	159.101
46	Houdini	238	5647	285	23.748	46	<0.005	1.143	1.208	266.91
4	Arti	86	3341	325	38.884	46	<0.005	1.39	1.437	166.307
56	Kermit	79	4610	2229	58.354	46	<0.005	0.779	0.808	111.411
34	Ebony	90	2785	228	30.978	43	<0.005	0.477	0.515	495.412
94	Tom	93	4511	741	48.516	40	<0.005	0.528	0.528	36.042
10	Blanchard	82	3254	370	39.659	40	<0.005	1.612	1.683	193.845
90	Steinieblue	161	4836	531	30.062	37	<0.005	0.978	1.031	163.397
1	Aloicious	55	3224	939	58.618	37	<0.005	1.466	1.558	237.753
12	Boris	178	5723	1763	32.169	34	<0.005	1.163	1.203	273.705
62	Muhammed	71	3541	366	49.887	34	<0.005	0.841	0.875	216.673
22	Chris	145	3125	132	21.559	31	<0.005	0.972	1.017	52.219
47	Hypotenuse	75	2854	210	38.08	31	<0.005	0.912	0.995	156.111
13	Borise	70	2057	449	29.386	31	<0.005	0.451	0.464	251.921
14	Bradwell	63	4645	702	73.73	31	<0.005	1.271	1.295	171.764
61	Mr Sumo	51	6000	5087	117.647	31	<0.005	2.173	2.239	229.726

ID number	Name	No. of fixes	Total days monitored	Max days between fixes	Mean days between fixes	No. of fixes to reach asymptote	P value of site fidelity displayed	Area of HR^{a}.	3D area of HR^{a}.	Est Biomass of HR^{a}.
11	Bob	42	1320	402	31.405	31	<0.005	0.637	0.68	303.536
36	Energizer	123	4783	384	38.894	28	<0.005	1.046	1.073	273.448
76	Rob	151	5100	381	33.755	25	<0.005	0.743	0.77	297.439
53	John	107	4132	1341	38.617	25	<0.005	0.583	0.623	106.083
84	Skinny	58	4022	1788	69.379	25	<0.005	3.894	4.047	196.5
66	Norman	56	4687	815	83.696	25	<0.005	0.852	0.874	323.869
73	Ralph	161	3088	140	19.193	22	<0.005	1.475	1.513	135.415
89	Starsky	153	4215	324	27.575	22	<0.005	0.658	0.659	34.357
43	Hazza	138	3570	319	25.862	22	<0.005	0.734	0.829	253.465
31	Dick	133	3660	398	27.541	22	<0.005	0.979	1.077	119.383
69	Poacher	106	3927	795	37.066	22	<0.005	0.596	0.619	193.088
75	Redband	102	3521	380	34.539	22	<0.005	1.338	1.398	141.562
80	s	73	2491	298	34.137	22	<0.005	1.652	1.706	248.191
85	Sneak	72	5907	2516	82.042	22	<0.005	0.679	0.679	48.123
82	Scooter	65	2132	168	32.831	22	<0.005	1.368	1.4	233.667
20	Charlie	59	3554	434	60.254	22	<0.005	0.726	0.786	526.798
79	Rupert	50	6181	3615	123.64	22	<0.005	0.83	0.862	182.302
98	Vinnie	44	1706	225	38.795	22	<0.005	1.278	1.28	70.175
40	Gertrude	44	967	509	22.023	22	<0.005	0.811	0.839	116.226
27	Dalcara	43	908	110	21.14	22	<0.005	1.798	1.859	155.186
67	Ohdub	37	3535	2290	95.568	22	<0.005	0.599	0.628	255.408
23	Clyde	35	2541	1326	72.629	22	<0.005	1.015	1.046	248.575
38	George	162	3390	517	20.951	20	<0.005	0.564	0.596	239.905
54	Johnny	32	1270	265	39.688	20	<0.005	0.603	0.646	182.438

ID number	Name	No. of fixes	Total days monitored	Max days between fixes	Mean days between fixes	No. of fixes to reach asymptote	P value of site fidelity displayed	Area of HR^a.	3D area of HR^a.	Est Biomass of HR^a.
48	Jack	270	5927	567	21.967	NR	0.074			
74	Rambo	76	3941	407	51.855	NR	0.271			
42	Grace	55	1805	365	32.818	NR	<0.005			
16	Callum	52	4984	1443	95.846	NR	<0.005			
100	Winston	51	1520	409	29.784	NR	<0.005			
97	Trevor	44	4332	1722	98.477	NR	<0.005			
19	Charger	43	3602	787	83.767	NR	<0.005			
5	Bart	39	1077	131	27.59	NR	0.095			
60	Mildred	35	1905	682	54.429	NR	<0.005			
30	Dibble	34	3371	866	99.147	NR	<0.005			
63	Mystery	33	3759	889	113.939	NR	<0.005			
18	Carlos	33	879	206	26.636	NR	<0.005			
50	Jenny	32	3312	2208	103.5	NR	<0.005			
25	Crumpy	31	2935	2431	94.677	NR	<0.005			
57	Kev	31	4911	3721	158.419	NR	<0.005			
78	Roscoe	28	2786	841	99.536	NR	<0.005			
87	Snufflupagus	28	1617	569	57.786	NR	<0.005			
7	Becky	28	355	63	12.679	NR	<0.005			
102	Xavier	27	568	125	21.037	NR	<0.005			
64	Namu	24	2949	904	122.792	NR	<0.005			
65	Nanananana	22	4035	1085	183.455	NR	<0.005			
96	Toy Boy	22	486	112	22.091	NR	<0.005			
33	Doris	21	3635	1482	173.048	NR	<0.005			
2	Anemone	21	3772	3182	179.667	NR	<0.005			

ID number	Name	No. of fixes	Total days monitored	Max days between fixes	Mean days between fixes	No. of fixes to reach asymptote	P value of site fidelity displayed	Area of HR[a].	3D area of HR[a].	Est Biomass of HR[a].
55	Kai	21	1153	661	55.048	NR	<0.005			
92	Three-pin	20	4899	2511	244.95	NR	0.025			
95	Totara	20	505	146	25.25	NR	<0.005			
99	Willy	20	1745	1537	87.25	NR	0.078			
	MEAN	**52.6**	**3354**					**1.058**	**1.102**	**201.685**

[a] Values calculated only for birds which reach asymptote and displaying significant site fidelity (P<0.05).

Table 9.2 Summary of data from ONE rowi used to calculate HR metrics.

ID number	Name	No. of fixes	Total days monitored	Max days between fixes	Mean days between fixes	No. of fixes to reach asymptote	P value of site fidelity displayed	Area of HR[a].	3D area of HR[a].	Est Biomass of HR[a].
140	Inca	76	2891	945	38.053	49	<0.005	5.411	5.611	107.529
167	Tote	76	4796	876	63.118	37	<0.005	6.452	6.815	190.405
153	Moonshine	105	3601	354	34.314	34	<0.005	3.181	3.376	163.747
139	Husky	84	4472	399	53.262	31	<0.005	3.249	3.336	84.895
124	CeeCee	85	4299	961	50.588	25	<0.005	4.35	4.546	100.646
143	Jim	32	4020	1861	125.656	25	<0.005	2.69	2.825	110.904
146	Jumping Jack	32	246	17	7.688	25	<0.005	0.89	0.936	217.461
163	Tane	28	3013	656	107.607	25	<0.005	3.52	3.701	191.005
137	Fancy	90	4930	763	54.778	22	<0.005	3.625	3.773	144.463
107	Annaboy	52	3384	343	65.115	19	<0.005	1.958	2.06	109.138

ID number	Name	No. of fixes	Total days monitored	Max days between fixes	Mean days between fixes	No. of fixes to reach asymptote	P value of site fidelity displayed	Area of HR[a].	3D area of HR[a].	Est Biomass of HR[a].
165	Tony	51	4411	559	86.529	19	<0.005	4.63	4.83	238.017
152	Molloy	40	2897	800	72.425	19	<0.005	2.117	2.261	105.292
138	Hughie	33	2522	1176	76.424	19	<0.005	2.871	2.968	117.972
115	Boof	29	4333	2201	149.448	19	<0.005	5.383	5.529	104.463
136	Doc	28	3721	1069	132.893	19	<0.005	3.016	3.106	116.425
169	Unkie	28	2202	853	78.643	19	<0.005	3.007	3.16	152.114
164	Tickles	22	122	56	5.545	19	0.007	0.694	0.736	215.173
172	White Eyes	38	4733	1148	124.579	NR	0.057			
119	Casey	35	4412	693	126.057	NR	0.058			
128	Cuba	29	753	394	26	NR	<0.005			
	MEAN	**49.6**		**806.2**				**3.355**	**3.504**	**145.273**

[a] Values calculated only for birds which reach asymptote and displaying significant site fidelity (P<0.05).