ANGLIA RUSKIN UNIVERSITY

FACULTY OF SCIENCE AND TECHNOLOGY

RUM RATS: ECOLOGY AND BEHAVIOUR

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Acknowledgments

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ABSTRACT

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The Isle of Rum hosts approximately 25% of the global population of Manx shearwaters, *Puffinus puffinus*. Potential for negative impacts on the shearwater colonies from introduced Norway rats, *Rattus norvegicus*, has highlighted the need to better understand the ecology of this island invader. Abundance and population estimates are often central to effective conservation and invasive species management. Despite their potentially catastrophic impacts on seabird populations, the ecology of Norway rats on islands is poorly understood. Developing an appropriate tool to measure rat population size is therefore important. Furthermore, an understanding of the movement patterns and diet of introduced Norway rats is vital to establishing the nature of their relationship with native species.

Optimisation (transect duration/length) of two common rodent activity survey techniques (tracking plates and chocolate-flavoured wax blocks) was carried out to derive parameters that resulted in a standard deviation of the bootstrapped distribution of the mean (precision) of less than 0.2. Activity survey scores were then calibrated against capture-mark-recapture population estimates for linear (coast, river, wall) and non-linear (grassland, heath, woodland) sites. An island-wide population estimate of Norway rats on Rum was calculated using extrapolated density estimates for linear features (boundary strip method) and non-linear vegetation types (SECR models). Home range size of 17 Norway rats, across three study sites (coast, heath, river) was estimated. Jacob's Index was used to compare vegetation availability (home range) with use (location points), and Spearman's correlation for a relationship between capture rates (C100TN) and distance to linear features. Stomach content analysis was used to describe the diet of 29 rats across three ecotopes (coast, grassland, urban) on Rum.

Activity indices reached an acceptable level of precision after three days and a grid size of 35 x 10m^2 from tracking plate (linear and non-linear sites) and wax block (non-linear sites only) surveys. Total population size of Norway rats on Rum was estimated at 11,844 ± 5,685 for non-linear/linear sites combined. Mean home range size (MCP100) was estimated at 2.32 ± 0.86 hectares, with differences between sex and site found. Distance to coast had a strong negative correlation with mean capture rates. Vegetation and invertebrates were the most frequent/abundant food types across all ecotopes.

Calibrated tracking plates are preferable for the use of estimating population size of Norway rats on islands. Coastal environments are likely to be an important resource for introduced rats; woodland may offer intra-island refugia to rats on Rum. Overall, Norway rats are unlikely to be a current threat to Manx shearwaters on Rum.

Key words: *Isle of Rum, Norway rats, invasive species, stomach content analysis, habitat preference, home range size.*

This thesis is dedicated to my family (past and present), without whom meaning would be lost.

Anaesthetised female rat 'Wanda', with a GPS tag attached (the rat was released after recovery from anaesthesia and re-trapped two weeks later to remove the tag).

Table of Contents

List of Figures and Tables

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RUM RATS: ECOLOGY AND BEHAVIOUR

SEAN BENJAMIN JAMES CARLISLE

Chapter 1 Introduction

1.1 General

1.1.1 What is an invasive non-native species?

A 'non-native' or 'alien' species has been described as, 'a species, subspecies or lower taxon, introduced outside its natural past or present distribution; includes any part, gametes, seeds, eggs, or propagules of such species that might survive and subsequently reproduce' (Convention on Biological Diversity 1992 (Decision VI/23)). For as long as humans have travelled, migrations and trade are thought to have transported new species from their native ranges, to many new unoccupied areas across the world (Defra 2003; Westphal *et al.* 2008).

In the UK, a species is considered to be non-native if it arrived in the UK as a consequence of the activities of Neolithic or post-Neolithic man, and/or their associated domestic animals (Webb 1985). Non-native species are found all over the world (Vitousek *et al.* 1997; Genovesi 2005), and in all taxonomic groups (IUCN 2000). Non-native species have diverse and often unpredictable effects on crops, ecosystems, human and livestock health (Pimentel *et al.* 2000; Hulme & Bremner 2006). The negative effects of non-native species include damage to agriculture and ecosystems, costs of prevention, control and management, and spread of disease (Lowe *et al.* 2000; Manchester & Bullock 2000; Courchamp *et al.* 2003; Towns *et al.* 2006; Jones *et al.* 2008). In the US, UK, Brazil, India, South Africa and Australia, more than 120,000 non-native species have become established, requiring an estimated $314 billion per annum spend on control and losses due to damage (Pimentel *et al.* 2000; Stokes *et al.* 2006). Non-native species can, however, also bring considerable benefits (Rodriguez 2006). These include new agricultural and horticultural species for food production and trade, bio-control agents for disease and pests, species for habitat management, and conservation (Williamson & Fitter 1996; Schlaepfer *et al.* 2011). In the UK for instance, the decline of the introduced rabbit, *Oryctolagus cuniculus*, during the 1950s, and subsequent reduced grazing of chalk downland, was linked to the extinction of the large blue butterfly, *Maculina arion* (Sheail 1991), indicating the potential conservation value of introduced rabbits. Conversely, the introduction of the American Mink, *Neovison vison*, during the 1950s, had significant conservation impacts on a range of native species, including (but not exclusively) brown trout, *Salmo trutta*, Atlantic salmon, *S. salar*, terns, *Sterna paradisaea/S.hidundo*, and the European protected water vole, *Arvicola amphibius*

(Barretto *et al.* 1998; Craik 1997). The effect of non-native species can therefore be positive or negative.

Invasive non-native species (INNS), however, have been defined as non-native animal or plant species which have the ability to spread rapidly and dominate ecosystems, causing adverse environmental, economic and human health effects (Non-native Species Secretariat 2016; Scottish Environmental Protection Agency 2017). Generally speaking only a small fraction of non-native species ever become established and/or invasive (Williamson 1999; Jeschke & Strayer 2005). The 'tens rule' states that only 10% of non-native species successfully invade and only 10% of those species become established pests (Williamson & Fitter 1996). Despite this, invasive non-native species are the second biggest threat to biodiversity behind habitat destruction, and historically have been responsible for hundreds of extinctions world-wide (Vitousek *et al.* 1997; Fritts & Rodda 1998). Invasive non-natives also impact heavily on the global economy with an estimated total cost of £1.7 billion in the UK alone. These figures are likely to be significantly higher if the indirect costs are also included (Williams *et al.* 2010).

1.1.2 Rodents as invasive non-natives

In part, the global success of established invasive non-natives can be attributed to their ability to adapt to new ecosystems (Jeschke & Strayer 2005). Mammals of the order Rodentia (characterised by a single pair of lower and upper jaw incisors (MacDonald 2009)) are considered one of the most successful groups of invasive non-natives (Ehrlich 1986; Clout & Russell 2008; Jones *et al.* 2008); and this may be in part due to their adaptability. Rodents are the largest taxonomic group of mammals, with approximately 2,367 species and can be found in almost every ecotope, continent, and island in the world (Roskov *et al.* 2018). Most rodents have an extremely high reproductive rate, with a gestation period of 21 days after which mating can begin again almost immediately (Meehan 1984; MacDonald 2009). Furthermore, Rodentia are typically social animals with aperiodic outbreaks attributed to their rapid reproductive response to changing environmental conditions, with huge aggregations of certain rodents often associated with abundance of food (Macdonald 2009). The house mouse (*Mus musculus*) in Australia, for instance, has been reported to increase density around wheat fields 200 fold, during outbreak years of optimal biotic and abiotic conditions (Brown *et al.* 2010). Various species within the order Rodentia are well-documented as invasive non-natives including the black rat (*Rattus rattus*), Norway rat (*Rattus norvegicus*), Polynesian rat (*Rattus exulans*) and the house mouse (Yom-Tov *et al.*

1999; Towns *et al.* 2006; Russell *et al.* 2008); rodents have invaded almost every continent in the world, and at least 80% of all islands (Atkinson 1985) (Table 1.1). Members of the genus *Rattus* are particularly opportunistic feeders and hence adaptable to new environments, with dietary plasticity and flexibility which varies between seasons, habitats, and ecosystems (Atkinson 1985; Towns *et al.* 2006). Rats that live in close association with humans (synanthropic species (Kucheruk 1965; Khlyap *et al.* 2010)) or cultivated fields (agrophilic species (Khlyap *et al.* 2010)), such as the black rat, Norway rat and Polynesian rat, are considered particularly invasive rodent species (Jones *et al.* 2008), as they can be readily transported through human activity.

The Norway rat is native to South East Siberia, North China, the Hondo region of Japan, and is a well-documented global invasive non-native species (Pascal & Lorvelec *et al.* 2006). Norway rats are typically a widespread synanthropic species found on every continent except Antarctica (Figure 1.1) (Pascal & Lorvelec *et al.* 2006; Lund 2015). Norway rats were first recorded in Europe around 1716, when they arrived in Denmark on Russian ships (Twigg 1975). Their spread to the UK followed closely behind, and the first introduction was recorded in England in 1728 (Meehan 1984).

Table 1.1 Summary of the distribution of invasive rats among major islands and island groups. Adapted from Atkinson (1985).

Rat Species Present	Number of Islands or Island Groups			
	Pacific Ocean	Indian Ocean	Atlantic Ocean	Total
R. exulans alone	2	-	-	2
R. norvegicus alone	4	1	5	10
R. rattus alone	6	17	3	26
R. exulans + *R. rattus*	7	-	-	7
R. exulans + *R. norvegicus*	6	-	-	6
R. rattus + *R. norvegicus*	4	4	5	13
All three species	15	-	-	15
One or more unidentified invasive rats present	9	7	6	22
Free of/probably free of invasive rats	12	5	5	22
Total	65	34	24	123

In the UK, Norway rats are now ubiquitous throughout all counties and most habitats with the exception of some offshore islands and mountainous regions (Non-native Species Secretariat 2016). Historically it was estimated that the UK population of Norway rats was around 2.5 rats per hectare of cultivated land; approximately 40 million rats (Boelter 1909). A more recent revision has, however, estimated a UK population of nearer 6.8 million (Harris *et al.* 1995). Disease transmission and damage to crops and buildings makes the management of Norway rats important to humans, and under the Prevention of Damage by Pests Act (1949) in Britain, landowners are obliged to control Norway rats (Mack *et al.* 2000).

Figure 1.1 Global distributions of the Norway rat *Rattus norvegicus* (Lund 2015).

1.2 Impacts of Invasive Rodents

1.2.1 Socio-economic and health

Several rodent species are considered some of the most important pest species worldwide. For instance, in Indonesia rodents (mostly *Rattus* spp*.)* are thought to be responsible for at least 15% of the annual loss of rice (Geddes 1992). In Tanzania rodents cause about 5 -15% of the annual maize losses; the food for approximately 2 million people (Leirs 2003). Singleton *et al.* (2003) estimated that rodents in Asia eat enough grain to feed 200 million people per year. Despite this, estimates for annual loses can be difficult to calculate with wide ranges often reported. For instance, in parts of South America estimates of losses have

ranged from 5% - 90% (Rodríguez 1993). The contamination of spoiled food sources could potentially lead to the spread of zoonotic diseases by rats, of which there have been many found (Webster *et al.* 1995). Webster & McDonald *(*1995) found evidence of 13 zoonotic parasites carried by Norway rats on UK farms. Norway rats have therefore been linked to the spread of numerous diseases such as Salmonella and Leptospirosis (Weil's disease). Davies & Wray (1997) recorded *Salmonella typhimurium* in populations of Norway rats on UK pig farms. More recently, Lin *et al.* (2012) linked the worldwide spread of the Seoul Virus to the migratory patterns of Norway rats.

With the increase of urbanisation and the movement of people across the world, invasive rodent species and their associated risks to humans are likely to follow (Mack *et al.* 2000).

1.2.2 Conservation

Invasive species can affect native species in a number of ways including habitat change, hybridisation, predator-prey interactions, direct predation and competition (Simberloff 1981; Ebenhardt 1988; Didham *et al.* 2007). Invasive rodent species, particularly from the genus *Rattus*, have effects on a number of native species across the globe including reptiles, insects, plants, mammals, and birds (Cree *et al.* 1995; Atkinson & Towns 2001; Stapp 2002; Donlan *et al.* 2003; Towns *et al.* 2006). The ecological impact can range from an individual to ecosystem level (Parker *et al.* 1999; Zavaleta *et al.* 2001). Rats are thought to be responsible for the eradication of at least 50 island species, although direct evidence of predation is difficult to obtain (Towns *et al.* 2006). In particular, rats have historically had an impact on bird species, especially seabird colonies (Bertram & Nagorsen 1995; Mulder *et al.* 2009). Atkinson (1985) reported that Norway rats were responsible for the extinctions of various species of seabirds on oceanic islands, although bird size and nesting behaviour have been found to affect predation risk by rats. For instance, large ground-nesting birds like masked boobies, *Sula dactylatra,* appear to co-exist with Norway rats on Tromelin Island, east of Madagascar (Le Corre 1996). Conversely Sooty terns, *Onychoprion fuscatus*, are particularly susceptible to rat predation and it appears that wherever rats and sooty terns are present there is a measurable predation effect (Taylor 1979). Overall it is generally accepted that the effect of rats on seabirds is a negative one; however, there is still a pressing need to understand the mechanisms of the interaction and which species are vulnerable. For the conservation of seabird species, an ecological understanding of the specific introduced rodent predators is therefore important.

1.3 Behavioural and Ecological Context of Rats

Despite the numerous eradication programmes covering a range of rodent species over several decades, surprisingly little research has gone into understanding the ecology of Norway rats on islands (Towns *et al.* 2003; Keitt *et al.* 2015). In order to optimise resources available for the management of invasive non-native species an understanding of their general ecology is useful. Most ecological research on introduced rats has been carried out on the Polynesian rat with the vast majority of island research on any rat species coming from New Zealand (Burbidge & Morris 2002; Campbell & Atkinson 2002; Hoare *et al.* 2007). Towns *et al.* (2006) concluded that of the three most successful rat invaders (black rat, Norway rat and Polynesian rat) the Polynesian rat was the most intensively studied. Very few studies in the northern hemisphere have investigated the ecology of Norway rats on islands, most were associated with eradications, and generally only concerned distribution. Taylor *et al.* (2000) recorded data on the density, distribution, habitat use, and diet of Norway rats on Langara Island, Canada, to establish the consequences of rat eradication. Major *et al.* (2007) measured habitat differences in Norway rat diet on Kiska Island, Alaska. On the Isle of Canna, following the suggestion of Norway rat eradication, the National Trust for Scotland carried out a series of mammal surveys on the island, reporting distributions of Norway rats (Patterson & Lloyd 2000; Patterson & Quin 2001; Patterson 2003). Distribution of Norway rats on Canna was associated with ecotope type and variation in densities and capture rates between ecotopes were reported (Patterson & Lloyd 2000; Patterson & Quin 2001). In the southern hemisphere, Harper *et al.* (2005) reported that Norway rat abundance was significantly higher in subalpine shrub land compared to river, forest and manuka shrubland on Stewart Island, New Zealand. Populations of Norway rats also varied seasonally, which is a similar pattern expected for most rodent species living naturally *i.e.* not associated with man (Mills & Childs 1998; Luis *et al.* 2010; Russell & Ruffino 2012). Harper *et al.* (2005) noted that in lowland forest in New Zealand, rat abundance numbers increased 20-fold following a heavy seed mast event of the southern beech, *Nothofagus* spp., in spring. When food availability is high, home range size is likely to be smaller, with individuals required to travel less to find resources. Home range size for Norway rats on farms was lower, with home sites closer to established food sources (Taylor 1978; Villafañe & Busch 2007; Lambert *et al.* 2008). Whilst home range size is affected by a number of factors, differences between sex, habitat, and season are regularly reported (McLoughlin & Ferguson 2000; Lambert *et al.* 2008). Diet in Norway rats also appears to

vary between habitats, and season, although there are still a wide range of habitats with little to no diet data available (Major *et al.* 2007).

Eradication of invasive non-native species has long been thought of as one of the most effective ways of conserving native species (Myers *et al.* 2000; Howald *et al.* 2007). However, rather than using a broad-brush approach with an accepted level of collateral damage, research is now moving towards addressing the specific conservation questions and species concerned (Zavaleta *et al.* 2001; Zavaleta 2002; Campbell *et al.* 2015).

1.4 Rat Management: Tools and Use

1.4.1 Rodenticides

Considering the environmental, social and financial implications of invasive rats, it is hardly surprising that control methods and applications have been extensively explored and implemented throughout the world. A large proportion of the early research on rat biology and ecology was indeed driven by the need to control rat pest species especially in relation to the risk of zoonotic disease (Meehan 1984). Live trapping and humane dispatch, lethal trapping, and rodenticides have all been commonly used but by far the most widely used control method for rats is the application of rodenticides (Taylor & Thomas 1993; Taylor *et al.* 2000; Towns & Broome 2003). Rodenticides were first popularised in the 1900s (Meehan 1984); however, records of plant derived rodenticides indicate their origins started much earlier (Freeman 1954). More recently, first and second generation anticoagulants have dominated. Anticoagulants reduce blood clotting activity, causing death by haemorrhaging (Hadler & Buckle 1992). Early development of anticoagulants began shortly before World War II, and interest picked up again in the 1950s (Bentley & Larthe 1959). By the 1970s several anticoagulants were available worldwide (Lazarus 1989). Extensive work was carried out during the 1970s and 1980s developing our physiological, behavioural and ecological understanding of rats in relation to the development of rodenticide baits (Kamil 1987; Cox & Smith 1992; Linhart *et al.* 1997). This new technology revolutionised rodenticides, and cleared the way for their success. Anticoagulants were initially believed to reduce any efficacy issues associated with rat neophobia; their slow mode of action reduces the likelihood that rats will associate subsequent symptoms of illness with their consumption of the bait (Quy *et al.* 1996; Priyambodo & Pelz, 2003). Initial success of first generation anticoagulant rodenticides was relatively short lived however, with widespread heritable physiological resistance being increasingly seen in rats and mice over the past 20 years (Buckle *et al.* 1994). The spread of resistance had a significant part to play in the

development of (more toxic) second generation anticoagulants. Recently, however, there appears to be a European and national level movement towards restricting the use of anticoagulant rodenticides. A report conducted by the Pesticide Safety Directorate (DEFRA 1997) stated that anticoagulant rodenticides should be regarded as being 'markedly inhumane'. Several other studies have also raised concerns about the long term suitability of anticoagulant rodenticides, given the questions raised about their humaneness (Mason & Littin 2003; Cowan & Warburton 2011). Furthermore, all anticoagulants inherently carry issues with primary and secondary poisoning of non-target species (Newton *et al.* 1990; Brakes & Smith 2005), and bioaccumulation (Cox 1991). This has led to research into alternative compounds suitable for rodenticides (Witmer *et al.* 2014), and the development of ecological (rather than chemical) based rodent pest management (Singleton *et al.* 1999). For instance, Lambert (2003) found that on UK farms habitat management compared well with rodenticide treatment for managing Norway rat populations.

Despite the apparent issues with anticoagulant rodenticides, they have been used extensively over the past 20 years for conservation purposes; allowing for the control of invasive rodents at the population level (Howald *et al.* 2007; Ruscoe *et al.* 2013). Most of the initial wildlife management research used ground-based delivery of rodenticide baits, but after a series of successful comparative trials, aerial broadcasting (using helicopters) was found to be marginally cheaper, and more importantly, more feasible in regions with difficult terrain (Parkes *et al.* 2011). Aerial broadcasting has now been successfully used throughout the world, and is often considered the most effective way of delivering rodenticide baits to large areas (Broome *et al.* 2014), although it inevitably poses more risks to non-target species as broadcast baits are unprotected. Regardless of the bait delivery system, having a firm understanding of the ecology of the target species will likely help minimise the biological impact of large scale eradications *e.g.* consequences for non-targets (Towns and Broome 2003; Caut et al. 2008). Furthermore, the timing of treatment phases can be optimised to seasons where alternative food for the target species is scarce, and densities are low (Keitt *et al.* 2015).

1.4.2 Island eradications

Typically, large scale regional eradications have been considered a desirable theoretical option with difficult practical implementation (Thomas & Taylor 2002). Despite this, there is clearly a need to manage invasive non-natives (Simberloff *et al.* 2013). This is extremely relevant to island ecosystems, where closed populations of native species, with high

biodiversity and endemism, have evolved without introduced species (Dulloo *et al.* 2002; Meyer & Cowie 2010). Islands represent approximately 4% of global land cover, but levels of endemism are 8-10 times higher than mainland ecosystems (Kier *et al.* 2009). For instance, in Hawaii it has been reported that up to 90% of species are endemic, and hence highly vulnerable to extinction following the introduction of a few voracious predators (Cowie & Holland 2008).

After the event of the first unintentional island-wide rodent eradication (by-product of rodent control efforts) in 1951 on Rouzic Island, France, intentional eradications of rodents have been conducted on at least 284 islands world-wide (Figure 1.2) (Towns & Broome 2003; Lorvelec & Pascal 2005; Howald *et al.* 2007). The first deliberate island eradications of invasive rodents on small islands began in New Zealand in the 1980s (Moors 1985; McFadden & Towns 1991); since that point Norway rats have been eradicated from over 104 islands.

A large proportion of invasive species removal projects have been carried out in Australasia (Mulder *et al.* 2009). Countries such as New Zealand, whose ecosystems have evolved without terrestrial mammals, have been particularly proactive in developing methods for eradication of invasive rodents (Thomas & Taylor 2002), with over 50 years of largely successful eradication attempts (Towns & Broome 2003).

Eradications have not always been successful however. Success is commonly declared if no evidence of the target species is found for at least two years after the cessation of toxic baiting; several eradication attempts have failed at least in part due to the difficulties in detecting rats at low densities. Other problems include non-target bait competitors, agriculture, and bait delivery methods (Parkes *et al.* 2011; Holmes *et al.* 2015).
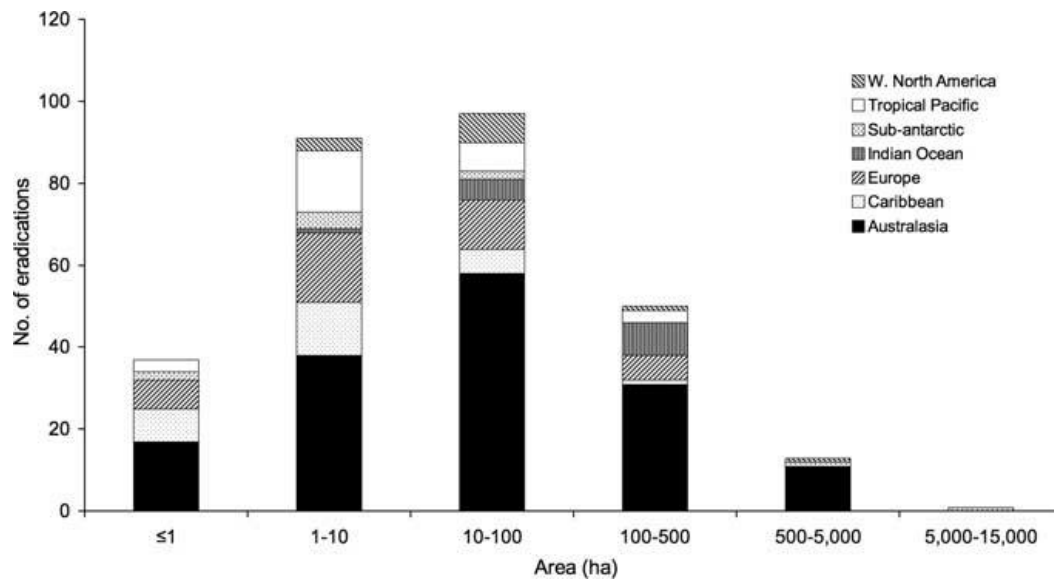
Figure 1.2 Summary of the number of successful global island eradications of invasive rodents carried out per location and island area (Howald *et al.* 2007).

1.5 Impact of Norway Rats on Manx Shearwaters in Britain

The storm petrel is considered a species of seabird that is highly vulnerable to rat predation considering their small size, lack of defensive behaviours to deal with predators, and their nesting habits (nesting in burrows or crevices - areas where rats may prefer to forage) (Jones *et al.* 2008). In Britain, Manx shearwaters are of particular interest due to their restricted breeding range and reliance on Scottish and Welsh islands for breeding (Ratcliffe *et al.* 2009). Manx shearwaters typically arrive at their UK breeding sites from their South American wintering sites between late winter/early spring for laying between early April – June (median laying 8 – 10th May) and fledging between August – October (Harris 1966; Thompson 1987; Guilford *et al.* 2009). The Scottish island of Rum hosts approximately one-quarter of the global breeding population of Manx shearwaters; the only breeding colonies that may be larger can be found on the islands of Skomer, Skokholm or Middleholm, Wales (Murray *et al.* 2003). Suggestions have, however, been made that the globally important Manx shearwater breeding colony on Rum may be in slow decline (Smith *et al.* 2001). In 2004, for example, the shearwater productivity on Rum was at its lowest recorded since 1999 (Mavor *et al.* 2005), and it has been suggested that introduced Norway rats may have contributed to this; although Thompson (1987) suggested that rats had little impact on the shearwater colony on Rum. Lambert *et al.* (2015) found that levels of Norway rat activity within three Manx shearwater colonies on Rum was too low in most years to cause measurable impacts on shearwater breeding success; but higher levels of rat activity in one

10

year were associated with impacts. It is clear overall that although the effect of rats on seabirds is generally negative, the relationship is affected by a number of factors, including the distribution and abundance of rats.

1.6 The Island of Rum

The Scottish island of Rum is the fifteenth largest Scottish island (10,684ha), the largest of the Small Isles, part of the Inner Hebrides, and lies approximately halfway between the Isles of Skye and Mull (Figure 1.3). Rum has a volcanic past with the mountain range (Cuillins) having formed some 60 million years ago (Scottish Natural Heritage 2009). Gale force winds occur for 50 days of the year, average temperatures are lowest in winter (5°C) and highest in summer (15°C), with mean annual rainfall of 2800mm and an average of 1100 hours of sunshine per year (Figure 1.4) (Met Office 2018). The landscape is varied and the climate is harsh, and given the influence of the sea and the isolation of Rum, a variety of distinctive habitats, plants and animals can be found there. Rum is one of Scotland's Wild Land Areas with limited human disturbance and is dominated by heath and mire across glens and moorland (Scottish Natural Heritage 2018). Rum supports important populations of resident and migratory bird species including golden eagle (*Aquila chrysaetos*), red-throated diver (*Gavia stellata*) as well as approximately 25% of the breeding population of Manx shearwater (*Puffinus puffinus*) (Wood 2000). Three rodent species are also resident on the island; wood mouse, *Apodemus sylvaticus*, Eurasian pygmy shrew, *Sorex minutus*, and the Norway rat.
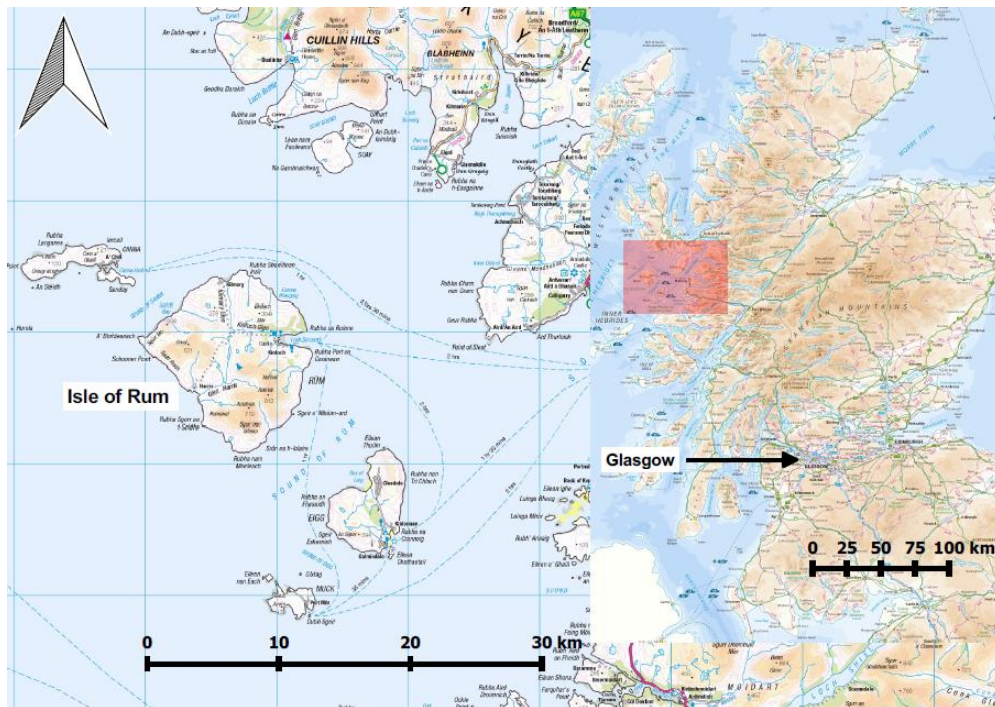
Figure 1.3 Map of Scotland and location of the Isle of Rum, approximately 180km northwest of Glasgow. Arrow (top left) indicates grid north. © Crown Copyright and Database Right 2018. Ordinance Survey (Digimap Licence).

The isle of Rum qualifies for Special Protected Area (SPA) status under Articles 4.1 and 4.2 of the EC Directive on the conservation of wild birds (79/409/EEC). Special Protected Areas are strictly protected sites classified for the protection of rare, vulnerable, and regularly occurring migratory species, such as Manx shearwater on Rum. SPAs are a way of formalising the legal mechanisms that Member States within the EU are expected to implement in order to fulfil EC Directive provisions such as:

● The maintenance of wild bird populations throughout their natural range and the support of various activities that encourage this.

● The identification and classification of Special Protection Areas (SPAs) for rare or vulnerable species and regularly occurring migratory species.

● The establishment of a protection scheme for wild birds.

In Scotland, legal responsibility for the management of SPAs is assumed by Scottish Natural Heritage (SNH), who manages the Isle of Rum as a National Nature Reserve.
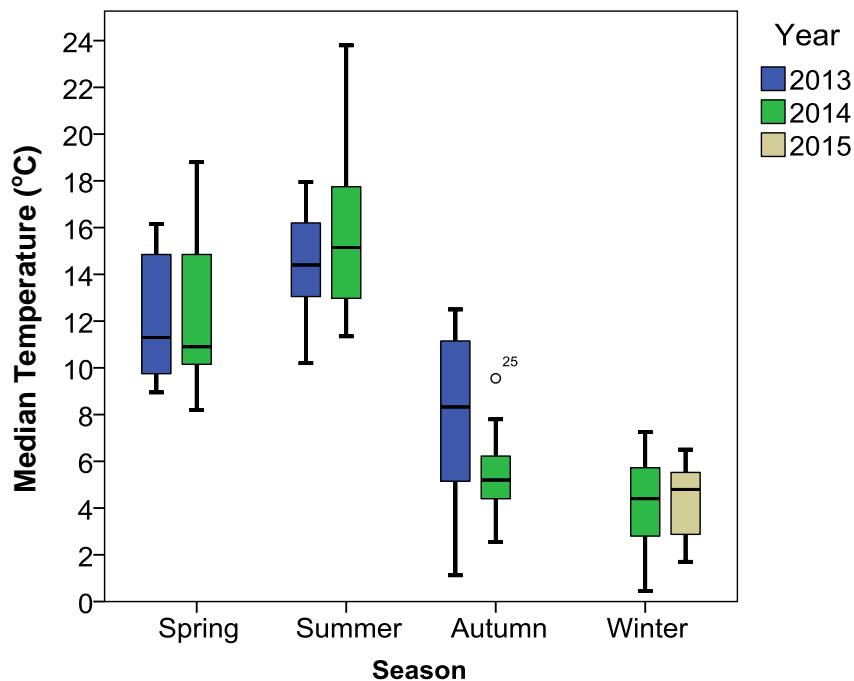
Figure 1.4 Median (IQR) seasonal (spring: 21st March – 21st June, summer: 21st June – 21st September, autumn: 21st September – 21 December, winter: 21st December – 21st March) temperatures (^{o}C) recorded on the Isle of Rum, Scotland, on the 13th May 2013 – 6th March 2015. Weather stations (CM7088 Wireless Rain Gauge, Climemet, Sudbury, UK) were located at 12 survey locations on Rum. Data was collected from a minimum of 6 survey sites per season over the two year period; stations were active for between 3 – 6 days per survey and were accurate to ± 1.0^{o}C.

1.7 Rationale and Research Questions

Considering the debate surrounding the long term productivity of Manx shearwaters on Rum and the widely reported negative effects of introduced Norway rats on native birds elsewhere, recent evidence suggesting co-existence on Rum has highlighted the need to know more about the general ecology of Norway rats on Rum, in light of some fundamental gaps in our ecological understanding of Norway rats on islands generally. The results of which should provide an evidence base for conservation policies, ensuring that global biodiversity is protected.

This thesis will address the following research questions:

1. What is the distribution and abundance of Norway rats on Rum and how is this related to shearwater breeding grounds?

2. Is there migration between sub-populations of Norway rats on Rum *e.g.* urban areas to shearwater breeding grounds?

13

3. Are there spatial differences in home range size and movement patterns of Norway Rats on Rum?

4. What are the habitat and feeding preferences of Norway Rats on Rum, and what role does avifauna play in the diet?

Chapter 2 - Optimisation of Two Common Rat Activity Survey Techniques: How Long is a Piece of Transect?

2.1 Introduction

2.1.1 General

Ecology is the study of plant and animal abundance and distribution and their interactions with their environment (Buckland *et al.* 2001). Estimating abundance, or population size, is an essential part of conservation, research, and the management of species. In order to calculate true abundance or distribution of animals, every individual within a given sampling area would need to be counted (Davies *et al.* 2012). Complete counts such as these may sometimes be achievable for large animals within restricted areas (Sutherland 2006; Elphrick 2008); however, for most species, sampling or surveying a (representative) proportion of the study population is a more feasible option (Seber 1982; Ross & Reeve 2003). Various survey techniques have been proposed and developed for surveying animal populations (Sutherland 2006). Distance sampling and capture-mark-release (C-M-R), for example, are considered useful methods when counting subjects within a given area, allowing estimates of density or population size to be achieved by calculating detectability, to account for missed individuals (Seddon e*t al.* 2003; Buckland 2004). Distance sampling requires a method of estimating the distance to a point *e.g.* a study subject, either from a given point or the perpendicular distance from the transect; hence the term 'distance' sampling, for observations made along linear transects through the landscape (Burnham *et al.* 1980). Distance sampling relies on direct observation of individual animals whilst indirect methods are based on sampling for signs of activity within the environment, to detect the presence of the animal. There are a number of indirect survey methods which are simpler and cheaper to carry out in (compared to direct methods *e.g.* trapping) and more applicable to surveying large areas, and these have been used for estimating density/abundance of animals (Rowcliffe *et al.* 2008). Furthermore, passive methods do not alter the behaviour of the subjects being investigated. Methods, however, must be specific to the question, habitat and species involved (Greenwood 1996; Krebs 1999).

2.1.2 Tools for studying populations: transects and plots

Transects are used as a way of collecting data from a number of sampling units within a sampling frame (Sutherland 2006). Transect surveys are carried out within a predetermined distance or area using signs of activity/presence to estimate ecological parameters, such as

density/abundance, where complete counts are impractical. There are various transect types commonly used throughout ecology, which vary between and within transect categories. Line and point transects, for instance, usually require observers to measure the distance (distance sampling) from the observation point or sampling line to the subjects' activity/presence (Buckland *et al.* 2001). Distance to the study subject is not, however, relevant when line transects are used for capture-mark-recapture surveys *i.e.* individuals are trapped (Buckland 2004). Quadrats are one of the most commonly used survey methods in population ecology and are particularly useful for density and abundance estimates for plants (Sutherland 2006; Begon *et al.* 2009). In essence, a square or plot of a given size is sampled within the survey area and all individuals are counted within this plot. A strip transect is a modification to the standard quadrat sampling which utilises a straight line to create a sampling strip of predetermined size and width to count individuals within a plot. The advantage to using strip transects over line transects is that it is often easier to count individuals inside an established boundary, thus reducing the difficulty of decisions about including or excluding organisms on the edge of the sampling area (edge effect) (Burnham *et al.* 1985).

The size and duration of sampling units should be relevant to the species and questions involved, with particular attention given to the spatial patterns of the species (Sutherland 2006; Nomani *et al.* 2012). For instance, if the research is investigating seasonal changes in behaviour, then the sampling period would need to cover at least two seasons to capture the appropriate data. The size of sampling units also varies according to the target species. For instance, a small quadrat size (1m x 3m) may be used for plants species, but size and shape of the quadrat should reflect the vegetation pattern being studied (Brummer *et al.* 1994). By comparison, Aars *et al.* (2009) used aerial line transects of up to 185km for estimating the Barents Sea polar bear, *Ursus maritimus*, sub-population size. Transect shape will also be determined by the way in which a study subject uses its environment (Merriam & Lanoue 1990; Pereboom *et al.* 2008). For instance, various species of birds and mammals have been shown to use linear features, and avoid open areas when travelling between habitat regions (Wegner & Merriam 1979). In this case, line/strip transects are more appropriate for capturing data along linear features, where subjects are likely to be found (Machtans *et al.* 1996). Clearly, however, in the case of linear features, subjects may travel back and forth along the linear transect more often than in an open areas, reducing the comparability between transect types. There are a number of proposed methods for calculating the correct size and shape of sampling units (Krebs 1999). The simplest method is to critically analyse similar work and replicate an appropriate peer-reviewed method. More robust and project

specific methods, however, need to take into account factors such as variability and cost, and there are now a number of software packages available that will help to refine your sampling parameters to suit your research questions and data type (Hendricks 1956; Dupont & Plummer 1990; Charan & Kantharia 2013).

Suitable sampling areas should consider habitat type and mobility of the species of interest but this must be balanced against the practicality of sampling (Seber 1982). Whilst highly mobile species would likely require larger sampling areas, if few samples can be practically achieved using this large sampling unit, then the number of replicates and subsequent precision of the data may suffer. Precision of an estimate can be considered to be how similar repeated estimates are to one another and broadly thought of as the square root of the number of replicate samples (Sutherland 2006). Often, however, there is variance between replicates in the rate at which subjects are encountered, which must also be considered when estimating precision (Fewster *et al.* 2009). Precision is therefore concerned with the level of confidence that data are free from random error (reliability). By contrast, whilst precision is concerned with the random error in the measurement, accuracy describes how close an estimate is to the true value, with any bias indicating the systematic error from the true values (validity) (Martin & Bateson 2007). Whilst maximising your precision provides more reliable measurements, as precision nears zero sampling effort becomes disproportionately larger and thus an acceptable level of precision is usually predetermined. Decision rules are therefore essential for estimating the required number of samples for a reasonable amount of accuracy (Ono 1967; Christenssen *et al.* 1977). Whilst a precision level (D) of 0.1 was suggested by Morris (1955), $D = \leq 0.2$ has been deemed acceptable in field studies (Christenssen *et al.* 1977; Addison 1989); where precision (D) is often considered the ratio of the standard error to the mean.

2.1.3 Activity indices

Tracking is one of the oldest and simplest passive methods used to get close enough to subjects to study their behaviour and distribution. With a trained eye, animal signs such as droppings, footprints and scratch marks can be used to confirm the presence, distribution and abundance of a particular species (Stander *et al.* 1997). This species-specific 'trail' that an individual animal leaves is something that has allowed for the development of various passive technologies. For instance, each mammal species has a unique footprint (Figure 2.1), although closely related species can be hard to differentiate.
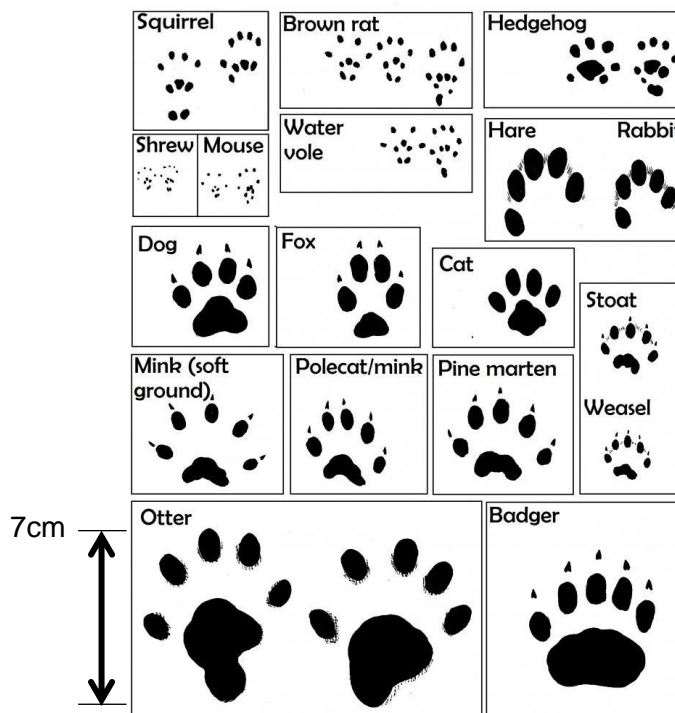
(The Mammal Society[©] <http://www.mammal.org.uk>)

Figure 2.1 Various examples of species-specific mammal footprint silhouettes. Eurasian otter *Lutra lutra* prints are typically 7cm x 6cm, whereas common shrews *Sorex araneus* are 1cm x 0.3cm (Olsen *et al.* 2013).

The uniqueness of animal footprints has led to the development of various tracking media such as tracking pads, tunnels, plates, and pits (Quy *et al.* 1993; Foresman & Pearson 1998; Blackwell *et al.* 2002). For instance, Ratcliffe *et al.* (2009) used a 1m diameter sand pit to detect the presence of domestic cats, *Felis catus,* on Ascension Island. Kauhala (1996) used tracking tunnels to detect the distribution of American mink, *N.* vison, in Finland. One of the main limitations of the tracking methods discussed, however, is that they only give researchers an index of activity or abundance, when often the objective is estimating true abundance.

Another possible technique for estimating abundance is census baiting (Quy *et al.* 1993; Webster *et al.* 1995). Bait inference uses the consumption of bait to indicate abundance of a target species. One of the problems with bait inference, however, is that the bait may be more or less palatable than the other food available to the target animals, potentially confounding activity estimates, particularly if alternative food availability varies temporally *e.g.* seasonally. Bait may also be consumed by non-target species, confounding the population estimates. Finally, dietary plasticity and flexibility varies spatially and temporally within and between species, family groups, populations and locations, making it difficult to assume that individuals consume a standard amount of daily bait (Barnett & Spencer 1953;

Meehan 1984; Caut *et al.* 2008). Non-toxic monitoring blocks use the same principle as census baiting. As with footprints, some mammal species have unique denture morphology, allowing chew marks to be identified to the species level. Chew marks, rather than bait consumption, give an indication of activity levels. Furthermore, wax blocks can be thought of as less nutritional than bait, which may reduce local immigration. Wax blocks are standardised blocks of non-toxic paraffin wax mixed with small quantities of attractant *e.g.* chocolate powder. Blocks are typically spaced in a uniform pattern across target areas to give an indication (chewmarks) of the presence of a target species. As such, non-toxic wax blocks are a standard tool for monitoring populations of target species during, for example, invasive mammal eradication projects (Towns & Broome 2003; Howald *et al.* 2007).

2.1.4 Transect parameters – how much is enough?

Transects are widely used for surveying rodent species to quantify a variety of factors relating to populations (Steen *et al.* 1996; Gentile *et al.* 2000; Previtali *et al.* 2009; Krebs *et al.* 2018). Transect methodology does, however, remain highly variable even when investigating the same research question on a single species; Shiels *et al.* (2013) and Sugihara (1997) both investigated the diet of island populations of black rats using differing transect lengths (300m, 600-1525m). Projects replicating 'tried and tested' survey parameters (duration, area/length) will usually be acceptable, but in the absence of a standardised protocol for your specific biological question, which method do you follow? Furthermore, how much data is enough? In any given project, resources are limited and it is essential that questions are asked about the power of a study to detect the phenomena of interest (Ellis 2010). In this sense, comparisons of previous studies can be a useful way of deciding on the number of samples required to estimate a parameter of interest given a certain effect size (the degree to which the phenomena are present in the population) (Ellis 2010). The effect size can be derived from published data and an estimate made of the sample size needed to detect an effect at an acceptable level of power *i.e.* 80% chance of detection. In the absence of suitable previous data, bootstrapping a small amount of pilot data may be useful.

2.2 Rationale and Research Questions

Previous surveys of rodents on Rum have used a variety of transect lengths; Lambert *et al.* (2015) used a series of 10 x 30m strip transects to survey rat activity on upland areas in and around Manx shearwater breeding colonies. Pankhurst *et al.* (2010) used line transect lengths of 250m to survey the distribution of wood mice across several vegetation types on

Rum. As such, a standardised method for surveying rodent activity on Rum has not been previously developed. This study will provide optimum survey parameters for two common survey techniques (tracking plates, chocolate wax blocks) across six sample groups (coast, river, wall, heath, grassland, woodland), in a non-urban, island population of Norway rats on the Isle of Rum, Scotland. The findings of this research will quantify the optimal transect parameters necessary for the assessment of rat activity and subsequent calibration against rat population estimates; allowing future sampling of rat activity on Rum to be standardised and providing an understanding of the activity of rats on Rum and elsewhere. These survey techniques will inform the Scottish Natural Heritage future management plan for the invasive non-native Norway rat on the Isle of Rum National Nature Reserve. The following research questions will be addressed in Chapter two:

1. What are the optimal parameters (number of survey days and transect intervals ($10m^2$)) for two common rat survey methods in high density linear environments on Rum?

2. What are the optimal parameters (survey days and transect intervals ($10m^2$)) for two common rat survey methods in low density non- linear environments on Rum?

3. What are the differences in activity estimates of Norway rats on Rum across two sample categories (linear, non-linear) and six sample groups (coast, river, wall, woodland, grassland, heath)?

2.3 Methods

2.3.1 Health and safety

In accordance with Anglia Ruskin University (ARU) Health and Safety Policies, a detailed research proposal was completed and approved prior to the start of data collection. This included a detailed plan of the experimental design, methodology, timescales, expected outcomes and a dynamic risk assessment. Procedures regulated by the Animals (Scientific Procedures) Act 1986, were carried out under a Home Office Project Licence (PPL 60/4485) held by the Animal and Plant Health Agency (APHA), York, UK, and were subject to approval by the APHA Animal Welfare and Ethical Review Body. Controlled veterinary drugs were stored, labelled and recorded in accordance with the Veterinary Medicines Directorate guidelines on controlled drugs. All fieldwork was conducted in accordance with ARU's health and safety guidelines (First Aid, Hazardous Substances and Lone Working).

2.3.2 Study sites

2.3.2.1 Preliminary site visits

Prior to the commencement of fieldwork proper, several *ad hoc* Norway rat surveys were conducted on a variety of vegetation types to assess the general suitability of spatial classifications. Walking transects were carried out to visually assess the frequency and density of signs of rat activity, such as rat droppings and burrows (Figure 2.2). It was hoped that there would be a range of rat densities associated with ecotopes/ecoelements allowing for a calibration of the survey techniques across several density strata. Whilst an ecotope is used to describe a homogenous spatial unit *e.g.* vegetation structure, an ecoelement is an individual feature such as a drystone wall (Whittaker *et al.* 1973; Klijn & de Haes 1994). As such, ecotopes (vegetation type) and ecoelements (linear features) were used to stratify samples. Based on the preliminary observations, and the site characteristics, it was expected that rat densities would be lower than would be expected for other sites such as UK farms, for instance.

Figure 2.2 A Norway rat burrow found during the preliminary site visits. Note the characteristic excavation pile containing common limpet, *Patella vulgate*, shells (arrow) from the adjacent foreshore. Limpets were commonly observed in the excavation pile of coastal rat burrows on Rum, but were never observed on interior sites. Shells can be up to 6cm in length.

2.3.2.2 Site selection

Stratified random sampling based on ecotope/ecoelement type was used to select 24 individual study sites, across six sample groups, divided into two categories (Linear; coast (*n*

= 4), river (n = 4), wall (n = 4) and non-linear; grassland (n = 4), heath (n = 4), woodland (n = 4)) (Appendix A, Figure 2.3). Sample groups were sampled once per season with individual sites only being sampled once during March 2013 – March 2015. Wall sites were not sampled in autumn but were sampled twice in winter. Seasons were defined using dates corresponding to the astronomical seasons as described in Figure 1.4.

Sample groups were decided upon using the following criteria:

1. Estimated Density: In order to optimise the survey techniques a variety of survey sites with a range of associated rat densities were required. Based on the preliminary *ad hoc* surveys an indication of the general range of densities was established, and coast and walls were identified as important linear features.

2. Biological Significance: The data collected during this project may contribute to the future management policy of Norway rats on Rum, with a particular emphasis on the possible impact on the Manx shearwater colony. Manx shearwaters breed on upland grassland on Rum; as such, this vegetation type was selected for sampling. Furthermore, rivers were identified as potential movement corridors for rats, allowing access to Manx shearwater colonies from surrounding areas.

3. Proportion of the total land cover on Rum; Heath accounts for a relatively large portion (approximately 33%) of the total land cover of Rum (Figure 2.4). As such, heath was selected for sampling.

4. Future Management: Scottish Natural Heritage is currently reviewing their woodland restoration plan for the island. As such, woodland was surveyed in order to estimate the impact any future vegetation changes may have on the ecology of Norway rats.

Non-linear groups were selected using shortened National Vegetation Classification community names (Rodwell 1991, 1992, 1995, 2000) (See Appendix A for a full list of vegetation types and plant communities). Linear groups were selected based on three linear features found on Rum (coast, river, wall). Within each group four study sites were selected for surveys. Study sites were randomly selected by community name in QGIS 1.8.0 Lisboa (QGIS Development Team 2012) using National Vegetation Classification data derived from Bates *et al.* (2002) (non-linear groups), OS VectorMap® District (Ordinance Survey 2016b) (coast sites), CEH Watercourse Network derived from Moore *et al.*(1994) (river sites) and OS MasterMap® Topography Layer (Ordinance Survey 2016a) (wall sites). In the case of wall sites, 'General Features-Obstructing' were selected from OS MasterMap® Topography data and either ground-truthed or confirmed using local knowledge to derive a wall spatial

data set for Rum. River data for Rum were extracted from the CEH Watercourse data by selecting 'Inland Water' to produce a standalone Rum river data set. Coastal sites were selected from the OS VectorMap® District Foreshore data for Rum. See Appendices B – D for maps created using the spatial data sets for all three linear features (coast, river, wall).
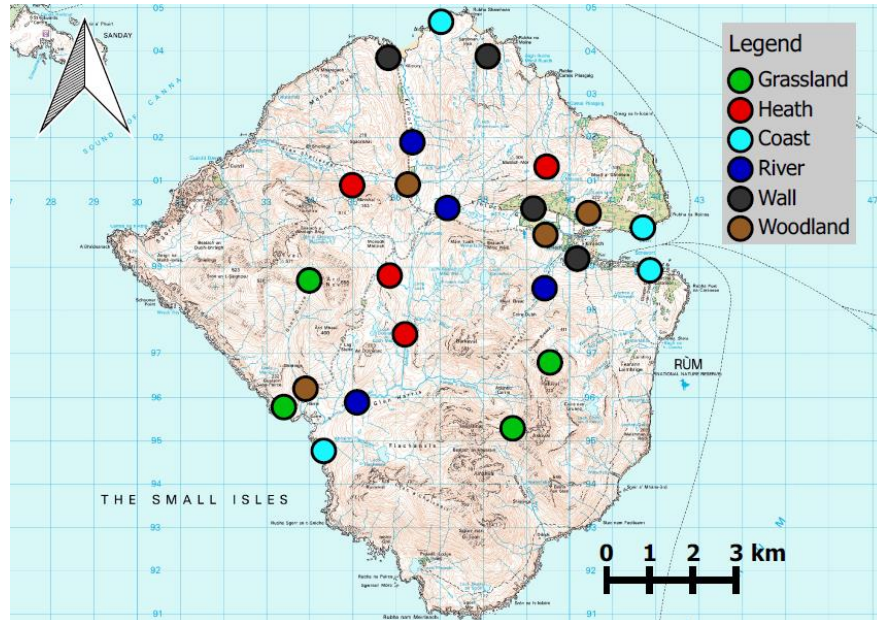
Figure 2.3 Map of 24 study sites across six ecotopes/ecoelements used to carry out two common rat activity survey techniques on Rum, 2013 – 2015. Arrow (top left) indicates grid north© Crown Copyright and Database Right 2018. Ordinance Survey (Digimap Licence).
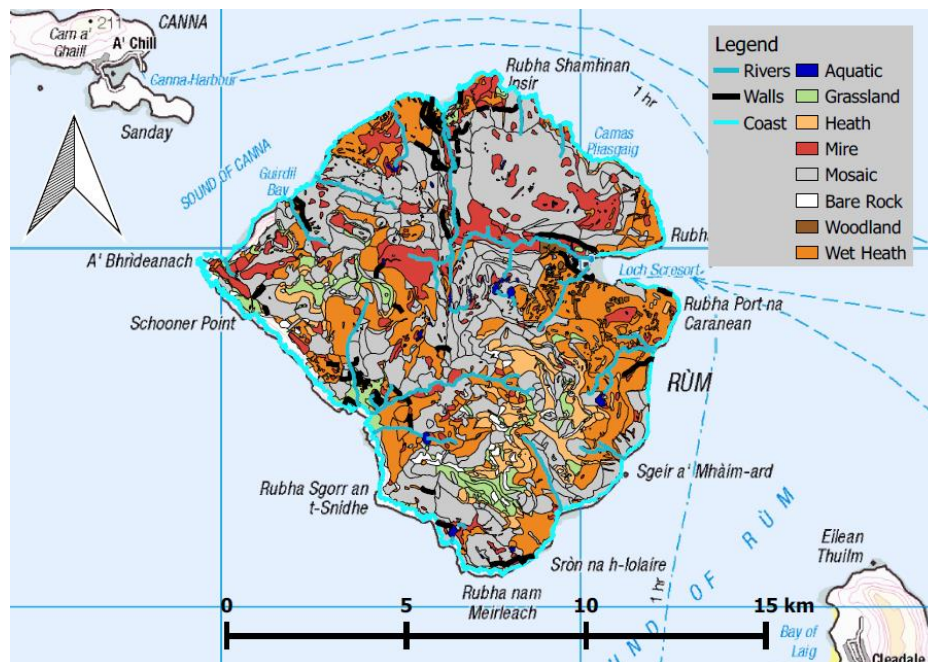
Figure 2.4 Map of ecotopes/ecoelements on the Isle of Rum, Scotland. Vegetation type based on NVC communities where appropriate. Wet heath was considered heath vegetation for survey site selection (data taken from Bates *et al.* (2002)). Arrow (top left) indicates grid north. © Crown Copyright and Database Right 2018. Ordinance Survey (Digimap Licence).

2.3.3 Transects

In preparation for transect setup, randomised transect start point grid references were downloaded to a hand-held Garmin GPS 60 (Garmin Ltd., Schaffhausen, Switzerland) via the software GPS Utility Version 5.19 (GPS Utility Ltd., UK). Initial attempts to remotely map whole transect survey areas using Transectizer Version 2.1 in QGIS were abandoned due to the topography on Rum. Digitized transects were produced in 2D and were unsuitable on steep terrain, producing transects of differing sizes. As such, a chalk line method was used to measure transect areas. A 100m x 1.5mm chalk line (Fisco FSCC4100, Fisco Tools Ltd., Essex, UK) was marked every 10m using permanent marker/insulating tape and a measuring tape. Strip/grid transects were used for linear/non-linear sites respectively. Transects were divided into 10m x 10m grids (intervals) arranged into the appropriate strip or grid design. Strip transect areas were marked out every 10m using the chalk line and spray paint (Templine Biodegradable Paint, M & P Survey Equipment Ltd., Chester, UK) and recorded in a GPS unit with a unique corresponding label. Grid transects were setup using two chalk lines and Pythagorean theory (right-angled triangle) to establish grid corners, ensuring the rectangular shape. Line A was used to measure 30m (10m points marked with paint). Line B was then attached to the start point of line A and rolled out to measure 40m, without ground marking, roughly perpendicular to Line A. The start point of Line A was then rolled out to 50m and moved to the 40m of line B. The point at which line A met the 40m point on Line B created a 90 degree angle at the initial start point (0m of Line A).This was repeated until all four grid corners were established, and the remaining internal 10m x 10m boundaries were marked using the chalk lines. Previous small mammal studies have used transect lengths ranging from 190- 250m (line transects) and 0.16 – 0.33ha (grid transects) with durations of one to three days (Pearson & Ruggiero 2003; Pankhurst *et al.* 2010; Stephens & Anderson 2014; Lambert *et al.* 2015). As such, an initial survey area of 0.50ha (500m x 10m, linear transects; 50m x 100m, non-linear transects) and six days was used to determine an appropriate (optimised) transect size and duration. A total of 12 study sites were sampled across two sample categories (linear *n* = 6; non-linear *n* = 6).

2.3.4 Tracking plates

Tracking plates were made by applying a clear, self-adhesive film (book-binding film) to standardised areas of white vinyl floor tile (100mm x 200mm). Activated carbon powder (Fisher Scientific UK Ltd., Loughborough, UK) was suspended in industrial methylated spirit (~25g litre^{-1}) and applied to the plastic coated side of the tile using a paint brush. Application

of the suspended carbon was carried out in a well-ventilated, dry atmosphere (when indoors). Plates were left to dry until the methylated spirit evaporated, leaving a thin weather-proof layer of carbon powder on the tile (Lambert 2003).

Following the method used on UK farms by Quy *et al.* (1993) and Lambert *et al.* (2008), tracking plates were placed where they were most likely to record rat activity *e.g.* beside burrows, runs, latrines or linear boundaries. Plates were placed at a density of 400ha^{-1} (four per 10m^2) and scored using a four-point system. An estimate of the percentage of each tracking plate covered in rat footprints was converted into scores using the following system: 0 = no prints; 1 = 1-25% of the plate covered; 2 = 26-95% covered; 3 = 96-100% covered (Figure 2.5). Plates with footprints were replaced daily. Scores were summed daily (total score) and then averaged to give a mean activity score per site.

A tracking plate pilot study was carried out prior to the commencement of the surveys proper in order to check the equipment, finalise the survey methods, and determine the type of data necessary. The pilot study was conducted on a coastal site, during the 21st January – 25th January 2013. Tracking plates were placed along a 150m transect line for 4/5 consecutive days, at a density of 400ha^{-1}. Plates were scored daily as described above.

Figure 2.5 A single tracking plate marked with rat footprints (activity score 2 = 26 – 95% footprint coverage). Animal and Plant Health Agency © Crown copyright, used with permission.

2.3.5 Wax blocks

Wax blocks were made by mixing 50g of wax pellets (iMelt paraffin-stearin blend, That Flaming Candle Company, UK) with organic cocoa powder (organic fairtrade cocoa powder, Green & Blacks, UK) at a ratio of approximately 1tsp of cocoa to every 150g of wax (Miller

2008). The cocoa powder was used as a rat attractant to encourage target species to chew the blocks (Figure 2.6). Wax was melted in a stainless steel jug, mixed with the appropriate amount of cocoa powder, and poured into pre-greased (vegetable oil) moulds. Moulds were placed on a top-pan balance (EMB 1200-1, Kern & Sohn GmbH, Balinger, Germany) to ensure 50g of wax mixture was poured into each mould. Once dry, wax blocks were removed and central holes were added using a heated Phillips-head screw driver. Blocks were then given a unique label underneath, and then reweighed. Wax blocks were placed at a density of 1 per 50m, a common spacing for toxic bait placement during eradication projects (Lock 2006; Bell *et al.* 2011). Wax blocks were randomly placed every 50m (to the nearest 1m), using tent pegs inserted through the central holes of the wax blocks. Blocks were left overnight and checked daily; chewed blocks were removed and replaced as necessary. Chewed wax blocks were scored using a similar method to the tracking plates. The percentage of the visible surface chewed by rats was estimated, and given an activity score using the same scoring as with tracking plates (0 = no chew marks, 1 = 1-25% of the wax block surface chewed, 2 = 26-95% of the surface chewed, 3 = 96-100% chewed). A general note on the amount chewed (no take, partial take, complete take) was also recorded. A score of 100% was given to any blocks that were completely missing, if confirmed by other signs of rat activity such as fresh droppings.
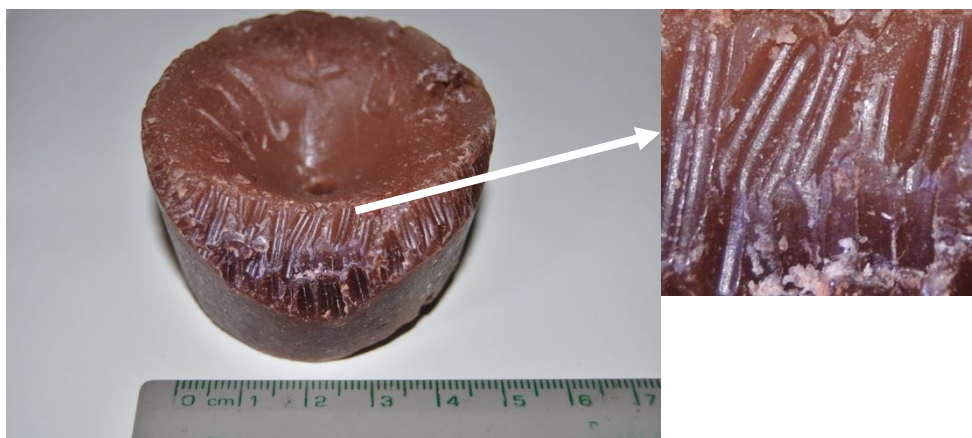
Figure 2.6 A Chocolate wax block (50g) with characteristic double tracked rat teeth marks. This block had an activity score of 1 (1-25% of surface chewed).

Tracking plate and wax block surveys were run sequentially on each study site (within 2 weeks). It was deemed that chocolate wax blocks may attract neighbouring rats from outside the study area and reduce the validity of the tracking plate surveys. As such, wax block surveys were conducted after tracking plate surveys.

Data was also collected on the number of tracking plates and wax blocks showing signs of wood mouse activity.

2.3.6 Analysis

Bootstrapping (with diminished returns) of the survey data was carried out in the software package RStudio 0.97.247 (RStudio, Boston, USA), to establish the optimal parameters (number of survey days, transect area) needed to achieve an acceptable level of precision (≤ 0.2 (standard deviation of the bootstrapped distribution of the mean)) in the data. Bootstrapping is a non-parametric resampling method used for estimating properties of an estimator (*e.g.* variance) by measuring those properties when sampling from an approximating distribution (Manly 2006). The bootstrap method treats the empirical distribution of the sample as the true distribution and resamples from this distribution (Manly 2006). The exact distribution of a statistic is then approximated using the empirical distribution and the bootstrapped data (Dixon 2002). Bootstrapping uses the variance of the sample data to calculate several random data sets, recalculates the mean and variance, and gives a range of possible sample means based on the parameters of the original sample data. The result is a mean of several means (often 10,000 randomised means) which is intended to better measure uncertainty to give a more reasonable level of confidence that the true value lies within the confidence intervals calculated by bootstrapping. Bootstrapping is a useful resampling tool for conducting power analysis (estimating samples sizes) with sparse data (Bros & Cowell 1987; Manly 1992).

Mean tracking plate and wax block activity scores per sampling unit (survey day, transect interval ($10m^2$)) from the six tracking plate/wax block surveys were resampled in accordance with the assumptions about independence between groups. The data was resampled (with replacement) 100,000 times resulting in a distribution of estimates used as the sampling distribution to estimate precision using the standard deviation of this distribution. Sample groups and categories were bootstrapped separately to establish the worst-case optimum parameters (all groups/categories had a standard deviation of the bootstrapped distribution of the mean (precision) of ≤ 0.2).

Daily activity score totals for tracking plates (% of plate covered in rat prints: 0 (no rat prints), 1 (1-25%), 2 (26-95%), 3 (96-100%)) and wax blocks (% of block surface with rat chew marks: 0 (no chew marks), 1 (1-25%), 2 (25-96%), 3 (96-100%) were averaged to give a mean activity score per survey type per site.

Mean activity scores were then analysed for differences between linear/non-linear categories, and ecotope/ecoelement groups, using a one-way ANOVA in SPSS version 20.0 (SPSS Inc., Chicago, USA) and Tukey's honestly significant difference test for pairwise

comparisons. The dependent variable was derived from percentages converted into discrete scores. These scores were then totalled daily and averaged per site, resulting in mean activity scores of continuous data. Furthermore, tracking plate data was $\log_{10}$ transformed to ensure the data were normally distributed.

Following the optimisation phase, a further 12 sites (linear $n = 6$, non-linear $n = 6$) were surveyed using the optimised transect parameter results.

2.4 Results

2.4.1 Optimisation of survey techniques

2.4.1.1 Optimisation of tracking plates

The bootstrapping output using six tracking plate surveys indicated that linear sites reached a precision of 0.2 (standard deviation of the bootstrapped distribution of the mean) at approximately 35 transect intervals (35 x $10m^2$ = 0.350ha) and three days (Figure 2.7). Non-linear sites produced better precision than linear sites; with a precision of 0.1 being achieved at approximately 10 transect intervals (10 x $10m^2$ = 0.100ha) across 1 day.
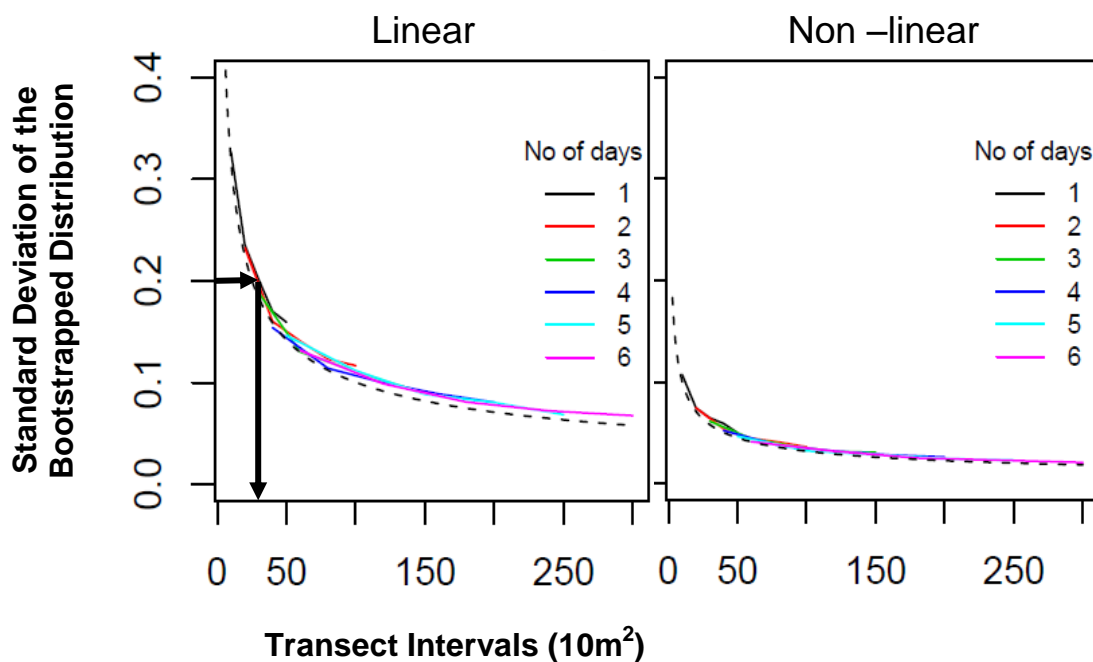
Figure 2.7 Bootstrapping results per sample category (linear/non-linear) for tracking plate surveys ($n = 6$ (per category)). Arrows indicate optimised parameters for a precision (standard deviation of the bootstrapped distribution of the mean) of 0.2. The dotted line shows the mean standard error as a function of the total number of transect intervals ($10m^2$), as expected given the "real" SD - calculated as "real" SD/sqrt (N). Note that the standard deviation of the (bootstrapped) sampling distribution tends to be higher than this.

2.4.1.2 Optimisation of wax blocks

Bootstrapping results using the six linear wax surveys suggested that linear sites did not reach the target precision of 0.2 (standard deviation of the bootstrapped distribution of the mean) within 300 transects intervals (300 x $10m^2$ = 3.00ha) across a maximum of 6 days (Figure 2.8). Bootstrapped non-linear wax surveys, however, produced a precision level of 0.2 at approximately 35 transect intervals (35 x $10m^2$ = 0.350ha) across 2 days.

Overall, only linear wax block surveys did not produce an acceptable level of precision (0 – 0.2), with all other surveys reaching acceptable precision by 35 transect intervals (35 x $10m^2$ = 0.350ha) across 3 days.
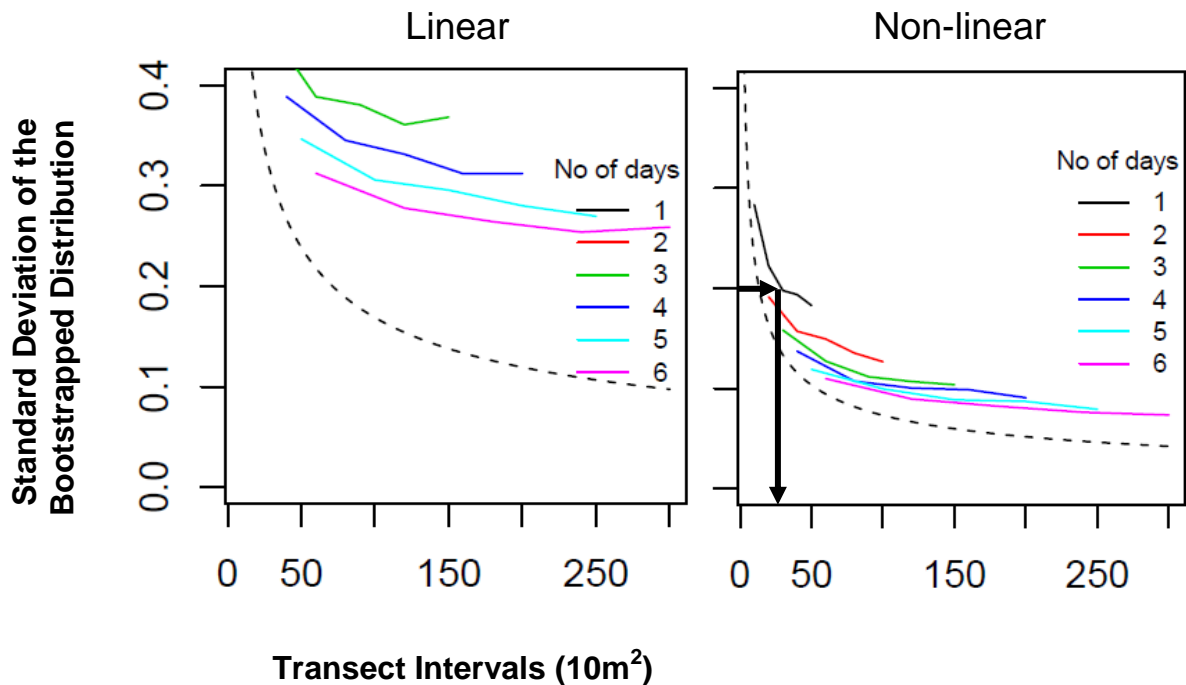
Figure 2.8 Bootstrapping results per sample category (linear/non-linear) for wax surveys (n = 6 (per category)). Arrows indicate the point at which a precision (standard deviation of the bootstrapped distribution of the mean) of 0.2 is achieved. The dotted line shows the mean standard error as a function of the total number of units, as expected given the "real" SD – calculated as "real" SD/sqrt (N).

2.4.2 Activity surveys

2.4.2.1 Tracking plates

A total of 12 sites per sample category were used for the tracking plate surveys (linear; grassland (n = 4), heath (n = 4), woodland (n = 4) and non-linear; coast (n = 4), river (n = 4),

wall (n = 4)). Tracking plate mean activity score for linear sites was 29.93 ± 7.13 (S.E.) and 13.77 ± 6.75 for non-linear (Figure 2.9). Coast (56.21 ± 9.58) had the highest mean activity score for tracking plates, and heath (1.87 ± 0.81) had the lowest (Figure 2.10).
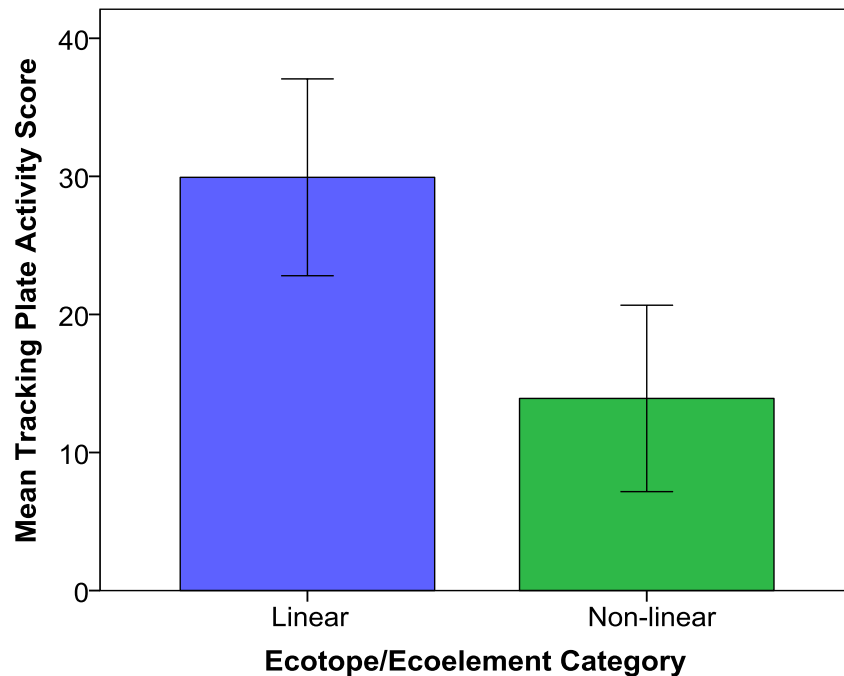
Figure 2.9 Mean tracking plate activity scores (S.E.) per ecotope/ecoelement category.

The Shapiro-Wilk's test (P>0.05), and visual inspections of their box plots, normal Q-Q plots and their histograms showed that both linear (Shapiro-Wilk's: W = 0.901, df = 12, P = 0.164) and non-linear (Shapiro-Wilk's: W = 0.971, df = 12, P = 0.923) sample categories were normally distributed. The linear category had a skewness of -0.325 (S.E. = 0.637), and a Kurtosis of -1.459 (S.E. = 1.232), whilst the non-linear category had a skewness of 0.210 (SE = 0.637), and a Kurtosis of -0.485 (S.E. = 1.232). In order to test for equality of variance a Levene's test was carried out and showed no difference in variance between sample categories for log_{10} mean tracking plate activity scores ($F_{1,22}$ = 1.335, P = 0.260).

There was a significant difference between the log_{10} transformed mean activity scores for tracking plates between sample categories (one-way ANOVA: $F_{1,22}$ = 7.031, P = 0.015) and sample groups (one-way ANOVA: $F_{5,18}$ = 6.220, P = 0.002). No difference was found between log_{10} transformed mean activity scores within linear sample groups (Post hoc Tukey: Coast/River, P = 0.454; Coast/Wall, P = 0.317; River/Wall, P = 1.000), but heath and woodland non-linear groups differed (Post hoc Tukey: P = 0.024). Mean log_{10} transformed tracking plate activity score was higher on the coast than both heath and grassland (Post hoc Tukey: P = 0.002 (heath), P = 0.010 (grassland)). No other differences were found.

Mouse footprints were recorded on 3 (coast), 28 (river), and 38 (wall) tracking plates on linear sites, and 2 (heath), 13 (woodland), and 117 (grassland) on non-linear sites.
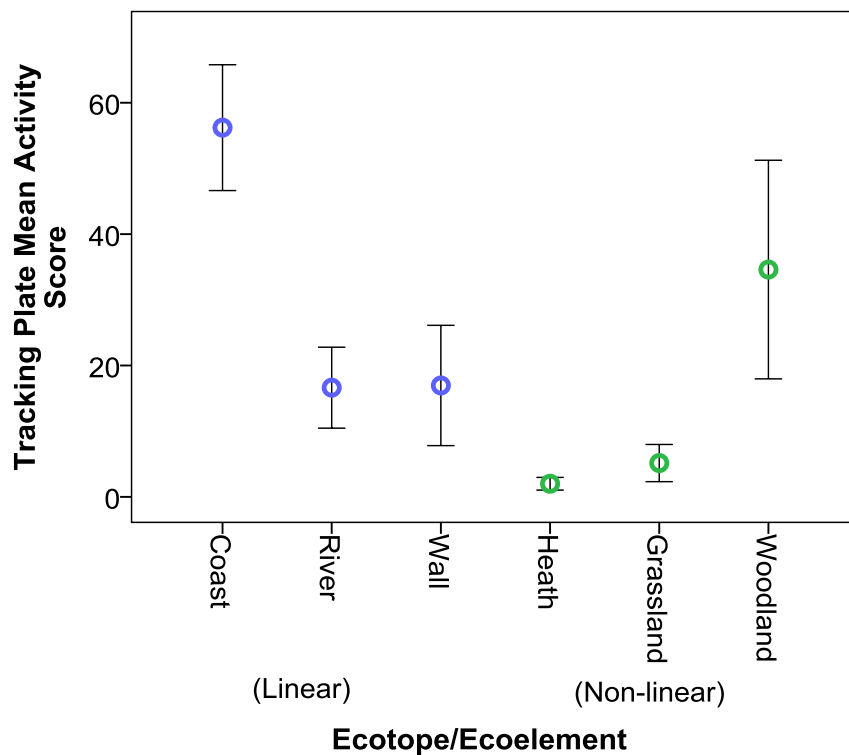
Figure 2.10 Mean tracking plate activity scores per ecotope/ecoelement with error bars (S.E.). Linear and non-linear categories are represented using blue and green markers respectively.
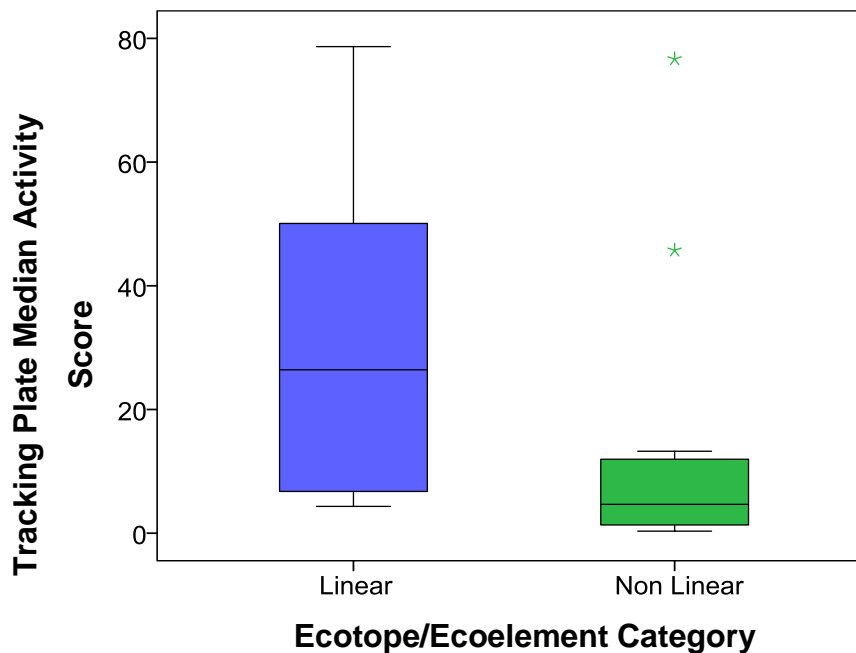
Figure 2.11 Boxplots of the median tracking plate scores per sample category. The two non-linear outliers (green asterisks) represent woodland 3 and woodland 4.

2.4.2.2 Wax blocks

A total of 12 sites per sample category were used for wax block surveys (linear; grassland (n = 4), heath (n = 4), woodland (n = 4) and non-linear; coast (n = 4), river (n = 4), wall (n = 4)). Mean wax activity score for linear sites was 11.28 ± 2.94 (S.E) and 6.55 ± 2.29 for non-linear (Figure 2.12). As with the tracking plate surveys coast sites (17.71 ± 7.45) had the highest mean wax activity scores; however, unlike tracking plates, grassland (1.69 ± 1.69) had the lowest mean wax activity score for non-linear sites (Figure 2.13).
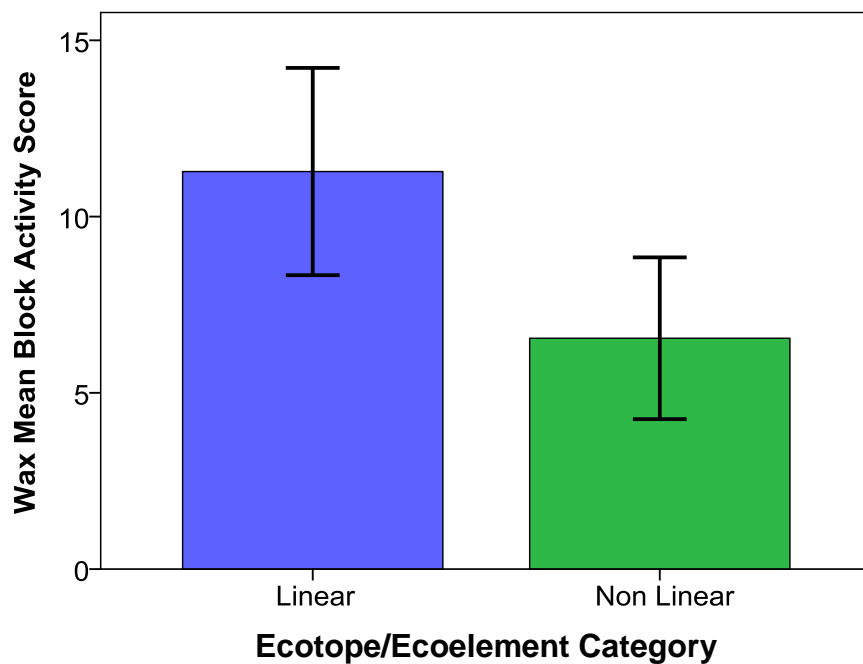
Figure 2.12 Mean wax block activity scores (S.E.) per ecotope/ecoelement category

Prior to analysis, a constant (10) was added to the mean wax activity score of each site (n = 24). Adding a constant allowed all mean wax activity scores (zero counts) to be included in the analyses. All data was then $\log_{10}$ transformed, to ensure they were normally distributed. The subsequent Shapiro-Wilk's test (P>0.05), and visual inspections of their box plots, normal Q-Q plots and their histograms showed that both linear (Shapiro-Wilk's: W = 0.959, df = 12, P = 0.763) and non-linear (Shapiro-Wilk's: W = 0.871, df = 12, P = 0.066) categories were normally distributed. The linear category had a skewness of -0.387 (S.E. = 0.637), and a Kurtosis of -0.400 (S.E. = 1.232), whilst the non-linear category had a skewness of 0.764 (S.E. = 0 .637), and a Kurtosis of -0.463 (S.E. = 1.232). In order to test for equality of variance a Levene's test was carried out and showed no difference in variance

between sample categories for $\log_{10}$ transformed mean wax activity scores ($F_{1,22} = 0.023$, $P = 0.881$).

There was no significant difference in $\log_{10}$ transformed+10 mean wax activity scores between sample categories (one-way ANOVA: $F_{1, 22} = 1.922$, $P = 0.180$) or sample groups (one-way ANOVA: $F_{5,18} = 2.147$, $P = 0.106$).
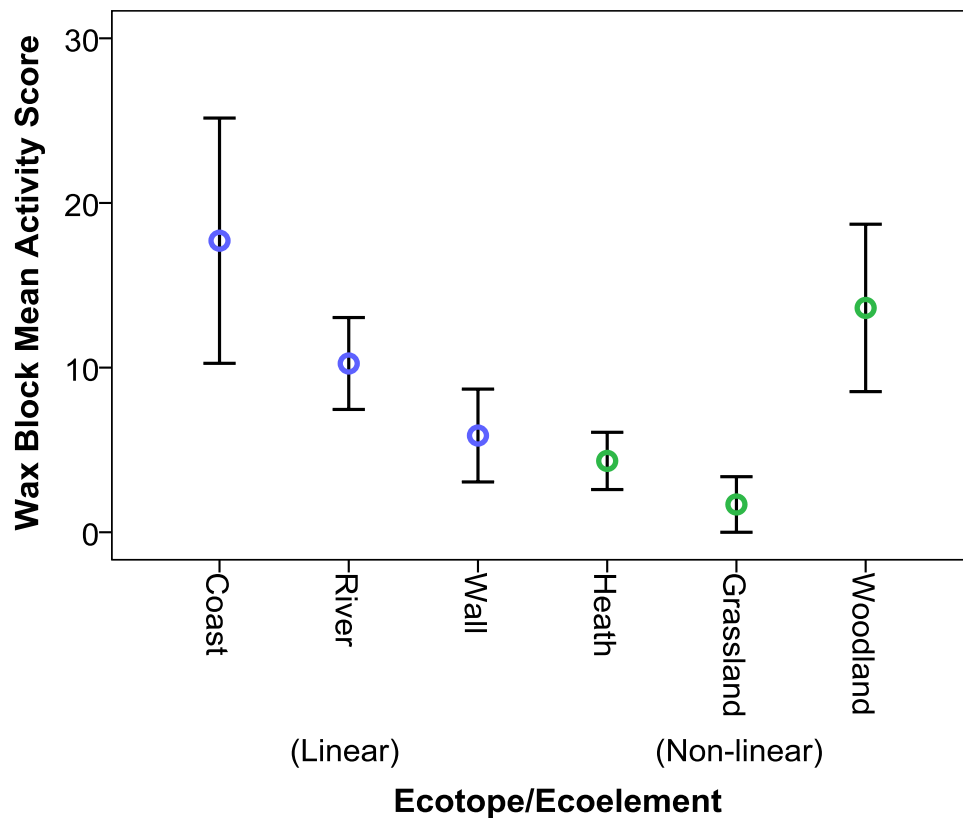
Figure 2.13 Error bars of wax block mean activity scores per ecotope/ecoelement. Linear/non-linear categories are represented using blue and green markers respectively.

Mice chew marks were recorded on 9 (coast), 24 (wall), and 51 (river) wax blocks on linear sites, and 0 (heath), 9 (wood), and 81 (grassland) on non-linear sites.

2.5 Discussion

2.5.1 Context: survey optimisation and activity scores

2.5.1.1 Optimisation

Optimisation of the tracking plate and wax block survey methods for both linear and non-linear sites on Rum provides a basis for predetermining transect parameters for Norway rat surveys on Rum. Furthermore, this may be useful for future studies on Rum and elsewhere if

conditions such as rat density and variation between transects are likely to be similar. Whilst methods such as sequential sampling have been used in the past, bootstrapping offers a potentially more robust novel option for optimisation of survey designs (Kuno 1969). Tracking plates reached an acceptable level of precision (standard deviation of the bootstrapped distribution of the mean) of ≤ 0.2, within three days and 35 transect intervals (35 x 10m^2). Similar optimisation parameters were found by Wood & Fee (2003) who suggested an increase in bias occurred at less than three days, and approximately 50 distance units (10m^2), when sampling wood rats using transect grids. Whilst non-linear wax block bootstrapped data reached an acceptable precision level within similar parameters to tracking plate data (35 transect intervals, 3 days), wax blocks in linear environments on Rum were much less precise and optimal parameters were not established within the maximum units sampled. The use of wax blocks may be less reliable as study subjects adjust to the novel food source (Chitty 1954; Meehan 1984). As such, tracking plates are preferred for producing rat activity indices over wax blocks in linear environments, with both survey techniques potentially suitable enough in non-linear environments.

2.5.1.2 Activity surveys

Previous work has suggested that linear features may be important movement corridors for several different species (Beier & Noss 1998; Dover *et al.* 2000). Norway rat mean activity scores (tracking plates) were higher on linear than non-linear sites on Rum, with no differences in mean activity score found within linear environments. This suggests that rats use linear environments (coast, river, wall) more than non-linear environments (heath, grassland, woodland) surveyed on Rum; if we assume activity indicates use. This result may be partly due to the requirement for Norway rats to have access to a water source, with two of the linear groups being associated with water (coast & river). For instance, in their native range in the Amur Basin, Russia, Norway rats have been reported on river banks up to 70km away from human habitation (Khamaganov 1972). Invasive Norway rats are frequently reported in wet habitats over arid ones; however, this may be in response to interspecies interaction, especially in the presence of black rats (Key & Muñoz 1994; Phillips 2010; Harper & Bunbury 2015). Taylor (1978) suggested that Norway rats use river banks in the presence of stoats. Hickson *et al.* (1986), however, reported that rat signs were not only found in close proximity to rivers or the coast, although 75m was considered 'away' from these linear features. On Rum, only two other rodent species are present (pygmy shrew, wood mouse) and the mean activity score from rats in woodland sites was the second highest score of all ecotopes/ecoelements surveyed on Rum. Norway rats are not typically

associated with woodland, given the competition for resources. The black rat, for instance, is thought to have largely pushed Norway rats out of most of the forested areas of New Zealand (King *et al.* 2011). Woodland tracking plate mean rat activity score also had a large range (5 – 76) on Rum. In particular woodland 3 and 4 were surveyed in autumn and winter and had high mean activity scores in relation to all other non-linear sites surveyed (Figure 2.11). The surrounding areas of woodland sites were grassland and heath; the two least active sample groups overall. Mean rat activity on coastal sites also differed from grassland and heath sites. It is possible that woodland offers an intra-island refuge for Norway rats on Rum, especially in the absence of interspecific competition. Woodland environments may also contain relatively high plant and invertebrate abundance and diversity, increasing food availability and subsequent survival of 'woodland' rats, but without evidence this needs evaluating.

Considering that grassland and heath (including wet heath) vegetation covers approximately 38% of the total land cover of Rum, it may be possible to consider the difference in rat activity on Rum as one between the interior and coast, as was previously suggested by Thompson (1987) on Rum. A similar pattern was also seen on Langara Island (Drever 1997; Kaiser *et al.* 1997). Furthermore, on the neighbouring isle of Canna, Norway rat signs were recorded in every ecotope surveyed but it was noted that the coast had the highest levels of activity (Patterson & Quinn 2001); a pattern also seen on Egilsay Island, Scotland (Lambert & Carlisle 2010).

Considering the potential for cascade effects on intertidal communities posed by invasive rats, and the evidence of their ability to consume a range of species from coastal communities, an indirect tool for measuring relative population size of rats along linear environments such as coastlines could become a useful tool for the conservation of coastal species, especially on islands with relatively large coastal environments (Navarette & Castilla 1993; Kurle *et al.* 2008). In particular, understanding the relative population size of invasive rats may help evaluate the factors limiting the locations, timings and intensity of their potential impacts on coastal environments, allowing the optimisation of future management resources; especially when using a less demanding, non-invasive (indirect) survey method when compared with the potential costs (practical and ethical) of direct measurement such as trapping. Furthermore, current methods for post eradication monitoring on large scale seabird recovery projects often use indirect methods (non-toxic blocks) to assess the presence of invasive rats and ultimately to confirm the success (or failure) of the project (Harper 2006; Towns *et al.* 2009). Whilst wax blocks can be used to confirm the presence of invasive rats, questions have been raised about their validity as a

tool for obtaining Norway rat activity indices on Rum. In particular, wax block surveys on linear sites on Rum (areas with the highest level of rat activity) did not reach an acceptable level of precision within reasonable practical transect parameters. It is possible that bait consumption does not reach an asymptote quickly in areas of high rat activity (and possibly high density), as rats adjust to a novel food source and/or neighbouring rats are attracted into the survey site. In non-linear sites on Rum, where rat activity was lower, wax block surveys performed well in the analyses. This suggests that wax blocks can a useful way of confirming the presence of invasive rats on islands but that their use for estimating activity may be more valid in non-linear low-activity environments.

2.5.2 Limitations

Tracking plates were usually placed on different rat runs; however, sites varied in their visible rat signs and as such, plates were occasionally laid close to one another. This was likely to happen on very few occasions and is not expected to have any substantial effect on activity scores.

Tracking plates conformed to a standardised size, but varied with age. Some new plates were produced for this project while others had been used previously. Worn or damaged plates were removed from the sampling pack, prior to the initialisation of the fieldwork phase of the project. Furthermore, no new plates were created after the start of the first survey. A 'smudge test' was carried out by the fieldworker if there was any concern about the reliability of any tracking plate and failed plates were excluded from the survey prior to use. Plates were replaced daily during active surveys and as such there may be a slight bias towards fresher tracking plates towards the end of surveys, although tracking plate scores did not increase daily, indicating if there was an effect it was likely to be small. Daily surveys were usually recorded every 24 hours; however, occasionally time between surveys was up to 30 hours; variations occurred consistently across every site surveyed and as such a systematic bias was not introduced. Tracking plates and wax blocks may therefore have slight temporal variation but the effect is likely to be even across sample groups and relatively small. Furthermore, surveys were all conducted during the day and Norway rats are considered primarily nocturnal (MacDonald 2009).

Despite making every attempt to balance seasonality within sample group, this was not always possible. For instance, wall sites were sampled twice in winter, and autumn was not studied at all. This may make comparisons between groups less reliable, but it is assumed that this effect will likely be small as a reasonable spread of seasons was sampled.

Comparisons within ecotope/ecoelement groups were not possible as sites were only sampled once per season; a lack of seasonal replicates within groups may therefore confound the data. For instance, whilst differences between and within sample categories (linear, non-linear) were found, these differences may be a result of season, site differences, or both.

2.5.3 Conclusions

Overall, optimised parameters were calculated to 35 transect length units (35 x 10m^2), across three days, to achieve a precision of 0-0.2, for tracking plates (linear & non-linear categories) and wax blocks (non-linear only). Precision for wax blocks in linear sites was lower and a precision of 0.2 was not reached within the transect parameters tested, meaning that the results from this survey method were considered unacceptably variable.

Mean tracking plate activity score was higher on linear sites (coast, river, wall) than non-linear sites (grassland, heath, woodland). An overall difference was found in mean tracking plate rat activity score between ecotope/ecoelement groups. No difference was found between linear groups but mean activity score differed between non-linear groups, with activity higher on woodland than heath sites.

Mean activity score did not differ between sample categories or sample groups using wax blocks.

2.5.4 Recommendations

Optimisation of the wax block survey method in linear environments was not achieved in this study and as such warrants further investigation especially in regards to optimum survey parameters for the study of invasive rats on islands.

Mean activity score for woodland sites was highest in winter, whereas for coastal sites mean activity score was highest in autumn. Given these differences a thorough investigation into the interaction between ecotopes and season and the effect this has on Norway rat activity would provide an understanding of the ecotopes essential for rat survival on Rum. For instance, does rat activity increase seasonally on key ecotopes on Rum, especially in relation to avifauna breeding seasons? Do woodlands provide overwinter refuge for rats on Rum? Do coastal populations of rats vary over seasons, or do they support year-round stable populations? Understanding the effect that season has on ecotopes and sub-

populations of rats on Rum would provide useful data for the management of these species, indicating when, where and how intensively to manage them in the future.

Chapter 3 – Movement Patterns and Habitat Use

3.1 Introduction

3.1.1 Rodents are defined by their habitat choices

Rodent species are commonly categorised by their habitat choices. Some genera including *Apodemus* for example, typically favour natural ecosystems and do not generally depend on man-made resources. Synanthropic species including Norway rats actively select man-made ecosystems, exploiting the more reliable (and abundant) resources (Meerburg *et al.* 2004; Harper 2005). Synanthropic rat species (and control methods) have been studied extensively in relation to their impacts on human interests (disease transmission, agriculture), whereas natural (field) species are often the focus of conservation efforts (Tew & MacDonald 1993; Ellis *et al.* 1999). Synanthropic and natural rodent species vary in their range of habitat choices; some are generalists while others are associated with a narrow range of habitats (Adler & Seamon 1991; Harper *et al.* 2005; Ruffino *et al.* 2011). Synanthropic rodents with a higher level of habitat plasticity (the generalists) have largely dominated ecological rodent research, due to their association with man. Rodent species not associated with man, however, are increasingly studied especially in relation to their invasive conservation threat in natural ecosystems (Towns *et al.* 2006; Jones *et al.* 2008; Mulder *et al.* 2009). The Norway rat, for instance, has been associated with the displacement and extinction of numerous species across the world, and their widespread distribution has far reaching consequences (Towns & Broome 2003; Travaset *et al.* 2009). The distribution of Norway rats covers most regions of the world including Asia, Africa, North, Central and South America, the Caribbean, Europe and Oceania and 35% of all islands (Atkinson1985; Schotman 1989; Tobin & Sugihara 1992; Global Invasive Species Database 2014). In the UK, Norway rats are ubiquitous, with the exception of some offshore islands (Global Invasive Species Database 2014).

3.1.2 What drives habitat selection?

3.1.2.1 Life history

Species can be described as having semelparous or iteroparous life cycles, depending on whether they exhibit a single reproductive period (semelparous) shortly followed by death, or many reproductive periods (iteroparous) throughout their life (Begon *et al.* 2006). The pacific pink salmon, *Oncorhynchus gorbuscha*, for instance, usually dies within days of spawning

(Heard 1991), whereas the African elephant, *Loxodonta africana*, can have several offspring throughout its lifetime, with the potential to breed for several decades until death (Stansfield *et al.* 2013). Vertebrates are usually iteroparous, and bacteria, plants and invertebrates are commonly semelparous, although there are always exceptions, such as the previously mentioned pink salmon and *Antechinus* spp. of marsupial mice, which usually only produce one litter followed shortly by parental death (Braithwaite & Lee 1979). Differences in life histories can be described in relation to reproductive allocation, with individuals investing the greatest contribution to the future of the population being naturally favoured (Van Noordwijk & de Jong 1986; Stearns 1989). In an environment with finite resources, however, trade-offs between resources have to be made, such as reproductive value versus age. Reproduction also comes at a cost with a likely decrease in individual survival and rate of growth (Zera & Harshman 2001). Classification of habitat types therefore may be considered in terms of their relative reproductive cost (RC), with some habitats comparatively higher RC than others (Bazzaz *et al.* 1987). In this sense life histories will play a major role in the selection of habitats by individuals. Habitat quality, however, will be determined by a number of factors such as competition, predation, and abiotic factors (Olsson *et al.* 2002; Martin & Joron 2003). Life histories are therefore often semi- permanent for individuals, and phenotypic plasticity will allow some species to adapt their behaviour in response to changes in environmental conditions (Stearns & Koella 1986; Nylin & Gotthard 1998). Thus, habitat types may be considered as *r* or *K*-selecting, that is we have habitats with limited environmental fluctuations and a large stable population, or habitats that are unpredictable with unstable populations (Davies *et al.* 2012).The convention, however, is to describe organisms rather than habitats as *r*/*K* selected, where *r* describes an organism that exhibits rapid reproduction, whereas *K* has lower reproductive allocation and fewer offspring. One of the simplest ways to view a population is as a single undivided entity, distributed more or less continuously across favourable habitat. In practice, however, populations of species are patchily distributed, generally due to the availability of resources and conditions for reproduction and survival (MacArthur & Pianka 1966; Guisan & Thuiller 2005; Begon *et al.* 2006).

3.1.2.2 Competition

Organisms can be distributed in a random, uniform or clumped spatial pattern (Krebs 1999). Species are therefore often distributed as collections of sub-populations (Begon *et al.* 2006). It has been widely reported that rodent species sharing habitats will partition resources (Harper 2006). Competitive exclusion dictates that two species exhibiting niche overlap

cannot exist at constant population values without a behavioural change (Hardin 1960). The mechanisms for interspecific partitioning will differ between changing activity budgets, change in diet, or division of habitats into micro-habitats (Price 1978; Kotler *et al.* 1993; Wisheu 1998). Intraspecific competition occurs when the combined demand by the same species for a resource exceeds its availability. Highly competitive individuals may be rewarded with preferred resource patches, but differences exist between patch profitability and competitive ability both within and between species; thus, animals compete with each other for space (Ranta *et al.* 2005; Svanbäck & Bolnick 2007). Competition may be indirect, with resource exploitation by one individual affecting another's ability to survive, grow and/or reproduce, or directly by interacting to protect preferred resources (agonistic behaviour *e.g.* fighting/territoriality) (Begon *et al.* 2006; Krebs & Davies 2009). As such, competition can limit the distribution and movement patterns of individuals by reducing available resources (Best *et al.* 2007). Competition between individuals may lead to dispersal; the movement an organism makes from its point of origin (Howard 1960; Hansson 1991). Movements within the same area over a given period of time (home range) also occur, with temporal shifts (migration) between seasons and timescales allowing organisms to seek vital resources (Burt 1943; Cox 1968; Branch 1975; Caughley 1977; White and Garrot 1990). Migration may result in immigration or emigration of individuals or a population (Pulliam 1988).

In the UK, Norway rats appear to out-compete related rat species in urban and agricultural environments (Gardener-Santana *et al.* 2009; King *et al.* 2011). In an island context, however, rats have been found in several environments not associated with man including; grassland, shrubland, rivers, and forests (Patterson & Lloyd 2000; Major *et al.* 2007). On the isle of Canna, for instance, Norway rats were found on all ecotopes, albeit with higher densities around the coast (Patterson & Quinn 2001). The greater use of natural ecosystems by rats on islands is not uncommon (compared to mainland contexts where they are more typically associated with human activities), and potentially reflects reduced competition for resources and a lack of interspecific competition compared to man-made ecosystems found in mainland contexts.

3.1.2.3 Biology and behaviour

Movement of individuals to selected resources is therefore influenced by competition and life history, but differences in movement patterns such as dispersal have been reported between individuals, sexes and ages (Greenwood 1980; Swingland & Greenwood 1983; Stenseth & Lidicker 1992). In highly social mammal species there is often a difference in dispersal rates

between sexes, although this is not always the case (Greenwood 1980; Dobson 1982). Krebs *et al.* (1976) found that dispersal rates of Townsend's voles, *Microtus townsendii*, were 25% higher in males than females. Female rodents of the squirrel Scuridae family typically remain close to their birth sites and set up home ranges adjacent to their family (Holekamp & Sherman 1989). Whilst the convention is to accept a general bias towards male dispersal in mammal species, Mabry *et al.* (2013) reported larger female dispersal distances in four species, with social mating systems playing an unknown role. The relationship between movement and resource selection is therefore not straightforward.

3.1.3 Movement and home range

3.1.3.1 Movement patterns of rats

Activity patterns of rodent species have been well documented and differences between and within species have been found (Kenagy 1973; Roll *et al.* 2006). Norway rats, for instance, are primarily nocturnal; however, factors such as predation, competition, and access to food can alter this adaptive mammal's behaviour (Macdonald 2009). Taylor (1978) found that Norway rats were mostly active at night on farms in the UK, however a few individuals did leave home sites during the day and one rat was primarily diurnal. Furthermore, activity patterns of individual rats also differ. For instance, Nieder (1985) found that whilst some of the study subjects showed a typical bimodal pattern of behaviour; peak activity shortly after sunset and shortly before sunrise, others displayed what appeared to be random patterns. These differences could be due to a number of factors including temperature, photoperiod, prey activity, individual differences, predation pressure, disturbance, competition, and social structure (Calhoun 1963). Like most group living rodents, Norway rats live in socially hierarchically structured groups, and in a population with a stable food source closely related females will defend neighbouring territories, forcing out unrelated intruders (MacDonald 2009). Temporal and spatial differences in movement patterns can also be due to a number of other factors including environmental conditions, habitat, resource availability, and interactions with conspecifics (Sanderson 1966). Male Norway rats generally have a larger home range size than females, although this is not always the case; Moors (1985) found male rats on Motohorupapa Island, New Zealand, moved distances more than twice that of females, whereas synanthropic populations tend to have more similar ranges (Lambert *et al.* 2008). Differences in home range size are often found between ecotope types, with resource-rich farm buildings supporting smaller home range sizes than less favourable field margins (Lambert *et al.* 2008). Norway rats have been known to develop groups around

stable food sources and will move nesting sites (home sites) once the resource has depleted; however, home sites are not always associated with potential food sources (Taylor 1978).

3.1.3.2 Studying rodent movement patterns

At a regional level, ecotopes such as vegetation type can be compared across spatial scales to give an indication of which vegetation types are selected, with comparisons of home 'core' areas and total areas indicating preference. For instance, if the use of a vegetation type, as indicated by the home range of an individual, is larger than the proportional availability, a selection is implied (Johnson 1980). Difficulties, however, are concerned with choosing the correct spatial scale to compare, and indeed their methods of estimation.

Various methods have been employed to study the movement patterns of rats (Hardy & Taylor 1980; Hickson *et al.* 1986; Key & Woods 1996; Ringler *et al.* 2014; Byers *et al.* 2017). Traditional capture-mark-recapture has been used extensively to study the small and large movement patterns used to estimate home range size derived from trap distances, although trap spacing can have an effect on this method of home range estimation (Stickel *et al.* 1980; Weatherhead & Hoysak 1989). Spool and line has successfully been deployed to trace fine-scale movement of individuals within their home ranges; however, this method can be labour intensive, does not provide any temporal data on movement, and may interfere with normal movement through spool entanglement (Key & Woods 1996; Mendel & Vieira 2003; Steinwald *et al.* 2006). With the development of increasingly light-weight technology using radio transmission backpack, tags and collars, these have been more commonly used to investigate the movement patterns of rats. Both manual and automated radio tracking has been successfully used for many rodent species (Taylor & Quy 1978; Dowding & Murphy 1994). Briner *et al.* (2003) developed an automated method for tracking movements of small mammals fitted with radio-transmitters, using fixed antennae and triangulation to obtain location estimates. More commonly, however, radio tracking data is collected manually. Rutherford *et al.* (2009) used radio collars to calculate the home range size of 14 black rats on Big South Cape Island, New Zealand, although new technologies are also becoming more popular; Global Positioning Technology (GPS).

GPS has been integrated into collars, with geolocations of study subjects being stored either passively (on collar) or actively (remote storage). Very few GPS studies have, however, tracked rodent species, with technology only recently becoming light enough for small mammals. Stevenson *et al.* (2013) tracked the movement of 9 grey squirrels, *Sciurus*

carolinensis, within fragmented habitats in Lancashire, UK. Byers *et al.* (2017) attempted to track 14 urban Norway rats using a mixture of passive and active GPS collars, but movement data was not obtained due to a variety of reasons *e.g.* tag loss, low recapture rates and tag malfunction.

3.1.4 Methods for studying home range and habitat use

3.1.4.1 Home range estimators

Home range size is the most commonly used spatial estimator in ecological studies of animal movement (Borger *et al.* 2009). Location data from radio tracking and GPS tagging is typically used to estimate home range sizes using two main approaches: minimum convex polygons (MCPs) and kernel density estimation (KDE) (Worton 1989; Harris *et al.* 1990; Nilsen *et al.* 2008). Minimum convex polygons are the oldest and most commonly used estimator of home range size (Powell 2000). MCP is the smallest possible polygon drawn where internal angles are not greater than 180 degrees and all locations are enclosed (Burgman & Fox 2003). Whilst this simple and easy method is still widely used it is likely to be influenced by extreme values, loses information from the internal location points, and may incorporate large areas unused by the organism (Powell 2000). As such, 95% MCPs are sometimes reported, which may at least reduce the effect of extreme outliers (Grinder & Krausman 2001; Herfindal *et al.* 2005). Whilst MCPs provide an estimation of the boundaries of a home range, kernel densities are increasingly popular as way of estimating home range (Hines *et al.* 2005; Katajisto *et al.* 2006; Hugh *et al.* 2015; Newsome *et al.* 2017). KDEs consist of placing a kernel (a probability density) over location points in a sample. A grid is superimposed on the data and an estimation of density is calculated at each grid intersection from the average densities of the overlapping kernels (Seaman & Powell 1996). The resulting densities are used to display the utilization distribution (the distribution of the organism's positions) (Worton 1989). As such, density estimations will be higher in areas with many observations, and lower with less observation. KDEs have therefore become a common method for studying animal-habitat relationships with multiple areas of a subject's activity easily being accounted for (Marzluff *et al.* 2004). Whilst KDEs do therefore appear to be a good method for estimating how an organism uses its environment, difficulties occur when choosing the exact kernel method (Hemson *et al.* 2005). In particular, decisions on optimal kernel width can be difficult and will affect the home range estimators, with narrow widths potentially highlighting measurement errors, and large widths losing local scale data (Silverman 2018). Many studies have therefore sought to establish a method for estimating

optimal band width (Bowman 1985; Silverman 1986; Worton 1989; Seaman & Powell 1996). In all cases of analysis, however, independence of data is a difficulty with most home range studies (Rooney *et al.* 1998). In particular, autocorrelation and time-to-independence of home range studies has received a lot of attention, despite some studies suggesting that removing autocorrelation may also remove important biological information (Blundell *et al.* 1999; Kernohan *et al.* 2001; Borger *et al.* 2006).

3.1.4.2 Habitat use

Home range studies are commonly used when estimating factors contributing to habitat selection and are often preferred in ecological studies (Cavanelli *et al.* 1994; Dickson & Beier 2002; White *et al.* 2006). Simply put, if the proportion (*i.e.* area) of an ecotope within a home range exceeds the proportion of the landscape composed of that ecotope then preference at the population scale is implied. Sampling design will therefore be important *e.g.* will data be collected on individuals, or will the populations be surveyed collectively? Also, if individuals are being studied, will ecotope attributes be recorded or just general categories used? Ecotope proportions of point locations and mean home range areas have both been used to compare spatial scales, and several methods are available to study habitat use (Morris 1987; Harris *et al.* 1990; Thomas & Taylor 1990).

Compositional analysis compares proportional use of ecotopes by comparing log-ratio transformed use and availability distributions with a log-likelihood ratio test (Aebischer *et al.* 1993; Beasley *et al.* 2007). It has been used frequently in habitat use studies, on a range of mammals including racoon dog, grizzly bear, and several species of bats. The test, however, requires a minimum of 10 tracked individuals, with more than 30 recommended (Aebischer *et al.* 1993).

Resource selection function (RSF) also uses proportional use, instead using utilization probabilities to determine a predictive model for a resource unit. RSF models are usually fitted using generalised linear models although a variety of models can be used (Boyce *et al.* 2002). In the case of used/unused ecotope data, logistic regression procedures can be useful. In the case of used/available data, however, used ecotopes may be considered a subset of available ecotopes and as such may not be an exclusive category in usual applications of linear regression, making analysis of this data potentially more difficult. Generally, however, RSF has often been used as a predictive tool for conservation planning and is increasingly being used for habitat use analysis (Boyce & McDonald 1999; Moorcroft & Barnett 2008).

Selection ratios/indices are perhaps the simplest methods for estimating habitat preferences. Early versions, for instance, simply compared percentages of use and availability (Manly *et al.* 2007). Variations since then, however, have tried to incorporate an electivity index where preference and avoidance can be described by the scale -1 (avoidance) to 1 (preference). Jacobs Index is one such selection index used to allow the comparison between selection and relative abundance of food types of several mammal species (Gregory & Baillie 1998). The index is an extension to the forage ratio and Ivlev's electivity Index, both of which may be less useful when relative abundance of food types vary (Ivlev 1961). In short, Jacob's Index is calculated using (Kauhala & Autilla 2010):

$$D = \frac{r - p}{r + p - 2rp}$$

EQ. 3.1

Where;

D = Jacob's Index

r = the proportion of a factor used by the study subject

p = the proportion of a factor available for the study subject

Use and availability therefore have to be defined before ecotope preference from movement patterns can be calculated. In this sense, we can consider habitat use as having three levels, in relation to home range size and ecotope type: Selection within a geographical area (order 1), use within the geographical range (order 2), and preference within the individual home range (order 3) (Kauhala & Autilla 2010). From this starting point, comparisons can be made between spatial scales to establish ecotope preferences, with larger scales often used as the available ecotope, and smaller scales indicating use from movement pattern data (Aebischer *et al.* 1993; Manly 2006; Kauhala & Autilla 2010).

3.1.5 Home range and habitat use in Norway rats

The majority of previous home range data available on Norway rat movement comes from habitats associated with agriculture, most of which comes from UK mainland studies (Taylor 1978; Taylor & Quy 1978; Quy *et al.* 1993; Lambert *et al.* 2008). Home range size estimates have been provided for poultry farms in Argentina (Villafañe & Busch 2008). MacDonald *et al.* (1999) reported home range lengths for Norway rats near UK farms but within woodland and river ecotopes also. Very little work has been done on the movement patterns of Norway rats on islands, with most of this research coming from New Zealand. Bramley (2014) radio

tracked the movement of eight Norway rats on Kapiti Island, New Zealand. Data are lacking on Norway rat movements on islands generally, with a substantial gap in the northern hemisphere. A difference in home range size is commonly reported between sexes of Norway rats, although this in not always the case. Taylor (1978) found that mean straight line measurements of home range were larger for male rats. Bramley (2014), however, reported similar home range size between sexes. Differences in home range size of Norway rats have also been reported across ecotopes (MacDonald *et al.* 1999; Lambert *et al.* 2008). MacDonald *et al.* (1999) reported differences in home range size between nutrient rich farmland and nutrient poor rivers. It seems clear therefore that whilst ecotope and sex differences are likely, availability and access to food may be a limiting factor for Norway rat home range size.

Norway rats have the potential for occupying a wide range of habitats and differences in ecotope use have evidently been recorded. On Stewart Island in New Zealand, Norway rats were found in all four defined ecotope types (manuka shrubland, podocarp-broadleaf forest, riparian shrubland and subalpine shrubland) with the highest density found in subalpine shrubland (Harper *et al.* 2005). Conversely, however, on Pearl Island in New Zealand, Norway rats were only present in coast trap sites, with no rats in forest or scrubland sites (Harper 2006). Norway rats are often associated with coastal and riverine environments. In the city of Salzburg, for instance, Norway rats generally preferred habitats with water, deciduous trees, and vegetation, avoiding areas of stone and no vegetation (Traweger *et al.* 2006).

3.2 Rationale and Research Questions

No previous research has investigated the habitat use or home range of Norway rats on the Isle of Rum. Bell & Ramsay (2011) lethal trapped rats in and around grassland sites (shearwater greens) on Rum, and found differences in the number of rats between shearwater grassland sites and non-shearwater sites, potentially indicating an effect of vegetation type (and associated food resources) - although this was not investigated. On the neighbouring island of Canna, rat abundance was surveyed using chew-sticks and showed that whilst Norway rats were found on all sites surveyed, coastal sites had the highest densities of chewed sticks of all ecotope types (Patterson & Quinn 2001).

The present study aims to investigate the movement patterns and habitat use of Norway rats on Rum. An understanding of the home range size will allow the potential of impacts to native species to be assessed, and will provide a comparison point for UK and European

island studies. Understanding habitat use of Norway rats on Rum will help the impacts of vegetation changes to be predicted; overall helping build a base of ecological knowledge in this understudied island setting. The following questions will be addressed in Chapter three:

1. What are the capture rates of Norway rats on Rum and do they differ between vegetation type, linear features and seasons?

2. What is the home range size of Norway rats on Rum, and do they differ between site/sex?

3. What are the habitat preferences in relation to vegetation type and linear features of Norway rats on Rum?

4. How feasible is the use of GPS tags to track the movement patterns of Norway rats on Rum?

3.3 Methods

3.3.1 Study sites

3.3.1.1 Live capture and release of rats

25 study sites including 24 from the optimisation and activity surveys as described in section 2.3.2.2 (Linear; coast ($n = 4$), river ($n = 4$), wall ($n = 4$) and non-linear; grassland ($n = 4$), heath ($n = 5$), woodland ($n = 4$)), were surveyed by repeated live trapping, with the intention of using the data later in the project to generate Norway rat population estimates from capture-mark-recapture (CMR) data (section 4.3.2.1) and to maximise the number of individuals PIT tagged and radio tagged for the home range and dispersal data. One heath site was trapped without previously carrying out activity surveys. Furthermore, repeated trapping was also carried out on several sites across seasons (Table 3.1)

Table 3.1 Details of repeated trapping per study site per season.

Site	Season			
	Spring	Summer	Autumn	Winter
Coast 1	May 2013	August 2013		
Coast 2	June 2013	August 2014		February 2014
River 1	June 2013	August 2014		February 2014
Wall 1	May 2014	July 2013		
Grassland 1		September 2014		March 2014

3.3.1.2 Radio tracking

Norway rats are generally associated with watercourses, and riverine environments are thought to provide movement corridors for rats to access the interior of islands (King *et al.* 1996; Traweger *et al.* 2006). Previous studies of introduced rats have also reported relatively high densities on island coastal sites (Harper 2006). Upland sites were considered an important region to study on the Isle of Rum as between 60,000 and 120,000 breeding pairs of Manx shearwaters nest above 450m elevation on the island. Three ecotope groups were therefore chosen to study Norway rat movement using radio-telemetry (river, coast and grassland/heath (high elevation)). Transect strips for site A and B were located within 5m of both river banks and 10m of the coastal 'splash line' respectively. Whilst river and coast may be considered linear features the surrounding vegetation types have been presented in Table 3.2.

Five study sites from the abundance and distribution surveys (Chapter two) were used for the radio-telemetry study; site A (river 1), site B (coast 2), site Ca (grassland 1), site D (coast 2), site E (river 2) and one new site was selected; site C (upland heath) (Figure 3.1). Abundance sites were reused (telemetry devices were fitted to rats during C-M-R trapping) to reduce the number of experimental animals used. The shortest distance between two radio-tracking sites was approximately 1.7km. Original abundance survey sites were selected using a randomised stratified design by ecotope/ecoelement strata using NVC data derived from Bates *et al.* (2002), OS VectorMap® District data (coast sites) and CEH Watercourse Network data (river sites) derived from Moore *et al.* (1994) (section 2.3.2.2). In short, QGIS was used to overlay 10m interval grid squares across the spatial data sets, with start points being randomly selected within ecotope/ecoelement type.

Site A (Corrie Dubh) was located on a river system which runs from the fringe of the Manx shearwater breeding colony on Rum, to the main village Kinloch approximately 1.9km north-east (Figure 3.1 & 3.2). Norway rats have been associated with water bodies in urban, agricultural and rural environments (Khamaganov 1972; Taylor 1978; Traweger *et al.* 2006). As such, Corrie Dubh may be a potential movement corridor between the village sub-population of Norway rats on Rum, and the globally important upland Manx shearwater breeding colony. A rough path runs along the west side of the river to its plateau where a working hydro-electric dam is situated.

Site B (Southshore) was located on the southern-shore of Loch Scresort; a sea loch found at the mouth of the Isle of Rum, where both the ferry port and Kinloch village are located. The

study site was approximately 2km east of Kinloch village, and 850m from the main ferry terminal (Figure 3.1). Approximately 400m east of the study site are the remains of a settlement established c.1830, surrounded by small numbers of foreshore breeding birds (oystercatchers, *Haematopus ostralegus*, common gulls, *Larus canus*).

Site Ca (Halival) was located within the shearwater colony, at approximately 460m elevation on the hillside of one of the Rum Cuillins, and 2.7km south of Kinloch village (Figure 3.1). The landscape is dominated by steep slopes, plateaus, bare rock and *Festuca ovina - Agrostis capillaris - Thymus praecox* grassland/*Calluna vulgaris - Erica cinerea* heath. Golden eagles (*A. chrysaetos*) and common ravens (*Corvus corax*) were frequently overhead. This site was selected for radio tracking because it was the only site from the original C-M-R grassland sites within the Manx shearwater greens. After an initially unsuccessful attempt to track the target number of rats on this shearwater grassland site (August 2014) a new site was chosen approximately 200m downhill, on the boundary of the winter snow line (site C) (Figure 3.1).

Site C (Halival South) is primarily heath vegetation at the foot of a small valley leading to one of the main breeding sub-colonies of Manx shearwaters on Rum. There is a small river running through the north-east corner which eventually forms part of a network of small rivers leading to a sandy beach on the east coast of Rum (Caves Bay), some 1.4km downhill (Figures 3.1 & 3.2). The river cuts through a pony path on the northern tip of the study site, which links Kinloch village to the south of Rum following the east coast.

Site D (North Shore) was located on the northern-shore of Loch Scresort, approximately 1.3km east of Kinloch village, and 800m adjacent to the main ferry terminal (Figure 3.1). The surrounding vegetation was dominated by plantation woodland (*Abies* spp., *Larix* spp., *Picea* spp., *Pinus* spp), heath (*Calluna vulgaris - Erica cinerea*) and small areas of mire (*Molinia caerulea - Potentilla erecta*). After an initial attachment of four TW-3 radio transmitter (Biotrack, Wareham, Dorset) collars to rats on site D (Coast, May 2013), radio tracking was delayed until a revised lone working protocol was approved (90 days). In particular, concerns were raised about the safety of working on rocky intertidal zones at night, especially given the increased risk of slips, trips and falls whilst lone working. Tagged rats either shed their collars ($n = 2$) or collars were never relocated ($n = 2$) once fieldwork restarted. Site B was therefore chosen to replace site D, to coincide with the C-M-R trapping schedule.

Site E (Kinloch River) was located along Kinloch River, approximately 3km west of Kinloch village, and 200m north of the main vehicle access route through Rum (Figure 3.1). Kinloch river travels east eventually leading to Loch Scresort, on the eastern edge of Kinloch village.

The site was located within an open valley/glen, with hills surrounding the north and south, frequently used for hunting by golden eagles. The vegetation was dominated by *Scirpus cespitosus - Eriophorum vaginatum* blanket mire. After an unsuccessful attempt at trapping a target number of individual rats in May 2014, site A was chosen to replace site E.
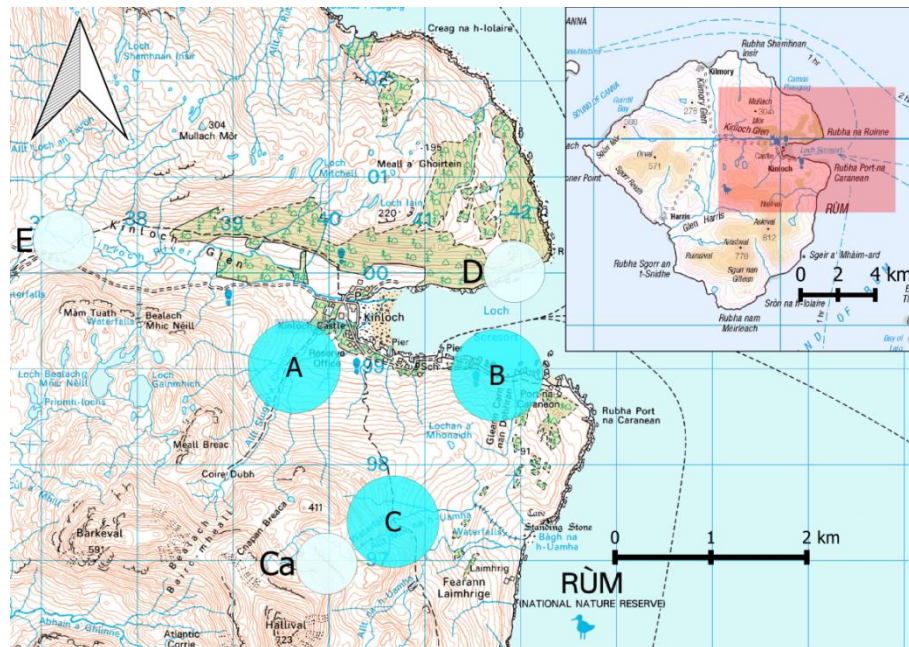
Figure 3.1 Map of the locations of radio tracking survey sites (site A (river), site B (coast), site C (heath)) for individual rats with complete data sets (>10 locations). Note the locations of unsuccessful radio tracking sites (site Ca, site D, site E). Arrow (top left) represents grid north. © Crown Copyright and Database Right 2018. Ordinance Survey (Digimap Licence).

Table 3.2 Ecotope details of radio tracking study sites with complete data sets (>10 locations), and surrounding vegetation.

Site	Ecotope Group	Surrounding Vegetation	NVC Community/Sub-community
A	**River**	Wet Heath	*Scirpus cespitosus–Erica tetralix; Carex panacea, Cladonia* spp.
		Mire	*Molinia caerulea–Potentilla erect; Erica tetralix*
		Heath	*Calluna vulgaris–Erica cinerea*
		Blanket Mire	*Scirpus cespitosus–Eriophorum vaginatum; Juncus squarrosus-Rhytidiadelphus loreus*
		Bog Pool	*Sphagnum auriculatum*
		Woodland	Plantation: *Abies* spp., *Larix* spp., *Picea* spp., *Pinus* spp.
B	**Coast**	Woodland	*Quercus petraea–Betula pubescens–Oxalis acetosella*
		Grassland	*Pteridium aquilinum–Galium saxatile; Anthoxanthum odoratum*
		Woodland	Plantation: *Abies* spp., *Larix* spp., *Picea* spp., *Pinus* spp.
		Mire	*Molinia caerulea-Potentilla erecta*
		Heath	*Calluna vulgaris-Erica cinerea*
		Wet Heath	*Scirpus cespitosus-Erica tetralix*
C	**Heath**	Blanket Mire	*Scirpus cespitosus-Eriophorum vaginatum; Drosera rotundifolia-Sphagnum* spp.
		Bog Pool	*Sphagnum auriculatum*
		Woodland	Plantation *Abies* spp., *Larix* spp., *Picea* spp., *Pinus* spp.
		Grassland	*Nardus stricta-Galium saxatile; Racomitrium lanuginosum*
		Wet Heath	*Scirpus cespitosus-Erica tetralix; Cladonia* spp.
		Heath	*Calluna vulgaris-Erica cinerea; Festuca ovina-Anthoxanthum odoratum, Thymus praecox-Carex pulicaris, Racomitrium lanuginosum*

Figure 3.2 Photographs of the three study sites used for radio tracking Norway rats (*n* = 17) on Rum in spring/summer 2014 & 2015.

3.3.2 Live capture and release of rats

Trapping commenced in May 2013 and ended in September 2015. A total of 9 – 12 live traps were set for four consecutive days, across one trapping period per site, at a density of 24/ha (12 traps (un-optimised transects), 9 traps (optimised transects)).Traps were placed every 40m in strip transects (linear sites), and every 20/40m for grid transects (non-linear sites). See below Figures 3.3 & 3.4 for further details on trap layout.
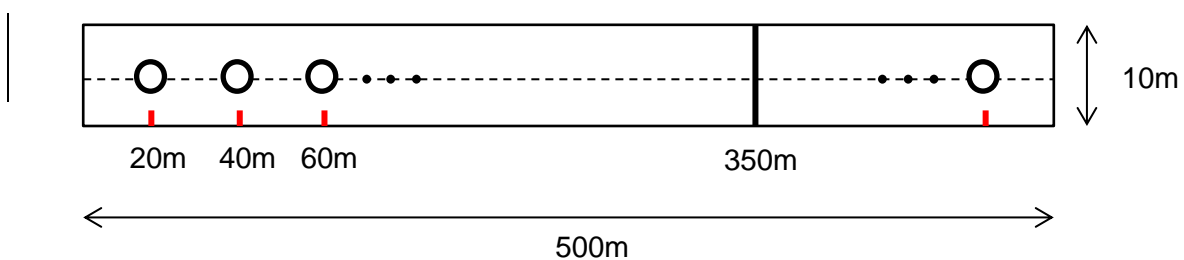
Figure 3.3 Trap layout for linear transects (circles). Ellipses (dots) indicate repetition of trap spacing. Bold line indicates the boundary of the optimised strip transect area.
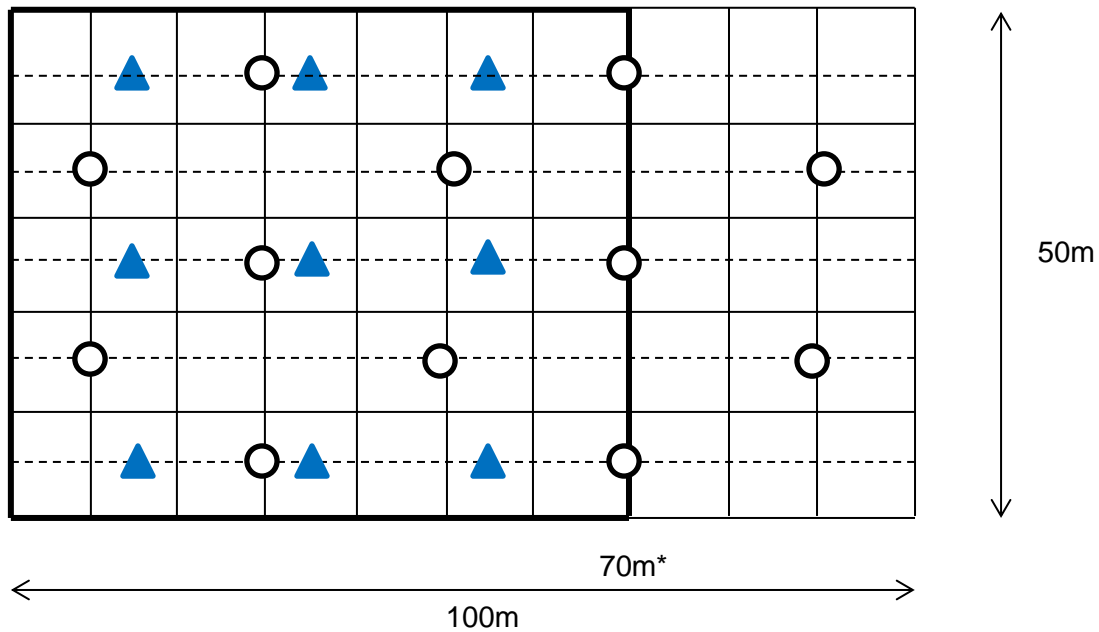
Figure 3.4 Trap layout for non-linear transects (circles). Optimised transects area and trap layout indicated by dark box and triangles respectively.

Combinations of three different live-capture trap types (SX Rat Trap, SX Environmental Supplies Ltd, Basildon, UK; Bledorberry Trap (two designs), MAFF, Surrey, UK) were used in equal proportions for each of the study sites. Trap type has been shown to effect capture rates of Norway rats (Taylor *et al.* 1981). As such, a randomised repeated pattern was used for the placement of traps on the study sites *e.g.* Trap B, Trap C, Trap A, Trap B, Trap C, Trap A. In the UK, whole wheat is the preferred bait in previous rat research projects (Chitty & Kempson 1949; Quy *et al.* 2003). Whole wheat was therefore placed in the internal bait troughs, and scattered immediately adjacent to the trap mouths (<10m^2). Traps were locked open and baited for a minimum of three days immediately prior to the trapping period. Pre-baiting allows the familiarisation of traps and consequently reduces the heterogeneity of capture probability. During trap-ups, traps were set 1-2 hours prior to sunset to allow fieldworkers sufficient time to exit the study sites prior to rat activity. Traps were then checked shortly before sunrise the following day to ensure subjects were not held for a period longer than 12 hours. Given the evidence of olfactory cues in rat communication (Galef & Heiber 1976), every attempt was made to reduce the possible transfer of anthropogenic and intraspecific odours onto traps (gloves were used when handling bait/traps, no food handled prior to trapping, waterproofs washed without the use of detergent, and odourless toiletries used). Prior to inclusion in the study, the general condition of potential study subjects was assessed visually to establish suitability of use as agreed by

the Animal and Plant Health Agency (APHA) Named Veterinary Surgeon and the Animal Welfare and Ethical Review Board (AWERB), using the following criteria:

- Awareness – the rat should be alert and respond to external stimuli *e.g.* a finger click, movement.

- Mobility – the rat should be able to move around, with a steady but agile gait.

- Injuries – the rat should have no significant injuries (*e.g.* broken limbs, non-superficial wounds).

- Appearance – the fur of the rat should appear clean and sleek, not raised ('staring coat').

- Posture – the rat should not be hunched or exhibit signs of breathing difficulties.

In order to reduce stress in study subjects and the risk to fieldworkers, individual rats were anaesthetised before processing using Isoflurane (Abbott Laboratories, Queenborough, Kent, UK); a method similar to that of Lambert (2003), Lambert *et.al.* (2008) and Parker *et al.* (2008) was used. Rats weighing over 200g were considered heavy enough to comfortably carry a radio transmitter (11g – 5.5% of subjects' body weight). Rats were transferred from traps to a bespoke anaesthetic inhalation chamber, preloaded with Isoflurane. A continuous visual assessment of the subject was made immediately after a rat was inserted into the anaesthetic chamber, and for the duration of anaesthetising. The anaesthesia chamber consisted of a cylindrical plastic chamber with a clear plastic lid (to allow close monitoring of the animal) and an internal baffle to separate the animal from the Isoflurane (Figure 3.5, left). The anaesthetic was inserted into the chamber via a tube connected to the underside of the internal cavity, leading to an absorption area (cotton wool) underneath a porous baffle floor. Once subjects were completely anesthetised (indicated by slow steady breathing, constant heart rate, relaxed muscles), rats were removed from the chamber and placed on a soft and dry sampling table.

Rats were fitted with TW-3 radio transmitters (Biotrack, Wareham, Dorset) using cable ties, allowing room for the tip of the fieldworkers' little finger between the neck and cable tie of the study subject. A syringe preloaded with an Identichip Passive Integrated Transponder (PIT) (Animalcare Ltd., York, UK) was inserted subcutaneously into the subject, allowing individuals to be uniquely marked for future identification. Insertion was just below the skin on the back of the neck (Figure 3.5, right). The following Biometric data was taken: sex (male or female), weight (± 0.1g), body length (tip of nose to base of tail ± 1mm), breeding

status (breeding or not breeding), maturity (mature or immature), body condition (poor or fair or good), evidence of ecto-parasites, and hair samples of >30 hairs were taken.

Breeding status and maturity was recorded in accordance with Greene (1935). In female rats, maturity was indicated by an open vagina. Furthermore, bald, as opposed to hairy nipples, indicated that the female rat was either lactating or gestating, giving an indication of the breeding status. Male rats were described as 'scrotal' or not, based on the position of the testes to indicate breeding status. In the apparent absence of testes, ano-genital distance was used to establish the sex of immature rats. Body condition was assessed palpably, to check for muscles and fat reserves, as an indication of general health as follows:

Poor - Little or no evidence of fat reserves around hip, vertebrae, rump and/or ribs. Bony/emaciated (released without radio tag attachment).

Fair - Reasonable amounts of fat reserves and muscle but major bone structures still easily felt. Lean.

Good - Substantial covering of fat (approximately ≥3mm) and muscle across the body.

The anatomical location of ecto-parasites found on study subjects was recorded *e.g.* ears, eyes, mouth. Hair samples were removed from the rump of subjects by gripping the skin with one hand and removing hair (against the direction of hair growth) with the other hand. Scales used for weighing subjects (EMB 1200-1 balance, Kern & Sohn, Balingen, Germany) were calibrated every field day using 1g and 10g test weights (327-61/327-64 test weight, Kern & Sohn, Balingen, Germany). Body length was measured using digital callipers (300mm Digital Caliper IP54 DC54300, Digital Micrometers Ltd., Sheffield, UK) from the tip of the nose to the base of the tail, with subjects in the supine (facing upwards) position.

Prior to release, subjects were returned to their traps and once again checked visually (as above) to ensure suitability for release, following a suitable recovery period (10 – 30 minutes). Trapped rats were released at the location of initial capture.

Figure 3.5 Picture of the anaesthetic chamber (left) and the insertion of a PIT tag into an anaesthetised Norway rat (right).

3.3.3 Radio tracking

Radio tracking commenced in May 2013 and ended in September 2015. Data was collected across three time periods: phase 1 (May 2013); phase 2 (February – August 2014); phase 3 April – September 2015).

In order to establish a general pattern of activity, rats fitted with radio collars were monitored during the day at least once prior to tracking, to establish their general behaviour (nocturnal or diurnal), and to record the location of any home sites in use. 'Active periods' of data collection were split into four time blocks. Time blocks were calculated using the total number of minutes during the period 30 minutes before sunset and 30 minutes after sunrise. Norway rats have been recorded leaving burrows prior to sunset and after sunrise (Taylor, 1978). The total number of minutes was then divided by four, giving four active time blocks (1, 2, 3, 4). Every attempt was then made to collect a balanced number of radio fixes per time block, across an equal number of active days. Initially, data collection was randomised daily for site and then individual; however, this was not always possible given the difficulty in locating specific individuals. As such, time block balance was prioritised. In order to reduce the potential for autocorrelation, individual radio fixes were never obtained closer than two hours apart (Borger *et al.* 2006). Tracking was achieved using a Sika radio tracking receiver and a flexible Yagi antenna (Biotrack, Wareham, UK). Rat locations were recorded using a Garmin GPS 60 (Garmin Ltd., Schaffhausen, Germany), typically accurate to 10 - 20m. Furthermore, hardcopies of GPS coordinates were recorded along with time, date, rat ID, and general activity (inactive inside or outside burrow, active inside or outside burrow). Surveyor movement and noise was kept to a minimum, and tracking was carried out downwind where possible, as with common animal tracking practice (Brown & Morgan

1998). Working distance was approximately 20 - 30m; however, when rats were stationary, distances of less than 10m could be achieved. Locations of subjects were confirmed using a close approach direction finding technique (Neill & Janson 2014). Upon arrival at each study site an aerial sweep was performed by the fieldworker; whilst holding the antenna forward at approximately shoulder length, a slow 360° rotation was carried out with the antenna elements in a vertical and then horizontal position, simultaneously listening to the receiver through headphones. This was usually performed at an elevated location to 'see' most of study site. Once a transmitter frequency had been received, direction of travel was chosen by either the volume of the associated beep (loudness indicating proximity) or the signal midpoint (the middle point between the left and right null (where a signal is no longer received)). Usually a second general sweep was carried out offset approximately 50m from the initial sweep in case topography was interfering with the initial signal direction. This was repeated several times, with workers moving towards the signal until a strong signal was received in every direction, indicative that subjects were nearby. At this point the gain/volume button on the receiver was lowered and aerial sweeps were made in a circling direction around the likely location of the transmitter. Once the location was confirmed the position was recorded using the GPS.

3.3.4 GPS tag

To test the feasibility of using GPS tags to track the movement of cryptic small mammals such as the Norway rat, one passive GPS tag for use with a cable tie collar (SnapTrax GPS tag, Skorpa Telemetry, Aberfeldy, UK) was attached to an adult female rat on radio tracking site B, in February 2014, for a total of 19 days. The trapping procedure followed that as outlined above (section 3.3.2). The total weight of the tag was 13g, or 5% of the total body weight of the study subject (265g) and location accuracy was within 9m. A VHF patch antenna was encased with the GPS tag to allow for the relocation and recapture of the tagged rat. The GPS schedule was set to 1 hour and successful locations were stored on board the tag, for download via a cradle (150mAH) attached to a computer and the appropriate software, upon recapture and removal.

3.3.5 Analysis

3.3.5.1 Capture rates

Norway rat Capture rates per 100 trap nights (C100TN) were calculated for each site (n = 25) using (Nelson & Clark 1973; Cunningham & Moors 1983):

$$\text{(Number of captures x 100)/corrected trap nights} \qquad \text{EQ. 3.2}$$

Where corrected trap nights are the number of traps used, multiplied by the number of nights traps were set, minus 0.5 for every unsuccessful trap that has been sprung *e.g.* trap closed with no animal inside. Capture rates were calculated from the number of unique individuals, and as such recaptures were excluded from estimations. Mean C100TN was compared using Kruskal-Wallis ANOVA in SPSS (SPSS Inc., Chicago, USA) for comparison across seasons and ecotopes/ecoelements. In the case of repeated trapping, mean C100TN per site was used.

3.3.5.2 Radio tracking

Prior to the initialisation of radio tracking, power analysis was used to estimate the minimum number of replicates needed to detect a difference in mean home range size between three sites, with power >80% (Cohen 1988). Home range estimates ($n = 30$) from non-urban populations of *R. rattus* across three sites in New Zealand were used (Hickson *et al.* 1986; Dowding & Murphy 1994; Hooker & Innes 1995). Initial attempts to find a large sample of reported home range estimates for non-urban Norway rats were unsuccessful; as such *R. rattus* estimates were used for the analysis. Using derived data ($\bar{x} = 0.81$ha, SD 0.5) bootstrapping in R 2.15.2 (R Development Team 2012) was used to simulate data, fitting the model 10,000 times for varying samples sizes ($n = 2 - 40$). The results indicated that a sample size of 17 rats was necessary to find a significant difference between the home range means across three sites (with power >80%) (Figure 3.6a). The expected standard error, and width of the 95% confidence intervals for the difference between the means was also calculated (Figure 3.6b).
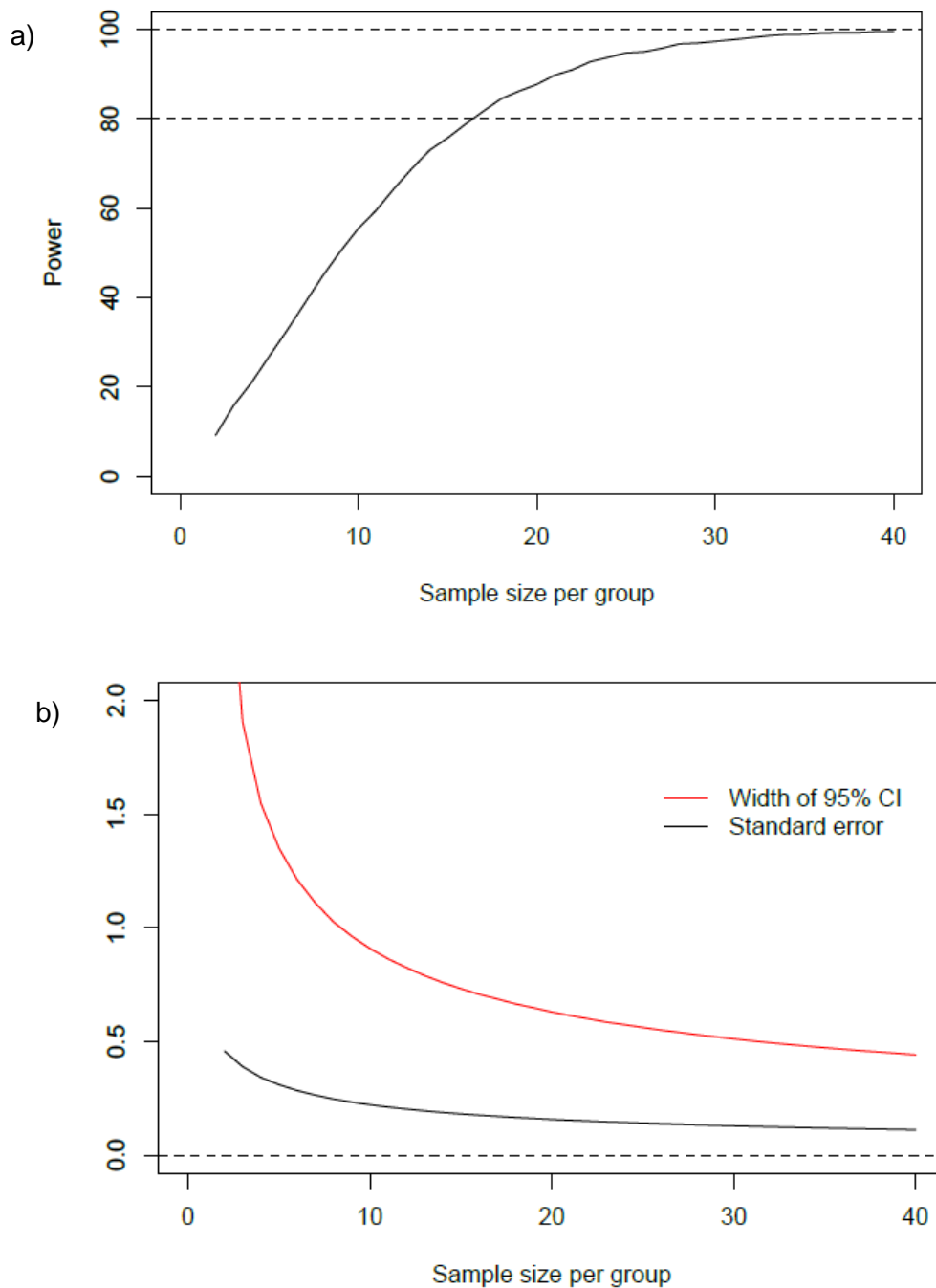
Figure 3.6 (a) and 3.6 (b) Power analysis estimates used to calculate the sample size needed to detect a statistically significant effect in home range size between three sites (a), and 95% confidence intervals (CI) calculated using the standard error of the difference between means (b).

Only radio tracking data for individual rats that reached the minimum threshold of fixes (>10) were used for the analysis (Hickson *et al.* 1986; Borger *et al.* 2006). Borger *et al.* 2006 found that a threshold of ten fixes per unit time was acceptable for the analysis of home range size, and that the largest variation in data arises from differences between individuals and sites. Complete data sets from the shearwater grassland site Ca (*n* = 1) and site C (*n* = 4) were

pooled for analysis to represent an 'upland' group located in and around the shearwater colonies. For analysis purposes this was considered as site C. Complete data sets were analysed from rats radio tracked during phases 2 & 3 (2014 & 2015) of the radio tracking data collection periods.

Raw radio telemetry data were digitised using QGIS 2.16 Nødebo (QGIS Development Team 2016) and analysed using the plugin AniMove 1.4.2 for minimum convex polygons (MCP).

MCPs (100% & 95%) were calculated using the location data. MCP100 was used for the analyses to allow for the comparisons with similar previous studies which primarily report MCP100 rather than MCP95 (Recht 1988; Quy *et al.*1999; Lambert *et al.* 2008; Villafañe & Busch 2008; Bramley 2014). Whilst MCPs may be linearly related to the number of sampled locations they are still commonly used, and can be useful for small samples (Powel 2000). Furthermore, concerns have been raised about the use of KDE to calculate home range size using data sets from a small number (<30) of radio locations per animal (Seaman & Powell 1996; Vokoun 2003). Data for home range size was not normally distributed (Shapiro-Wilk) and were $\log_{10}$ transformed for analysis. Home range size was investigated using a general linear model in SPSS for explanation by site, sex (male or female) and weight (g). A one-way ANOVA was used to analyse site differences in home range size within males and females separately.

3.3.5.3 GPS tag

Location data from the GPS tag was analysed using the same method as described above (section 3.3.5.2) for calculating MCP100.

3.3.5.4 Habitat use

3.3.5.4.1 Vegetation types

Habitat use was analysed using the home range area estimates from radio tracked rats described in section 3.3.5.2.

Total area of ecotope (vegetation) type per home range of individual rats was calculated by intersecting home range estimations with NVC polygon data for Rum (Bates *et al.* 2002) in QGIS, to create home range estimators with associated vegetation type geometries. Jacob's Index (EQ. 3.1) was used to compare vegetation proportions between home range and location points, as an indication of availability versus use (Jacob 1974; Revilla *et al.* 2000;

Boulanger *et al.* 2009; Kauhala & Autilla 2010; Hawley *et al.* 2015). Jacob's indices were tested for significance by calculating the 95% confidence limits of the means of indices for individual rats per ecotope type, to test for a significant difference from the 'neutral' value (0), where proportional use of vegetation type is equal to its availability. The use of a vegetation type was considered non-random (*i.e.* preferred or avoided) if 0 was not included in the confidence interval range (Boulanger *et al.* 2009; Kauhala & Autilla 2010; Hawley *et al.* 2015).

3.3.5.4.2 Distance to linear features

Mean capture rates (C100TN) were tested for a correlation with mean trap distance to three linear features (river, wall, coast) using Spearman's correlation in SPSS 20.0 (SPSS Inc., Chicago, USA). Maps of linear features were obtained using the method described in section 2.3.2.2 (site selection). Linear feature polylines were converted into equidistant points (0.5m) using the QChainage plugin in QGIS 2.16.0 Nødebo (QGIS Development Team 2016). The distance to each trap location was then calculated using the 'distance to nearest hub' processing tool in QGIS, to give an estimate of the distance between each trap and the linear feature (converted into points), to give a mean distance to linear feature per site. Activity and CMR surveys were only carried out on walls and rivers with a minimum length of 350m. It is unknown what effect linear feature length may have on rat distribution. As such, only rivers and walls of a minimum length of 350m were used to calculate mean trap distance per site.

3.4 Results

3.4.1 Capture rates

A total of 308 Norway rats were caught on Rum, across 25 study sites and six ecotope/ecoelement types between May 2013 and September 2015. Average recapture rate was 51%; linear sites (56%) had a better recapture rate than non-linear (46%) sites. Both sexes were trapped roughly equally; 49% were male and 51% were female. More females were caught than males on coastal (56%) and grassland sites (54%); more males were caught than females on woodland (58%), heath (58%), wall (54%), and river (53%) sites. Mean weight was estimated at 232 ± 67g (SD) with males (256 ± 67g) being heavier than females (210 ± 60g). The heaviest male (420g) and female rats (470g) were both trapped on a grassland site within the shearwater colony in late summer. The heaviest rat caught on Rum was therefore a female, which more than doubled its body weight between winter

(205g) and summer (470g) in 2014. Without further information on this individual (breeding status, age, diet) it was impossible to deduce why the heaviest rat captured on Rum was female. Mean body length was estimated at 197 ± 21mm, with males (206 ± 18mm) being longer than females (187 ± 20mm). PIT tags were used to ensure subjects were uniquely identified. Tag loss was recorded at 0.33% (confirmed with fur clip), much lower than that recorded in previous studies (Lebl & Ruf 2010).

Shapiro-Wilk's test ($P<0.05$), visual inspections of box plots, normal Q-Q plots and their histograms showed that mean C100TN data for linear (Shapiro-Wilk's: $W = 0.829$, $df = 18$, $P = 0.004$) and non-linear (Shapiro-Wilk's: $W = 0.755$, $df = 14$, $P = 0.001$) sample categories were not normally distributed.

Mean C100TN was calculated as 15.96 ± 2.76 (S.E.) for rats on Rum. Mean C100TN differed between sample categories (Kruskal-Wallis: X^2_2: 8.476, $n_1 = 18$, $n_2 = 19$, $P = 0.004$) with linear sites having a larger mean C100TN ($\bar{x} = 22.35 ± 4.05$) than non-linear sites ($\bar{x} = 9.57 ± 3.11$). Mean C100TN differed between ecotope/ecoelement groups (Kruskal-Wallis: X^2_2: 20.345, $n_1 = 7$, $n_2 = 5$, $n_3 = 5$, $n_4 = 6$, $n_5 = 5$, $n_6 = 4$, $P = 0.001$), with mean C100TN for coast sites ($\bar{x} = 37.43 ± 6.91$) being larger than all other groups except woodland ($\bar{x} = 22.05 ± 7.69$) (Mann-Whitney U tests, $P<0.05$) (Figure 3.7). No differences were found between any other ecotope/ecoelement types ($P >0.05$).
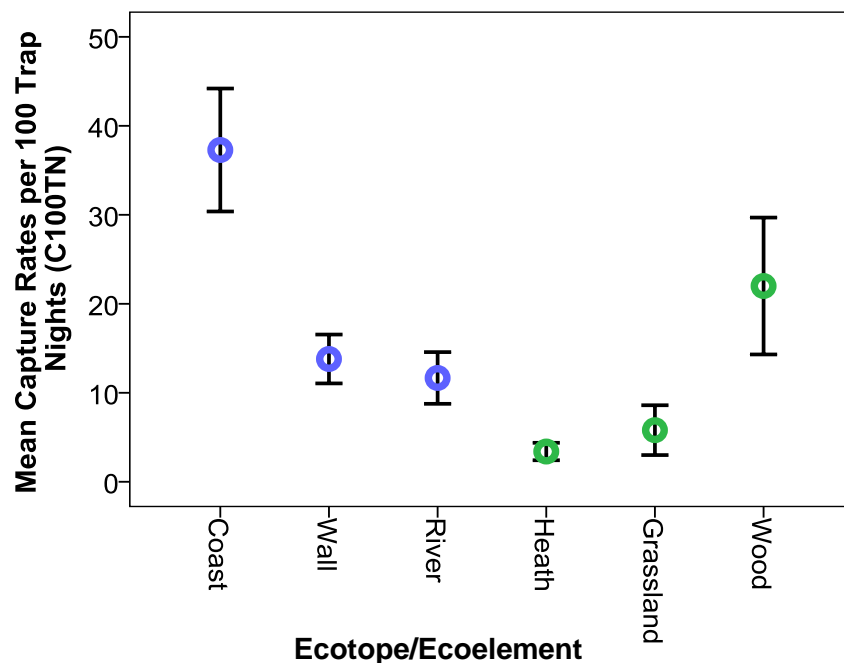
Figure 3.7 Mean capture rates per 100 trap nights (SE) of Norway rats per ecotope/ecoelement, pooled across seasons and years (May 2013 – September 2015).

Mean capture (C100TN) rates were highest in autumn and lowest in spring (Figure 3.8), although no significant effect of season was found ($P>0.05$). Mean capture rates were lowest in spring for both linear and non-linear categories but were highest in autumn and winter for linear and non-linear categories respectively. Woodland 3 was sampled in winter and had a higher mean capture rate ($\overline{x} = 38.9$) than all other non-linear sites; which may explain why mean C100TN was highest in winter on non-linear sites.
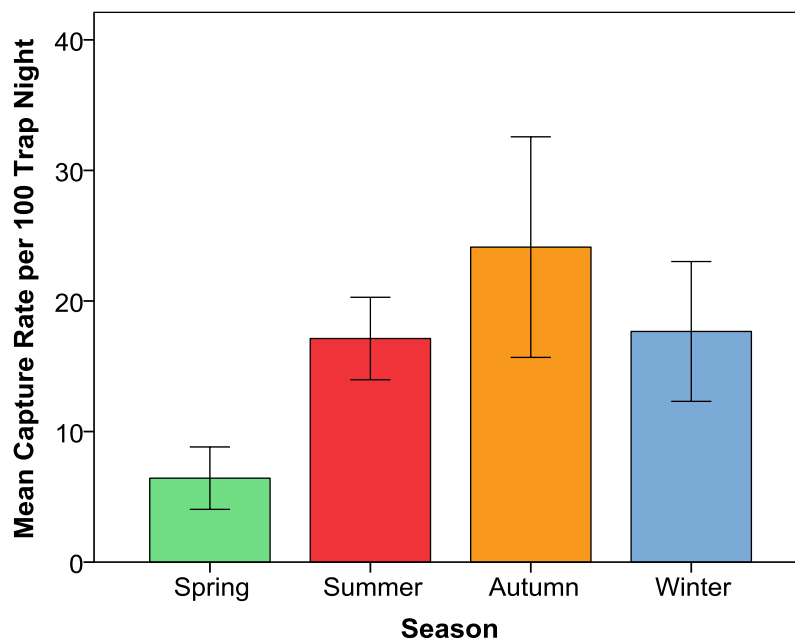
Figure 3.8 Mean capture rates per 100 trap nights (SE) of Norway rats on Rum separated into season, pooled across ecotopes/ecoelements and years (May 2013 – September 2015).

3.4.2 Radio tracking

Forty rats (13%) trapped on Rum were radio tagged, across six study sites (Appendix E) (three sites with sufficient data), and four ecotope/ecoelement types (three with sufficient data). Seventeen tagged rats (42.5%) were successfully tracked (fixes >10), of which 53% (n = 9) were male, and 47% (n = 8) were female (Table 3.3, Figure 3.9 – 3.11). Ten (25%) tagged subjects could not be relocated after data collection had been completed. Eight (20%) tagged rats could not be located after the initial transmitter attachment, of which 75% (n = 6) were male, and 25% (n = 2) were female. Seven (17.5%) tagged rats were found dead during the active period of data collection, of which 57% (n = 4) were predated (found within 50m of buzzards nest, 1.5 – 3km from last known location), and 43% (n = 3) were likely to have died of natural causes (individuals were found within the nest chambers with collars still attached and no obvious signs of tag related death *e.g.* suffocation from tags). Seven (17.5%) of the tagged population either removed their collars or died during data

collection (inaccessible burrow). Five (12.5%) of the tagged population removed their collars, of which 60% ($n = 3$) was within 5 days of initial attachment. Two collars were removed under anaesthetic, either on welfare grounds (tight collar/infected neck abrasions) or completion of data collection. Only one of the collars used was found to be faulty. No radio tracked rats were found outside their burrows during the day although day time data collection was restricted to one day per individual. Norway rats were tracked on three study sites for an average of 12.6 days and 12.5 fixes. See Appendix E for full details on Norway rats fitted with radio collars.

Table 3.3 Summary of the number of radio tracked rats, mean number of fixes, duration, and home range (MCP100) per site used to estimate home range size.

	Site A	Site B	Site C	Mean
Number of rats (male/female)	6.0 (3/3)	6.0 (3/3)	5.0 (3/2)	5.7
Mean no. of fixes (range)	13.0 (12 - 14)	12.0 (11-13)	12.5 (12 - 13)	12.5
Mean no. of days (range)	16.7 (9 - 39)	13.7 (11-16)	7.4 (6 - 11)	12.6
Mean MCP100ha (SE)	4.18 (2.22)	0.62 (0.15)	2.13 (0.94)	2.32 (0.86)
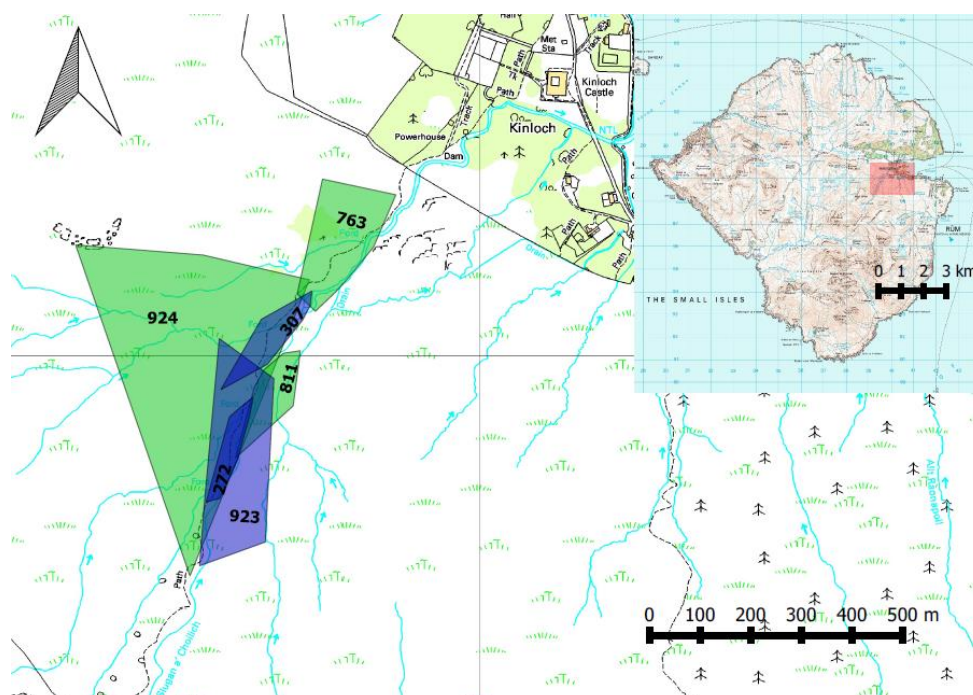
Figure 3.9 Home ranges (100%MCPs) of complete data sets (>10 locations) for individual Norway rats ($n = 6$) on site A (river), Isle of Rum. Data collected in spring and summer 2014 & 2015. Male ranges in green; female ranges in blue. Arrow (top left) indicates grid north. © Crown Copyright and Database Right 2018. Ordinance Survey (Digimap Licence).
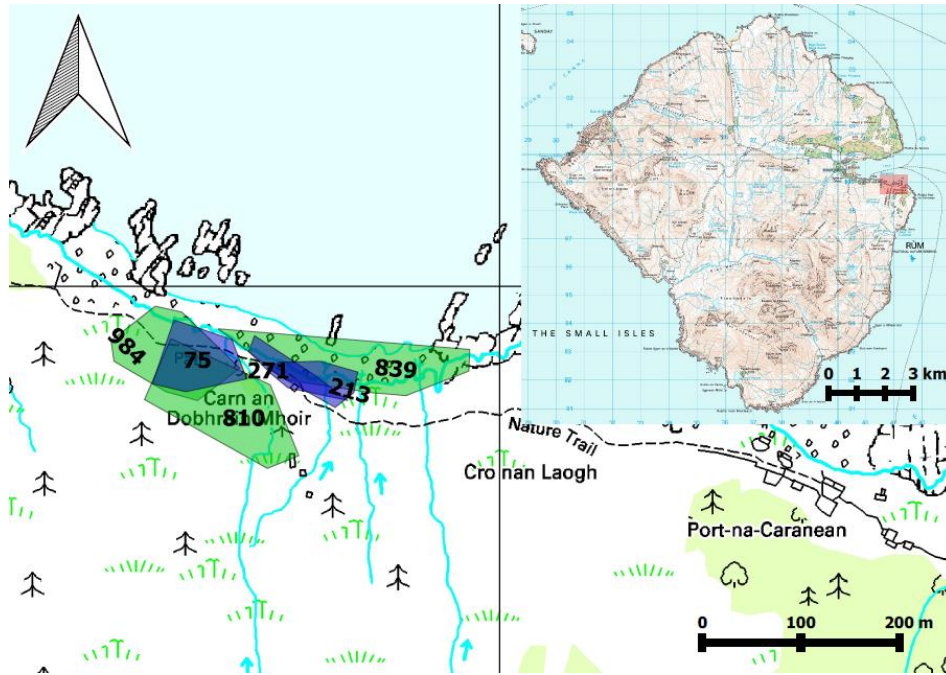
Figure 3.10 Home ranges (100%MCPs) of complete data sets (>10 locations) for individual Norway rats (*n* = 6) on site B (coast), Isle of Rum. Data collected in spring and summer 2014 & 2015. Male ranges in green; female ranges in blue. Arrow (top left) indicates grid north. © Crown Copyright and Database Right 2018. Ordinance Survey (Digimap Licence).
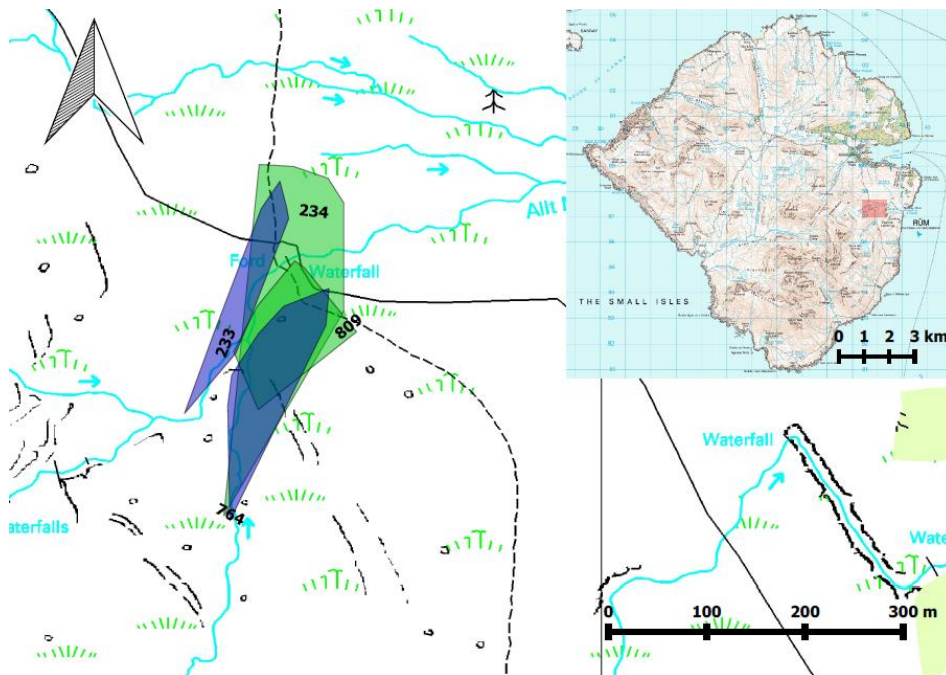
Figure 3.11 Home ranges (100%MCPs) of complete data sets (>10 locations) for individual Norway rats (*n* = 5) on site C (heath), Isle of Rum. Data collected in spring and summer 2014 & 2015. Male ranges in green; female ranges in blue. One rat tracked for estimation of home range size on heath habitat (rat 323, Appendix BE) was located 250m uphill and is excluded from this map. Arrow (top left) indicates grid north. © Crown Copyright and Database Right 2018. Ordinance Survey (Digimap Licence).

Mean home range size varied with estimator (MCP100 = 2.32 ± 0.86ha; MCP95 = 1.62 ± 0.62ha) (Table 3.4), with mean $\log_{10}$ MCP100 being significantly larger than $\log_{10}$ MCP95 (paired t-test: t = 6.669, df = 16, P = 0.0001). Home range size as estimated by MCP100 was largest at site A (river), followed by site C (heath), with the smallest home range found at site B (coast) (site A = 4.18 ± 2.22ha; site B = 0.62 ± 0.15ha; site C = 2.13 ± 0.94ha) (Table 3.4). Overall, there was a significant effect of site on $\log_{10}$ mean home range size (MCP100) (GLM: F_2 = 6.030, P = 0.014) (Table 3.4), but a post hoc Tukey test showed that only site A (river) and B (coast) significantly differed from one another at the 5% level (P = 0.007), although site A (river) and C (heath) did at the 10% level (P = 0.076). Average home range size (MCP100) was significantly higher for males ($\overline{x}$ = 3.39 ± 1.51ha, n = 9) than females ($\overline{x}$ = 1.08 ± 0.52ha, n = 8) (($\log_{10}$ MCP100) GLM: F_2 =8.022 P = 0.014) (Figure 3.12, Table 3.4). No site differences were found in the home ranges ($\log_{10}$ MCP100) within males or females (P = >0.05).
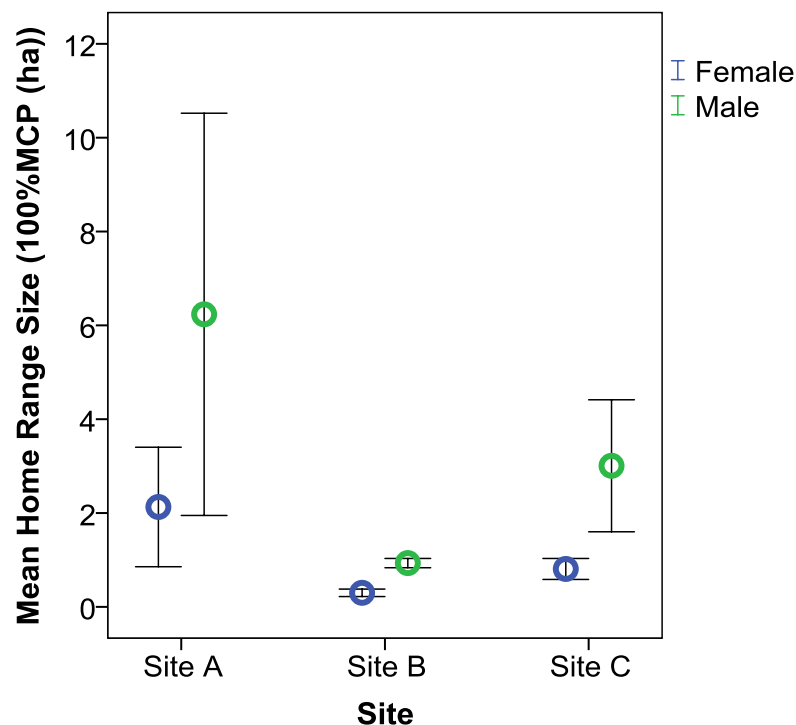
Figure 3.12 Estimates of mean home range size ± S.E. (100% minimum convex polygons) per sex and site (site A (n = 6); site B (n = 6); site C (n = 5)).

Weight can be used as a rough guide to rat age and as such was initially considered for the final GLM selection; however, an interaction was suspected between sex and weight. Whilst the interaction was not significant at the 5% level, it was at the 10% (GLM: F_2 = 3.108, P = 0.076). Furthermore, significant differences in weight were found between the sex of radio

tracked rats (t-test: $t = 2.985$, $P = 0.009$; difference = 55.97, 95% CI = -95.94 to -16.00). As such, weight was removed from the model prior to analysis.

Table 3.4 Summary of the mean home range sizes and *P* values from a general linear model used to explain the differences in home range size of Norway rats on Rum per home range estimator (ha). The associated effect size is indicated by the R^2 value.

Home Range Estimator	Home Range Size (ha) (SE)	R^2	Site	Sex
MCP100	2.32 (0.86)	0.611	0.014	0.014
MCP95	1.62 (0.62)	0.567	0.020	0.028

3.4.3 GPS tag trial

A total of 23 location fixes were successfully retrieved from the GPS tagged rat, covering a period of 9 days (5th – 14th February 2014). MCP100 home range (Figure 3.13) was estimated at 0.89ha, with only three ecotope types represented within the home range; heath (29% of total area), mosaic (22%), and woodland (47%). The remaining 2% was recorded in the intertidal zone.
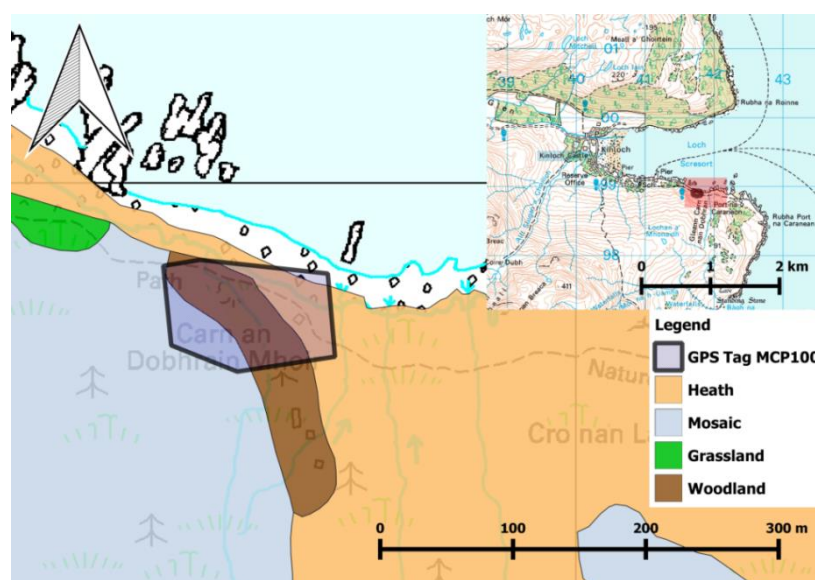
Figure 3.13 Home range area (black boundary) of a single female Norway rat 'Wanda' located on the south shore of Loch Scresort, Isle of Rum. The rat was tagged in February 2014 and tracked for a total of 9 days before recapture and tag removal. Arrow (top left) indicates grid north. © Crown Copyright and Database Right 2018. Ordinance Survey (Digimap Licence).

3.4.4 Habitat use

3.4.4.1 Vegetation types

Ecotope proportions of the study area (MCP100) and density of intra-territorial locations (radio location fixes) appeared very similar (Table 3.5). Only four vegetation types (heath, mire, mosaic, woodland) were represented in both the study area and location point data. Rock, sand dune and aquatic ecotopes were absent from both the study area and location points. Heath vegetation accounted for approximately 81.0% of the proportions of the study area and locations points (Table 5.3) and was not avoided or preferred within the study area (Jacob's Index = 0) (Figure 3.14). Mosaic accounted for 8.3% and 13.4% of the study area and used area (location points) respectively, and a mild preference was indicated (Jacob's Index = 0.3), although this was not found to be significant (0 was included within the confidence intervals of the mean of indices for individual rats per ecotope type) (Jacob's index 95% CI: $\overline{x}$ = -0.17 ± 0.39). Woodland was found in both the study area and location points (7.5%, 5.1%) with a mild avoidance indicated (Jacob's Index = -0.21) but no significance was found (Jacob's index 95% CI: $\overline{x}$ = -0.34 ± 0.42). Mire vegetation was also represented in the study area and location points (3.1%, 0.5%), with a strong avoidance suggested (Jacob's Index = -0.75); however, only one individual was found within mire vegetation and as such significance could not be tested. Grassland was found within the study area (0.1%) but was not represented in the location data and as such a strong avoidance of this habitat was indicated (Jacob's Index = -1), but significance could not be tested.
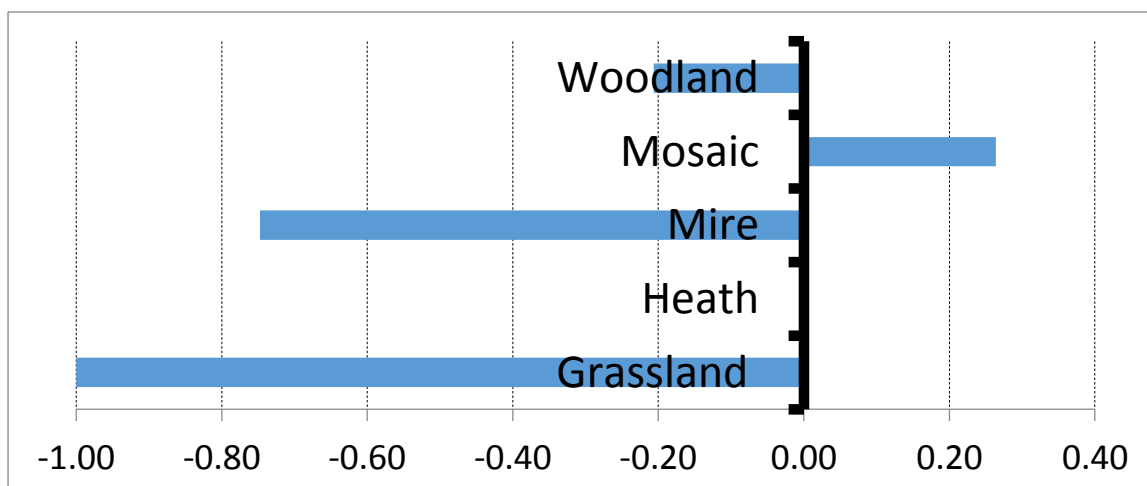
Figure 3.14 Proportions of vegetation type within the study area (MCP100) compared against densities of radio location fixes per ecotope using Jacobs Index. Indices close to 1 and -1 indicate a preference or avoidance of ecotope type respectively.

Table 3.5 Summary of total areas or counts and percentages per vegetation type across three spatial scales (whole-island, MCP100, location points) on Rum. NVC areas derived from Bates *et al.* (2002). Area in hectares (whole-island, MCP100) and number of fixes (location points) displayed with percentages (parentheses). Discrepancies due to rounding error.

Vegetation Type (NVC Community)	Whole-island	MCP100	Location Points
Aquatic	68.37ha (0.7%)	0	0
Grassland	531.00ha (5.1%)	0.04ha (0.1%)	0
Heath (including wet heath)	3426.72ha (32.7%)	31.48ha (81.0%)	175 (81.0%)
Mire	1266.66ha (12.1%)	1.21ha (3.1%)	1 (0.5%)
Mosaic	4915.39ha (46.9%)	3.22ha (8.3%)	29 (13.4%)
Sand Dune	5.03ha (0.1%)	0	0
Woodland (including plantation)	107.012ha (1.0%)	2.93ha (7.5%)	11 (5.1%)
Bare Rock	171.51ha (1.6%)	0	0
Total =	10491.69ha	38.88ha	216

3.4.4.2 Linear features

A strong negative correlation was found between mean distance to coast and mean C100TN (Spearman correlation: $r_S = -0.576$, $N = 25$, $P = 0.005$). No correlation was found between the mean C100TN and mean distance to either river (Spearman correlation: $r_S = -0.024$, $N = 25$, $P = 0.911$) or wall linear features (Spearman correlation: $r_S = -0.247$, $N = 25$, $P = 0.235$).

3.5 Discussion

3.5.1 Context: capture rates, home range and habitat use

3.5.1.1 Capture rates

Mean capture rate per 100 trap nights (C100TN – EQ. 3.2) was used to analyse capture rates of Norway rats on Rum between experimental groups, and across studies. Mean C100TN on Rum was estimated at 15.96, which falls within the range estimated for all rats species on oceanic islands (5 -20 C100TN) (King 1990). A very similar estimate was reported by Drever (1997) in spruce vegetation (16.9) on Lanagara Island, NZ, although kill traps were used to calculate capture rates as opposed to live trapping (CMR). C100TN estimates from CMR may not be directly comparable to C100TN estimates using kill traps as recaptured individuals from live trapping may reduce the number of traps available for new individuals. Differences in capture rates between ecotopes/ecoelements were found on Rum; patterns were similar to that found with tracking plate results - linear sites had a higher mean C100TN than non-linear sites, and coast differed from all sites accept woodland. The highest capture rates on Rum were found on the coast ($\overline{x}$ = 37.43); much lower C100TN estimates were reported by Harper (2006) for coastal rats on Stewart Island, NZ (13 C100TN). The largest C100TN estimate on Rum was found on coast 3 in autumn (58 C100TN) which was more similar to the capture rates calculated from live trapping for up to five consecutive nights, found in the wet season on the tropical island of Conception, Seychelles (60 C100TN) (Hill *et al.* 2003). Norway rat capture rates on the Isle of Canna, Scotland were also higher on the coast compared to interior environments (Patterson & Quinn 2001).

Previous capture estimates of rats from sites surrounding Manx shearwater colonies on Rum were found to be as high as 4.2 C100TN (Bell & Ramsay 2011). The majority of which was recorded either in grassland or heath. Similar mean C100TN estimates were found for rats on grassland and heath vegetation in this study ($\overline{x}$ = 5.8 C100TN (grassland), $\overline{x}$ = 3.3 C100TN (heath)). Weihong *et al.* (1999) found much higher mean capture rates of Norway rats on grassland ($\overline{x}$ = 10.5 C100TN) on Motukorea Island, New Zealand. Shearwater colonies are, however, situated on Rum upwards of approximately 450m, and the majority of vegetation types on Rum can be considered part of upland habitats (Averis *et al.* 2004). Very few studies have looked at the capture rates of Norway rats in upland habitats. Drever (1997) trapped Norway rats across three vegetation types on Langara Island (NZ), with only upland bog snap traps failing to capture any rats. Key *et al.* (1994) found Norway rats at high

altitude areas on Santa Cruz Island, Galapagos, concluding that soil type, moisture, and water access may allow survival, again highlighting the potential association between Norway rats and water. King *et al.* (1996) found that 81% of Norway rats trapped in Pureora Forest Park, New Zealand, were trapped within 1m of a river bank, albeit at very low capture rates (0.12 – 0.27 C100TN). Harper *et al.* (2005), however, concluded that Norway rat relative abundance (C100TN) was higher on subalpine shrubland than riparian shrubland on Stewart Island, NZ. Riparian environments may therefore be less important to Norway rat populations on islands, with mean river C100TN estimations on Rum ($\overline{x}$ = 11.92) around the median for oceanic rats (5 – 20 C100TN).

Capture rates for woodland rats ($\overline{x}$ = 22.05) on Rum were the second highest of all ecotopes/ecoelements and was the only ecotope/ecoelement type that did not differ significantly from coastal sites. It may be possible that habitat quality is overall very poor on Rum, and as such woodland vegetation provides the least bad alternative to most interior ecotopes/ecoelements surveyed. Rum also has very few competitors or predators for Norway rats, potentially allowing them to utilise vegetation types they are not usually associated with.

3.5.1.2 Home range and movement

Home range size of Norway rats on islands across the world is understudied with most of the few published studies coming from New Zealand (NZ) (Moors 1985; Hickson *et al.* 1986; Bramley 2014; Harper & Bunbury 2015). Mean home range size (MCP100) for 17 Norway rats (9 males, 8 females) on Rum during spring and summer across three sites (coast, river, heath) was estimated at 2.32ha. Hickson *et al.* (1986) reported a similar mean home range size (2.2ha, MCP100) for three Norway rats on a coastal forest in spring and summer on Stewart Island, NZ; although the mean number of radio fixes used to estimate home range size ($\overline{x}$ = 24) was nearly twice that recorded here ($\overline{x}$ = 13). Moors (1985) reported similar home range sizes ($\overline{x}$ = 1.2ha) of three Norway rats from forests in Motuhoropapa Island, NZ; although home range was estimated using trap distances and data was pooled across three seasons. Bramley (2014) reported a much larger home range size (5.5ha, MCP100) for eight Norway rats on a grassland site in winter on Kapiti Island, NZ, using a similar mean number of radio fixes ($\overline{x}$ = 28) to Hickson *et al.* (1986), but a disproportionate amount of males were tracked (males; n = 7 and females; n = 1).

Most mainland studies of Norway rat home range size have almost exclusively been concerned with urban and agricultural environments (Recht 1988; Quy *et al.*1999; Lambert

et al. 2008; Villafañe & Busch 2008). Research on Norway rat home range in Europe and the UK focuses on farms and surrounding arable land (Taylor 1978; Taylor & Quy 1978; Hartley & Bishop 1979; Quy *et al.* 1999; Cowan *et al.* 2003; Lambert *et al.* 2008). Lambert *et al.* (2008) radio tracked Norway rats for 11 – 30 days on UK farms (prior to habitat modification) with relatively low home range estimates (MCP100) for Norway rats around farm buildings ($\overline{x}$ = 0.02ha, *n* = 27) and field margins ($\overline{x}$ = 0.38ha, *n* = 5) (lowest estimate on Rum: $\overline{x}$ = 0.6ha (site A, coast); although specific timings of tracking *e.g.* season, is unclear. Quy *et al.* (1999) reported much larger home range sizes (MCP100) of Norway rats around UK farm buildings ($\overline{x}$ = 1.55ha); although mean duration of tracking ($\overline{x}$ = 53 days) was much greater than that reported by Lambert *et al.* (2008).

Home range size of rats on Rum significantly differed between sites; a pattern similar to that reported in the UK between farm buildings and field margins (Hardy & Taylor 1980; Cowan *et al.* 2003; Lambert *et al.* 2008). Site differences in Norway rat home range sizes have also been reported between resource rich environments such as garbage tips and farm buildings, and resource poor environments such as streams (MacDonald *et al.* 1999; Quy *et al.* 1999). Whilst access to food will likely influence home range size, this is not always the case. MacDonald *et al.* (1999) reported a retraction in the mean linear home range length of male Norway rats surrounding farm fields after harvest; an effect likely to be related to an increased risk of predation in open areas.

An effect of sex on the home range size of Norway rats on Rum was detected, with males generally having a larger home range than females. MacDonald *et al.* (1999) also reported that female Norway rats generally had smaller home range sizes than males around UK farms although no statistical analysis was provided. Lambert *et al.* (2008) observed sex differences in rat home range size around UK farms but this was only found to be mildly significant (male; 0.38ha and female; 0.02ha; *P*<0.1). Villafañe & Busch (2008) did not find sex differences in the home ranges of Norway rats on poultry farms in Argentina; although differences in movement were assessed using the maximum distance between localization points (Lmax). Quy *et al.* (1999) observed very little variation between home range sizes of female and male rats located near farm buildings (male;1.60ha and female;1.50ha), but did observe sex differences in home range estimates in arable fields near a pond (male; 1.51ha and female; 18.2ha) and stream (male; 2.99ha and female; 0.50ha); although no analysis on sex effects was conducted. Quy *et al.* (1999) noted that the unusually large female home range size found near a pond was attributed to a single female rat moving 650m and back from her initial release site. In a non-urban setting data is lacking on the sex differences in home range size between Norway rats. Bramley (2014) observed that home range size

(MCP100) was larger for males than females but again no statistical analysis was provided to confirm the existence of a meaningful difference. With such limited information on Norway rat home range size in relation to sex, general patterns are difficult to conclude. Furthermore, differences in home range size of rats on islands may be attributed to a number of factors including site, season, sex, predation, and density (Russell *et al.* 2011; Ringler *et al.* 2014). As such, comparison of 'similar' studies may not reflect real differences between results especially given the variety of methods available for estimating home range size (Borger *et al.* 2006).

3.5.1.3 GPS trial

Home range size (MCP100) was successfully estimated for one female Norway rat on Rum using a GPS tag; indicating its potential use for other small mammals. In comparison, Byers *et al.* (2017) unsuccessfully trialled the use of GPS tags on 14 Norway rats in Vancouver, Canada; with tag malfunction a possible reason for difficulties obtaining location fixes. Furthermore, in Byers *et al.* (2017) tags were attached to the backs of Norway rats using veterinary adhesive of which 21% were dislodged from recaptured rats. Stevenson *et al.* (2013) successfully used GPS tags to investigate the movement patterns of another rodent species (grey squirrel, *Sciurus vulgaris*) in the UK. As with this study, GPS tags were attached using a collar; potentially a useful attachment method for GPS tags to other species of small mammals. Regardless of the attachment method, an inherent problem with increasingly relying on modern technology is technology failure *e.g.* tag malfunction; however, this is likely to be outweighed by the benefit of obtaining fine scale movements of 'difficult' study organisms (Hebblewhite & Haydon 2010). Home range size of the single female Norway rat on Rum using data from the GPS tag was estimated at 0.9ha; within the range of female rats on Rum (0.2 – 4.6ha) but much larger than other females from radio tracking site B (0.2 – 0.5ha), where the GPS collar was attached. Nearly twice as many location fixes (23) were, however, used to estimate MCP100 using the GPS data, within a similar sampling period (GPS tag: 9 days, radio tracking: $\bar{x}$ = 12.6 days). The variation in number of location fixes may explain some of the difference in home range size between radio tracked rats and the single GPS tagged rat from site B.

3.5.1.4 Habitat selection

Habitat use for Norway rats in non-urban environments is understudied; a small number of studies have mostly been conducted on islands in New Zealand and no analysis of ecotope use against availability has been attempted (King *et al.* 1996; Innes *et al.* 2001; Harper *et al.*

2005; Bramley 2014). Harper *et al.* (2005) trapped Norway rats across four vegetation communities (*Leptospermum* shrubland, riparian shrubland, podocarp-broadleaf forest, subalpine shrubland) on Stewart Island (NZ) and concluded that the relative abundance of Norway rats was highest on subalpine shrubland. Harper (2006) trapped three species of *Rattus* across four ecotope types (coast, forest, river, shrubland) on Pearl Island (NZ) and only recorded Norway rats on coastal sites. In the UK, Patterson (2006) used chew sticks to survey the activity of Norway rats on the Isle of Canna, reporting the highest activity at coastal sites.

In an urban landscape Traweger *et al.* (2006) used trapping locations to calculate electivity indices to estimate habitat preference of Norway rats within the city of Salzburg, Austria. A significant preference for running water and woodland (conifers/deciduous) was found, whilst an avoidance of rock and no water was also reported. Jacob's indices from Rum rats suggested that woodland was not preferred within the home range of Norway rats in spring/summer; however, a significant avoidance was not found. Furthermore, no rats radio tracked on Rum had any rock within their home range or location points. Habitat availability in an urban setting, however, is likely to be significantly restricted *e.g.* due to the presence of roads and as such direct comparison of ecotope preference between urban and non-urban landscapes should be approached with caution.

3.5.2 Limitations

Minimum convex polygons have been criticised as providing only crude outlines of animal home ranges, are sensitive to extreme data points which can result in large areas that are never used, and have a linear relationship to fix number; reaching asymptotic values of home range area with a large number of replicates (White & Garrott 1990; Powel 2000; Borger *et al.* 2006). Despite this, MCPs are commonly used, easy and simple to calculate, and do not assume an underlying statistical distribution (Powell 2000). As with most home range estimators, including MCP, time-to-independence can also be an issue (Rooney *et al.* 1998). The assumptions of independent data points necessary for most analyses may be compromised if data points are related *i.e.* radio location can be predicted from other data points. Without quantifying the level of relatedness between locational fixes validity of analyses may be questionable (Rooney *et al.* 1998; Kenward 2001; Kernohan *et al.* 2001); however, removing autocorrelation may have negatives effects on interpretation of the underlying behaviour of the study organism (Blundell *et al.* 2001). The use of MCP100 to estimate home range size in this study provides a basic understanding of the short-term movements of Norway rats on Rum across a limited number of study sites. Without

estimating autocorrelation or understanding the underlying behaviour that drives movement, it is unclear to what extent MCP100 accurately reflects the home range size of rats on Rum, or to what extent autocorrelation has affected the analyses. In particular, if autocorrelation is high, assumptions about independence of data points may not be met, posing uncertainties about the conclusions of the GLM and one-way ANOVAs when comparing home range size across site and sex. Furthermore, extreme data points may have increased the home range size of individual rats resulting in larger mean home range sizes across sexes and sites. Lastly, if extreme values have resulted in large areas of MCP100 containing vegetation that is actually unused, analyses (Jacob's Indices) and subsequent conclusions on habitat use in relation to vegetation type may also be compromised.

In this study, standard error of the mean home range size (MCP100) for males from site A was relatively large. Variation in male home range size on site A was large. In particular male home range size on site A ranged from 14.8ha (rat 924) – 1.2 ha (rat 811); rat 924 visited what appeared to be a nesting site at a rocky outcrop approximately 450m away from the initial trapping point near the main river, but would return to the river each night; resulting in a large estimate of home range. Taylor (1978) also described similar ranging behaviour by a rat on a UK farm, suggesting that rats can be temporarily disoriented by predator attacks. The Isle of Rum, however, has no mammalian predators and as such another cause is likely. Taylor & Quy (1978) described exploratory ranging behaviour in Norway rats on UK farms where male rats would occasionally travel to areas not associated with a food source, possibly in relation to mating. On Rum, Rat 924 was reproductively active (descended testes) so this may well explain the roaming behaviour observed. The large home range size of rat 924 may also have affected the comparison of sex differences in home range size of rats on Rum. Excluding rat 924 reduced male home range sizes of rats on Rum (3.9ha → 2.0ha); also highlighting how sensitive MCP100 can be to outliers.

Sample size and number of replicates per individual was also small for home range size data, and any non-significant results may not reflect biological conditions. This is especially true for radio tracking site C where difficulties in trapping adequate rat numbers (due to extreme weather) resulted in a reduced tracking period ($\bar{x}$ = 7.4 days) when compared with site A ($\bar{x}$ = 13.7 days) and site B ($\bar{x}$ = 16.7 days). Also, whilst differences in mean home range size between sites were found, no replication within ecotope/ecoelement was carried out and as such any differences in home range size between ecotope/ecoelement such as vegetation type could not be assessed.

Analysis of ecotope selection between home range (MCP100) and intra-territorial locations (radio tracking fixes) using Jacob's index described no significant preference or avoidance of any of the vegetation types analysed (grassland, heath, mire, mosaic, woodland). In particular, only four vegetation types were represented in both the study area and the location point data (heath, mire, mosaic, woodland) and only two were suitable for analyses. Grassland was only represented at the home range scale (MCP100) and sample size ($n = 1$) was too low to estimate confidence in the data. It also highlights the limitation of using proportional comparisons; un-sampled ecotopes cannot be compared. Furthermore, the majority of grassland vegetation on Rum is found within patches of mosaic communities, therefore it is likely that grassland is underrepresented in the habitat analysis. This is especially important when considering the seasonal grassland greens created by Manx shearwater colonies. Mire was represented at both the home range and intra-territorial scale but again sample size was too low ($n = 1$) to estimate confidence in the data. The remaining two vegetation types showed no significant difference between use and availability. As such, confidence in the habitat analysis overall is low due to low sample size and lack of statistical analysis for several vegetation types. Furthermore, determining what is considered 'available' habitat appears to vary between studies, with some researchers preferring the use of 95% kernel density estimators to reflect true availability (Kauhala *et al.* 2006; Palphramand *et al.* 2007). Also when using home range/location points to indicate habitat use the underlying assumption is that location = ecotope preference, which may not be the case given the absence of data on the behavioural mechanism driving movement (Beyer *at al.* 2010). Kauhala & Autilla (2010) also highlighted the difficulty in finding habitat preferences within home ranges when using location points, which requires large sample sizes and no locational errors.

Ecotope areas per home range size were estimated using data from NVC surveys carried out in 1997 and 1998 (Bates *et al.* 2002); any changes in vegetation since the original surveys would reduce the accuracy of these results. No island-wide National Vegetation Surveys have been conducted on Rum since the aforementioned data set. Regardless of this, it seems unlikely that at a landscape level at least, vegetation will have dramatically changed, and no evidence of this was seen during any of the surveys carried out. Furthermore, the Isle of Rum is a National Nature Reserve and conservation of the associated vegetation types is fundamental to its status.

3.5.3 Conclusions

Mean capture rates (C100TN) were higher on linear than non-linear sites and differences were found between the mean C100TN recorded on coastal sites and all other ecotopes/ecoelements (grassland, heath, river, wall) except woodland. No seasonal differences were found in the mean C100TN data but samples did not include seasonal replication within sites.

Mean home range size (MCP100) for Norway rats on Rum in spring and summer was estimated at 2.32ha; however, data were pooled across two years. Furthermore, low sample size, low replication and large variation in the data potentially reduce confidence in the data, with independence of the data not quantified. Differences in the home range sizes of rats were found between sites and sexes. Rats from Site B (coast) had the smallest home range size ($\overline{x}$ = 0.62ha), whilst rats from site A (river) had the largest ($\overline{x}$ = 4.18ha). Males ($\overline{x}$ = 3.39ha) had larger home range sizes than females ($\overline{x}$ = 1.08ha). Home range size did not differ between sites within males or within females. Not enough data was collected to determine the effect of ecotope/ecoelement on home range size.

No significant differences were found between the use and availability of vegetation types (Jacob's index) by rats in spring and summer; although sample size was very low and several ecotopes were un-sampled or sampled only once preventing analysis from being carried out. Despite this, mean C100TN did show variation across ecotope/ecoelement type with capture rates significantly higher on coast than all other sites except woodland; which was the highest all of all non-linear sites.

3.5.4 Recommendations

Home range size was estimated for Norway rats on Rum using data pooled across seasons (spring and summer) and years (2014 and 2015). As such, generalisations about home range size of rats on Rum are difficult to justify. Given the lack of data available on Norway rat movement in natural settings it would be useful to fully understand the differences in home range size between ecotopes/ecoelements and across seasons in a natural environment. In particular no data is currently available on the winter movement of rats on Rum which may be crucial to understanding their overwinter survival. Furthermore, home range data across seasons and ecotopes/ecoelements may provide useful information on the role that unstable food sources *e.g.* seabirds, play in the dispersal of Norway rats on Rum.

Habitat use and preference of Norway rats is also understudied and a more thorough investigation on this topic would yield meaningful results, especially in relation to rat management and species conservation. For instance, which vegetation types hold the key to rat survival in insular environments?

Chapter 4 – Calibration of Survey Methods and a Whole-island Population Estimate for Norway Rats on Rum

4.1 Introduction

4.1.1 General

A population is defined by Krebs (1999) as a *'group of organisms of the same species occupying a particular space at a particular time'*. Knowledge of population size is often vital when managing species (Sinclair *et al.* 2006), with distribution and abundance being the core subjects of ecology (Andrewartha & Birch 1986). Abundance can be considered the number of organisms of the same species within an area, whereas density is the number of individuals per unit area. For example, if you counted 100 leatherback turtles, *Dermochelys coriacea*, on a 2km^2 stretch of beach, the count or abundance on that beach would be 100, whereas the density would be 25/km^2, commonly converted into hectares to give 0.25/ha. The basic estimator for abundance is considered (Schaffer 1974; Strum & Western 1982; Coulson *et al.* 2001):

$$N = \frac{n}{p}$$

EQ. 4.1

N = Abundance

n = Number of unique animals observed

p = Estimated probability that an individual is detected

The method chosen for estimating abundance will vary depending on the question being investigated. For instance, does the biological question require absolute numbers of individuals in a unit area to be understood or is the rate of change between units more important? Furthermore, it may be possible to census every individual in a given area (total counts), usually, however, species abundance is calculated by estimating the population size from a sample of the total population (Sutherland 2006). Small sampled areas can then be used to estimate larger spatial scales (scaling up) with landscapes being described as nested hierarchies in which information is translated between scales (Urban *et al.* 1987). Levels of organisation within landscapes increase across time and space with lower levels characterised by smaller spatial and temporal scales *e.g.* leaf physiology, and higher levels with larger scales *e.g.* regional dynamics (Allen *et al.* 1984; Urban *et al.* 1987) (Figure 4.1).

With an appropriate experimental design hierarchical levels within a landscape can be explicitly linked. For instance, manipulations to the spatial or temporal resolution of the observation data (grain) and the time or area (extent) of the observation set allows for information to be translated between scales (King 1991). Essentially, therefore, scaling up is an increase in the extent; differences in spatial heterogeneity and temporal scale, however, complicates the scaling up process.
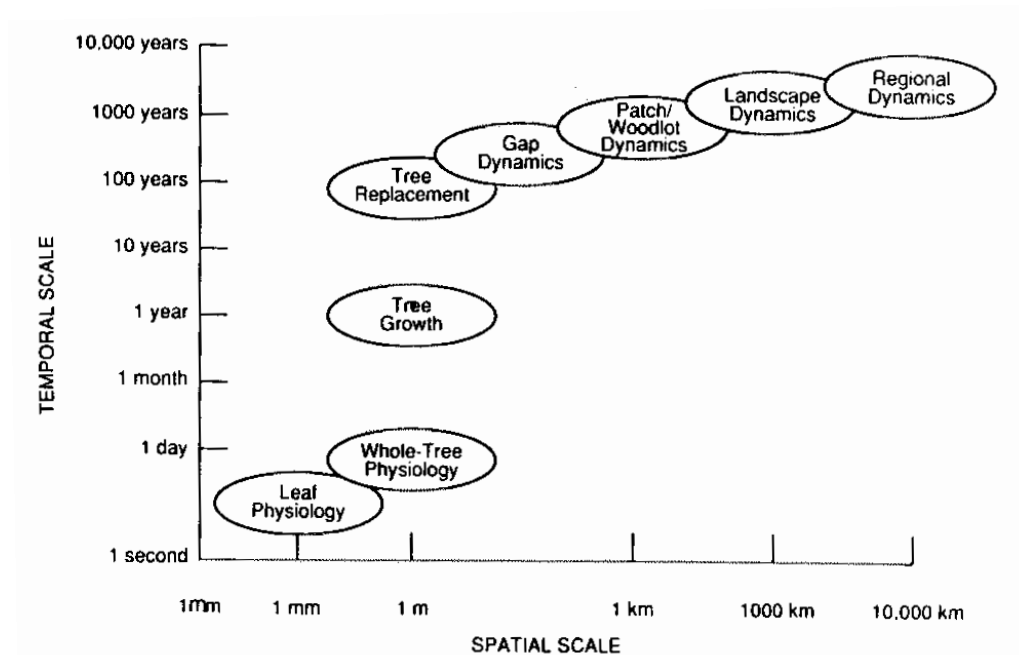
Figure 4.1 A hierarchical representation of biomass in a forested landscape (King 1991).

An important aspect of scaling up therefore is aggregation of data. There are several methods used for aggregating data to allow for spatial and temporal differences between scales, with varying grain (resolution) and model extent (time or area) (King 1991). Sampled data can be averaged across whole areas (lumping), although assumptions are made that processes are linear across scales (Welsh *et al.* 1988). Samples can also be collected across a variety of patches *e.g.* vegetation type, to reflect the spatial heterogeneity at the landscape scale, and then directly extrapolated. The difficulty, however, is deciding which factors should be patched, especially if the landscape has a large amount of heterogeneity (Band & Wood 1988). Furthermore, the method and associated data used to sampled patches will also vary.

81

4.1.2 Tools for estimating abundance from capture-mark-recapture (CMR)

Whilst indirect sampling techniques *e.g.* tracking plates, only provide indices of abundance, direct survey methods where subjects are captured, marked, and recaptured (CMR) to estimate population size from the proportion of marked versus unmarked animals, can be used to calibrate abundance indices against sample population estimates (Eberhardt & Simmons 1987). Direct survey methods such as trapping are capable of providing reliable and robust population estimates (Burnham & Overton 1979; Pollock 1982; Chao 1987). As such, trapping has been used extensively to estimate distribution and population sizes of most classes of animals including fish, amphibians, reptiles, birds, mammals and various invertebrate groups (Greenslade 1964; Wilson & Anderson 1985; Sharp & Lokemoen 1987; Dunham *et al*. 1988; Bradshaw *et al.* 2007; Mazerolle *et al.* 2007).

Using two occasions of capture-recapture for estimating population size was first used to estimate the population size of humans in England and France in the early 1800s and 1600s respectively (Cochran 1978; Hald 1990). It was not until 1930 that Lincoln used a derivation of this for wildlife, to estimate the population size of ducks. The simplest population estimate can be achieved using Petersen's/Lincoln's method (Caughley 1977; Amstrup *et al.* 2010):

$$N = M / \frac{m}{n}$$
EQ. 4.2

Where;

N = Total population size

M = Marked animals in the population

m = Marked animals recaptured in subsequent sample

n = Number of animals in subsequent sample

Numerous models have since been suggested to estimate population size from capture-recapture studies, with variations to capture method (Zippin 1958; Chao 1988), capture occasions (Schnabel 1938; Darroch 1961), population dynamics during trapping (Leslie 1945; Seber 1982; Pollock 1991), catchability (Burnham & Overton 1979; Pollock 1991) and individual covariates (Huggins 1991) all having been discussed. Very thorough reviews on suitable models for estimating various types of population variables from trapping have been published by Otis *et al.* (1978), Seber (2001) and Amstrup *et al.* (2005). Generally speaking,

however, models can be grouped into either open or closed depending on whether the population during trapping is constant or not *i.e.* free from immigration and emigration, births and deaths (Williams *et al.* 2002; Amstrup *et al.* 2010).

As with any model its success will depend on the data meeting specific assumptions and capture-recapture models are no different. The assumptions of closed capture models are:

1) The population remains constant over the study period
   (no emigration/immigration, no births/deaths).

2) Animals do not lose their marks or tags.

3) All marks or tags are correctly recorded.

4) All animals have a constant (equal) probability of capture on each trapping occasion.

Most of the four assumptions can be reasonably met with an appropriate study design (short trapping period (constant populations), permanent marking (animals do not lose their marks) and careful scientific manner (marks recorded correctly). Assumption four (equal catchability), however, is not so straightforward and is widely accepted as biologically unlikely and commonly not met (Carothers 1979; Pollock *et al.* 1982; Jolly & Dickson 1983). As such, a lot of research has been carried out to understand the deviations from this assumption; starting from Pollock's sequential framework (Pollock *et al.* 1974; Otis *et al.* 1978; Pollock 1982; Seber 1986; Chao 1989; Pledger *et al.* 2003). These deviations have resulted in up to 12 closed capture models being offered in standard software such as MARK, each consisting of parameters *p* (probability of initial capture), *c* (probability of recapture), and *pi* (proportion of the population with a particular mixture *i.e.* heterogeneity). The advantage of using more recent models over classic closed capture models such as Petersen-Lincoln and Schnabel is that the assumption of equal catchability can be relaxed, with the effects of time, behaviour, and heterogeneity compared using model selection (Huggins 1989). In short, three main variations within sampled populations have been proposed:

1) Model M_t – Capture probability varies with time/trapping occasion *e.g.* effect of weather on animal activity.

2) Model M_b – Capture probability varies due to behavioural response (trap happiness/shyness) *e.g.* animal behaviour altered due to fear from first capture occasion.

3) Model M_h – Capture probability varies with individual animal differences (heterogeneity*) e.g.* sex, age, social dominance.

Several combinations of the above have been combined by Otis *et al.* (1978) to create a suite of simple 'classic' models each allowing variations in capture probability: M_o (equal catchability), M_b (behavioural (trap) response only), M_t (variation in time only), M_h (heterogeneity of individuals only), M_{tb} (time and behavioural variation), M_{th} (time and individual heterogeneity), M_{bh} (behaviour and heterogeneity) and M_{tbh} (time, behaviour and heterogeneity). Whilst it is clear, therefore, that a number of models exist to aid the analysis of trapping data, deciding on the 'ideal' candidate is essential for applying the models. Traditional null and alternative hypothesis tests using associated *P*-values have successfully allowed binary interpretations of predefined questions; however, their formal evidence has been questioned (Burnham *et al.* 2011; Royall 2017). For example, using *P*-values allows the judgement of rejection or failed rejection of a null hypothesis but there is no comparative estimation of the strength of this hypothesis against multiple alternatives. Following on from the strategy of 'multiple working hypotheses', comparing the strength of evidence using multimodal inference is therefore more suitable (Chamberlin 1890; Burnham & Anderson 2003). This information-theoretic approach has been extensively documented, and essentially compares the statistical distances between the set of models against either approximate full reality (Kullback-Leibler) or the best model in the set (Akaike Information Criterion) (Burnham & Anderson 2001, 2003; Burnham *et al.* 2011).

Kullback and Leibler (1951) made the link between information theory and statistics and the Akaike Information Criterion (AIC) is often used to determine which of the models is most parsimonious with the data investigated (Akaike 1973; Burnham & Anderson 2003). Given that adding parameters to a model is likely to improve the model fit, an end point that adequately represents the data needs to be sought. In this sense a trade-off is being met between model bias and variance to determine the 'best' model (Figure 4.2).
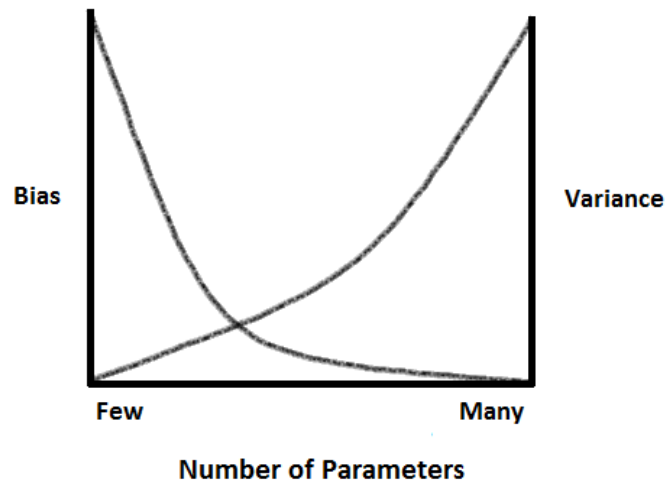
Figure 4.2 Theory of parsimony, with bias decreasing but uncertainty (variance) increasing with the number of parameters added to a model (Burnham & Anderson 2003).

4.1.3 Estimating density

Ecological practitioners and policy makers alike often want to know not only how many individuals there are but also how this relates to area. Density can help understand a vast array of biological questions within conservation and species management, inter/intraspecific interactions and game quotas (Gittleman 2001; Sinclair *et al.* 2006). Despite this requirement, the relationship between true density and estimated density can be difficult to determine. For instance, if we take the naïve estimator of density (*D*), given the abundance (*N*), within a sample area (*A*) (Wilson & Anderson 1985):

$$D = \frac{N}{A}$$
EQ. 4.3

This seemingly simple estimator is called the naïve estimator primarily due its simplistic view of sample area, *A*. In particular, whilst surveyors may clearly map out predefined sampling areas, study subjects rarely recognise these boundaries. Within any given sample area subjects' home range will be partially or completely enclosed, with many individuals on the edge of the sample area coming in and out of the sample area during surveying (McArdle *et al.* 1990; Caley *et al.* 1996; Ivan 2008). Consider Figure 4.3 below:

85
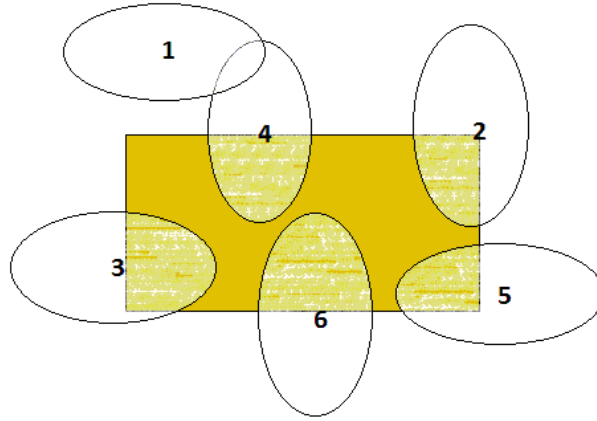
Figure 4.3 Theoretical home range areas (ovals) with varying proportions overlapping the sampling grid (orange), adapted from Ivan (2008).

The naïve estimator has therefore been heavily criticized for the exclusion of the 'edge effect', particularly with small-scale trapping grids. As such, several methods for estimating density from trapping grids have been developed to deal with difficulties in establishing what the effective sampling area is.

Dice (1938) proposed adding a boundary strip to a trapping grid (W) equal to half the average diameter of a home range size to the sampling perimeter, such that (Wilson & Anderson 1985):

$$D = \frac{N}{A(W)}$$

EQ. 4.4

Where;

D = Density estimation

N = Number of individuals

A = Sample area

W = boundary strip area

This method, however, assumes that data is available on the home range size of the study subjects. Several methods have been developed to obtain data for W from trapping alone, ranging from home range estimates from trap distances to outright estimations of W. For instance, O'Farrel *et al.* (1977) used trap assessment lines to estimate the effective trapping

area of live captures of the oldfield mouse, *Peromyscus polionotus*, and the cotton rat, *Sigmodon hispidus.* Otis *et al. (*1978) investigated the use of a trapping grid made up of a series of sub-grids to allow an estimation of the effective trapping area to be inferred. Despite these methods for assessing the effective trapping area, mean maximum distance moved (MMDM) by individuals between trapping events has been suggested and frequently used to estimate a boundary strip for sampling areas (Otis *et al.* 1978; Wilson & Anderson 1985; Soisalo & Cavalcanti 2006; Obbard *et al.* 2010). Combining Dice's suggestion of using half the home range diameter and MMDM has resulted in the use of MMDM/2 to calculate the effective trapping area (Krebs *et al.* 2011; Noss *et al.* 2012). Regardless of the method used to calculate effective trapping area, most have been criticised as *ad hoc* methods lacking theoretical foundations, with logistical and data size issues (Sarmento *et al.* 2014). Two methods have been successfully used without the need to calculate an effective trapping area: trapping webs and spatially explicit capture recapture (SECR) (Anderson *et al.* 1983; Link & Barker 1994; Efford *et al.* 2009; Royle *et al.* 2009). Anderson *et al.* (1983) proposed the use of trapping webs to estimate density, with distance from web centre combined with the number of captures to produce an estimate of density. More recently however, the use of SECR has become an increasingly popular method for calculating densities for a wide range of mammal species (Thapa *et al.* 2014; Mohamad *et al.* 2015; Boron *et al.* 2016). Probability models are fitted to the data using the probability of capture as a function of the distance from the home range centre to the trap; home range centre is usually assumed to follow a 2-D distribution (Poisson) with density *D* (Efford & Fewster 2014).

4.1.4 Population estimates

Landscape level population estimates for small mammals are notoriously difficult to reliably achieve (Atkinson 1985). Plasticity in social organisation and home ranges, coupled with spatial and temporal changes in resources and environmental conditions, alter population dynamics and abundance (Calhoun 1963; Meehan 1984). Fluctuations in small mammal densities are well reported, with outbreaks in rodents not uncommon, albeit mostly in association with humans (Brown *et al.* 2010). In Baltimore, rat population numbers varied between 165,000 in 1947 to 60,000 in 1949 using the same method, and 48,420 in 2004 using a different method (Davis & Fales 1950; Easterbrooke *et al.* 2005). In New York, a previous total population estimate for rats was reported at 250,000 (Davis 1950); however, recent estimates suggest a figure closer to 2 million rats (Auerbach 2014), which may reflect real variation in abundance although methods also differed between estimates. The

population of Norway rats in the UK has been estimated at roughly 6.8 million (Harris *et al.* 1995).

4.1.5 Population estimates and calibration of survey techniques for rats

Population estimates of Norway rats on islands have typically been associated with conservation *e.g.* seabird recovery projects. A successful eradication of Norway rats was recently carried out on St. Agnes and Gugh islands, UK, with Norway rat numbers estimated at 3,100 shortly before eradication (Bell 2011). The Isle of Canna, located approximately 6.5km north-west of Rum, had a rough estimate of 3,000 – 5,000 Norway rats in 2005, prior to eradication (Bell *et al.* 2011). Estimates were derived from extrapolations of density estimates.

Very few papers have sought to calibrate indirect abundance indices for rats against population estimates from direct methods such as trapping. Brown *et al.* (1996) successfully calibrated tracking tunnels against ship rat abundance in New Zealand. Quy *et al.* (1993) calibrated Norway rat activity indices against population estimates on UK farms; these appear to be the only published calibration of tracking activity indices for rats. Despite the use of non-toxic blocks for the post eradication monitoring of invasive rodents on islands, wax block activity indices have never been calibrated against population size from trapping. Thomas (1999) investigated the feasibility of using wax block bite marks to measure changes in the abundance of black rats and possums, *Trichosurus vulpecula*, in New Zealand forests. It was concluded that the frequency of bite marks in wax blocks was a feasible method for measuring abundance in rats and possums. Trapping numbers did, however, only follow a similar trend to the frequency of wax blocks bitten by possums and only on one of the three sites sampled. Furthermore, no analysis or calibration between trapping and wax block bites was attempted.

4.2 Rationale and Research Questions

In order to make effective conservation decisions, an understanding of any potential limiting factors to migratory seabird survival, such as predation by invasive rats, would assist the Scottish government to '*take the requisite measures to maintain the population*', under the European Commission 'Bird Directive' (Directive 2009/147/EC). Considering the conservation value of the Isle of Rum (host to roughly 25% of the world's Manx shearwater population (60,000 – 120,000)) and the presence of invasive Norway rats on the island, a population estimate of Norway rats could therefore provide data to inform the future

management of rats on Rum. Calibrating activity indices against population estimates provides a useful conservation tool by allowing indirect survey methods to be used to estimate population size; potentially suitable for use in other similar island environments. Chapter four examines the following research questions:

1. What are the calibration curves (activity scores vs. population estimates from CMR data) for two survey methods (wax blocks, tracking plates) used in linear and non-linear contexts on Rum?

2. What are the differences in abundance estimates and density of Norway rats on Rum, across six ecotope/ecoelement groups (coast, grassland, heath, river, wall, woodland)?

3. What is the total population size of Norway rats on Rum?

4.3 Methods

4.3.1 Study sites

4.3.1.1 Activity scores calibrated against CMR data

Activity scores (from tracking plates and wax blocks) were calibrated against CMR population estimates using data from the 24 study sites as described in section 2.3.2.2.

4.3.1.2 Island-wide population estimate

Abundance estimates from 25 study sites (including repeated sites) described in section 3.3.1.1 were used to calculate a total population estimate of Norway rats on Rum.

4.3.2 Calibrating activity indices against rat population estimates

4.3.2.1 Estimating population size from CMR data

A closed capture 'Huggins' model was selected to estimate population size per site (Huggins 1989, 1991) using the software MARK 8.0 (MARK, Fort Collins, Colorado, USA) (White & Burnham 1999; Lukacs 2009). A 'Huggins' model was chosen because population estimate, N, is conditioned out of the Huggins likelihood using (with no individual covariates) (Cooch & White 2010):

$$\frac{M\,(t+1)}{[1-\,(1-p)(1-p)(1-p)]} \qquad \text{EQ. 4.5}$$

M = Number of marked animals in the population

t = Time

p = Probability of first capture

As such, abundance estimates using Huggins models are therefore conditioned on captured individuals only, and are therefore more stable when dealing with small sample size, as with this study (Huggins 1991).

General assumptions of closure were also expected to be met through the use of a short trapping period (constant population), PIT tags and hair clips (to check for loss of tags) and duplicate PIT tag records (tags correctly recorded). Furthermore, data came from a single trapping period of live individuals, individuals were not misidentified (permanently marked and fur clipped), data were not analysed across strata, the fate of the individual was unknown and population abundance was the only parameter of interest *e.g.* not survival (Brownie *et al.* 1985; Pradel 1996; Williams *et al.* 2002; McClintock & White 2009; Cooch & White 2010).

Following the suggestions by Otis *et al.* (1978), a set of simple classic models were tested hierarchically for their suitability, starting with the simplest model (M_o = no variation) to the most complex (M_{tbh} = time, behaviour and heterogeneity effects). Anomalous results were excluded from the final selection process *e.g.* those with huge (3000) or impossibly small (0) standard errors. Models were tested for their agreement with the data, as indicated by the corrected AIC value (AICc), suitable for assessing model agreement when dealing with small sample sizes (Hurvich and Tsai 1989). Models with the lowest AICc/highest model likelihood score were selected for each site. Linear regression in SPSS version 20.0 (SPSS Inc., Chicago, USA) was used to calibrate linearity between mean activity scores per site and abundance estimates. Ecotope/ecoelement categories (linear/non-linear) were analysed separately. For comparisons between ecotope/ecoelement groups (coast, heath, grassland, river, wall, woodland) a one-way ANOVA was used at a significance level of $P<0.05$.

4.3.2.2 Calibrating activity scores to population estimates

Mean activity scores for tracking plate ($\log_{10}$ transformed) and wax block ($\log_{10}$ + 10 constant) survey techniques were calibrated against CMR abundance estimates from 24 study sites using a linear regression in SPSS.

4.3.3 Island-wide population estimate

4.3.3.1 Density estimates: non-linear sites

Density was estimated using CMR data collected on non-linear sites using spatially explicit capture-recapture estimates (SECR) in DENSITY 5.0.3.1 (Borchers & Efford 2008; Efford 2012) with the exception of two sites (woodland 1, heath 2) which had too few data points to analyse using SECR and instead were calculated using MMDM in DENSITY. Heath 2 had very low capture rates and as such MMDM was pooled across all trapped individuals in all heath sites to obtain MMDM ($\overline{x}$ = 35m) which was used to estimate heath 2 density.

SECR estimates remove the need to produce an estimate of trapping area, but assume the following:

1) The population is closed (*i.e.* no births, deaths or dispersal during a trapping session).

2) Capture does not affect the movement patterns of animals within a trapping session.

3) Tags are not lost, and each recaptured animal is located and identified accurately.

4) Traps are set at known locations for a fixed time.

5) Trap placement is random in relation to the location of animal ranges and animal ranges are randomly orientated.

6) Home ranges of animals do not change during a trapping session.

7) Home range sizes are similar between animals.

8) Home-range centres are scattered throughout the sample area, or home-range centres are scattered within mapped subsets of the landscape (*e.g.* vegetation areas).

Efford's Maximum Likelihood was used to estimate density per site, using the default settings (Buffer Width = 100m, Full Likelihood, Poisson Distribution Model, Half Normal Probability Model).

4.3.3.2 Density estimates: linear sites

For linear sites (coast, river, wall), rat abundance estimates from CMR were calculated using MARK, as described in section 4.3.2.1; however, estimates used for the whole island population estimate were based on the mode model *i.e.* the model commonly at the top of model selection tables, rather than models with the lowest AICc per site.

Abundance estimates were then converted into density estimates (rat/ha) using Dice's boundary strip method (EQ. 4.4), where effective trapping area *A* (*W*) was estimated using mean distances moved (Wilson & Anderson 1985; Soisalo & Cavalcanti 2006; Obbard *et al.* 2010). The width of the boundary strip was calculated using half the mean maximum distance moved (MMDM/2) (Dillon & Kelly 2008; Mondal *et al.* 2012; Krebs *et al.* 2011; Noss *et al.* 2012), from a linear feature (van der Ree 2002) using radio tracking data (Tioli *et al.* 2009) for rats whose home range intersected the linear features class, *i.e.* MMDM/2 for river sites was calculated using the radio tracking data for rats trapped at river study sites. The maximum distance a study subject was found from a linear feature was calculated in QGIS. Linear features from the spatial data sets (section 2.3.2.2) were converted into equidistant points (0.5m) using the QChainage plugin in QGIS. The distance to each radio tracked location was then calculated using the 'distance to nearest hub' processing tool in QGIS, to give an estimate of the distance each radio fix was from a linear feature (converted into points). Radio fixes furthest away from the linear feature were then averaged to give a MMDM from the linear feature. MMDM was calculated using data from radio tracking site B (Southshore – coast, *n* = 6) to estimate an appropriate boundary strip for the Rum coastline (high water line) (MMDM/2 = 25m). Radio tracking data from site A (Corrie Dubh – river, *n* = 6) was used to calculate MMDM for the appropriate river linear feature boundary strip (MMDM/2 = 64m). No radio tracking data was collected on a wall linear feature sites and as such MMDM for the wall boundary strip was calculated using the mean distance of all radio tracked individuals (*n* =17, MMDM/2 = 45m) from coast and river linear study sites (site A & B). The calculated boundary strips were then added to the linear transect lines to create an effective trapping area for each linear transect. Transect lengths were calculated using the Points2One 1.0.2 plugin in QGIS 2.16 Nødebo, to calculate the total straight line distance (m) between trap locations per site.

4.3.3.3 Land cover data

Total areas per vegetation type were calculated using NVC polygon data derived from Bates *et al.* (2002). Total vegetation on Rum was grouped into eight main ecotopes (aquatic, grassland, heath, mire, mosaic, rock, sand dune and woodland) according to their general plant communities, covering a total of 10,491.69ha (Table 3.5). Aquatic, bare rock and sand dune were not used to estimate total population size of rats on Rum. Although Norway rats are commonly associated with water bodies, they are not considered aquatic mammals. Aquatic communities contribute 0.7% (68.37 ha) of the total land cover on Rum. Bare rock and sand dune were also excluded from the estimate as it is assumed that neither can provide adequate resources suitable for rat survival (food/shelter) and density is therefore assumed to be very close to zero. Sand dune contributes 0.1% (5.03 ha) of the total land cover on Rum, of which 61% is *Festuca rubra - Galium verum* fixed dune grassland (3.07 ha), whilst the remainder is either semi or mobile dune communities. Bare rock covers 1.6 % (171.51 ha) of the land cover on Rum.

Mosaic areas were divided into separate vegetation types by calculating the total area of each vegetation type per mosaic polygon. Proportions of vegetation types in each mosaic polygon were recorded during the original surveys (0% - 100% (0 – 1)) allowing the total area of that polygon to be divided into vegetation types. The resulting areas were then added to the vegetation type totals until no mosaic was left.

Mire and heath were pooled into one group. Whilst mire was not chosen during the initial randomisation process for survey site selection, several wet heath (commonly considered as mire) sites were surveyed and as such heath and mire was grouped into one stratum.

4.3.3.4 Converting density estimates into total rat population estimate

Total population estimates were analysed in two groups:

1) Non-linear population estimate - non-linear ecotope (vegetation type) density estimates were combined to give a non-linear total population estimate.

2) Combined population estimate - non-linear/linear ecotope/ecoelement (vegetation type & linear feature) density estimates were pooled to give a combined total population estimate.

Linear features occur along NVC communities on Rum and the extent to which Norway rats use linear features in relation to its surrounding vegetation is unknown. As such, double

counting and independence of data had to be considered. To eliminate this error a boundary strip method similar to van der Ree (2002) was used. MMDM/2 estimates that were calculated previously for density estimation for linear sites (4.3.3.2) were used to add a boundary strip (*W*) to all locations of surveyed linear feature types (coast, river, wall), using the spatial data sets (2.3.2.2) created previously for Rum. The areas of NVC communities that overlapped with the linear boundary strip were then removed from the vegetation type area totals to ensure that rats counted on linear features were not double counted when non-linear/linear total abundance estimates were combined. This created adjusted non-linear total areas per vegetation type, and total areas (transect length x boundary strip) per linear feature type.

Total abundance was estimated for each ecotope/ecoelement group using a formula similar to the naïve estimator (EQ. 4.3), as follows:

$$N_h = D_h A_h$$

<div align="right">EQ. 4.6</div>

Where;

N_h = Total abundance per ecotope/ecoelement group

D_h = Mean density of rats (ha) per ecotope/ecoelement type

A_h = Total area of ecotope/ecoelement type (ha)

Estimating total population size by multiplying ecotope/ecoelement density estimators by total areas may only provide a basic estimate of total abundance but it can still be a useful option when scaling up stratified data (Siniff & Skoog 1964; Miller *et al.* 2004; Sutherland 2006; Mathews *et al.* 2018;). In this study, the stratification process included several ecotope/ecoelement groups and replication within ecotope/ecoelement, ensuring that a gradient of densities that represent the population of rats on Rum was captured in the data. Density estimates per ecotope/ecoelement were also either calculated using spatially explicit capture recapture methods (non-linear sites), which are unbiased to edge effects (Efford 2009), or the boundary strip method (linear sites), which accounted for any possible edge effects (Dice 1938). Furthermore, ecotopes unlikely to be occupied by rats (bare rock, aquatic, dune) were not included in the estimate and only ecotopes/ecoelements occupied by rats (presence confirmed through activity surveys or trapping) were used to estimate total population size of rats on Rum.

Total estimate of population size (N_T) was analysed using the following formula (Caughley 1977):

$$N_T = \sum N_h \qquad \text{EQ. 4.7}$$

Standard deviations of mean density per ecotope/ecoelement were calculated in SPSS and then multiplied against the total ecotope/ecoelement areas to give extrapolated standard deviations per group (Sutherland 2006). Extrapolated ecotope/ecoelement standard deviations were then pooled using the Satterthwaite approximation (which does not assume equal variances between samples) to estimate a pooled standard error (Satterthwaite 1946):

$$S_e = \sqrt{(s_1^2/n_1 + s_2^2/n_2)} \qquad \text{EQ. 4.8}$$

Where:

S_e = Pooled standard error

s_1 = Standard deviation from the first sample

n_1 = Sample size from the first sample

These were then converted into confidence intervals using the appropriate degrees of freedom.

4.4 Results

4.4.1 Calibration of population estimates per site against activity scores

4.4.1.1 Population estimates from CMR data

The largest Norway rat abundance estimate across all sites on Rum was found on a coastal site (coast 3: $N = 27$), with the lowest on grassland (grassland 2, grassland 3) and heath (heath 1) sites, where no rats were found (Table 4.1). Within non-linear sites, the largest rat abundance estimate was found on a woodland site (woodland 3: $N = 16$).

Model selection differed between sites with the null model (H_o) usually performing the best and a mixture of other models (M_t, M_{th}, M_{tb} and M_b) being selected less often (Table 4.1, Appendix F). Three sites (heath 2, river 1, woodland 1) did not have high enough recapture

rates to estimate population size using capture probabilities and as such only the minimum number alive (MNA) was reported.

Table 4.1 Summary of the C-M-R population estimates (MARK) and models used for the calibration of two rat activity survey techniques (tracking plates, wax blocks) against abundance estimates for Norway rats on Rum. Occasionally recapture rates were too small to estimates population size and instead minimum number of rats alive (MNA) is reported.

Site	Population Estimate (S.E.)		Model Selected
Coast1	9	(0.62)	Huggins M_{tb}
Coast2	11	(0.45)	Huggins M_b
Coast3	27	(10.04)	Huggins M_o
Coast4	26	(2.85)	Huggins M_o
River1	2	-	MNA
River2	5	(1.28)	Huggins M_o
River3	14	(1.82)	Huggins M_t
River4	5	(2.37)	Huggins M_o
Wall1	11	(1.81)	Huggins M_o
Wall2	12	(2.25)	Huggins M_o
Wall3	4	(0.79)	Huggins M_o
Wall4	2	(0.18)	Huggins M_{th}
Grassland 1	3	(0.7)	Huggins M_o
Grassland 2	0	(0)	-
Grassland 3	0	(0)	-
Grassland 4	3	(1.3)	Huggins M_o
Heath 1	0	(0)	-
Heath 2	2	-	MNA
Heath 3	2	(0.18)	Huggins M_{th}
Heath 4	1	(0.4)	Huggins M_o
Woodland 1	4	-	MNA
Woodland 2	5	(0.54)	Huggins M_{tb}
Woodland 3	16	(2.2)	Huggins M_o
Woodland 4	11	(1.0)	Huggins M_o
Mean =	**7.29**	**(1.28)**	

A significant linear relationship was found between $\log_{10}$ transformed mean tracking plate activity scores and CMR population estimates per site for linear (Regression: $y = 0.045x + 0.813$; $F_{1,10} = 19.75$; $P = 0.001$; $R^2 = 0.664$) and non-linear surveys (Regression: $y = 0.116x + 0.181$; $F_{1,10} = 15.989$, $P = 0.003$; $R^2 = 0.615$) (Figure 4.4). A significant linear relationship was found between $\log_{10}$ transformed + 10 mean wax block activity scores and population estimates for non-linear surveys (Regression: $y = 0.33x + 1.051$; $F_{1,10} = 28.572$, $P = 0.0001$; $R^2 = 0.741$) but not for linear surveys (Regression: $F_{1,10} = 0.995$, $P = 0.342$) (Figure 4.5). Despite an apparent linear relationship between activity scores from non-linear activity surveys and abundance estimates, it should be noted that data points from woodland sites had high leverage. Tracking plate boxplots reveal that two woodland sites(woodland 3, woodland 4) may be considered outliers (Figure 2.11) and indeed a linear relationship was not found when they were removed from tracking plate and wax block non-linear analyses (tracking plates: $F_{1,10} = 1.700$, $P = 0.229$; wax blocks: $F_{1,10} = 3.395$, $P = 0.103$).
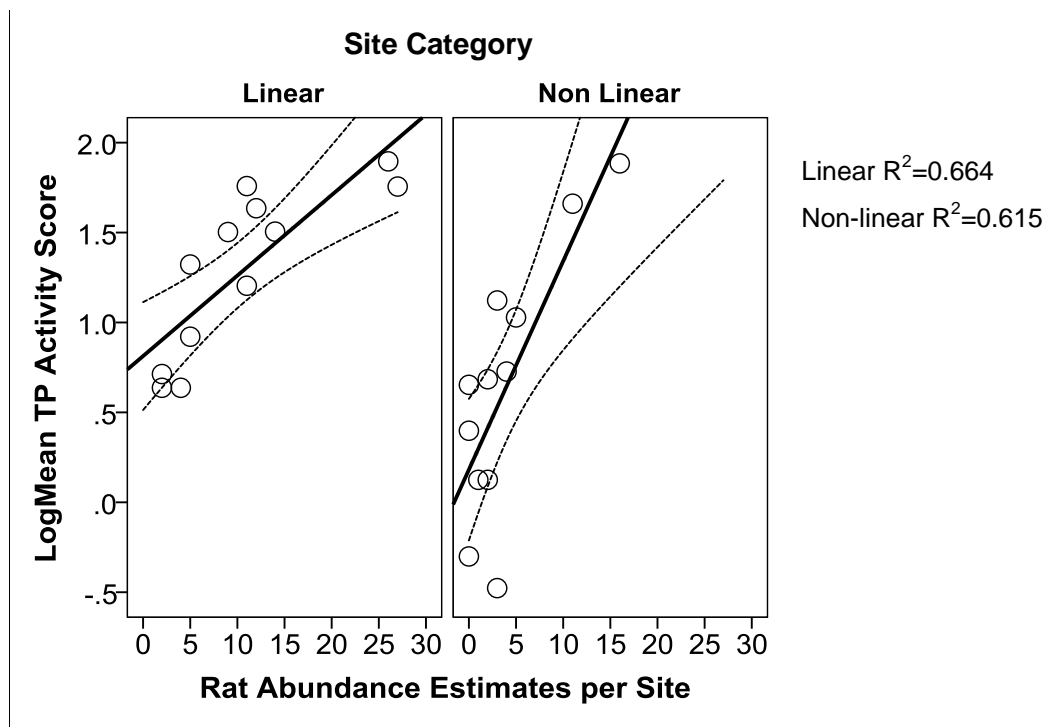
Figure 4.4 Linear regression calibration curve of $\log_{10}$ transformed mean tracking plate (TP) activity scores and population estimates, with linear line and confidence intervals (broken lines) for linear and non-linear site categories.
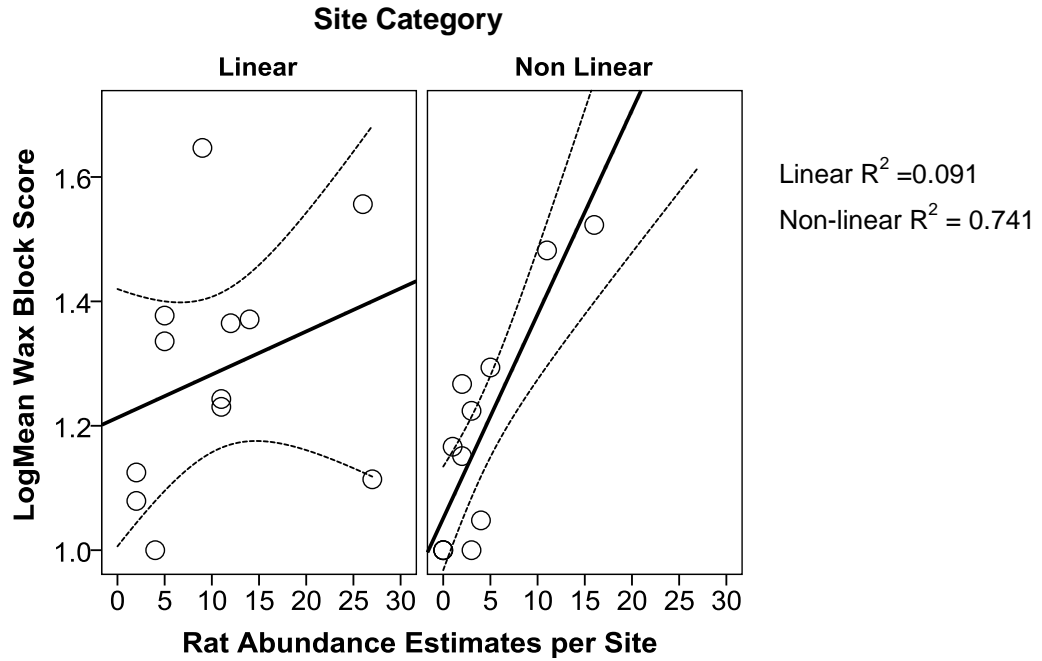
Figure 4.5 Linear regression calibration curve for mean wax block activity scores (log$_{10}$ + 10constant) and population estimates, with linear lines and confidence intervals (broken lines) for linear and non-linear site categories.

4.4.2 Island-wide population estimate

4.4.2.1 Densities estimates by ecotope and ecoelement

Mean density was estimated at 2.92 ± S.E.1.74 rats/ha for non-linear sites and 6.10 ± 1.41 rats/ha for linear sites (Table 4.2 & 4.3). Density was highest on coastal sites ($\overline{x}$ = 13.01 ± 2.86 rats/ha) and lowest on heath ($\overline{x}$ = 0.52 ± 0.25 rats/ha) sites (Table 4.4). Density was highest on Coast 3 (30.72 ± 11.36 rats/ha) and lowest on heath 1, grassland 2 and grassland 3 (0 rats/ha) (Table 4.2 & 4.3). The highest density of rats on a non-linear site was found in Woodland 3 (17.94 ± 9.00 rats/ha) (Table 4.2). Grassland site 1/1B was located within the shearwater colony on Rum and had a mean density of 4.34 rats/ha (summer = 4.7 rats/ha, winter = 3.98 rats/ha); the highest of all grassland or heath density estimations (Table 4.2).

Table 4.2 Summary of non-linear site density estimates (DENSITY) used for an island-wide population estimate of rats on Rum.

Site	Density Estimate - rat/ha (S.E.)		Density Method
Woodland 1	1.81	-	MMDM
Woodland 2	1.06	(0.52)	ML
Woodland 3	17.94	(9.00)	ML
Woodland 4	8.10	(4.70)	ML
Heath 1	0.00	(0.0)	-
Heath 2	1.46	-	MMDM
Heath 3	0.36	(0.29)	ML
Heath 4	0.22	(0.25)	ML
Heath 5	0.57	(0.58)	ML
Grassland 1	3.98	(3.55)	ML
Grassland 1B	4.70	(4.96)	ML
Grassland 2	0.00	(0.00)	-
Grassland 3	0.00	(0.00)	-
Grassland 4	0.74	(0.52)	ML
Mean =	**2.92**	**(1.74)**	

Table 4.3 Summary of rat abundance and associated models, and density estimates for linear study sites. Densities were converted from abundance using the boundary strip method (Dice 1938), where effective trapping area was calculated by adding a strip (MMDM/2) around transects.

Site	Abundance Estimate - no. of rats (S.E.)		Density Estimate - rat/ha (S.E.)		Abundance Model (MARK)
Coast1	9.18	(0.46)	3.81	(0.19)	Huggins M_o
Coast1B	13.24	(2.22)	5.50	(0.92)	Huggins M_o
Coast2	12.35	(1.45)	5.76	(0.68)	Huggins M_o
Coast 2B	33.10	(6.08)	15.43	(2.83)	Huggins M_o
Coast 2C	21.33	(3.98)	10.12	(1.89)	Huggins M_o
Coast3	27.16	(10.04)	30.72	(11.36)	Huggins M_o
Coast4	25.93	(2.85)	19.70	(2.17)	Huggins M_o
River1	2.00	(0.00)	0.36	(0.00)	MNA
River 1B	6.48	(2.02)	1.14	(0.36)	Huggins M_o
River1C	8.45	(2.91)	1.49	(0.51)	Huggins M_o
River2	4.76	(1.28)	0.85	(0.23)	Huggins M_o
River3	14.29	(2.21)	2.69	(0.42)	Huggins M_o
River4	5.63	(2.37)	1.41	(0.59)	Huggins M_o
Wall1	10.59	(1.81)	2.55	(0.44)	Huggins M_o
Wall1B	10.56	(5.26)	2.50	(1.24)	Huggins M_o
Wall2	12.20	(2.25)	3.18	(0.59)	Huggins M_o
Wall3	4.38	(0.79)	1.56	(0.28)	Huggins M_o
Wall4	2.82	(1.68)	1.03	(0.61)	Huggins M_o
Mean =	**12.47**	**(2.76)**	**6.10**	**(1.41)**	

Table 4.4 Summary of rat density per ecotope/ecoelement pooled across seasons and years.

Ecotope/ Ecoelement	n	Density Estimate - rat/ha (S.E.)	
Coast	4	13.01	(2.86)
Wall	4	2.16	(0.63)
River	4	1.32	(0.35)
Wood	4	7.23	(3.90)
Grassland	4	1.88	(1.02)
Heath	5	0.52	(0.25)
Mean =		**4.35**	**(1.50)**

4.4.2.2 Total population estimate of rats on Rum

Total population size of Norway rats on Rum in May 2013 – March 2015 was estimated at 7,444 ± 5,497 for non-linear sites and 11,844 ± 5,685 for non-linear/linear sites combined (Table 4.5). Approximately 1075ha of grassland, heath/mire and woodland ecotope overlapped with the linear feature boundary strip and as such was removed from the total areas (ecotope/ecoelement area (adjusted)) (Table 4.5).

Table 4.5 Summary of the island-wide rat population estimates, mean density estimates and abundance totals per ecotope/ecoelement type. Approximately 1075ha of non-linear ecotope area was excluded from the calculation for the pooled (non-linear/linear) population estimate of rats on Rum to adjust for overlap. Confidence Intervals for population estimates were calculated by pooling S.E. (Satterthwaite 1946) and using the appropriate $t_{critical}$ value for n-1 degrees of freedom.

Ecotope/ Ecoelement	Mean Rat Density (± S.E.)	Ecotope/ Ecoelement Area	Total Rat Abundance (± S.E.)	Ecotope/ Ecoelement Area Adjusted to Remove Overlap	Total Rat Abundance Adjusted to Remove Overlap (± S.E.)
Grassland	1.88/ha (± 1.02)	1020.70ha	1,919 (± 1041.11)	911.07ha	1,713 (± 901.96)
Heath/Mire	0.52/ha (± 0.25)	9117.13ha	4,741 (± 2279.28)	8175.47ha	4,251 (± 2043.87)
Woodland	7.23/ha (± 3.90)	108.46ha	784 (± 422.99)	84.40ha	610 (± 329.16)
non-linear population estimate =			**7,444 ± 5,497**		
Coast	13.01/ha (± 2.86)			303.61ha	3,950 (± 868.32)
River	1.32/ha (± 0.35)			665.91ha	879 (± 233.07)
Wall	2.16/ha (± 0.36)			204.17ha	441 (± 73.50)
combined population estimate =					**11,844 ± 5,685**

4.5 Discussion

4.5.1 Context: calibrations and population estimates

4.5.1.1 Calibration of survey methods

Calibration of tracking plate activity scores against CMR data was successful for linear and non-linear sites, but wax block calibration was only successful for non-linear sites on Rum. Despite the apparent success of the calibration of tracking plates and wax blocks against CMR data in non-linear environments, inspections of the calibration curves (Figures 4.4 & 4.5) reveal variability is high at low population estimates; for instance, an activity score of 0-20 could relate to a population estimate of 5 rats. It is possible that the inclusion of woodland sites (woodland 3 & 4), where population estimates were relatively high, was essential for the calibration of non-linear sites. This suggests that the calibration curves may produce inaccurate population estimates at low densities and the (unconverted) activity index should be used instead. One of the four grassland survey sites was located within the Manx shearwater breeding colony on Rum (grassland 1) and two of the four grassland sites had population estimates of zero. Given the low mean activity scores found in vegetation where shearwaters are present (grassland), it is unclear how useful a conservation tool the calibration curve is in relation to estimating invasive rat populations around shearwater greens. Further investigation is needed because seasonal replication within ecotope/ecoelement was rarely carried out, data were pooled across years, and sample sizes were small; as such, it is possible that calibration could be successful in areas of low densities of rats, such as those surrounding shearwater colonies on Rum, but further work is required. On linear sites (higher density), tracking plate calibration against abundance estimates was successful, whereas no calibration was achieved for wax blocks in linear sites. Furthermore, tracking plates were successfully calibrated against Norway rats on UK farms where activity scores were high (did not drop below approximately 25) and rat population estimates were over 20 rats per site (Quy *et al.* 1999). Whilst wax blocks therefore may be a useful conservation tool for establishing the presence of a target rodent species, the inclusion of an attractant (chocolate) may alter the behaviour of rats. For instance, wax block consumption on linear sites on Rum uniformly increased every day on most survey sites. It is therefore possible that rats are adjusting to a novel food source and gradually increasing their consumption or rat numbers are increasing in the study area. Regardless of the reason, it appears that wax blocks may not be a suitable method for estimating rat abundance or density, particularly in areas of low activity.

4.5.1.2 Population density estimates

The mean density estimate for Norway rats on non-linear sites (grassland, heath, woodland) was estimated at 2.92 rats/ha and 6.10 rats/ha on linear sites (coast, river, wall) on Rum. Bell (2011) reported much higher figures for Norway rats on the Isles of Scilly (23 rats/ha), UK, but non-linear and linear estimates were combined. Mean density of rats estimated on non-linear sites on Rum was, however, very similar to the mean density estimate of Norway rats on other islands including Motuhoropapa, New Zealand (3.3 rats/ha) and St.Clement's Island (3.3 rats/ha), USA, but lower than that found on Raoul (8.94 rats/ha) and Breaksea (13 rats/ha) islands in New Zealand (Lattanzio & Chapman 1980; Moors 1985; Taylor & Thomas 1993, Harper & Veitch 2006).

4.5.1.3 Whole island population estimates

The population size of Norway rats on Rum was estimated at 7,444 ± 5,497 (non-linear category) and 11,844 ± 5,685 (pooled linear & non-linear categories). Previous density estimates for Norway rats on other UK islands have been much higher. Bell (2011), for instance, estimated the population size for Norway rats on St. Agnes and Gugh islands prior to eradication. Mean density estimate was calculated using a trapped population of 56 rats to produce a mean estimate of 23 rats/ha and a total abundance estimate of 3,100 rats for St Ignes and Gugh. Using the same density estimator extrapolated to the area of Rum produces a population estimate of approximately 245,000 rats on Rum. Bell *et al.* (2011) also estimated the population size of Norway rats on the Isle of Canna, Scotland; using bait inference, Norway rat population size on Canna was estimated at 3,000 – 5,000, despite being nearly 9.5 times smaller than Rum (Canna; 1,130ha and Rum; 10,684ha).

4.5.2 Limitations

Total sampling period per site (start of tracking plate survey – end of trapping period) varied between sites but was usually within four weeks, with the exception of Coast 1 which was active for seven weeks. Norway rats have a gestation period of approximately 21 days, with offspring weaned after a further 21 days (Meehan 1984). As such, a limited number of new rats were expected to be born within the four week sampling period. Whilst trapping and surveys should preferably be as contemporaneous as possible, it can be assumed that populations would remain stable enough during the sampling period to regard sampling as contemporaneous. Radio tracking and C-M-R data suggest that dispersal (as indicated by a failure to locate the animal immediately after attachment) was approximately 20%, although

failure to locate does not necessarily indicate dispersal (Appendix E). A total of 308 rats were trapped during this project but only four rats were recaptured at different study sites (section 5.4). Successful calibration of the survey techniques also suggests that the sampling period was short enough to be representative. Wax block surveys did not, however, calibrate well to abundance estimates for linear sites, which is likely to be a biological difference (immigration, adjustment to novel food) rather than a sampling error; wax block surveys were carried out after tracking plate surveys and therefore closer in time to trapping events.

Linear site abundance estimates used to calculate linear density estimates for the pooled total population estimate of rats on Rum were achieved using the simple model (M_o) for ease of comparison between ecotope/ecoelement groups. The null model is a good starting point for model selection but is unreliable if any heterogeneity exists in the data and in biological terms is likely to be an oversimplification (Otis *et al.* 1978). Estimates from M_o therefore should be considered naïve and potentially unreliable.

Density estimates for non-linear sites were achieved using ML in DENSITY. Krebs *et al.* (1999) suggested that ML methods overestimate density at low densities (<1.5/ha). Considering that mean densities of rats on non-linear sites on Rum ranged from 0.52 – 7.23 rats/ha it is likely that the ML estimates for rats on Rum were less accurate on some non-linear sites, especially on heath sites were mean density was very low (0.52 rats/ha). ML does also require a reasonable amount of data, with recommended sample size for use in DENSITY at >20 recaptures per site (Efford 2012). Despite this, ML estimates are still preferred over alternatives that require the estimate of effective trapping given the difficulties in estimating trapping area especially using small samples (Krebs *et al.* 1999). Non-spatial methods using MMDM/2 to calculate effective trapping areas have, however, been shown to produce similar density estimates to SECR models, albeit mostly using camera trapping methods for studying cryptic mammals (Balme *et al.* 2009; Pesenti & Zimmermann 2013). Confidence in the density estimates of this study is potentially therefore relatively low, especially for most non-linear sites, where capture rates were very low.

Population estimates described above were calculated across seasons and years. Study sites were mostly only surveyed once (one site per season) and as such no seasonal replication within ecotope/ecoelement type was achieved. Whilst some seasonality may have been captured in the data when sites were pooled into ecotope/ecoelement groups, site differences confound any possible inference. Furthermore, site abundance estimates were pooled across years and any differences observed may be an interaction between

season and year, with some sites likely to be effected by season more than others. As such, the population estimates provided for Norway rats on Rum may be considered very broad and may not accurately reflect population estimates of rats on Rum at any specific time period *e.g.* year or season.

4.5.3 Conclusions

Tracking plates were successfully calibrated against abundance estimates for Norway rat populations living in non-urban, non-agricultural linear and non-linear environments for the first time. Wax blocks were successfully calibrated against abundance estimates for rats living in non-linear environments but were not successfully calibrated in linear environments; possibly because an asymptote of consumption was not reached within the duration of the surveys. Precision of population estimates from the calibration curves decreased with population density and where density of rats is low the (unconverted) activity indices should be used instead.

Mean density of Norway rats on Rum was estimated at 2.92 rats/ha on non-linear sites and 6.10 rats/ha on linear sites.

Total population size of Norway rats on Rum was estimated at 7,444 ± 5,497 for non-linear environments and 11,844 ± 5,685 for non-linear/linear environments combined. Site abundance estimates were, however, pooled across seasons and years and as such the population estimate for Norway rats on Rum does not account for temporal changes.

4.5.4 Recommendations

Given the use of non-toxic monitoring blocks for post-eradication monitoring of invasive rats during seabird recovery projects, a calibration of this method using abundance estimates from a range of ecotopes/ecoelements (and associated densities) would provide a useful tool for estimating population size of invasive rats on islands. In particular, whilst wax blocks were successfully calibrated against abundance estimates from non-linear sites on Rum, the calibration was dependent on data from the woodland sites which had high leverage (because of their high densities). Furthermore, wax blocks did not calibrate against abundance estimates from linear sites, an effect which warrants more investigation, especially given the evidence that invasive Norway rat density is higher along island coasts. Calibrating wax blocks would therefore provide a useful tool for estimating rat population numbers on seabird conservation projects to aid in the management decisions of invasive rats on islands.

An island-wide population estimate of Norway rats on Rum was calculated using pooled data across seasons and years. As such, it is unclear what effect season or year have on the population size of Norway rats on Rum. Future studies addressing these issues could provide valuable insights into the long term population dynamics of rats on Rum and their potential impact on native species. In particular, do rat populations fluctuate between seasons, and if so which season and why? Do rat populations change in response to seasonal resources such as Manx shearwaters? Is this effect constant over time or do rat populations show annual differences in response? What role does climate play in this?

A further understanding of these patterns may provide valuable data for assessing the factors limiting population size of rats on Rum, which could be used to establish the potential impact they have on native species.

Chapter 5 - Diet

5.1 Introduction

5.1.1 General

The variety of feeding mechanisms found in the animal kingdom is diverse, with species' grouping generalised into trophic levels such as herbivores and predators, with variation in species commonality (dominant species) and importance (keystone species). Nutrients *i.e.* energy, are passed between trophic levels in a series of interactions between food chains, connected to larger food webs (Begon *et al.* 2009). For instance, Kurle *et al.* (2008) describes the relationship between rats and rocky intertidal communities (Figure 5.1):
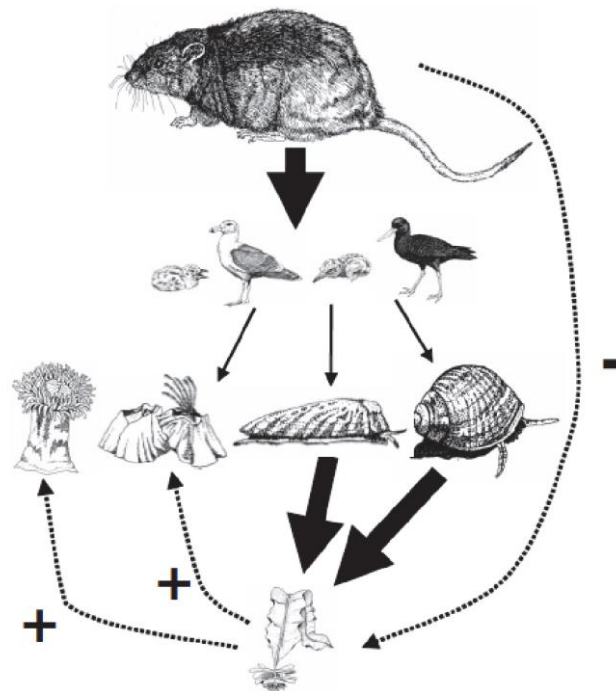
Figure 5.1 Direct (arrows) and indirect (dotted lines) effects of Norway rat predation on foreshore communities in the Aleutian Islands, Alaska. Rats predate birds which increases intertidal invertebrates which reduces algae cover and increases available space for more invertebrates. Note also the Aleutian Islands are located at similar latitude to Rum at ~54 and 57° N respectively (taken from Kurle *et al.* 2008).

The connectedness of organisms within a food web means that changes to the abundance of species at one trophic level can impact the abundance at other levels. These interactions occur in terrestrial and aquatic ecosystems, can be direct or indirect, positive or negative,

107

and across several trophic levels (Elser *et al.* 2000; Williams & Martinez 2000; Borer *et al.* 2005). For instance, Price *et al.* (1980) investigated the relationship between plants and herbivores, emphasising the impact that plants can have on natural selection across several trophic levels. Courchamp *et al.* (1999) describes the indirect effect of rabbit herbivores on seabirds through their interaction with carnivorous feral cats. Numerous examples of these cascade effects have been seen (Fritts & Rodda 1998; Pace *et al.* 1999; Shurin *et al.* 2002; Amori & Clout 2003). Communities exist along an equilibrium/non-equilibrium scale with spatial patchiness, interaction within (competition) and between (predation) trophic levels all contributing to the community stability (Schmitz *et al* 1997; Begon *et al.* 2006).

Predation can be described as the consumption of part or all of a living individual by another (Sinclair *et al.* 1998; Begon *et al.* 2009). Generalists tend to choose many prey items and exhibit typically short catching and feeding (handling time) times in comparison to time searching for prey. Specialist species tend to choose single or few species but have relatively short searching times in comparison to their handling time (Schoener 1971; Martin *et al.* 1995; Shipley *et al.* 2009). For instance, lions, *Panthera leo*, will often live in close proximity to their chosen prey and therefore searching time will be low, but handling times will be relatively high (Caraco & Wolf 1975; Carbone *et al.* 2007). Conversely, many species of insectivorous, woodland birds will have relatively long searching periods but relatively low handling times (Lima 1986; Dolman *et al.* 2007; Bell 2012). Differences in diet can therefore be broadly explained in terms of energetics and risk (Schoener 1971; Charnov 1976; Pianka 2011). In a theoretical sense, diet selection depends on prey energetic profitability and abundance, with a preference for items with a high energy and low handling time ratio. In the real world of heterogeneously distributed prey items, patches of resources will therefore exist, with associated competition and predation risks for highly profitable resources (Schoener 1974; Lima & Dill 1990; Elmhagen *et al.* 2000; Sorensen & Dearing 2003; Wiggins *et al.* 2006).

The introduction of exotic predators can be particularly devastating to native prey species, especially where ecosystems have been 'closed' for relatively long periods. Island species of birds in New Zealand, for instance, have evolved without the presence of mammalian predators (Atkinson 1985; Vitousek *et al.* 1997; Chapin *et al.* 2000; Mack *et al.* 2000; Steadman 2006; Cheke & Hume 2008). As such, evolved behavioural and phenotypic defences have been naturally selected without these alien predators. Numerous expirations and extinctions across several taxa have been associated with introduced mammals (Courchamp *et al.* 2003; Caut *et al.* 2008; Clout & Russell 2008; Simberloff *et al.* 2013).

Furthermore, the destruction, fragmentation and disturbance of habitats are likely to increase the success of other predatory, generalist mammal invaders by reducing habitat, biodiversity and abundance of prey species (Courchamp *et al.* 1999; Amori & Clout 2003).

5.1.2 Rat impact

Norway rats are considered one of the most successful global invaders and amongst the most problematic of the island invaders (Towns & Broome 2003; Towns *et al.* 2006; Angel *et al.* 2009; Drake & Hunt 2009; Shiels 2010), with evidence of suppression, extinction and displacement, as well as multi-trophic cascade effects on native species (Peay *et al.* 2013) (Figure 5.2).
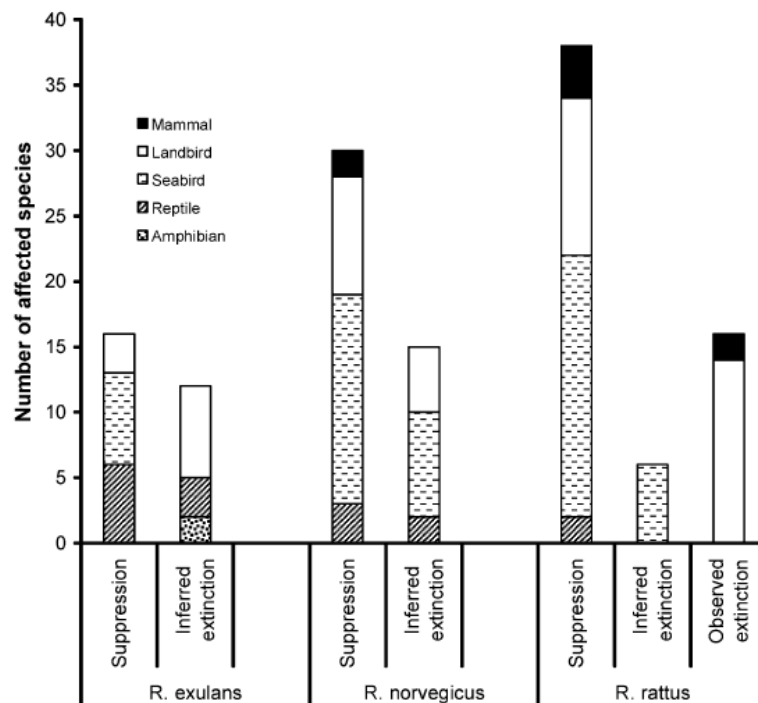
Figure 5.2 Summary of the number of island species (mammals/birds/reptiles/amphibians) affected (suppressed/extinct) by three species of introduced rats (Towns *et al.* 2006).

Several papers have thoroughly reviewed the impacts of Norway rats on seabirds and whilst the general impact is negative, examples of co-existence do exist (Moors *et al.* 1992; Major & Jones 2005; Major *et al.* 2006). It is possible that over time, well-established invasive species, such as rats, reach equilibrium with their surrounding environments and that changes in seabird and invasive rat abundance cannot wholly be explained through their

predator-prey interactions (Martin *et al.* 2000; Begon *et al.* 2006; Theoharides & Dukes 2007; Gallien *et al.* 2012).

Debate surrounds which of the 'big three' (*Rattus exulans, Rattus norvegicus, Rattus rattus*) rat invaders have the potential to cause the most harm, with varying numbers of direct (suppression, extinction) and indirect (trophic cascade) impacts being documented across the world (Athens 2009; Meyer & Butaud 2009; Traveset *et al.* 2009). Atkinson (1985) found Norway rats preyed on the highest number of seabirds; however, Jones *et al.* (2008) found that black rats had the highest negative mean impact on seabirds. Furthermore, McDonald *et al.* (1997) suggested that food supply for seabirds was a larger concern than black rats, at least where rat populations were low in comparison to seabird numbers. Regardless of the 'winner', the impacts of all invasive non-native rat species on seabirds can be broadly attributed to several factors (Atkinson 1985; Towns *et al.* 2006; Jones *et al.* 2008; Latorre *et al.* 2013):

- Relative size and behaviour (arboreal or ground nesting) of the rat species

- Seabird nest position

- Seabird body size

- Seabird behavioural response to predator *e.g.* aggressiveness

- Seabird egg size and/or shell thickness

5.1.3 Rat diet

Rats are omnivorous with a variable diet likely to change with food availability (Harper & Bunbury 2015). Several studies have identified feeding preferences in Norway rats; however, the results vary between studies (Hobson *et al.* 1999; Major *et al.* 2007; Caut *et al.* 2008). For instance, Meehan (1984) noted that rats consumed all 15 different food types presented, with a preference only seen when food types were presented together and acceptance effected by the method of presentation (whole or pellets). Rejection of food is also often associated with an introduction of a new object (neophobia) into the rat's immediate environment. Chitty & Kempson (1949) noted that the introduction of an unfamiliar object onto the path of a rat, prevented use of that path, and subsequent consumption of nearby food. Furthermore, Norway rat diet has high dietary plasticity, allowing diet to adjust to changes to their environment (Robinet *et al.* 1998; Towns *et al.* 2006; Caut *et al.* 2008). Not only do Norway rats vary their diet considerably, they may also vary their mechanism for eating. Whilst it is common for Norway rats to remove food items,

either to eat elsewhere or to hoard, they have also been well documented feeding on site (Takahashi & Lore 1980). It has been suggested that hoarding behaviour is, at least in part, due to the permanency of the food type, although several other factors such as predation risk, food type, rank, gender, reproductive status and age can all have an effect (Barnett & Spencer 1951; Galef & Whiskin 2004; Leaver 2004). For instance, Berdoy (1991) found that social status had an impact on Norway rat feeding behaviour with lower ranking individuals preferring to feed when dominant rats were inactive. Twigg (1975) also noted that Norway rats gradually increased both their duration and frequency of visits to unfamiliar food items. Nonetheless, the variation in diet and behaviour of the Norway rat contributes to its successful global invasion.

5.1.4 Tools for studying diet

The study of diet is essential for the understanding of interactions between organisms and their survival. As such, many methods are available, depending on the question and species concerned. For instance, scat analysis has been used extensively in terrestrial mammal studies (Litvaitis 2000; Trites & Joy 2005; Klare *et al.* 2011). Seabird diet studies are commonly conducted using data from the regurgitation of stomach contents (prey identification) (Hyslop 1980), although popularity of modern chemical techniques is growing (Rau *et al.* 1992; McInnes *et al.* 2016) (Figure 5.3). Diet studies can therefore be split into two broad categories: biochemical and morphological. Morphological techniques include any which utilise physical prey items including stomach content analysis, scat samples and regurgitation. Classic morphological techniques are, however, making way for modern molecular biochemical techniques with methods including immunological techniques, stable isotope analysis (SIA) and DNA-PCR based methods (Boreham & Ohiagu 1978; Peterson & Fry 1987; King *et al.* 2008; Carreon-Martinez & Heath 2010).

Despite this, both methods have strengths and weaknesses. Whilst historically, biochemical analyses, such as stable isotopes, allowed for the analysis of data on trophic levels suitable for separating terrestrial vs. aquatic prey, significant advancements have been made recently allowing for the identification of prey within biomes (Gannes *et al.* 1997; Clementz & Koch 2001; Rundel *et al.* 2012; Oelze *et al.* 2014; Cerling *et al.* 2015; Lerner *et al.* 2018). Morphological techniques may theoretically allow the collection of species level data; however, variation in digestion rates can make interpretation with soft bodied organisms likely to be underestimated (Sheppard & Harwood 2005). As such, a number of studies have

used a combination of both methods, with morphology adding depth to biochemical data (Burns *et al.* 1998; Beaudoin *et al.* 1999).
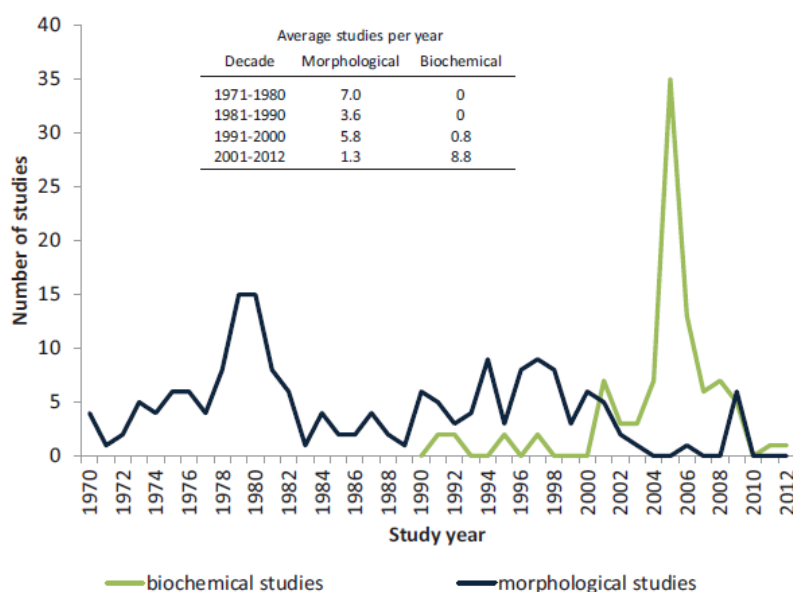
Figure 5.3 Pattern of change in the method used to study albatross diet covering a 42 year period (McInnes *et al.* 2016).

5.1.5 Norway rat diet on islands

Norway rat diet in an island setting has been notably understudied, with most information on diet and food preferences in relation to bait development in mainland synanthropic populations (Meehan 1984). Stomach content analysis was carried out on 80 Norway rats from Langara Island, Canada, with differences observed between coastal and interior habitats (Drever & Harestad 1998). Stable isotope analysis of Norway rats trapped on Pearl Island, New Zealand, showed similar results, with Norway rats located on the coast consuming a primarily marine diet, although specific prey items were not identified (Harper 2006). Norway rat diet was also studied in the Noises Islands, New Zealand, with invertebrates, vegetation and seeds dominating contents (Moors 1985). Rat diet is understudied in UK or European islands; with only a handful of studies reporting on the diet of two species of rats; black rat and Norway rat (Thompson 1987; Stapp 2002; Bell & Ramsay 2011; Ruffino *et al.* 2011). Stapp (2002) used stomach contents and stable isotopes to analyse the gut contents of black rats on the Shiant Islands, Scotland, and concluded that marine food groups including seabird feathers, fish scales and muscle tissue of molluscs, are an important feature of black rat diet, potentially allowing rat populations to survive when

terrestrial food sources are scarce. Ruffino *et al.* (2011) investigated the diet of black rats on Bagaud Island, France, with different food types consumed across three habitats.

5.2 Rationale and Research Questions

Only two previous studies have looked at Norway rat diet on Rum, with information lacking on winter seasonal diet (Thompson 1987; Bell & Ramsay 2011). Thompson (1987) looked at the relationship between Norway rats and Manx shearwaters on Rum and found that plants and invertebrates made up most of the rat dropping samples, with scavenged remains of birds found in autumn and winter. Bell & Ramsay (2011) also reported high numbers of rats with vegetation and invertebrates in the stomach contents on Rum, but a large percentage of rats had remains of 'live' shearwaters in their gut during autumn - towards the end of the shearwater breeding season when late chicks are fledging.

Considering the wide variety of food types consumed by the Norway rat, global comparisons may not be useful, especially in relation to conservation. In this case, the understanding of Norway rat diet in an island setting such as Rum will provide a comparison point for future studies on Norway rat diet on islands, especially in the UK and Europe, where island data is relatively sparse. In Chapter five, the following questions are investigated:

1.   What, if any, are the spatial patterns of Norway rat diet on the Isle of Rum?

2.   Does diet vary between seasonal groups on Rum?

5.3 Methods

5.3.1 Study sites

A total of five sites across three sample groups (coast: $n = 2$; grassland: $n = 2$; urban $n = 1$) were used for the analysis of Norway rat diet on Rum. Sites were randomly selected per sample group using NVC (grassland sites) and linear feature data (coast sites) as described in section 2.3.2.2, with the exception of the urban site and grassland 1 (see below).

Kinloch village (urban site), was located on the eastern 'mouth' of the island, adjacent to Loch Scresort (NM 140197 799530; elevation: 10m). The village was typical of a Scottish rural village with a mixture of bothies, detached houses, and farm buildings. There were no tarmacked roads on the island but there were managed tracks for vehicle access running through the village and connecting the disused townships elsewhere on the island. The population size of the village was approximately 30 people with several domestic cats, dogs,

chickens, ponies, and a flock of Soay sheep being kept. The north of the village was surrounded by fields of *Lolium perenne - Cynosurus cristatus* grassland, with the south and west dominated by mixed woodland. To the east of the village was an extensive area of tidal mudflats/intertidal zone. Rodent control was carried out on an *ad hoc* basis by community residents and reserve staff, with rodenticide rarely used during the study period. Rat carcasses were donated to this study by community members, with the majority of rats being dispatched by domestic cats.

Coast 1 was located in the northern coast of Rum (Figure 5.4), within the deer research area, approximately 6.5km north-west of Kinloch Village (NG 35557 04262; Elevation: 2m). As such, the site was near the rutting greens that host the annual red deer rut. The surrounding habitat was dominated by *Scirpus cespitosus - Erica tetralix* wet heath and *Festuca ovina - Agrostis capillaris - Galium saxatile* grassland, and had an intertidal zone width up to 200m immediately adjacent. The remains of a previous township were approximately 800m southwest of the site, with dry stone walls and a burial ground associated with this.

Coastal site 2 was located on the northern shore of Loch Scresort, the main sea loch on the east coast of Rum, approximately 1.5km east of Kinloch village (NM 41785 99964; elevation: 12m). The surrounding habitat was dominated by a mosaic of conifer woodland plantation; *Scirpus cespitosus - Erica tetralix* wet heath, *Molinia caerulea - Potentilla erecta* mire, *Pteridium aquilinum - Galium saxatile* community and *Calluna vulgaris - Erica cinerea* heath, with approximately 30 – 40m of intertidal width. The surrounding coast is also frequently used by otters, with an otter holt approximately 400m away from the site.

Grassland 1 was located approximately 500m southwest of coast 1 (NG 35973 03896; elevation: 12m), and roughly 6km northwest of Kinloch village. The surrounding habitat was dominated by *Pteridium aquilinum - Galium saxatile* community and *Scirpus cespitosus - Erica tetralix* wet heath, with small patches of *Carex echinata - Sphagnum recurvum/auriculatum* mire and *Calluna vulgaris - Erica cinerea* heath. The site was located within the deer research area and centred on a bothy (and associated outbuildings), frequently used by researchers. The bothy was completely surrounded by open grassland 'deer greens', which hosted some of the highest density of red deer found on grassland on Rum. Researchers donated rat carcasses obtained either by cat predation or sporadic lethal trapping.

Grassland 2 was located approximately 3.4 km southwest of Kinloch village, in a mountainous region on Rum, host to the Manx shearwater breeding colony (NM 37848 97033; elevation 547m). As such, the surrounding habitat was dominated by a mosaic of *Festuca ovina - Agrostis capillaris-Thymus praecox* grassland/*Calluna vulgaris - Erica cinerea* heath and bare rock. The landscape was dominated by steep slopes and views of 'shearwater greens', with golden eagles frequently nesting nearby.
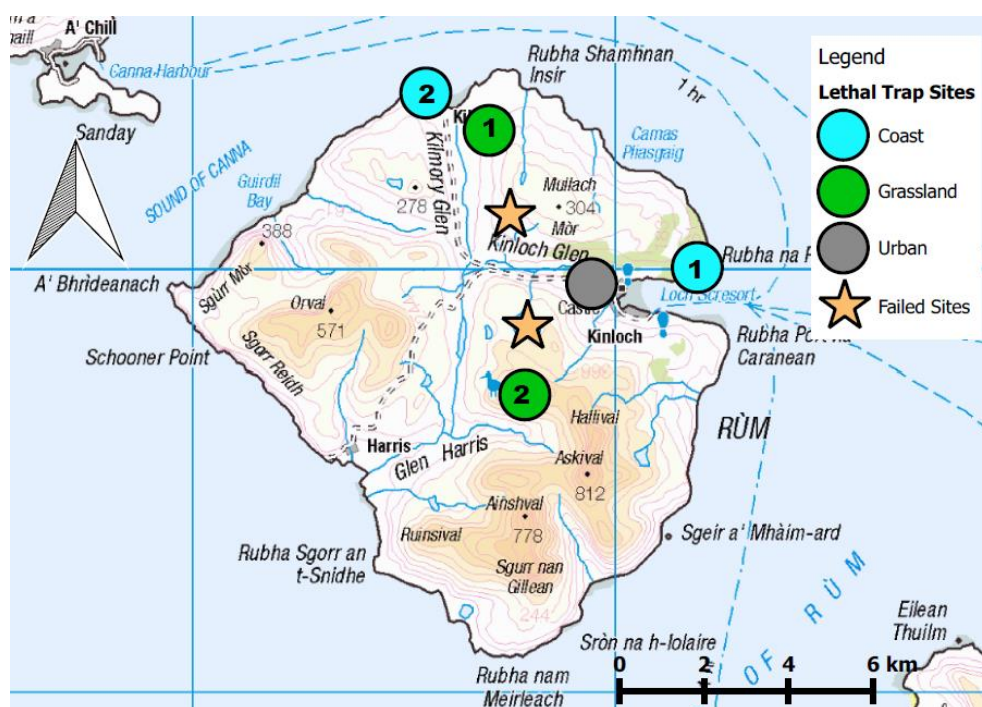
Figure 5.4 Map of the study sites used for diet analysis on Rum. Rats were dispatched during March 2014 – October 2015. Stars indicate sites where lethal traps failed to capture any rats. © Crown Copyright and Database Right 2018. Ordinance Survey (Digimap Licence).

5.3.2 Lethal trapping

With the exception of the urban and grassland 1 sites described above, lethal trapping was used to collect Norway rat carcasses from the remaining sites (n = 3) for stomach content analysis. Lethal trapping was carried out in March 2015, after the cessation of activity and abundance surveys and prior to the final phase (phase 3; April – September 2015) of radio-tracking. Lethal trapping was carried out 1 – 4 months prior to radio tracking phase 3 and 3 – 8km away from radio sites, with the exception of one lethal trapping session which was carried out on grassland 2 in March 2014 (two rats caught). 12 Fenn traps (MK4 Fenn Trap, The Trap Man, Ormskirk, UK) were spaced 40m apart, baited with whole wheat, set shortly before sunset and checked at least every 24 hours. Carcasses were then scanned for PIT tags, numbered, labelled, bagged and frozen immediately (0– 3 days) after collection, for

analysis at a later date. Kinloch Village (urban) and grassland 1 rats were dispatched using a variety of methods as per usual management practice by residents on Rum (trapping and predation by cats) and frozen immediately after collection. There was no formal use of rodenticide on Rum during the fieldwork period; no rats used for stomach content analysis were believed to have been killed by poison and no evidence was found to contradict this *e.g.* pale liver.

5.3.3 Stomach contents

Stomachs were dissected from the internal cavity and rinsed with a 2% detergent solution to allow the viewing and removal of any connecting, intestinal, or oesophageal tissue from the external surface of the stomach. Stomachs were then dried with paper towel to remove any solution and weighed on Kern EMB1200-1 top pan balance (Kern & Sohn GmbH, Balingen, Germany). Scales were calibrated using Kern OIML F1 (327-6/7) 1g and 10g weights immediately before use. Following the method previously described by Sugihara (1997) and Shiels *et al.* (2013), a medial longitudinal incision was made to each stomach, which was then rinsed into a beaker using a 2% detergent solution after peeling back the stomach wall. The stomach was then removed, leaving the stomach contents and solution in the beaker, and towel dried prior to re-weighing. Stomach content weight was then calculated by subtracting the reweighed empty stomach from the initial full stomach weight. Stomach contents were then shaken in 50ml of detergent solution for five minutes, to allow the dissolving of fats, grease and other non-particulates. The contents of the beaker were then poured into a 0.4mm sieve, and rinsed with tap water to remove any detergent /non-particulate solution. Contents were examined in a petri dish using a Prior Z6B222 dissecting microscope (Prior Scientific Instruments Ltd., Cambridge, UK) at 10.5 – 67.5x magnification. Empty stomachs were removed and all tissue collected and incinerated as per standard practice for biological tissue.

Based on previous work by Bell & Ramsey (2011) on Norway rat diet on Rum, stomach contents were classified into 12 subgroups; fish, invertebrates, vegetation, seeds, blood, fur, bones, flesh, feathers, egg(bird), adult (bird) and chick (bird). For ease of comparison with other similar studies these subgroups were subsequently merged into 7 main groups; bait/feed, fish, invertebrates, other animal matter (including bird), seeds, stones, and vegetation.

5.3.4 Analysis

Dissected rat stomachs with no contents were excluded from analysis. Presence and absence and visual estimates (%) of abundance per food type in each stomach, were recorded for the 12 food groups and then given an index score; 0 (absent), 1 (<0.5%), 2 (0.5-5%), 3 (>5 to 25%), 4 (>25 to 50%) and 5 (>50%). Following the 'points method', mean relative abundance of each food type per sample group was then calculated using the following formula, where F values were calculated for each food group within individuals (Hynes 1950; Sugihara 1997);

$$ F_a = \frac{\sum \left(\frac{F_1}{T_1} + \frac{F_2}{T_2} \ldots . . \frac{F_i}{T_i} \right) 100}{N} \qquad \text{EQ. 5.1} $$

Where;

F_a = Relative abundance of each food group

F_i = Food group index score per individual i

T_i = Total index score per individual i

N = Number of individuals per sample/seasonal group

Percentage occurrence was also calculated as the percentage of total stomachs containing each food group.

Data were not normally distributed (Shapiro-Wilk's test (P>0.05), Q-Q plots). To test for equality of variance relative abundance scores for individual rats were ranked then aggregated using sample groups (coast, grassland, urban) to create mean rank scores per sample group. Variance from the mean ranked scores was calculated by subtracting the individual rank scores from the sample group means. The difference was then converted into a positive integer to allow a non-parametric Levene's test to be carried out. Only vegetation, invertebrates and stones had equal variance between sample groups (Levene's test; invertebrates: $F_{2,26} = 2.160$, $P = 0.136$; stones: $F_{2,26} = 0.668$, $P = 0.521$; vegetation: $F_{2,26} = 2.685$, $P = 0.087$). As such, only mean ranks were used to interpret results. For comparisons between seasons, data were pooled into two general groups (spring and summer; autumn and winter) based on the warmest and coldest seasons on Rum respectively (Figure 1.4).

Analysis of relative abundance was conducted in SPSS version 20.0 (SPSS Inc., Chicago, USA) using a Kruskal-Wallis ANOVA and pairwise comparisons using Mann-Whitney U tests.

5.4 Results

A total of 29 rats were used for stomach content analysis (three rats were excluded prior to analysis – no stomach contents) of which 18 were female and 11 were male. Rats were dispatched from March 2014 – October 2015. Four rats used for stomach content analysis were previously trapped on activity survey sites. Three rats were trapped on a coast site approximately 200m away and 4 months after being trapped at a wall site; one rat was trapped (community donation) in the urban site approximately 1.5km away and 9 months after being initially trapped on a river site. A total of 15 rats used for stomach content analysis were dispatched in spring and summer and 14 individuals in autumn and winter, of which 9, 11, and 9 rats were taken from urban ($n = 1$), coast ($n = 2$) and grassland ($n = 2$) sites respectively.

Vegetation and invertebrates made up the highest estimated percentage of stomach contents overall (Figure 5.5, Table 5.1), occurring in 97% ($n = 28$) and 90% ($n = 26$) of all stomachs analysed, at a mean relative abundance (EQ. 5.1) of 43.7% and 43.3%. 8.8% ($n = 3$) of the rats trapped had no contents in their stomach, all of which were males from grassland sites (Appendix G).

Fragments of leaves, stems, roots and rhizomes (vegetation) occurred in 88.9 - 100.0% of stomachs, with a mean relative abundance of 37.7 - 52.4% (Table 5.2). Fragments of chitin from adult arthropods (predominantly marine crustaceans), insect larvae and worms (Annelida & Nematoda) (invertebrates) were found in 77.8 - 100.0% of stomachs, with a mean relative abundance of 33.7 - 53.0%. Only two of the 26 stomachs containing invertebrates had a large quantity of non-crustacean remains. One urban rat had an estimated 45% abundance of invertebrate remains in its stomach, of which 100% was insect remains. One grassland rat had an estimated 98% invertebrate stomach contents, of which 50% was insect and 50% crustacean. No coast rats had more than 5% insect remains in their stomachs. Fish scales were only found on coastal sites in 18.2% of stomachs, with a mean relative abundance of 2.4%. Seeds occurred in 27.3 - 33.3% of stomachs analysed, at a mean relative abundance of 2.9 - 4.8%. No seeds were found in any urban rat stomachs. Stone fragments occurred in 11.1 - 22.2% of stomachs analysed, at a mean relative abundance of 1.7 - 3.3%. Bait/feed was found in 66.7% of urban rats at a mean relative

abundance of 19.9%. Other animal remains (fur) occurred in 11.1 - 18.2% of stomachs examined, at a mean relative abundance of 0.9 - 1.6%. Fur was found in the stomachs of coast and urban rats, but not grassland.
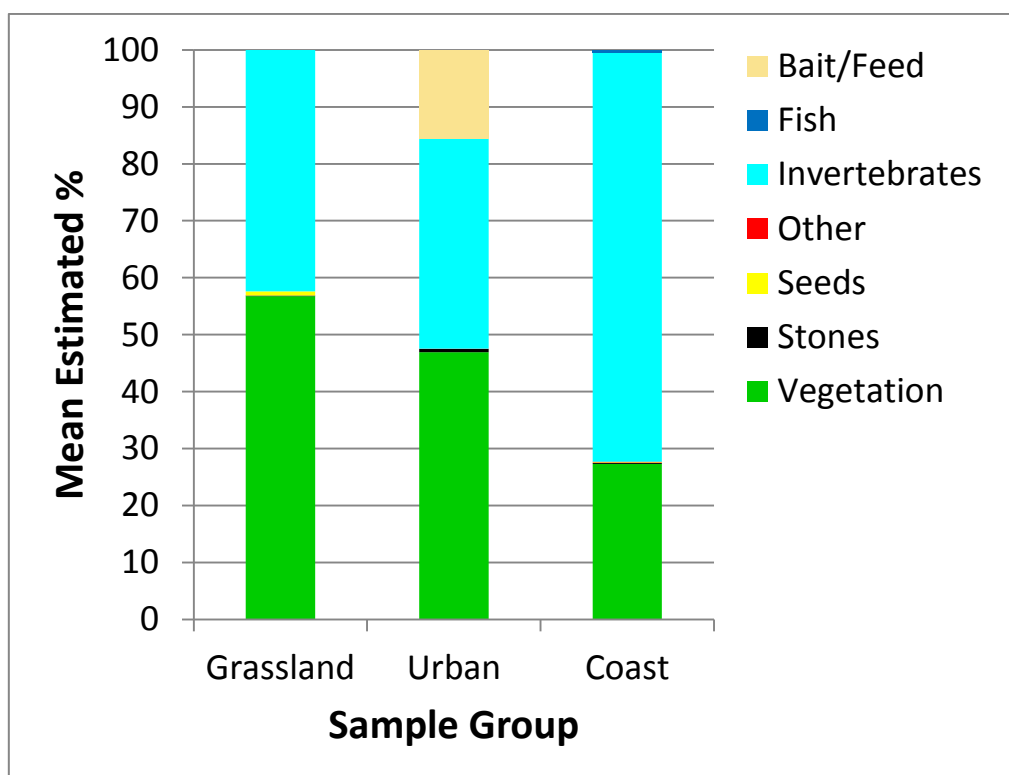
Figure 5.5 Mean estimated percentage of each food type per sample group. Visual estimates (%) of each food type in the stomach contents of individual rats were averaged per sample group. Exacts percentages and associated errors can be found in table 5.1.

Table 5.1 Details of mean estimated percentages (± S.E.) of food groups in the stomach contents of Norway rats from urban, coast and grassland sites pooled across seasons (spring/summer and autumn/winter) and years (March 2014 – October 2015) on the Isle of Rum.

Food Group	Grassland (n = 9)		Urban (n = 9)		Coast (n = 11)	
Vegetation	56.78	(± 13.42)	46.89	(± 9.25)	27.3	(± 10.82)
Invertebrates	42.39	(± 13.49)	36.91	(± 9.52)	71.8	(± 10.85)
Stones	0.11	(± 0.11)	0.61	(± 0.55)	0.14	(± 0.10)
Seeds	0.72	(± 0.55)	0		0.14	(± 0.07)
Other (Animal)	0		0.06	(± 0.01)	0.09	(± 0.06)
Fish	0		0		0.50	(± 0.45)
Bait/Feed	0		15.56	(± 6.06)	0	

Table 5.2 Percentage occurrence (% of rat stomachs the food type occurred in) and mean relative abundance ± S.E. (parentheses) of food groups in the stomach contents of Norway rats from coast, grassland and urban sites on Rum. Seasonal groups (spring and summer; autumn and winter) and years (March 2014 – October 2015) were pooled.

Food Group	Grassland ($n = 9$)	Urban ($n = 9$)	Coast ($n = 11$)
Vegetation	88.9 (52.4 ± 11.0)	100 (42.3 ± 4.7)	100 (37.7 ± 5.7)
Invertebrates	77.8 (41.1 ± 10.9)	88.9 (33.7 ± 5.2)	100 (53.0 ± 5.7)
Stones	11.1 (1.7 ± 1.7)	22.2 (3.3 ± 2.4)	18.2 (2.4 ± 1.7)
Seeds	33.3 (4.8 ± 2.5)	0	27.3 (2.9 ± 1.6)
Other (Animal)	0	11.1 (0.9 ± 0.9)	18.2 (1.6 ± 1.1)
Fish	0	0	18.2 (2.4 ± 1.6)
Bait/Feed	0	66.7 (19.9 ± 5.8)	0

There was a significant difference in the mean ranked relative abundance of bait/feed between sample groups at the $P<0.05$ level (Kruskal-Wallis: $X^2_2 = 15.95$, $n_1 = 11$, $n_2 = 9$, $n_3 = 9$, $P = 0.0003$). In particular, mean ranked relative abundance of bait/feed was greater in urban than both grassland (Mann-Whitney U test: $U = 13.50$, $n_1 = 9$, $n_2 = 9$, $P = 0.01$) and coast sites (Mann-Whitney U test: $U = 82.50$, $n_1 = 11$, $n_2 = 9$, $P = 0.01$). Furthermore, whilst there was no effect of sample group on the mean ranked relative abundance of invertebrates overall, coast did have a significantly higher mean ranked abundance of invertebrates than urban (Mann-Whitney U test: $U = 21.50$, $n_1 = 11$, $n_2 = 9$, $P = 0.03$).

Relative abundance of seeds differed between seasons (Kruskal-Wallis: $X^2_2 = 7.97$, $n_1 = 1$, $P <0.01$), with relatively more seeds found in the stomach contents of rats in autumn and winter than in spring and summer (Figure 5.6, Table 5.3). No other significant effect of season on food group was found.
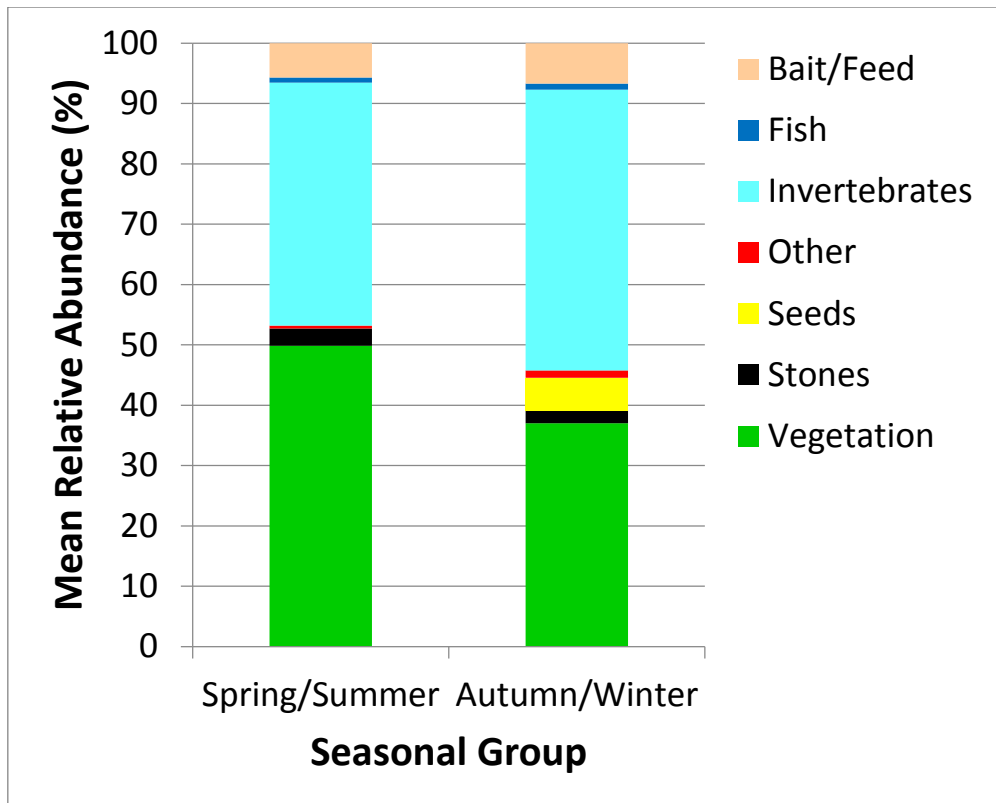
Figure 5.6 Mean relative abundance estimates of food types per seasonal group in the stomach contents of Norway rats on Rum. Data were pooled across sample groups (coast, grassland, urban) and years (March 2014 – October 2015).

Table 5.3 Details of mean relative abundance estimates (± S.E.) for food types recorded in the stomach contents of Norway rats, per seasonal group.

Food Group	Spring/Summer	Autumn/Winter
Vegetation	49.87 (± 7.06)	37.01 (± 4.28)
Invertebrates	40.27 (± 6.76)	46.53 (± 5.77)
Stones	2.83 (± 1.60)	2.12 (± 1.44)
Seeds	0	5.41 (± 1.85)
Other (Animal)	0.51 (± 0.51)	1.22 (± 0.85)
Fish	0.83 (± 0.83)	1.02 (± 1.02)
Bait/Feed	5.68 (± 3.48)	6.69 (± 3.59)

5.5 Discussion

5.5.1 Context: diet

As with previous island studies, Norway rat diet on Rum contained mostly vegetation and invertebrates across all seasons and sites (Bremner *et al.* 1984; Thompson 1987; Bell & Ramsay 2011). Moors (1985) reported that plants, seeds, fruits and invertebrates (including insects and crustaceans) occurred most frequently in the stomach contents of Norway rats in the Noises Island (NZ), of which invertebrates and plant materials occurred the most. Despite previous evidence of bird remains in Norway rat stomach contents on Rum and Kiska Islands, no incidence of other animal matter (*e.g.* birds) was found in this study (Major *et al.* 2007; Bell & Ramsey 2011). Only a small number of rats had animal matter (tightly woven balls of hair) other than invertebrates in their stomach ($n = 3$) and it is likely these hair samples can be attributed to either allo or auto-grooming; grooming behaviour in rats has been shown to account for up to 40% of their waking time (Bolles 1960). Two of the three individuals with fur in their stomachs were also likely to be from the same social group (trapped 80m and three days apart). Furthermore, no other animal matter (bones/flesh) was present in the stomach contents of the rats with hair balls; predation of any vertebrate species was therefore unlikely. Two grassland rats were trapped within the shearwater colony in winter (Rat 020 & 021, winter 2014, Appendix G) and had similar percentage of occurrences/relative abundance scores of food types in comparison to other grassland rats.

Differences were found in the mean ranked relative abundance of bait/feed between sample groups overall, and in the relative abundance of invertebrates between the coastal and urban sites. Major *et al.* (2007) also noted spatial differences in the diet of Norway rats on Kiska Island, Alaska; although analysis was done using stable isotopes and replication within sample group was much larger ($n = 78$). Bait/feed consumption in Norway rat diet on Rum differed between urban and grassland/coast sites on Rum; reflecting the availability of bait/feed rather than a biological phenomenon. Mean ranked relative abundance of invertebrates was higher on coastal sites than the urban site, possibly reflecting the variety of invertebrate prey available on coastal sites in comparison to urban environments. Navarrete & Castilla (1993) reported on the remains of up to 40 species of intertidal organisms (decapods, gastropods, bivalves) located in burrows of Norway rats ($n = 20$) in Chile; with keyhole limpets being found at the highest relative abundance of all organisms (42%). Moors (1985) also reported marine foods (molluscs, polychaetes, crustaceans) occurring in 27% of the stomach contents of Norway rats ($n = 36$) in the Noises Islands (NZ).

Taylor *et al.* (2000) reported that marine invertebrates (including amphipods) occurred in 26% of the stomach contents of Norway rats (*n* = 80) on Langara Island, British Columbia. Harper (2006) suggested that in the presence of a competitor, Norway rats may be excluded from preferred food sources and utilise a marine food source. On Rum, however, in the absence of competitive exclusion, coast sites may offer better resources in comparison to potentially resource poor interior habitats containing moorland (Twigg 1975). Coastal sites are likely to be a highly profitable and therefore desirable resource for invasive Norway rats (Harper 2006). Seasonal differences in rat diet on Rum was low with only the mean ranked relative abundance of seeds differing between seasons, with more abundance in autumn and winter than spring and summer. Seasonal variation in invasive rat diet on islands is, however, understudied; Sturmer (1988) found the frequency of occurrence of vegetation and invertebrates varied between seasons on Stewart Island (NZ), with more vegetation in autumn and winter, and more invertebrates in spring and summer; seasonal changes in availability of plant leaf matter may explain this.

Considering that Norway rats are omnivorous with highly variable diets, comparisons between studies and indeed generalisations about their diet are difficult (Harper & Bunbury 2015) to justify. Despite this, it does appear that plant material and invertebrates are important aspects of Norway rat diet, with spatio-temporal variations in their consumption by rats (in response to changing conditions) likely (Bremner *et al.*1984*; Sturmer 1988)*. Vertebrate species such as birds have been reported in the diet of numerous invasive rat species, with predation by rats potentially resulting in population level consequences to bird populations (Atkinson 1985); but assumptions on Norway rat diet should be used with caution given the variability in their diet.

5.5.2 Limitations

Sample groups were selected using broad spatial categories (*e.g.* urban) to provide a practical way of creating stratified samples for the analysis of rat stomach contents on Rum. In reality, however, it is likely that broad categories contain mosaics of ecotopes *e.g.* plant communities and often sub-communities (with associated prey items) within them, not accounted for when selecting sites. Furthermore, physical barriers between categories rarely exist and it is likely rats use a variety of ecotopes to fulfil their nutritional requirements. For instance, three rats previously trapped during a CMR session on an activity survey site (wall 3) in October 2014, were re-trapped in March 2015 at a coast site approximately 200m away from the initial activity survey site. The large quantities of (marine) crustaceans found in the

stomach contents of most grassland rats on Rum may be attributed to this movement between ecotopes. Navarrete and Castilla (1993) also found remains of intertidal organisms in the burrows of Norway rats up to 200m from the littoral zone.

Sample sizes per sample group and per season were low (<20) and as such biological differences may have been missed. In particular, only one urban site was sampled for rat diet, which may be useful for spatial comparisons of Norway rat diet on Rum but it is unlikely to accurately reflect a general urban environment. Furthermore, whilst the urban site was the only village populated on Rum, human population was low (<30 residents, buildings were spread across a large area) and was located within close proximity to the coast (ca 200m).

Also, classification of food types had low resolution with differences potentially being found if dietary groups were divided into smaller strata. Major *et al.* (2007) found a difference between the proportions of marine and terrestrial invertebrates consumed by black rats on Kiska Island, Alaska; an effect unlikely to be observed had invertebrates been pooled.

5.5.3 Conclusions

Norway rat diet on Rum did not vary greatly between sites or seasons. Mean ranked relative abundance of bait/feed differed between sample groups with urban rats consuming more bait/feed than grassland and coastal rats. Mean ranked relative abundance of invertebrates differed between coast and urban rats. No other significant differences between sample groups were found. Sample size was, however, low and an effect may have been missed.

Norway rat diet on Rum did not vary greatly between seasons with the only difference being found between the mean ranked relative abundance of seeds; more seeds were consumed by rats in autumn and winter than in spring and summer. No other seasonal differences were found.

Vegetation and invertebrates occurred in the highest percentage of stomachs and had the highest relative abundances across all sites and both seasonal groups. Fur was found in the stomach contents of three rats but may be accounted for by grooming behaviour. No other evidence of vertebrate animal matter was found in the stomach contents of any Norway rats on Rum during this study.

5.5.4 Recommendations

A relationship between coastal areas and rat diet has been reported across several studies with coastal environments potentially providing stable high-protein food resources for

invasive Norway rats (Moors 1985; Taylor *et al.* 2000; Stapp 2002). Introduced rats also have the ability to change the communities of intertidal zones (Kurle *et al.* 2008; Fukami *et al.* 2006). Despite this, no experimental work has investigated the multi-trophic effect of introduced rat diet on these communities and any such study could be of conservation value to coastal species, such as ground nesting birds, and their associated invertebrate prey.

Previous work on Rum has shown that Manx shearwater remains were present in the gut of Norway rats within the shearwater colony in autumn (Bell & Ramsay 2011), but no animal matter (other than fur and invertebrates) of any species was found in the stomach contents of rats across seasons or sites in this study. These differences between studies could be attributed to small sample size, site differences, or year. Therefore, it is recommended that research be carried out on the long term effects of season and vegetation type on the diet of Norway rats on Rum. In particular, replication should be high within vegetation type using repeated sites across seasons, with a particular focus on grassland (including shearwater greens) to establish the extent to which Manx shearwaters are found in the diet of Norway rats on Rum.

Chapter 6 - General Discussion

6.1 Context: Ecology of Rats on Rum

The potential for negative impacts of invasive non-native rats on island populations of seabirds is widely reported across the world (Atkinson 1985; Towns *et al.* 2006; Jones *et al.* 2008); recent evidence demonstrating the coexistence of Norway rats and Manx shearwaters on Rum has, however, raised some important ecological questions about the nature of this relationship (Lambert *et al.* 2015). Fundamental gaps in our understanding of Norway rats in an island setting has led to an investigation into their biology on Rum and any implications this may have on Manx shearwaters. The work presented in this thesis aims to address these gaps in knowledge and provide essential data to inform management practices in a key conservation area.

6.1.1 Spatial patterns of abundance, distribution and density

To begin with, an understanding of the general distribution of Norway rats on Rum and how this relates to previously reported Manx shearwater distribution was established. Optimal survey parameters for two common rat survey techniques (tracking plates, chocolate wax blocks) were established and activity scores were calibrated against population size estimates from CMR trapping data.

A total population estimate of Norway rats on Rum was calculated at 7,444 ± 5,497 (non-linear sites) and 11,844 ± 5,685 (non-linear/linear sites combined) with rat signs (activity, trapping) being recorded on every ecotope/ecoelement group and all 25 sites surveyed. In this sense, Norway rats are ubiquitous on Rum, at least present on all of the ecotopes/ecoelements surveyed across the island (coast, grassland, heath, river, wall, woodland).

Norway rat mean density was estimated at 2.92 rats/ha (non-linear sites) and 6.10 rats/ha (linear sites). To put this into context, Bell (2011) estimated an average density of rats on St. Agnes and Gugh Island, UK, of 23 rats/ha, which if extrapolated by the area on Rum would provide an estimate of approximately 245,000 rats; clearly, however, this is a generalisation without scientific validity. Mean densities of Norway rats on islands across the world range from 3.3 – 13.0 rats/ha (Lattanzio & Chapman 1980; Moors 1985; Taylor & Thomas 1993; Harper & Veitch 2006); indicating that non-linear density estimates for rats on Rum are slightly lower than other studies. In urban environments, rat densities are typically much

higher, with estimates from urban rats varying between 25 – 73 rats/ha (Traweger *et al.* 2006).

Whilst density estimates using CMR data are calculated using the proportion of captured rats versus recaptured rats to estimate an encounter probability for un-trapped individuals (Cunningham & Moors 1996; Efford 2012); the more commonly used C100TN reports the total number of unique individuals encountered per 100 trap nights during an individual trapping period and represents a useful index for comparative purposes between rat studies on islands (Nelson & Clark 1973; Cunningham & Moors 1983). In this sense, comparing capture rates between ecotopes/ecoelements may provide crucial information on the factors limiting distribution and abundance of Norway rats on Rum. Mean C100TN on Rum was estimated at 15.96, which is within the normal range estimated for rats on oceanic islands (5 – 20 C100TN) (King 1990). C100TN varied between ecotope/ecoelement categories for rats on Rum, with mean C100TN being higher on linear sites ($\bar{x}$ = 22.35) than non-linear sites ($\bar{x}$ = 9.57). Mean activity scores (tracking plates) were also found to be higher on linear sites ($\bar{x}$ = 29.93) than non-linear sites ($\bar{x}$ = 13.77) for rats on Rum. To put this into context, mean activity score on UK farms using tracking plates was estimated at 50 – 98 (Quy *et al.* 1993; Lambert *et al.* 2008). The use of linear features as a movement corridor has been reported in other species and indeed, based on the data from this project, linear habitats do appear important for rats on Rum also (Wegner & Merriam 1979). Several other studies in urban and non-urban settings have concluded that Norway rats are often associated with riverine environments (Major *et al.* 2007; Innes *et al.* 2001; Traweger *et al.* 2006). Differences reported here in the C100TN and activity scores between ecotope/ecoelement categories may therefore be a feature of the ecotope/ecoelement types included in the linear category, rather than in relation to linearity *per se*. In a more general sense it is widely accepted that Norway rats prefer wet environments to arid ones (Harper & Bunbury 2015). Mean activity score for rats was highest on coastal sites ($\bar{x}$ = 56.21) and was significantly higher than grassland and heath mean activity scores during this study. Differences in mean activity and C100TN between ecotope/ecoelement categories may therefore be a result of the inclusion of coastal sites in the analysis, rather than the inclusion of rivers in the linear category. Moors (1985), for instance, concluded that Norway rats were not always trapped in close proximity to rivers on Motohorupapa Island, New Zealand. Furthermore, a correlation was found on Rum between the mean C100TN and distance to coast but not for distance to river or wall linear features. Previous studies have highlighted the importance of coastal areas to the distribution of invasive Norway rats on islands and it seems likely that this is the case for rats on Rum also (Harper 2006; Patterson 2006).

Mean tracking plate activity scores, C100TN and density for grassland sites were the second lowest of all ecotopes/ecoelements surveyed. In 2014, (year two) of the study, several failed attempts were made to trap wintering rats in a grassland site within the shearwater colony. It seems reasonable to assume that the extensive snow cover above 350m (where shearwaters nest during warmer months) reduced the survival of Norway rats and localised extinctions may have occurred. Whilst it is unclear what effect snow cover will have on Norway rat abundance, temperature and snow cover has been shown to reduce activity (Calhoun 1962). Despite previous levels of C100TN for Norway rats in grassland on islands being reported within the normal range for oceanic islands (King 1990; Weihong *et al.* 1999), reports of Norway rats during this project were low and it is unlikely that grassland is suitable to sustain dense populations of Norway rats on Rum. Seasonal resources such as Manx shearwaters may temporarily increase rat activity on grassland sites, with a small increase in density seen on grassland 1 (shearwater colony) in summer when compared with winter. Clearly, however, a single site is not representative of all shearwater sites on Rum and the effect of seasonality on activity and C100TN within grassland requires further investigation. Approximately 75% of the grassland and heath sites surveyed on Rum had low C100TN (<5) when compared with estimates for all rat species on oceanic islands (5 – 20 C100TN) (King 1990); with only two rats (one male and one female) being caught on most of these sites, which were likely to be reproductive pairs. Mean tracking plate activity scores in woodland sites were the highest for all non-linear sites surveyed and differed significantly from heath activity scores; mean C100TN for woodland was the second highest of all ecotopes/ecoelements surveyed. Mean tracking plate activity scores and C100TN for woodland 3 and woodland 4 were relatively large in comparison to all non-linear and most linear sites surveyed. These sites were surveyed within isolated pockets of woodland surrounded by a large amount of poor quality (low activity and C100TN) vegetation (grassland and heath). Considering how sparsely woodland is distributed on Rum (1% of the land cover) it is possible woodland offers an intra-island refuge for Norway rats by providing a more suitable micro-climate with associated resources (food and nesting sites), when surrounded by open unfavourable vegetation. It is unclear, however, what effect season may have on the activity and C100TN of rats on Rum in woodlands, with no repeated surveys carried out on woodland sites and all sites sampled during different seasons. Conifer plantations produced the lowest woodland activity and C100TN estimates, but were sampled in winter and spring, and deciduous woodlands produced the highest estimates, but were sampled in summer and autumn. The extent to which woodland provides suitable resources for high activity and abundance of rats on Rum is therefore unclear.

6.1.2 Diet and impact on avifauna

Invertebrates and vegetation were the main dietary components (recorded in the highest mean relative abundance within stomach contents) of Norway rats across three sample groups surveyed (grassland, coast, urban) on Rum; invertebrates and vegetation are regularly reported in the stomach contents of invasive Norway rats on islands (Taylor *et al*. 2000; Major *et al.* 2007; Bell & Ramsay 2011). A significantly higher relative abundance of invertebrates were found in the stomachs of coastal rats in comparison to the urban rats; the majority of which consisted of marine crustaceans. The importance of coastal prey to Norway rats on other islands is well documented (Moors 1985; Taylor *et al.* 2000; Stapp 2002). Harper (2006) concluded that coastal environments provide high quality food (protein) for invasive Norway rats in comparison to interior island habitats. Navarette & Castilla (1993) reported up to 40 species of marine foods in the stomach contents of Norway rats on coastal sites in Chile, of which keyhole limpets were found at the highest frequency of rat stomachs. So it seems likely that the results reported in this study confirm that coastal environments on Rum provide a plentiful supply of food for Norway rats, with marine invertebrates playing an important role in rat diet on Rum. No evidence of avifauna remains was found in the stomach contents of any rats during this study, contrary to the previous findings of Bell & Ramsay (2011) who did report bird remains in between 30 – 50% of the stomach contents from rats trapped near shearwater breeding colonies on Rum. It is clear, therefore, that rats on Rum do have the potential for predation of avifauna but to what extent is unclear. Furthermore, sample sizes between this study and Bell & Ramsay (2011) differed, with the later reporting on the findings from 52 rats whereas only 29 were used during this study. Also, all rats trapped previously by Bell & Ramsay (2011) were surveyed within or near the shearwater colony during the Manx shearwater breeding season, whereas only two rats were caught within the shearwater greens in this study and both were caught outside the shearwater breeding season. As such, rats on Rum have been previously reported with shearwater remains in their stomach contents but the importance of this prey and indeed avifauna on the rat population across ecotopes and seasons is unclear, given the absence of avifauna reported here.

The two rats trapped at the shearwater greens in winter were reported here with invertebrates, vegetation and seeds occurring at the highest percentage and relative abundance of all food types recorded. Whilst the relative abundance of seeds was relatively low overall for all rats on Rum, the highest relative abundance of seeds was found in the two grassland rats found within the shearwater greens.

It is clear therefore that invertebrates and vegetation are an important resource for Norway rats across all seasons on Rum, but with such low sample sizes it is unknown what effect, if any, season has on the diet of rats on Rum, with very little seasonal difference in diet found here. Relative abundance of seeds was, however, greater in autumn and winter than spring and summer, and may play an important role in the overwinter survival of rats on Rum. Seeds have frequently been reported in the diet of Norway rats in other studies of invasive Norway rats on islands (Moors 1985; Taylor *et al.* 2000; Bell & Ramsay 2011).

Kurle *et al.* (2008) suggested the possibility of a top-down cascade effect of Norway rats on intertidal communities, through the predation of coastal birds and the associated effect on bird prey items. Furthermore, whilst the direct predation of invasive rats on coastal birds and the associated potential for cascade effects on coastal communities has been reported, it is possible that rats are indirectly affecting coastal birds through prey competition (Kurle *et al*. 2008). For instance, common limpets are an important dietary resource for oystercatchers and whilst no limpets were found in the stomach content of rats on Rum, soft bodied animals are frequently under-reported in stomach content studies (Sheppard & Harwood 2005). Furthermore, Navarette & Castilla (1993) concluded that limpets were found in the highest frequency of Norway rat burrows along coastal sites in Chile; on Rum, limpet shells were often a diagnostic feature of Norway rat coastal burrows observed during the preliminary surveys in comparison to interior sites, where no evidence of limpets were present outside rat burrows. The limpit shells outside coastal rat burrows could also be a result of rats tunnelling into shell middens, resulting from historic human activity, and may not necessarily indicate that rats utlise limpets as a food source.

Given the risk of rat predation to small ground nesting birds (Atkinson 1985; Jones *et al.* 2008) and the evidence from this project of high density and activity of coastal rats on Rum, it is more likely that bird species typically associated with coastal areas are at a higher risk to negative effects of invasive rats than inland birds associated with poor rat habitats (low rat activity and density and C100TN) on Rum *e.g.* Manx shearwaters on upland grassland. These may include Eurasian oystercatchers, *Haematopus ostralegus*, ringed plovers, *Charadrius hiaticula,* common sandpipers, *Actitis hypoleucos,* and common/artic tern, *Sterna hirundo/paradisaea,* with previous studies reporting negative impacts by invasive rats to these bird species across the world (Norman 1975; Wragg & Weisler 1994; Pierce & Blanvillain 2004; Harper & Bunbury 2015). High density of invasive rats does not, however, necessarily increase the risk of negative impacts on birds, with alternative food sources potentially reducing any possible impact invasive rats may have on seabirds (Harper &

Bunbury 2015). In this sense it is unclear what impact Norway rats may have on shoreline bird species on Rum.

6.1.3 Movement and dispersal of rats

Dispersal rates were not estimated for Norway rats on Rum but general patterns of movement were assessed during this project, with home range and trapping providing some insight on the spatial differences in movement patterns of the invasive Norway rat on this globally important island.

Mean home range size on Rum was estimated at 2.32ha which falls within the home range estimates for other Norway rat populations on islands (1.2 – 5.5ha) (Moors 1985; Hickson *et al.* 1986; Bramley 2014) and is higher than estimates found for Norway rats living in areas associated with humans on the UK mainland (0.02 – 1.55ha) (Quy *et al.* 1999; Lambert *et al.* 2008). Differences between home range size in synanthropic and island populations may be explained due to the increased food availability and shelter, and higher densities available to mammal species in urban environments (Iossa *et al.* 2010; Bateman & Fleming 2012). Šálek *et al.* (2015), for instance, concluded that mammal home range size decreased as density increased in association with urban environments. During this study, the site with the smallest home range (site B) was located on a coastal site. Coast sites also had the highest activity and C100TN and density estimation of all ecotopes/ecoelements studied, including river (radio site A) and heath (radio site C). It is therefore possible that density affects the home range size of rats on Rum on coastal sites when compared with heath and river sites. No replication was, however, carried out within ecotope/ecoelement so whilst site differences were found in the home range of rats on Rum, the extent to which this is related to vegetation type, linear features or associated densities is unknown.

Home range size was estimated using MCP100 and was higher in male than female rats on Rum. A total of eight rats failed to be located after initial radio tag attachment, of which 75% were male. Whilst exploratory behaviour is common in Norway rats, dispersal is typically male-biased in rodent species (Calhoun 1963; Taylor & Quy 1978; Krebs *et al.* 2007). The longest straight line distance moved in a single night by any rat (1.5km) during this study was by a male from a study site which had too few rats to include in the radio tracking study (river, site E). It is unclear whether this movement was within the home range of the subject, exploratory behaviour, or dispersal. It is, however, unlikely to be explained through dispersal as movement from the initial capture was towards an established nesting site (indicated by an established burrow - multiple droppings and flattened vegetation surrounding burrow).

131

Three rats (2 male and 1 female) were re-captured on a coast site (lethal coast 1) approximately 200m and 4 months from their initial capture point (wall 2); one male rat was trapped at the urban site approximately 1.5km and 9 months from the initial capture point (river 1).

Thompson (1987) theorised that Norway rats on Rum may disperse seasonally to upland areas associated with Manx shearwaters. The shortest distance from the coast to shearwater colonies on Rum is roughly 1.2km to the Cloughs Crag colony. Lambert *et al.* (2015) reported relatively high activity of rats on Cloughs Crag in 2013 when compared with two other study sites within the shearwater colony on Rum. Furthermore, it was suggested that elevation may play some part in the survival of rats around shearwater colonies. Rats were reported within and around the shearwater colonies by Bell & Ramsay (2011) and Lambert *et al.* (2015) during spring and summer seasons; during this study, Norway rats were live-trapped within the shearwater colony (grassland 1) in winter and summer 2014. Furthermore, two rats were lethal trapped during this study in the shearwater colony in winter. Considering the evidence reported that Norway rats on Rum can move up to 1.5km in one night and move between ecotopes seasonally, it is possible that at least some rats on Rum move from the coast to shearwater colonies seasonally; it is clear from this project's trapping data that rats on Rum are, however, found within the shearwater colony outside shearwater breeding seasons.

Dispersal rates were, however, not quantified in this study and the extent to which the movement observed reflects the population ecology of rats on Rum is unknown. Whilst trapping occurred across 25 study sites on Rum, areas of low rat activity and abundance reduced the sample size, especially on less favourable ecotopes of high conservation value *e.g.* grassland. As such, sample sizes were low with a lack of seasonal data on home range size and a lack of within site seasonal data across most aspects of this study.

6.1.4 Predation of rats

The Isle of Rum is free from mammalian predators of rats; however, avian predators are present. In particular, three radio collars were retrieved during this study within 50m of a known buzzard's nest located approximately 1.5km from site B (coast). In mainland Scotland, rabbits, *Oryctolagus cuniculus,* are the primary prey item of buzzards, although Rooney & Montgomery (2013) found evidence of Norway rat remains in 50% of buzzard nests checked in Ireland. Predators can affect the ranging behaviour of Norway rats, with home range movements likely to be smaller in the presence of predators especially near

open areas (Taylor 1978; Taylor & Quy 1978). Mean home range size of rats on Rum reported here were smallest on site B (coast) where the predated rats were initially tagged. Given the lack of ground cover on intertidal zones, it is possible that predation threat has some impact on rat movement on Rum. Without further information on buzzard diet and distribution, however, the extent to which rats make up the diet of buzzards on Rum is unknown, or indeed to what extent buzzard predation may affect the behaviour or ecology of rat populations. Furthermore, whilst it is possible that rats play a role in buzzard diet on Rum, it is unclear if this is scavenging or predation, given differences in activity patterns between the species *e.g.* rats are nocturnal and buzzards are diurnal.

Another possible predator of rats on Rum is the golden eagle, *A. chrysaetos*. One golden eagle nest was checked for the presence of Norway rat PIT tags from the CMR surveys. One rat PIT tag from radio tracking site A (river) was found in the nest of a golden eagle, which was located approximately 3km away from the initial rat trapping site. Whitfield *et al.* (2009) also found Norway rat remains in the pellets of golden eagles on nearby Uist Islands, Scotland. It is unclear what role rats play in the diet of golden eagles on Rum, especially in the absence of their preferred Leporidae prey (Watson 2010).

6.1.5 Competition between rodent species

Distribution of rats may be limited by the presence of rodent competitors (Ruscoe *et al.* 2011; Dammhahn *et al.* 2013; Bramley 2014). Harper (2006), for instance, suggested that in New Zealand black rats competitively exclude Norway rats from forested areas. On Rum, three rodent species (wood mouse, pygmy shrew, Norway rat) are found but it is unclear whether competition for resources exists between the species. It is, however, unlikely that in a shared environment no interaction occurs.

The extent to which wood mice and rats compete for resources on Rum is unknown. It is clear, however, that agonistic interactions exist between rats and mice, with rats often killing mice, typically for predation purposes (Karli 1956; O'Boyle 1974). Karli (1956) reported that some Norway rats would kill mice during their first interaction, whilst other rats would not kill even in starved conditions. Wood mice are typically granivorous with some studies suggesting that up to 70% of their diet constitutes seeds (Griffin *et al.* 2000; Khammes & Aulagnier 2007; Rogival *et al.* 2007). During this study, relative abundance of seeds found in the stomach contents of rats was reported at 2.9 - 4.8%, with significantly more in autumn and winter; as such, competition for seeds may occur between rats and mice on Rum, at least during autumn and winter. Without detailed knowledge on the diet of mice on Rum, or

specific information on seed types, conclusions on competition cannot, however, be made. Furthermore, no evidence of mouse predation was found in the stomach contents of rats on Rum, suggesting either that the sample size was too small to pick up an effect or rats on Rum do not predate on wood mice. It is possible that the effect is small because rats and mice occupy different areas on Rum and as such interactions occur infrequently. Mean tracking plate activity score was highest for rats on Rum in coast and woodland sites and lowest in grassland. Conversely, however, mouse activity on Rum was recorded during this study on the highest number of tracking plates in grassland sites, and lowest in coast, although the effectiveness of using tracking plates for activity surveys of wood mice is untested. Also, despite the collection of some basic activity data for wood mice on Rum, no statistical analysis was carried out, with apparent spatial differences in mouse activity potentially not reflecting any real differences. Pankhurst *et al.* (2010) found wood mice on all ecotope types surveyed (grassland (including shearwater colonies), woodland, coast and heath) but reported the highest capture rates in woodland and grassland and the lowest in coastal areas. Furthermore, evidence was reported on the damage to occupied traps by rats, potentially indicating a predation attempt by rats on mice; although the extent to which the bait within the traps attracted rats is unclear. Given that Norway rats have a preference for wet environments, have a strong swimming ability and can exhibit diving behaviour for catching prey, perhaps they are more suited to coastal environments than wood mice (Galef 1980; Russell *et al.* 2005; Harper & Bunbury 2015).

Considering the presence of mice within shearwater colonies on Rum and the potential for dietary niche overlap (seeds) with rats, the relationship between rats and mice on Rum requires further investigation. In particular, both rats and mice are a potential threat to island avifauna (Atkinson 1985; Cuthbert & Hilton 2004; Jones et al. 2008). Ruscoe *at al.* (2011) reported that when black rats were removed from four areas of New Zealand forests, house mouse numbers increased by 300%, an effect attributed to competitive release. In an island setting, Caut *et al.* (2007) reported an increase in mouse populations following the eradication of rats from Buck Island, US Virgin Isles. Prior to management of a single rodent species on Rum, an understanding of the relationship between rodent species would therefore aid in predicting the outcome of any management by reducing the chance of unexpected outcomes to populations of invasive rodent species on the island.

6.2 Conclusions

6.2.1 Distribution and abundance of rats and relation to shearwaters

Total population size of Norway rats on Rum in May 2013 – March 2015 was estimated at 7,444 ± 5,497 for non-linear sites and 11,844 ± 5,685 for non-linear/linear sites combined.

Evidence of Norway rats (tracking plates, wax blocks, CMR) was recorded on every study site and ecotope/ecoelement surveyed (coast, grassland, heath, river, wall, woodland), including shearwater breeding grounds. Shearwater greens were sampled within the grassland group.

Norway rat tracking plate mean activity score was higher on linear sites ($\overline{x}$ = 29.93 ± 7.13) (coast, river, wall) than non-linear sites ($\overline{x}$ = 13.77 ± 6.75) (grassland, heath, woodland). Mean activity scores differed between ecotope/ecoelement types with coastal ($\overline{x}$ = 56.21 ± 9.57) activity scores being higher than heath ($\overline{x}$ = 1.88 ± 0.81) and grassland ($\overline{x}$ = 5.1 ± 2.8) scores, and woodland ($\overline{x}$ = 34.6 ± 16.6) scores being higher than heath.

Mean activity score using chocolate wax blocks did not differ between ecotope/ecoelement categories or types.

Mean capture rates (C100TN) were higher on linear ($\overline{x}$ = 22.35 ± 4.05) than non-linear ($\overline{x}$ = 9.57 ± 3.11) sites. Differences were found between the mean C100TN recorded on coastal ($\overline{x}$ = 37.3 ± 6.91) sites and all other ecotopes/ecoelements (grassland, heath, river, wall) except woodland ($\overline{x}$ = 22.05 ± 7.69). No seasonal differences were found in the mean C100TN data but samples did not include seasonal replication within sites.

Mean activity scores, C100TN and densities were low for grassland sites with data from the single shearwater grassland site exhibiting typical patterns in comparison to the other grassland sites surveyed. Abundance was therefore low in shearwater breeding grounds but only one site was sampled so generalisations cannot be made.

6.2.2 Rat migration between sub-populations and implications for shearwaters

Data on general patterns of movement as assessed by home range analysis and trapping indicate that Norway rats do occupy different habitats seasonally. Given the limited data, however, the extent to which this occurs is not known. Four rats were recaptured at different survey sites across ecotopes/ecoelements and seasons, of which one rat was lethal-trapped on the urban site approximately 1.5km away and nine months after its initial capture.

Furthermore, a single male rat was recorded moving up to 1.5km in one night. It is therefore possible that Norway rats could migrate between sub-populations on Rum, such as urban and coast areas to shearwater breeding grounds, but with limited data robust conclusions cannot be made.

6.2.3 Spatial differences in home range and movement

Mean home range size (MCP100) for Norway rats on Rum in spring and summer was estimated at 2.32ha; however, data were pooled across two years. Furthermore, low sample size, low replication and large variation in the data determine that confidence in the data is low, with independence of the data not quantified. Differences in home range size of rats were found between sites and between sexes. Site B (coast) had the smallest home range size ($\overline{x}$ = 0.62 ± 0.15ha) whilst site A (river) had the largest home range size ($\overline{x}$ = 4.18 ± 2.22ha), which was significantly larger than site B. Males ($\overline{x}$ = 3.39 ± 1.51ha) had significantly larger home range sizes than females ($\overline{x}$ = 1.11 ± 0.52ha). Home range size did not differ between sites within males or within females. Not enough data were collected to determine the effect of vegetation or linear features on home range size.

6.2.4 Habitat and feeding preferences and implications for avifauna

Norway rat diet on Rum did not vary greatly between sample groups (coast, grassland, urban). Mean ranked relative abundance of bait/feed differed between groups with only rats living in or near the village consuming bait/feed. Mean ranked relative abundance of invertebrates differed between coast and urban sites. No other significant differences between groups were found; however, sample size was low (n = 29) and an effect may have been missed.

Norway rat diet on Rum did not vary greatly between seasons with the only difference found between the mean ranked relative abundance of seeds; more seeds were consumed by rats in autumn and winter than in spring and summer. No other seasonal differences were found.

Vegetation and invertebrates were found in the highest frequencies of stomachs and had the highest relative abundances across all sites and both seasonal groups. Hair was found in the stomach contents of three rats but may be accounted for by grooming behaviour. No other evidence of vertebrate animal matter including avifauna was found in the stomach contents of any Norway rats on Rum in this study. Given previous evidence of avifauna in the stomach content of rats on Rum, it is clear that avifauna do play some role in the diet of

Norway rats on Rum, but at a population level it is unclear how frequently this occurs or what role avifauna play in rat survival on Rum.

No significant differences (Jacob's index) were found between the availability (MCP100) and use (density of location points) of vegetation types (grassland, heath, mire, mosaic, woodland) by rats on Rum during spring and summer; although sample size was very low and several vegetation types were un-sampled or sampled only once, preventing analysis from being carried out.

A correlation was found between mean C100TN and distance-to-coast but was not found between mean C100TN and distance-to-river or distance-to-wall.

These findings could now be applied to the management of a key conservation area and, furthermore, expand the literature on the management of invasive rat populations. This highlights the importance of establishing ecological information appropriate to the invasive rat population in question.

6.3 Recommendations

Given the contradictory evidence surrounding the role of avifauna in the diet of rats on Rum, an understanding of the distribution, abundance and diet of Norway rats across seasons and years would be beneficial to clarifying this relationship. In particular:

a) How frequently do rats consume shearwaters or their eggs or chicks?

b) What is the nature of consumption - predation or scavenging?

c) Under what circumstances does it happen - when resources are limiting *e.g.* during years of rat abundance or low seed abundance, or when there is significant shearwater chick mortality?

Understanding this relationship will provide helpful data for future management decisions on the potential impacts of Norway rats on this globally important colony of Manx shearwaters on Rum.

Coastal sites are an important resource for Norway rats on Rum, with high levels of abundance and density reported there; however, there is limited information available on the potential threats rats may pose to shoreline ground-nesting birds. Furthermore, the potential for cascade effects by Norway rats on intertidal zones has been previously reported. As such, a Norway rat removal experiment conducted on coastal sites across Rum could

potentially provide an understanding of the multi-trophic effects of Norway rats on tidal communities. In particular:

d) What impact do rats have on the breeding success of shoreline birds?

e) What are the long term effects of Norway rats on tidal invertebrate communities and how does this impact on the breeding success of shorebirds?

Dispersal rates were not quantified for Norway rats in this study and the extent to which the limited data on movement reflects the movement patterns of rats on Rum is unknown. A thorough understanding of the dispersal rates of Norway rats on Rum could potentially allow their impacts on avifauna to be fully assessed. For instance:

f) How frequently do Norway rats disperse and what are the limiting factors *e.g.* resources, density and competition?

g) Does dispersal vary between seasons and sex and how is this related to avifauna breeding?

h) Do rats on Rum disperse from high density coastal areas to shearwater breeding grounds?

Understanding the long term movement patterns of Norway rats on Rum will provide the information necessary to understand and minimise any potential impact Norway rats may have on native avifauna.

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Appendices

Appendix A Full list of NVC plant communities per vegetation type. Red indicates communities included in different vegetation types in British Plant Communities Volumes.

Vegetation Type	Shortened Community Names (British Plant Communities Volumes)
Aquatic	A – Aquatic sub-communities not described during original surveys
Grassland	CG10 *Festuca-Agrostis-Thymus* grassland CG11 *Festuca-Agrostis-Alchemilla* grass-heath CG12 *Festuca-Alchemilla-Silene* community CG13 *Dryas-Carex* heath MC5 *Armeria-Cerastium* community MC6 *Atriplici-Betetum maritimae* MC8 *Festuca-Armeria* grassland MC9 *Festuca-Holcus* grassland MC10 *Festuca-Plantago* grassland U4 *Festuca-Agrostis-Galium* grassland U5 *Nardus-Galium* grassland U6 *Juncus-Festuca* grassland U17 *Luzula-Geum* tall-herb community U20 *Pteridium-Galium* community
Heath	H7 *Calluna-Scilla* heath H10 *Calluna-Erica* heath H14 *Calluna-Racomitrium* heath H20 *Vaccinium-Racomitrium* heath H21 *Calluna-Vaccinium-Sphagnum* heath M15 *Scirpus-Erica* wet heath U7 *Nardus-Carex* grass-heath U10 *Carex-Racomitrium* moss-heath

| Habitat	Shortened Community Names (British Plant Communities Volumes)
Mire	M6 *Carex echinata-Sphagnum* mire M10 *Pinguiculo-Caricetum dioicae* mire M17 *Scirpus-Eriophorum* mire M23 *Juncus-Galium* rush-pasture M25 *Molinia-Potentilla* mire M30 *Hydrocotylo-Baldellion* *(*Related vegetation of seasonally-inundated habitats) M31 *Sphagno auriculati-Anthelietum julaceae* spring M32 *Philonoto-Saxifragetum stellaris* spring
Rock	R,R1a,R1b,R1c,R2a,R2b,R3a,R3b,R3c
Sand Dune	SD6 *Ammophila* community SD7 *Ammophila-Festuca* community SD8 *Festuca-Galium* community
Woodland	P Plantation W7 *Alnus-Fraxinus-Lysimachia* woodland W11 *Quercus-Betula-Oxalis* woodland W23 *Ulex-Rubus* scrub

Appendix B Map of rivers located on the Isle of Rum, Scotland. Extracted from CEH Watercourse Network data (Moore *et al.* 1994) using the 'Inland Water' category. Arrow (top left) indicates grid north. © Crown Copyright and Database Right 2018. Ordinance Survey & NERC (CEH) (Digimap Licence).
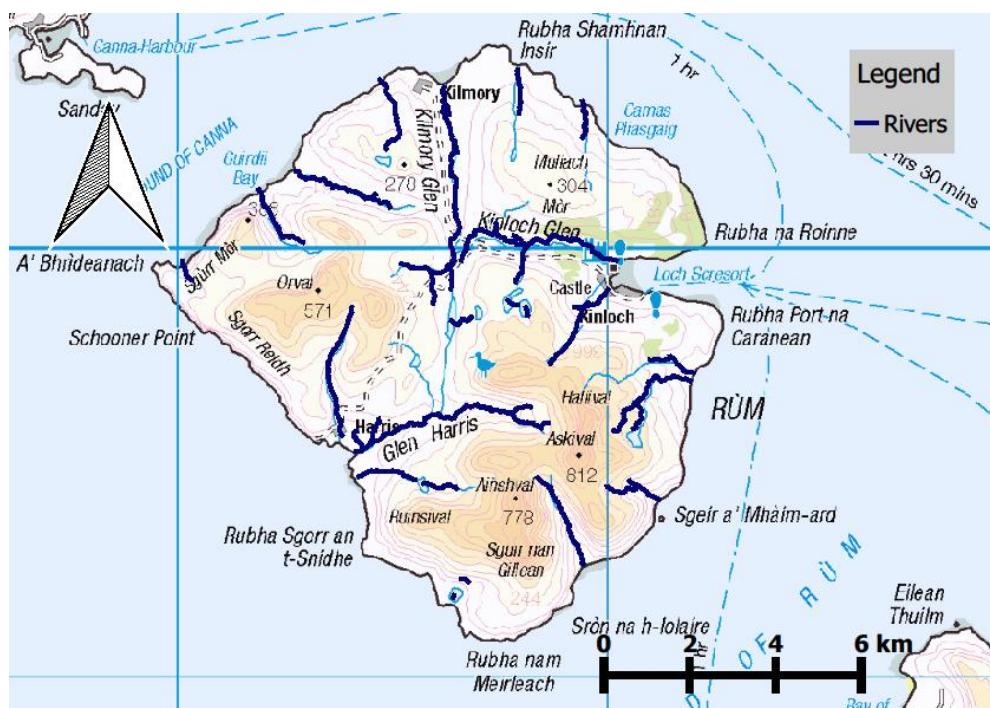

Appendix C Map of the coastline of the Isle of Rum, Scotland. Extracted from OS VectorMap® District using 'Foreshore' data. Only coastline with an adjacent foreshore was included in the map. Arrow (top left) indicates grid north. © Crown Copyright and Database Right 2018. Ordinance Survey (Digimap Licence).
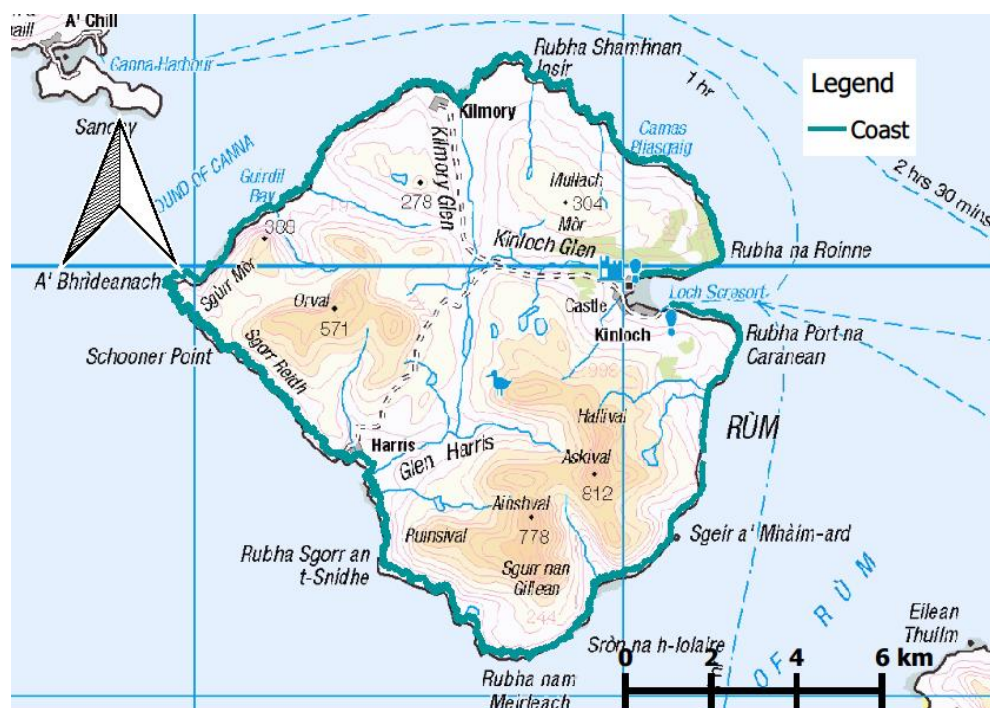
**Appendix D Map of walls located on the Isle of Rum, Scotland. Extracted from OS MasterMap®
Topography Layer (wall sites) using 'General Features-Obstructing'. Walls were either ground-
truthed or confirmed using local knowledge to verify the location of walls. Arrow (top left)
indicates grid north. © Crown Copyright and Database Right 2018. Ordinance Survey (Digimap
Licence).**
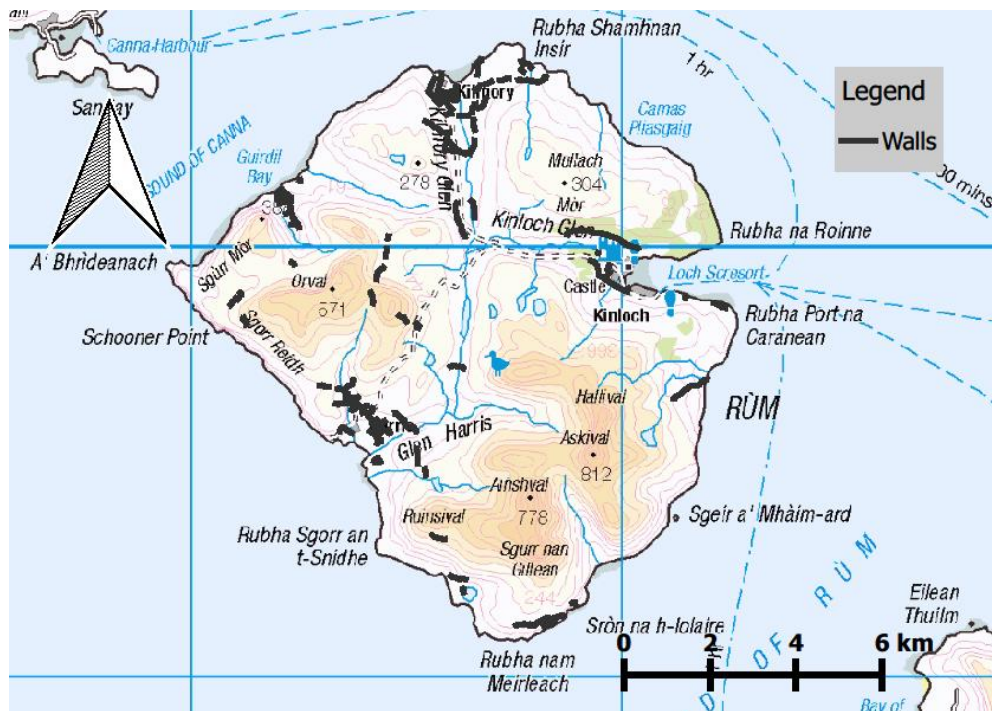
Appendix E Data table of all individual Norway rats fitted with radio transmitters in May 2013 – September 2015.

Rat	Site	Sex	Weight (g)	Breeding	Attach. Date	Active (days)	No. of Fixes	Fate	Notes
811	A	M	240	Y	Apr-15	11	14	Died (Natural)	Found dead in nest chamber, 2 months after last fix (June 2014)
924	A	M	301	Y	Apr-15	39	13	Lost signal	Failed to relocate post data collection (Nov 2015)
272	A	F	230	N	Apr-15	9	13	Lost signal	Failed to relocate post data collection (Nov 2015)
984	B	M	320	Y	Jul-15	14	13	Lost signal	Failed to relocate post data collection (Nov 2015)
213	B	F	195	Y	Jun-14	15	13	Collar removed/ died	last fix located at inaccessible burrow
323	C2	M	260	Y	Aug-14	7	13	Collar removed/ died	Collar at inaccessible burrow 3 months after last fix (Jan 2015)
234	C	M	205	N	Apr-15	6	13	Collar removed/ died	Inaccessible burrow
271	B	F	210	Y	Jul-15	13	13	Collar removed/ died	Inaccessible burrow
763	A	M	250	Y	Jun-14	16	13	Died (Predated)	Collar near buzzards nest, 3 months/3 km from last fix (Sept 2014)
75	B	F	265	N	Mar-14	12	13	Collar detached	Rat recaptured after fixes threshold reached
307	A	F	200	Y	Jun-14	12	12	Lost signal	Failed to relocate 6 months from last fix (Dec 2014)
233	C	F	230	Y	Sep-15	6	12	Lost signal	Failed to relocate post data collection (Nov 2015)

Rat	Site	Sex	Weight (g)	Breeding	Attach. Date	Active (days)	No. of Fixes	Fate	Notes
809	C	M	310	Y	Sep-15	7	12	Lost signal	Failed to relocate post data collection (Nov 2015)
923	A	F	200	Y	Jun-14	13	12	Died (Natural)	Collar in burrow with rat bones, 150 days after last fix (Dec 2014)
810	B	M	220	Y	Jun-14	15	12	Collar removed	Collar located on path 150 days after last radio fix (Dec 2014)
764	C	F	200	N	Apr-15	11	12	Collar removed	Retrieved from burrow
839	B	M	340	Y	Jul-15	13	11	Lost signal	Failed to relocate post data collection (Nov 2015)
237	B	M	295	Y	Jun-14	16	9	Died (Predated)	Collar on cliff edge with bones/fur, 60 days from last fix(Aug 2014)
296	D	F	280	?	May-13	9	6	Lost signal	Unsuccessful tracking after fieldwork restart (August 2013)
850	D	F	300	?	May-13	8	5	Lost signal	Unsuccessful tracking after fieldwork restart (August 2013)
257	B	F	195	N	Jun-14	5	5	Collar removed	Retrieved from burrow
723	A	M	265	Y	Jun-14	5	5	Collar removed	Retrieved from burrow
947	E	M	250	Y	May-14	33	4	Lost signal	Relatively large distances between initial fixes then signal lost
703	D	M	275	?	May-13	9	4	Collar removed/ died	Inaccessible burrow

Rat	Site	Sex	Weight (g)	Breeding	Attach. Date	Active (days)	No. of Fixes	Fate	Notes
923	D	M	330	?	May-13	9	3	Collar removed/died	Collar at inaccessible burrow 3 months after last fix (Aug 2015)
777	B	M	270	Y	Feb-14	6	2	Died (Predated)	Collar found on cliff 1.5km/120 days after attachment (Aug 2014)
270	C2	M	290	N	Aug-14	5	2	Collar removed	Retrieved from burrow
778	A	F	225	N	Aug-14	6	2	Faulty	Restricted transmission range and Intermittent signal
908	A	M	270	Y	Aug-14	1	1	Did not locate	Single fix 500m from trap point but failed to relocate
723	A	M	350	Y	Aug-14	2	1	Collar removed/died	Likely died, appearance indicated old rat. Inaccessible burrow
838	B	F	310	N	Feb-15	11	1	Died (Natural)	Animal found dead in burrow
345	A	M	210	N	Feb-14	0	0	Did not locate	Attempted to relocate up to 60 days after attachment
745	B	F	225	N	Feb-14	0	0	Did not locate	Attempted to relocate up to 60 days after attachment
893	B	F	270	N	Aug-14	0	0	Did not locate	Attempted to relocate up to 60 days after attachment
872	B	M	250	Y	Aug-14	0	0	Did not locate	Attempted to relocate up to 60 days after attachment
964	B	M	265	N	Feb-15	0	0	Did not locate	Attempted to relocate up to 60 days after attachment
255	B	M	210	N	Feb-15	0	0	Did not locate	Attempted to relocate up to 60 days after attachment
765	C	M	235	Y	Sep-15	0	0	Did not locate	Attempted to relocate up to 60 days after attachment

Rat	Site	Sex	Weight (g)	Breeding	Attach. Date	Active (days)	No. of Fixes	Fate	Notes
252	B	F	260	Y	Aug-14	0	0	Died (Predated)	Collar beside buzzards nest, 10 days/3km from trap point
983	C2	M	280	Y	Aug-14	0	0	Collar detached	Removed on welfare grounds - too tight

Appendix F Model selection statistics for abundance estimates per site calculated in MARK. Bold underlined indicates model selected for abundance estimates.

Site	Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance
	{Mtb}	**48.35**	**0.00**	**0.40**	**1.00**	**4**	**34.48**
	{Mo}	48.88	0.53	0.31	0.77	1	42.18
Coast 1	{Mb}	51.10	2.74	0.10	0.25	2	42.15
	{Mh}	51.13	2.77	0.10	0.25	2	42.18
	{Mt}	51.58	3.23	0.08	0.20	4	37.71
	{Mo}	**59.19**	**0.00**	**0.41**	**1.00**	**1**	**52.53**
	{Mb}	60.20	1.01	0.25	0.60	2	51.34
	{Mtb}	60.71	1.52	0.19	0.47	4	47.12
Coast 1B	{Mh}	61.39	2.20	0.14	0.33	2	52.53
	{Mt}	65.87	6.68	0.01	0.04	4	52.28
	{Mth}	69.78	10.59	0.00	0.01	9	41.92
	{Mb}	**60.42**	**0.00**	**0.43**	**1.00**	**2**	**43.93**
	{Mo}	60.94	0.52	0.34	0.77	1	46.64
	{Mh}	63.14	2.72	0.11	0.26	2	46.64
Coast2	{Mt}	64.27	3.85	0.06	0.15	4	43.04
	{Mtb}	64.58	4.15	0.05	0.13	4	43.35
	{Mth}	75.64	15.22	0.00	0.00	9	40.14
	{Mo}	**112.17**	**0.00**	**0.58**	**1.00**	**1**	**120.43**
	{Mb}	114.26	2.09	0.20	0.35	2	120.43
	{Mbh}	116.40	4.23	0.07	0.12	3	120.43
Coast 2B	{Mt}	116.50	4.33	0.07	0.11	4	118.34
	{Mtb}	116.71	4.53	0.06	0.10	4	118.55
	{Mth}	119.51	7.34	0.01	0.03	9	109.62

Site	Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance
	{Mo}	**81.29**	**0.00**	**0.62**	**1.00**	**1**	**74.39**
	{Mb}	83.39	2.10	0.22	0.35	2	74.36
Coast 2C	{Mtb}	84.87	3.58	0.10	0.17	4	71.36
	{Mt}	85.85	4.56	0.06	0.10	4	72.34
	{Mth}	94.08	12.79	0.00	0.00	9	67.91
	{Mo}	**62.00**	**0.00**	**0.64**	**1.00**	**1**	**58.60**
	{Mh}	64.15	2.15	0.22	0.34	2	58.60
Coast 3	{Mt}	66.00	4.00	0.09	0.14	4	55.88
	{Mtb}	66.84	4.84	0.06	0.09	4	56.72
	{Mo}	**117.33**	**0.00**	**0.52**	**1.00**	**1**	**109.49**
	{Mb}	117.89	0.56	0.39	0.76	2	107.95
Coast 4	{Mtb}	121.43	4.10	0.07	0.13	4	107.15
	{Mt}	123.31	5.99	0.03	0.05	4	109.04
	{Mth}	128.88	11.55	0.00	0.00	9	102.78
	{Mo}	**27.30**	**0.00**	**0.58**	**1.00**	**1**	**18.55**
	{Mb}	28.54	1.24	0.31	0.54	2	17.31
River 1B	{Mtb}	31.55	4.26	0.07	0.12	4	14.37
	{Mt}	32.70	5.41	0.04	0.07	4	15.52
	{Mbh}	36.56	9.27	0.01	0.01	5	15.76
	{Mo}	**31.1816**	**0.00**	**0.50**	**1.00**	**1.00**	**27.2489**
	{Mbh}	32.24	1.06	0.29	0.59	5.00	17.1557
River 1C	{Mb}	33.4744	2.29	0.16	0.32	2.00	27.152
	{Mt}	36.2197	5.04	0.04	0.08	4.00	24.3635
	{Mtb}	38.2928	7.11	0.01	0.03	4.00	26.4366

Site	Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance
River 2	**{Mo}**	**23.15**	**0.00**	**0.48**	**1.00**	**1**	**16.13**
	{Mb}	24.66	1.51	0.22	0.47	2	15.00
	{Mt}	24.67	1.51	0.22	0.47	4	8.29
	{Mtb}	26.80	3.65	0.08	0.16	4	10.43
River 3	**{Mt}**	**64.18**	**0.00**	**0.35**	**1.00**	**4**	**50.50**
	{Mo}	64.68	0.50	0.27	0.78	1	57.84
	{Mh}	65.52	1.33	0.18	0.51	3	54.22
	{Mb}	66.62	2.44	0.10	0.30	2	57.60
	{Mtb}	66.96	2.78	0.09	0.25	4	53.28
River 4	**{Mo}**	**21.6189**	**0.00**	**0.75**	**1.00**	**1.00**	**14.5989**
	{Mb}	24.1917	2.57	0.21	0.28	2.00	14.5344
	{Mtb}	28.4993	6.88	0.02	0.03	4.00	12.1287
	{Mt}	30.0424	8.42	0.01	0.01	4.00	13.6718
	{Mbh}	32.472	10.85	0.00	0.00	5.00	11.7377
Wall 1	**{Mo}**	**49.32**	**0.00**	**0.50**	**1.00**	**1**	**38.80**
	{Mb}	50.68	1.36	0.25	0.51	2	37.92
	{Mh}	51.57	2.25	0.16	0.33	2	38.80
	{Mt}	54.09	4.77	0.05	0.09	4	36.40
	{Mtb}	54.57	5.24	0.04	0.07	4	36.87
	{Mth}	62.89	13.56	0.00	0.00	9	29.56
Wall 1B	**{Mo}**	**28.74**	**0.00**	**0.59**	**1.00**	**1**	**20.99**
	{Mb}	31.08	2.34	0.18	0.31	2	20.94
	{Mh}	31.13	2.39	0.18	0.30	2	20.99
	{Mt}	35.38	6.64	0.02	0.04	4	19.70
	{Mtb}	35.60	6.86	0.02	0.03	4	19.93
	{Mth}	49.59	20.84	0.00	0.00	9	13.16

Site	Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance
	{Mo}	**53.6823**	**0**	**0.70117**	**1**	**1**	**41.2793**
	{Mb}	55.76	2.08	0.25	0.35	2	41.14
Wall 2	{Mtb}	60.21	6.53	0.03	0.04	4	40.77
	{Mt}	60.45	6.77	0.02	0.03	4	41.01
	{Mth}	72.48	18.80	0.00	0.00	9	38.18
	{Mo}	**23.86**	**0.00**	**0.45**	**1.00**	**1**	**16.84**
	{Mb}	24.33	0.48	0.35	0.79	2	14.68
	{Mh}	26.49	2.64	0.12	0.27	2	16.84
Wall 3	{Mtb}	27.72	3.86	0.07	0.15	4	11.35
	{Mt}	31.27	7.42	0.01	0.02	4	14.90
	{Mbh}	35.38	11.53	0.00	0.00	5	14.65
	{Mth}	**-125.23**	**0.00**	**1.00**	**1.00**	**8**	**1.39**
	{Mo}	12.33	137.56	0.00	0.00	1	8.28
	{Mb}	16.03	141.26	0.00	0.00	2	8.25
Wall 4	{Mh}	16.07	141.29	0.00	0.00	2	8.28
	{Mt}	28.92	154.15	0.00	0.00	4	6.20
	{Mtb}	29.24	154.47	0.00	0.00	4	6.52
	{Mo}	**18.58**	**0.00**	**0.61**	**1.00**	**1**	**13.17**
	{Mb}	20.39	1.81	0.25	0.40	2	12.05
Grassland 1	{Mh}	21.51	2.93	0.14	0.23	2	13.17
	{Mt}	28.63	10.06	0.00	0.01	4	11.91
	{Mtb}	28.77	10.19	0.00	0.01	4	12.05
	{Mo}	**17.74**	**0.00**	**0.81**	**1.00**	**1**	**12.33**
Grassland 4	{Mh}	20.68	2.93	0.19	0.23	2	12.33
	{Mth}	**16.77**	**0.00**	**0.98**	**1.00**	**7**	**1.39**
Heath 2	{Mtb}	24.11	7.33	0.02	0.03	4	1.39

Site	Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Num. Par	Deviance
	{Mth}	**-125.23**	**0.00**	**1.00**	**1.00**	**8**	**1.39**
	{Mo}	12.33	137.56	0.00	0.00	1	8.28
	{Mb}	16.03	141.26	0.00	0.00	2	8.25
Heath 3	{Mh}	16.07	141.29	0.00	0.00	2	8.28
	{Mt}	28.92	154.15	0.00	0.00	4	6.20
	{Mtb}	101.55	226.77	0.00	0.00	6	4.16
Heath 4	**{Mo}**	**9.39**	**0.00**	**1.00**	**1.00**	**1**	**5.39**
	{Mo}	**12.33**	**0.00**	**0.80**	**1.00**	**1**	**8.28**
Heath 5	{Mb}	15.16	2.83	0.20	0.24	2	7.38
	{Mt}	28.92	16.58	0.00	0.00	4	6.20
	{Mtb}	**25.50**	**0.00**	**0.63**	**1.00**	**4**	**11.09**
	{Mt}	28.53	3.03	0.14	0.22	4	14.12
Woodland 2	{Mo}	28.55	3.05	0.14	0.22	1	22.59
	{Mb}	30.32	4.82	0.06	0.09	2	21.87
	{Mh}	31.04	5.54	0.04	0.06	2	22.59
	{Mo}	**75.61**	**0.00**	**0.51**	**1.00**	**1**	**62.17**
	{Mb}	77.45	1.83	0.20	0.40	2	61.85
	{Mh}	77.77	2.15	0.17	0.34	2	62.17
Woodland 3	{Mtb}	80.29	4.67	0.05	0.10	6	55.20
	{Mt}	80.57	4.96	0.04	0.08	4	60.41
	{Mbh}	82.01	6.39	0.02	0.04	4	61.85
	{Mth}	86.58	10.97	0.00	0.00	9	53.29
	{Mo}	**61.64**	**0.00**	**0.55**	**1.00**	**1**	**52.89**
	{Mh}	63.51	1.87	0.21	0.39	3	50.25
Woodland 4	{Mb}	63.75	2.11	0.19	0.35	2	52.79
	{Mt}	67.88	6.24	0.02	0.04	4	52.19
	{Mbh}	67.94	6.30	0.02	0.04	5	49.71

Appendix G Summary of relative abundance estimates (index scores) of stomach content analysis per individual rat.

Rat No.	Date	Season	Site	Stomach Weight (g)	Food Weight (g)	Veg.	Invert.	Fish	Seeds	Stones	Feed/ Bait	Other Animal Matter
013	03/15	Winter	Coast 1	11.6	8.3	5 (2)	95 (5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
016	03/15	Winter	Coast 1	5.8	2.3	35 (4)	65 (5)	0 (0)	0 (0)	0 (0)	0 (0)	0.5 (1)
018	03/15	Winter	Coast 1	4.3	1.0	95 (5)	5 (2)	0 (0)	0.5 (1)	0 (0)	0 (0)	0 (0)
014	03/15	Winter	Coast 1	4.8	3.3	25 (3)	68 (5)	5 (2)	0.5 (1)	1 (2)	0 (0)	0.5 (1)
015	03/15	Winter	Coast 1	5.2	1.2	10 (3)	90 (5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
017	03/15	Winter	Coast 2	5.3	2.5	5 (2)	95 (5)	0 (0)	0.5 (1)	0 (0)	0 (0)	0 (0)
012	07/15	Summer	Coast 2	1.5	0.6	15 (3)	85 (5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
006	08/15	Summer	Coast 2	4.5	2.6	5 (2)	95 (5)	0.5 (1)	0 (0)	0 (0)	0 (0)	0 (0)
004	09/15	Summer	Coast 2	3.4	0.8	100 (5)	0.5 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
005	09/15	Summer	Coast 2	5.0	2.0	1.5 (2)	98 (5)	0 (0)	0 (0)	0.5 (1)	0 (0)	0 (0)
007	09/15	Summer	Coast 2	5.6	1.9	5 (2)	95 (5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
008	06/14	Summer	Grassland 1	6.8	2.3	2 (2)	98 (5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
023	08/14	Summer	Grassland 1	2.9	1.8	100 (5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
029	08/14	Summer	Grassland 1	0.9	0.1	100 (5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

Rat No.	Date	Season	Site	Stomach Weight (g)	Food Weight (g)	Veg.	Invert.	Fish	Seeds	Stones	Feed/ Bait	Other Animal Matter
028	11/14	Autumn	Grassland 1	9.4	6.2	0 (0)	100 (5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
034	12/14	Winter	Grassland 1	1.9	0.0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
022	03/15	Spring	Grassland 1	2.5	0.0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
010	06/15	Summer	Grassland 1	0.8	0.3	95 (5)	5 (2)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
011	06/15	Summer	Grassland 1	1.3	0.4	20 (3)	80 (5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
001	10/15	Autumn	Grassland 1	4.5	0.8	65 (5)	35 (4)	0 (0)	0.5 (1)	0 (0)	0 (0)	0 (0)
003	10/15	Autumn	Grassland 1	3.1	0.0	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
020	03/15	Winter	Grassland 2	23.1	16.0	65 (5)	30 (4)	0 (0)	5 (2)	0 (0)	0 (0)	0 (0)
021	03/15	Winter	Grassland 2	3.4	0.9	64 (5)	34 (4)	0 (0)	1 (2)	1 (2)	0 (0)	0 (0)
033	05/14	Spring	Urban	1.1	0.1	80 (5)	20 (3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
031	06/14	Spring	Urban	2.9	0.5	50 (4)	45 (4)	0 (0)	0 (0)	5 (2)	0 (0)	0 (0)
032	09/14	Summer	Urban	4.0	2.2	55 (5)	0 (0)	0 (0)	0 (0)	0 (0)	45 (4)	0 (0)
026	12/14	Winter	Urban	1.9	0.7	60 (5)	40 (4)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
027	12/14	Autumn	Urban	11.1	4.1	85 (5)	5 (2)	0 (0)	0 (0)	0 (0)	10 (3)	0 (0)
024	01/15	Winter	Urban	13.7	3.8	25 (3)	60 (5)	0 (0)	0 (0)	0 (0)	15 (3)	0 (0)

Rat No.	Date	Season	Site	Stomach Weight (g)	Food Weight (g)	Veg.	Invert.	Fish	Seeds	Stones	Feed/ Bait	Other Animal Matter
025	01/15	Winter	Urban	20.4	13.1	40 (4)	20 (3)	0 (0)	0 (0)	0 (0)	40 (4)	0 (0)
030	03/15	Spring	Urban	7.4	3.3	10 (3)	60 (5)	0 (0)	0 (0)	0 (0)	30 (4)	0.5 (1)
009	08/15	Summer	Urban	8.2	3.6	10 (3)	89 (5)	0 (0)	0 (0)	0.5 (1)	0.5 (1)	0 (0)

END