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Ecology of an island mouse, *Apodemus sylvaticus hirtensis*

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Abstract

An island subspecies endemic to the remote St Kilda archipelago, *Apodemus sylvaticus hirtensis* is considered of national importance but has been little studied, despite its inclusion in the criteria for the islands' designation as a World Heritage Site. This study expands our knowledge of the core ecology of the mice; distribution, morphology, age structure, breeding phenology, population density, range size, survival and fecundity are all described and quantified using data collected from 4462 captures of 787 individuals between 2009-2012 on three sites (Carn Mor, Glen Bay & Village Bay), 1-2km apart on the main island of Hirta. Morphological analysis confirmed the reputed gigantism the mice, with maximum body weights of 60g for males and 50.5g for a non-gravid female both being approximately double that of a mainland specimen (the heaviest gravid female caught weighed 56g). Sexual dimorphism was evident, with males >1 year old being 8.7% heavier than females on average. Significant geographical variation in size was also found; mice on the seabird breeding colony of Carn Mor were heavier, longer and in better condition than mice elsewhere. Mice were observed to have a well-defined breeding season between April and September, shorter than on the mainland, with most individuals not breeding until their second year and very few surviving two winters. No geographical differences were found in the proportion of adult mice more than a year old that were in breeding condition at any given time, although there were significant geographical differences in the proportion of individuals in breeding condition for 'young adult' mice entering their first spring and sub adult mice in the autumn of the year in which they were. Spatially explicit capture-recapture (SECR) methods were used to quantify population densities free from *ad hoc* methods of trapping area estimation. Temporal variation in population size typical of temperate small mammals was found, with densities as low as 2 mice/ha in spring, increasing through summer and autumn with juvenile recruitment until reaching a peak at the beginning of winter of up to 50 mice/ha. Geographical variation was again observed, with frequent significant differences between trapping sites and an overall trend of highest population densities on the seabird breeding site. Mean individual range sizes varied between 0.3-3.0ha and were largest in Village Bay and in males in breeding condition. Pradel robust design recruitment models were used to quantify monthly survival (0.67-1.00) and fecundity (0.03-0.41) and overall rate of population change (0.81-1.52) between sessions. Survival varied little between grids outside of the breeding season, but tended to be greater in Carn Mor than Village Bay during the summer. Fecundity rates varied little between years and grids, with one exception where increased summer fecundity followed a severe winter decline on Carn

Mor. The possible role of differences in the quality of the food supply (in particular the seabird breeding colony and spatial variation in sheep grazing pressure) on creating geographical variation in body size, condition, breeding phenology, density and population dynamics are discussed in detail, as is the overall pattern of insular traits found in the mice.

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Lay Summary of Thesis

The lay summary is intended to facilitate knowledge transfer and enhance accessibility, therefore the language used should be non-technical and suitable for a general audience. This should be a brief summary.

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The St Kilda field mouse, *Apodemus sylvaticus hirtensis*, is a sub species of the long-tailed field mouse (also known as the wood mouse), which is common across much of mainland Europe and the UK. St Kilda is a remote island chain off the west coast of Scotland, and having been introduced by man sometime in the distant past, the mice have lived in isolation from the rest of their species, becoming larger and adapting to the local conditions. They are considered an important natural asset and are protected under St Kilda's designation as a World Heritage Site, but have been studied very little. This study aims to expand our knowledge of the basic ecology of the mice by studying whereabouts on the island they live, their size, age and breeding seasons, how abundant they are and how the size of their population changes through time as a result of the balance between births and deaths.

Generally, the mice were large, weighing as much 60 grams and up to 20cm in length, including the tail. Males were typically slightly bigger than females of the same age. The mice had a well-defined breeding season, with pregnancies occurring between April and September. This meant that the number of mice tended to be greatest at the start of winter, after all the juveniles had left the nests, with as many as 50 mice per hectare (100 metres x 100 metres), fslling to as few as 2 mice/ha in the spring. Most mice do not try and breed until the year after they are born, and they are generally short lived, with about half dying in their first winter and almost none surviving two winters. We studied the mice at three different sites on the island and found considerable differences in size, body weight, and the number of mice at each site, which could be due to differences in food availability – the largest and most numerous mice were found at Carn Mor, which is a breeding site for tens of thousands of seabirds who's guano enriches the soil and increases the amount of food available, and mice may even scavenge or predate bird eggs. Elsewhere on the island they are even known to feed on dead sheep.

Declaration

I hereby declare that the work reported in this thesis was undertaken by myself, unless otherwise acknowledged, that the thesis itself is of my own composition and that the work has not been submitted for any other degree or professional qualification.

Thomas Black
September 2013

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CHAPTER 1

1.1 Introduction

1.1.1 Distribution of *Apodemus sylvaticus*

Apodemus sylvaticus is a common and generalist rodent distributed throughout much of continental Europe and northwest Africa, where it's tendency to inhabit a mixture of woodland and grassland has led to it being commonly referred to as both wood mouse and field mouse. A very adaptable species, it is also found in an array of other habitats including moorland, steppe, Mediterranean scrubland, sand dunes, suburban and urban parks, gardens, wastelands, arable fields and forestry plantations (Montgomery 1989). As well as abundant populations throughout most of mainland Europe (with the exception of Finland and the northern parts of Scandinavia, the Baltic and Russia), *A. sylvaticus* is also found on a large number of offshore islands within its range, including the British Isles, Iceland, the Danish archipelago and many Mediterranean islands (Fig. 1.1). This study focuses on a population of field mice (*Apodemus sylvaticus hirtensis*) found on the remote Scottish archipelago of St Kilda.

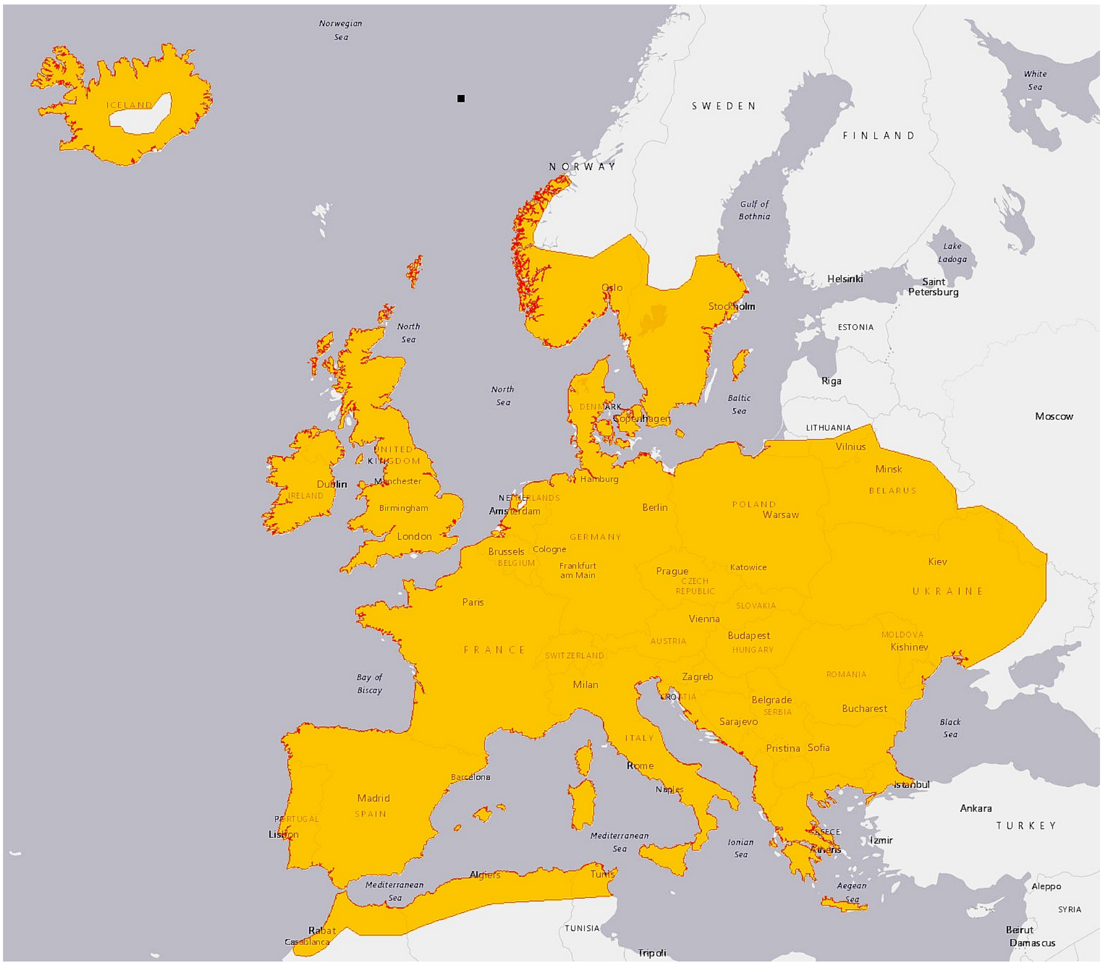

Figure 1.1 Geographical range of *Apodemus sylvaticus*. Adapted from IUCN Red List data (IUCN 2014).

1.1.2 Island populations

Islands represent a huge diversity of habitats, but are typified by their isolation, distinct boundaries and small size relative to equivalent mainland habitats. These traits can result in restricted colonisation and local adaptation, producing island biota with reduced species richness but high endemism – up to 10 times higher than equivalent continental habitats (Kier *et al.* 2009). Islands pack 15% of the world's bird, reptile and plant species into just 3% of its land area and 30% of designated biodiversity hotspots, 25% of global terrestrial ecoregions and 40% of Alliance for Zero Extinction sites are islands. They are even more important in terms of marine ecosystems; 67% of 'centres of marine endemism' are islands (Menon *et al.* 2010).

Ever since Darwin and Wallace's pioneering works on the theory of evolution, oceanic islands have made attractive sites for ecological research. Compared to mainland areas, their discrete nature and isolation tends to result in 'microcosm' ecosystems with fewer interspecies interactions and populations that are effectively closed to immigration and emigration. As such they can act as natural laboratories – simplified systems for the study of many aspects of ecology, evolution and biogeography (Whittaker & Fernandez-Palacios 2007). In particular, island communities tend to exhibit high levels of disharmony (Juan *et al.* 2000), endemism (MacArthur & Wilson 1967) and relictualism (Cronk 1992) while individual species may exhibit reduced dispersal capabilities (Williamson 1981), unusual traits or innovations (Baldwin & Sanderson 1998), extremes of size (Meiri *et al.* 2008) and shifts in life history strategies (Grant 1998).

Island populations also provide the opportunity to study several ecological and evolutionary processes. The tendency for bias of recent colonisation events towards younger islands demonstrates the importance of availability of 'vacant niche space' in determining the success of colonization events (Funk & Wagner 1995), whilst the frequent diversity of forms found in species groups stemming from single colonisers provides insight into the mechanisms of population divergence involved in adaptive radiation (Givnish *et al.* 1997).

Conversely, the small range and population sizes of island biota can leave them more susceptible to species loss, either through biotic factors such as competition, alien species invasion and demographic stochasticity, or abiotic factors including geological and climatic change. They are particularly susceptible to human disruption and extinction rates are far higher on islands than on continents (Steadman 1995). There are perhaps some positives to consider however, in that the simplified and discrete nature of island ecosystems can make the causes and risks of extinctions easier to pinpoint and identification and implementation of management or restoration practices a more practical possibility (Towns *et al.* 1997).

1.1.3 Gigantism and competition

First coined by Van Valen in 1973, the 'island rule' attempts to explain why many animals change size on islands. Island populations will share much of their phylogenetic history with their mainland counterparts, and yet often demonstrate a considerable phyletic shift in size (Lomolino 1985). Among mammals, insular dwarfism can be observed among carnivores, lagomorphs, elephants and artiodactyls, while murid rodents often exhibit insular gigantism (Meiri *et al.* 2008).

Although the above clades do show fairly strong directional patterns, for many other groups the data is less than unequivocal and the validity of the island rule, as well as various hypotheses for its underlying processes, have been fiercely debated (see Lomolino 1985 and

Meiri *et al.* 2008). Of those hypotheses, several have fallen from favour including the viewpoint that some giant species may be relics of once more widespread populations; that reduced prey size on islands may promote dwarfism in predators; that sexual selection on islands may promote gigantism where other selective pressures present on the mainland have been removed; that gigantism is due to founder effects stemming from size selection on immigration success and most recently that there might be a tendency for mammals to move towards an optimum body size at which energy capture from the environment is maximised, once competition or other selective pressures are removed (see Benton *et al.* 2010 for a synthesis of these).

Several further hypotheses are still generally considered favourably (Benton *et al.* 2010). Firstly, that ecological release plays a key role, whereby island populations encounter reduced pressure from competition, predation and parasitism and are able to change body size as a result. Since species richness declines with diminishing island size (MacArthur & Wilson 1967) and mammal species numbers are generally impoverished, those mammals that are present on an island will typically face less competition for food and shelter and less predation. Small mammals therefore have less need to remain small and cryptic and may increase in size, whilst large mammals can become smaller without increased predation risk (Van Valen 1973, Raia & Meiri 2006). Linked to this is the concept of niche expansion (Van Valen 1973), whereby unoccupied ‘niche space’ on islands with impoverished fauna allow animals to take advantage of new diets, allowing small mammals to increase their size range or even take over the roles of intermediate sized species. Insular dwarfism amongst large species may also be due to resource limitation; large herbivores and carnivores both tend to require large foraging areas which may simply not be available on small islands, creating selective pressure for smaller size (Raia & Meiri 2006). Finally, life history models provide possible evolutionary mechanisms for explaining size shifts. Reduced extrinsic mortality rates and decreased resource availability may produce genetic and phenotypic responses in age and size at maturity, and the relative significance of these two responses may determine the direction of body size change; reduced extrinsic mortality is expected to increase body size while reduced resource availability is expected to decrease it (Palkovacs 2003).

Body size change on islands is therefore unlikely to follow any strict rule; rather it is probably the result of intensified natural selection promoting directional shifts in mean body size in response to complex interactions between different processes, contingent on the circumstance of biotic and abiotic factors of a particular island, although patterns amongst some clades remain fairly strong, including that of gigantism in murid rodents such as *Apodemus* (Meiri *et al.* 2008).

1.1.4 Community and cross-boundary trophic interactions

Cross-boundary trophic subsidies refer to the process whereby organisms or materials dispersing from one habitat patch into another may significantly impact food web dynamics and interactions of resident species. Trophic subsidies can be particularly important in island ecosystems where differences in productivity between marine and terrestrial systems may be encountered and where the coastal ecotone makes up a far larger proportion of the terrestrial biome than on the mainland (Polis & Hurd 1996). Seabirds can provide a major source of cross-boundary subsidies when they come ashore to roost and nest; food scraps, failed eggs and carrion can directly influence the productivity of detritivores and scavengers (Sanchez-Pinero & Polis 2000, Stapp & Polis 2003) and with along with guano, can increase the productivity and nutritional value of the plants that form the basis of terrestrial food webs (Anderson & Polis 1999).

Stable isotope analyses have shown that *Peromyscus* mice, generalist and omnivorous rodents that occupy very similar niches to *Apodemus*, benefit from littoral and seabird-transported marine subsidies which lead to increased abundance on small islands in the Gulf of California (Stapp & Polis 2003). Similarly, several rodent species (*Rattus spp.* and *Mus musculus*) sampled across four islands in four different oceans have all been shown to be recipients of marine-derived subsidies. Moreover, seabird breeding periods were shown to correspond to increased plant growth and rodent reproduction (Caut *et al.* 2012).

The appetite of island rodents for marine-derived subsidies can also be seen in the direct predation of seabirds and eggs. This is an issue of major concern for many seabird conservation programmes, with invasive *Rattus spp.* alone known to predate 75 species of island-nesting seabirds across 10 families (reviewed in Jones *et al.* 2008). There is also now unequivocal proof of seabird predation by mice, with predation by introduced *Mus musculus* known to be a significant cause of poor breeding success in the Tristan albatross (*Diomedea dabbenena*) and Atlantic petrel (*Pterodroma incerta*) on Gough Island. Predation of wandering albatross (*Diomedea exulans*) chicks on Marion Island is also suspected (Wanless *et al.* 2007). On St Kilda there is circumstantial evidence for possible predation or scavenging of Leach's storm petrel (*Oceanodroma leucorhoa*) eggs by Apodemus sylvaticus hirtensis (Bicknell 2009).

There may also be some trophic interactions between the Soay sheep (*Ovis aries*) of St Kilda and the mice. These unmanaged sheep graze heavily across the island, significantly impacting vegetation composition and abundance. It is conceivable that they may alter food availability for the mice by reducing seed production of grasses, which *Apodemus sylvaticus* are known to feed on (Watts 1968). Grazing by sheep has been demonstrated to impact negatively some small rodents such as field voles (*Microtus agrestis*), but not bank voles (*Clethrionomys glareolus*) (Steen *et al.* 2005, Wheeler 2008). Conversely, mice have been observed to feed on freshly deceased sheep (pers. obs.), which could potentially prove to be a valuable food source, especially during sheep mortality events in winter and spring.

1.1.5 Boom bust; St Kilda's oscillating sheep

The only other extant land vertebrate on St Kilda, the Neolithic Soay sheep have been present on the archipelago for three to four thousand years (Clutton-Brock & Pemberton 2004), although they were only introduced to the island of Hirta in 1932, where they now exist as an unmanaged approximation of a wild population. They are remarkable both for their insular dwarfism and their population dynamics. Despite being fairly long-lived with an almost total lack of predation and inter-specific competition, the Soay sheep on Hirta demonstrate frequent population oscillations, sometimes decreasing or increasing by more than 60% in a year (Clutton-Brock & Pemberton 2004) in response to variation in overwinter mortality rates and density-dependent fecundity in young and old ewes. Both density and climate appear to directly affect overwinter mortality and the growth of early-life individuals, which again is linked to subsequent mortality and fecundity. Overall, survival rates demonstrate strong over-compensation with respect to density, which can lead to chaotic population dynamics when coupled with their relatively high fecundity (individuals regularly conceive at less than one year old, and incidences of twinning are relatively high), although it generally requires at least three breeding seasons for a population that has suffered heavy mortality to reach a level where it is liable to crash again (Clutton-Brock & Pemberton 2004).

1.1.6 Conservation concerns

Insular island populations tend to be particularly susceptible to disruption by both biotic and abiotic changes in their environment; of the 88 documented mammal extinctions since 1500, 57 have been insular small mammals (MacPhee & Flemming 1999) and the recorded extinction rate for island mammal species over the same time period is 100 times greater than for mainland species (Loehle & Eschenbach 2012). As a highly adaptable generalist omnivore, *Apodemus sylvaticus* has an extensive range and is categorised as of Least Concern by the IUCN Red List. However, insular populations tend to show increased specialisation, reduced genetic variation and morphological, behavioural and life history changes that can make them more susceptible to extinction. On St Kilda itself, the endemic house mouse *Mus musculus muralis* – an insular form of another widespread, successful, generalist omnivore with a global range – rapidly became extinct following changes in the management of the islands and in the face of competition from the field mouse (Harrison 1933).

Elsewhere, insular *Apodemus sylvaticus* have been shown to be negatively impacted by introduced competitors such as bank voles (Montgomery *et al.* 2015) and to possess distinctly shaped mandibles and molars suggestive of localised feeding adaptations (Renaud & Michaux 2003, Renaud & Michaux 2007), while many insular rodents demonstrate reduced reproductive effort and shorter breeding seasons which may hinder population recovery following perturbation (Adler & Levins 1994).

Of particular concern is the potential introduction of other rodents, particularly *Rattus spp*. and *Mus musculus* which pose a considerable risk to insular small mammals, although it is often unclear whether this is due to predation in the case of rats, competition or disease introduction, although the latter is increasingly being seen as a major risk for island populations that may never have been exposed to a particular disease (e.g. Wyatt *et al.* 2008).Furthermore, whenever the interaction between introduced rodents and insular small mammals has been investigated experimentally, a negative impact has been found (Harris 2009). Certainly this is the scenario of greatest concern on St Kilda, which now sees considerable boat and helicopter traffic.

Further concerns have been raised regarding interactions with St Kilda's seabird colonies. Seabirds are in global decline (Croxall *et al.* 2012) which may negatively impact the mice by reducing any marine-derived trophic subsidies, or by creating pressure for control of the mouse population on St Kilda's internationally important seabird nesting sites if there is further evidence for seabird predation by the mice.

1.2 St Kilda

Lying 40 miles west of the Outer Hebrides and 100 miles from the Scottish mainland (Fig. 1.2), St Kilda is a remote archipelago formed from the remains of an extinct ring volcano. Rising as high as 430 metres from the Atlantic, it has an oceanic climate with typically cool temperatures, high rainfall and moderate to strong winds, which have resulted in a treeless landscape typified by mixed grassland complexes, heathered moorlands and peat bogs, bounded by maritime swards and steep-sided sea cliffs (McVean 1961).

Figure 1.2. The major islands of St Kilda, and their position relative to the rest of Scotland. Image courtesy of The National Trust for Scotland.

St Kilda is a designated UNESCO World Heritage Site on account of its cultural history, physiographical features, importance as a seabird breeding station, marine life, the opportunities for scientific research and the presence of two endemic subspecies; the St Kilda wren (*Troglodytes troglodytes hirtensis*) and the St Kilda field mouse (*Apodemus sylvaticus hirtensis*). A second endemic mouse subspecies, the St Kilda house mouse *Mus musculus muralis*) became extinct in the early 1930s following the evacuation of the human population on whom it apparently relied for scavenging food (Boyd 1956).

Having evolved in island isolation from the long-tailed field mouse or wood mouse (*A. sylvaticus*) common across most of Europe, the St Kilda field mouse was designated as a separate species (Barrett-Hamilton 1899) and then subspecies (Barrett-Hamilton 1900) over a century ago, primarily on account of its larger size and different colouration compared to mainland populations of field mice (Figure 1.3).

Figure 1.3. Comparative skins of the subspecies *A.s. fridariensis* (Fair Isle, left), *A.s. hirtensis* (St Kilda, centre) and *A.s. sylvaticus* (Sussex, right). Image © P. Morris, skins courtesy of The Natural History Museum (reproduced from Harris & Yalden, 2008).

Despite being included in the islands' designation as a World Heritage Site, its protected status under that designation and having been described as of national importance (Ratcliffe 1977), relatively little is known about the ecology of *A. sylvaticus hirtensis*. Specimens collected using kill traps in the early twentieth century (Eagle Clarke 1905, Waterston 1905, Waterston 1906, Eagle Clarke 1914) provide some basic observations on size, morphology, diet and parasites, whilst short-term live trap surveys expanded this to include descriptions of distributions, habitat preference, population size, breeding status (Harrison 1933, Boyd 1956, Boyd 1959) and a comparison of morphology with other Scottish races of *A. sylvaticus* (Berry 1969). Whilst these studies do provide some useful information about the St Kilda field mouse, their sporadic and opportunistic nature make it difficult to draw many detailed ecological conclusions from (see section 1.3.1 for summary) and the methodologies used would be difficult to replicate due to incomplete descriptions, changes in available equipment and human impacts on some of the areas of study.

The islands of St Kilda have undergone considerable changes in land management over the last century, with the evacuation of the resident human population in 1930, the subsequent removal of cats and dogs and the establishment of an unmanaged population of Soay sheep on the main island of Hirta. Today, St Kilda is managed by the National Trust for Scotland (NTS) and its Partner Group and is an increasingly popular tourist attraction and the site of a permanently manned Ministry of Defence facility. The increasing human traffic has led to concerns about the possibilities of accidentally introducing rats or other predatory mammals to the archipelago. Competition, disease or even direct predation from such an introduction, or poisoning by a subsequent eradication campaign, probably pose the biggest single risk to the field mice. Further research into the mice has therefore been identified as a priority in the current St Kilda Management Plan (NTS 2003) in order to inform management strategies for the islands, particularly given the potential impact of any future rat eradication programme and the fact that a previous change in management led to the extinction of the endemic house mouse (Harrison 1933). A recent rat eradication campaign on the similar-sized Scottish island of Canna succeeded in removing Norway rats (*Rattus norvegicus*) without wiping out the resident field mouse population (Bell *et al.* 2011), by taking advantage of the different range sizes of the two species and spacing poisoned bait stations such that they were encountered by every rat, but not every mouse. Range size is therefore a key metric for informing potential eradication campaigns.

Figure 1.4. A wide view of Village Bay, with the island of Dun (separated from Hirta by a narrow channel) in the foreground and Boreray on the horizon.

1.3 The comparative biology of *Apodemus sylvaticus hirtensis*

1.3.1 Distribution, abundance and population dynamics

Presumably introduced by man sometime in the distant past, *A. sylvaticus hirtensis* is known to occur on the main island of Hirta at present and was found on Dun during trapping sessions in 1905 (Eagle Clarke 1905). The presence or otherwise of mice on Boreray and

Soay appears to be unknown, except for one unreferenced anecdotal mention of their presence on both islands (Harrison 1933). No mouse activity was noted during a multi-day research expedition to Boreray in 1980, although specific attempts to find them were not made (Duncan *et al.* 1981). Baiting (without traps) was carried out on Boreray in 2000 and 2010 and on Soay in 2000 and failed to reveal any mouse activity (S. Murray, pers. com.). Given that the mice are usually very quick to locate introduced food sources (pers. obs), this can probably be regarded as a genuine null finding.

The first reported trapping of mice on St Kilda in the scientific literature comes from 1894, where nine house mice and a single field mouse were caught in kill traps in the Village Bay area (Elliot 1895). Further kill trapping took place over the course of a month in July 1905 and found field mice in several locations around Hirta, including Village Bay and Glen Bay, particularly in the vicinity of hay-filled cleits (stone storage structures), and in greater numbers on Dun (Waterston 1905). Autumn kill trapping in October and November of 1910 and 1911 found mice "everywhere in the crofted area, in the neighbourhood of the houses, on the face of cliffs, on the sides and hill-tops; finding congenial retreats in the rough stone-built cleits, and in the walls surrounding the crofts" (Eagle Clarke 1914).

The first attempt to establish a repeatable live trapping regime began in July and August 1931, a year after the evacuation of the human population (Harrison 1933). A transect was established in Village Bay that ran along the 'dry burn' between its exit into the sea at the edge of the beach and the stone enclosures above the village at An Lag Bho'n Tuath. Along this transect were nominated five stations, each of which consisted of a line of traps parallel to the transect. However, the precise layout and number of traps was not reported, other than to say that a "typical" trapping success for 50 live traps (of two different designs) produced 47 captures over 13 nights.

An attempt was made to repeat this transect in May 1955 (Boyd 1956) with the new style Longworth traps (as used in this study), which succeeded in capturing 50 mice with just 20 traps over 5 nights. It would appear therefore that the mouse population within the village area had expanded considerably in the 25 years since the evacuation, although a direct comparison between the two trapping efforts is difficult given the different designs of traps used and the low repeatability of trap placements. Today the 1931 transect is rendered unrepeatable as much of it is now the site of the military base and numerous buildings have been erected across its length.

The 1931 and 1956 surveys trapped further afield as well, and found field mice to be common throughout the meadow and transitional moorland areas of Village Bay, where they were strongly associated with the walls, cleits and cottages (Harrison 1933, Boyd 1956, Boyd 1959) which presumably act as diurnal cover and nesting sites. The 1931 survey found fewer mice above the head dyke than within its perimeter, and no mice on the slopes above 350 feet, regardless of the presence of cleits. They also trapped at unspecified locations in the Glen Bay area in the north-west of Hirta and on the higher *Festuca-Calluna* moorlands above 300 feet. The mice were deemed to be fairly common in Glen Bay in the relatively few areas with cleits and walls, and essentially absent from the higher moorland slopes above 400 feet regardless of the presence of cleits, although the authors did note the anecdotal record of a mouse having been caught on the top of Conachair, the island's highest peak.

More extensive trapping in April 1957 in cleits across Hirta found the mouse to be ubiquitous, with successful trappings in 28 of 30 locations, including near the tops of all major summits, although the mice still seemed most abundant in the Village Bay lowlands. It seems on this evidence that the large number of dry-stone structures and natural talus slopes greatly enhance the distribution and abundance of field mice across Hirta, given that the otherwise shallow and waterlogged soils are likely to be unsuitable for burrowing (Boyd 1959).

It is interesting to note that prior to the evacuation of Village Bay in 1930 much of the low-lying meadow was cultivated land in which the now extinct house mouse was abundant enough to be described as 'swarming' around the cleits and houses (Waterston 1905). It would seem they were outcompeting the field mice in an environment with extra food provided by human activity and in the presence of cat predation. Just one year after the evacuation, however, the house mouse population was apparently reduced to less than 25 individuals surviving off stores left behind in two of the cottages (Harrison 1933). Furthermore, although the trapping techniques differed, the 1955 survey caught more than six times as many field mice (corrected for trapping effort) as the 1931 survey in the Village Bay area (Boyd 1956), suggesting a large population expansion into the previously inhabited area following competition and predation release. Summaries of previous trapping efforts on St Kilda are provided in Table 1.1.

Unfortunately, it is difficult to derive any more meaningful estimates of abundance from previous studies and they have been rendered unrepeatable due to the construction of the MoD base across the line of the main transect (Harrison 1933, Boyd 1956, Boyd 1959). Nor do they provide sufficient information to give an accurate indication of population dynamics, other than the observation that juvenile recruitment into the active population began in late June (Boyd 1959). Measurement of population dynamics requires regular ongoing trapping sessions due to the tendency for survival rates and breeding seasons of *A.*

sylvaticus to vary within and between years (Watts 1969). Elsewhere in northern Europe, *A. sylvaticus* generally undergo a seasonal cycle typified by low spring densities prior to the onset of breeding and a late autumn maximum at the end of the breeding season (Flowerdew 1985, Montgomery 1989,Bengtson *et al.* 1989). Within- and between-year density fluctuations can be considerable but there is little evidence for inter-annual cyclic patterns (Montgomery 1989, Gorman & Ahmad 1993). Population densities are considered to vary according to habitat type. Minima can be as low as 0.5mice/ha in sand dunes (Gorman & Ahmad 1993), although around 7 is more typical for deciduous woodland (Montgomery 1989). In British mainland populations, woodland densities (20-55 mice/ha) are generally higher than in grassland (15-20 mice/ha) or in maritime sand dunes (10-12 mice/ha) (Flowerdew 1985, Wilson *et al.* 1993, Gorman & Ahmad 1993). Greater densities have been observed elsewhere; insular Icelandic populations with no competitors and reduced predation pressure fluctuate seasonally from 22-150 mice/ha in areas with an especially plentiful autumn seed supply (Bengtson *et al.* 1989). In more typical grassland areas, Icelandic populations can have annual density maxima of less than 3 mice/ha, demonstrating considerable effects of habitat quality on population density (Unnsteinsdottir & Hersteinsson 2011).

Table 1.1 Summary of notable previous trapping efforts of mice on St Kilda and their findings, 1933-59.

Reference	**Period**	**Location**	**Description**	**Measurement method**	**Findings**
Harrison & Moy-Thomas, 1933	July-August 1931	Hirta, 13 sites across habitat types and elevations, mostly in Village Bay. (Description of sites very	Trap survey describing distribution and relative abundance of *A. sylvaticus hirtensis* on Hirta with regard to habitat type (elevation, vegetation, dry-stone structures), a year after evacuation [of the human population].	Rows of "about 50" traps per site, at "about 5 yards" intervals, left for "about 10 days". Two types of live traps used. (Methods described too briefly to be repeatable in later studies.)	"Field mice fairly numerous over most of the island below 400ft, common in long grass areas and abundant near stone walls or cleits at low level." (Average number of mice caught nightly per site ranged from 0 to 5, including retrapping.)
J.M. Boyd, 1956	May 1955	Hirta, Village Bay, 5 stations along the Dry Burn	Trap survey of mice in the village area of Hirta.	Lines of 4 Longworth traps (at 10 yard intervals) at 5 stations along a transect. Traps cleared and rebaited in the field for five consecutive nights of trapping. Mice marked by ear clipping.	"Village area population seems to have increased since 1931 study, taking into account differences in method and time of year." (Total of 50 mice, 33 individuals, caught in 100 trap-nights.)
J.M. Boyd, 1959	June 1956	Hirta, Village Bay, 4 stations along the Dry Burn	Trap survey of mice in the village area of Hirta.	Lines of 5 Longworth traps (at 10 meter intervals) at 4 stations along a transect. Traps cleared and rebaited in the field for five days, then moved for the last two days of trapping. Mice marked by ear clipping.	Decrease in mice caught per trap-night compared to 1955, but not significant when retrapped individuals are discounted. Significantly fewer adults caught than in 1955 (19 against 35 per cent).
J.M. Boyd, 1959	April 1957	Hirta, 30 stations throughout the island	Trap survey on whole island of Hirta (limited to areas with sufficient numbers of cleits), to determine density patterns across the island.	10 Longworth traps per station, placed inside 5 neighbouring cleits.	"Field mice are present all over Hirta, densest in the village area and rarest on the ridges."
J.M. Boyd, 1959	June 1957	Hirta, Village Bay	Trap surveys in the village area of Hirta, to determine influence of stoneworks and talus and of RAF operations on distribution.	Six lines each of 10 or 20 Longworth traps set for one night, situated around the newly constructed RAF buildings and equipment near the shore of Village Bay.	Lines with 10 traps caught between 1 and 9 mice each, the single 20 trap line caught 12. Mice seemingly not displaced by the human activity.

Island rodent populations are often typified by high densities relative to their mainland counterparts (Adler & Levins 1994). Examples from the British Isles include bank voles (*Myodes glareolus skomerensis*) on Orkney and Skomer with remarkable densities of up to 500 voles/ha and 475 voles/ha respectively (reviewed in Harris *et al.* 1995) compared to typical maxima of 11-34 voles/ha on the British mainland (Flowerdew *et al.* 2004). *Apodemus sylvaticus* are also found on Skomer but their abundance has been less well studied that that of the voles, although they are known to have distinct distribution from the voles, preferring rocky headlands and 'rabbit lawn' over the bracken and rushes in which the voles are primarily found (Healing *et al.* 1983). House mice (*Mus musculus*) are known to reach densities of up to 50 mice/ha averaged across the whole 100ha of Skokholm island, although some areas of the island have more favourable habitat than others and local densities may be considerably greater in preferred habitats (Berry 1968). The tiny 4ha Crabapple Island in the freshwater Beldany Lake, Poland, has been known to hold combined populations of yellow-necked mice (*Apodemus flavicollis*) and bank voles (*Myodes glareolus*) of up to 170/ha (Bujalska & Gruem 2008). Deer mice (*Peromyscus maniculatus*) occupy very similar niches to *Apodemus* and are considered to exist at relatively low and stable densities but demonstrate multi-annual cycles and extremes of density (5-430 mice/ha) on the small island of Santa Barbara, California (Drost & Fellers 1991). Similarly, experimental introductions of deer mice to an island off the coast of Maine resulted in a population whose density was 13 times that of the nearby mainland (Crowell 1983).

Conversely, there are numerous examples of small mammal island populations, including those of *Apodemus sylvaticus*, that do not exhibit elevated density (Delany 1970, Adler & Levins 1994, Crowell 1983), and this is broadly considered to be due to the relative lack of suitable habitat for the species in question. For example, house mice are generally considered human commensals and may do poorly on uninhabited islands (Berry 1968). However, there is still frequent evidence for increased density among many insular rodent populations, possibly due to reduced dispersal opportunities, reduced inter-specific competition, absence of predators or niche expansion (Adler & Levins 1994).

1.3.2 Ranging behaviour

None of the previous trapping efforts on St Kilda examined ranging behaviour of the mice, but examples from elsewhere can be found. Intuitively, range sizes should reflect the distribution of key resources required by an individual, including shelter, food and access to mates, which are likely to vary seasonally and between habitats. A comparison of range size in two mainland populations of *A. sylvaticus* occupying deciduous woodland and sand dunes found large differences between habitats, seasons and sexes. Mean range sizes for males increased from 0.3 to 0.6ha during the breeding season in woodland, and from 1.8 to 3.6ha in sand dunes. Female range sizes fluctuated less, remaining around 0.2ha in woodland regardless of season and varying from 1.2 to 1.6ha in sand dunes (Attuquayefio *et al.* 1986). Although estimates of home range size can vary considerably according to habitat and the method used to calculate them, the patterns of variation between sex and season appear to be largely consistent for *A. sylvaticus* populations found in woodland and arable farmland (reviewed in Wolton 1985) where range size is typically less than 1ha. The increase in range size in male *A. sylvaticus* during the breeding season seems to reflect non-random patterns of territorial overlap with several female territories (Brown 1969, Randolph 1977), which reflects the normal perception of *A. sylvaticus* employing a polygynous or promiscuous breeding system.

1.3.3 Breeding ecology and phenology

Although typically summer and autumn breeders in temperate climates, *A. sylvaticus* is well known for its variable breeding seasons and litter numbers and it may extend reproduction into or even through the winter depending on food availability and population density, even under snow (Smyth 1966). Elsewhere in Britain, *A. sylvaticus* typically breeds from March through to October, peaking in the summer months. Females produce up to 7 litters a year usually of 4-7 young each with gestation taking around 25 days. The young are fully weaned after about 18 days, and usually start to breed the year after their birth, but if they were born early in the year they may breed during the year of birth (Harris & Yalden 2008). Boyd (1969) found that females on Hirta were in breeding condition between April and August, with a peak in May/June, although this was inconsistent across years. Juveniles began to enter the trappable population in the second half of June which points to conceptions from late April onwards (assuming normal *A. sylvaticus* gestation and weaning durations).

Figure 1.5. Portraits of an adult St Kilda field mouse (left) and a younger individual undergoing post-juvenile moult (right).

As for the mating system, *A. sylvaticus* have been described as polygynous or even monogamous on the basis of home range data in some studies (Randolph 1977), but more recent work based on paternity analysis using microsatellite data has demonstrated high levels (means of 53-85%) of multiple paternities within litters, with up to three or four fathers per litter, suggesting a polyandrous or promiscuous mating system is more likely (Bartmann & Gerlach 2001, Booth *et al.* 2007, Bryja *et al.* 2008). Individual breeding success has been shown to positively correlate with weight at the onset of the breeding season in male, but not female *A. sylvaticus*, and there was no significant difference in variance of breeding success when comparing males and females (Bartmann & Gerlach 2001). However, the above study was performed on a captive population with only four individuals of each sex per replicate and may not be representative of wild populations of *A. sylvaticus*.

Whilst breeding ecology and population dynamics have been a major topic of research for many other *A. sylvaticus* populations, there is essentially no information available for the mice of St Kilda, other than the observation that juvenile recruitment into the trappable population does not occur until the middle of Jun, pointing to a rather late onset of breeding in late May (Boyd 1959). This would be in keeping with many other island populations of rodents, which often show patterns of shortened breeding seasons, delayed onset of sexual maturity and reduced fecundity, balanced against increased survival and population density (Adler & Levins 1994).

1.3.4 Evolutionary history and size

Field mice populations on many of the Scottish isles are of unusual size and morphology, and for some time it was posited that they may be remnant populations that, unlike mice on the mainland, survived the last ice age on island refugia and have evolved these differences in the 5000 years since the isles became separated from one another by rising sea levels (Berry 1969). However, morphometric analyses suggest complex relationships between populations on the different isles that are more easily explained as the result of post-glacial colonisation through accidental introductions by man (Berry 1969). On the basis of morphology, the St Kilda field mouse is more closely related to field mice populations in Northern Ireland and Norway than it is to those elsewhere in the Outer Hebrides, suggesting it may have been introduced by Viking sailors who were established throughout the Scottish Isles and Northern Ireland from the 8th century onwards – the so called 'Viking mouse' theory (Berry 1969).

Recent examination of the genetic diversity of the mice on St Kilda (using samples collected during this study) found very low levels of allelic variation in the eight microsatellite loci investigated, which suggests that the mice have remained genetically isolated since their introduction. In fact, with a maximum of six alleles at any of the loci studied, introduction of a single pregnant females carrying a multiple-paternity litter could theoretically account for all the observed genetic diversity of the mice on St Kilda (Robertson 2011). However, apart from geographical isolation there is little evidence of functional speciation between *A. sylvaticus hirtensis* and other nearby populations, as experimental breeding studies have shown that they will readily interbreed with *A. sylvaticus* from mainland Northern Ireland and southern England populations, as well as the Fair Isle field mouse, *Apodemus sylvaticus fridarensis* (Berry 1969). It is perhaps safest therefore to consider *A. sylvaticus hirtensis* as an ecotype (a genetically distinct population found in a particular) rather than race or subspecies.

Populations that evolve on islands often provide remarkable examples of body size evolution. Among island mammals, the tendency for small species to evolve toward a larger size and large species toward a smaller size is known as the island rule (Van Valen 1973). Various mechanisms have been posited to explain this pattern, but in general it is believed to be due to small mammals growing larger to control more resources and enhance metabolic efficiency, while large mammals evolve smaller size to reduce resource requirements and increase reproductive output. This frequently coincides with release from competition/predation pressure that may otherwise keep body size evolution in check. However, modern thinking is that the size evolution on islands is likely to be governed by the biotic and abiotic characteristics of different islands, the biology of the species in question and contingency. Although examples of size evolution in both directions are numerous, when investigated using methods that use full phylogenetic control the island 'rule' appears almost to be made to be broken, being true in only a few clades; carnivores, heteromyid rodents and artiodactyls typically evolve smaller size on islands whereas murid rodents usually grow larger (Meiri *et al.* 2008).

Interestingly, the two mammal species found on Hirta both belong to one of the clades mentioned above; the already diminutive Soay sheep (*Ovis aries*) found on Soay and Hirta has shown a measurable negative trend in body size over the last 23 years in response to changing environmental conditions (Wilson *et al.* 2007, Ozgul *et al.* 2009) and the St Kilda field mouse was primarily classified as a distinct subspecies on the basis of its large size (Barrett-Hamilton 1899). Similarly, the extinct house mouse and extant wren subspecies are larger than their mainland counterparts.

St Kilda is not unique in being home to *A. sylvaticus* of unusual size; as a species it shows considerable variation in size and many other islands around Scotland, Britain and Europe hold races of field mice that are larger than those on the mainlands (Berry 1969, Angerbjorn 1986), although the St Kilda strain appears to be amongst the very largest, at least in terms of body length. Whilst the biotic and abiotic factors affecting body size are undoubtedly complex, increased size in *A. sylvaticus* is perhaps most strongly correlated with competitive release from other mouse and vole species (Angerbjorn 1986). Angerbjorn also examined the hypotheses that the degree of gigantism in island populations may be related to climatic differences between island and mainland populations, island size or distance between islands and the mainland but found no observable trends. Elsewhere however, insular *Apodemus speciousus* populations around the Japanese archipelago do conform to both the island rule (larger body size on smaller islands) and Bergmann's rule (increased body size with latitude), presumably in response to climatic variations (Millien & Damuth 2004).

1.3.5 Diet

Although known to eat a wide range of foodstuffs, *Apodemus* are considered primarily granivorous, and the 1931 survey stated that grass (*Holcus lanatus, Anthoxanthum odoratum* and *Festuca ovina*) forms the bulk of the diet, along with the seeds of *Cochlearia anglica,* *Statice maritime, Ranunculus acris* and *Rumex acetosa* (Harrison 1933), presumably on the basis of faecal or gut contents. However, the survey was made in August when seeds would have been relatively plentiful and the mice may rely on switching prey types at other times of year (they may also cache seeds and other food items). As on the mainland, the mice may also eat plant buds and stems, invertebrates and fungi (Churchfield & Brown 1987, Green 1979, Rogers & Gorman 1995, Watts 1968, Zubaid & Gorman 1991, Harris & Yalden 2008) and are thought to eat petrel eggs (Bicknell 2009) and dead sheep (pers. obs.) on St Kilda.

The mice have no direct competitors on St Kilda, but share the herb and grass food supply with one other mammal, the Soay sheep. With few or no predators on St Kilda, the mouse population is presumably ultimately controlled by the food resource, disease and climatic conditions. The Soay sheep population undergoes population crashes at erratic intervals, which are associated with high density, low food and poor over-winter weather (Coulson *et al.* 2001), but it is not known if the same factors affect survival in the mouse population, or indeed if such fluctuations may benefit the mice by reducing competition for plant resources or providing dead sheep as an additional food source.

The extent to which the mice may predate seabird eggs is also potentially important as 95% of the European population of Leach's Storm-petrel *Oceanodroma leucorhoa* breeds on the archipelago and its main colony on St Kilda is reported to have declined by 48% between 1999 and 2003 (Newson *et al.* 2008). It is believed that the mice may have had a role in the recent failure of up to 15,000 Leach's Storm-petrel nests on St Kilda in a single breeding season, although there is no direct evidence for this (Bicknell 2009).

1.3.6 Parasites and disease

A slight account of some of the parasites of the St Kilda field mouse can be found in Boyd 1959. Ectoparasites consisted of fleas (*Ctenophthalinus nobilis vulgaris, Nosophyllus fasciatus* and *Typhloceras poppei*) and mites (*Laelaps festinus* and *Enlaelaps stabularis*). Endoparasites were identified as *Rictularia cristata*, a species of nematode not usually found in Great Britain, and a cestode *Hymenolepis diminuta*. Earlier studies found *Cysticercus fasciolaris* cestodes whose primary host is the cat, but these were not found by Boyd, presumably due to the removal of the cat population with the evacuation of the human population in 1931.

Mainland populations are known to harbour a diverse array of micro- and macroparasites, with a recent study of gastrointestinal and blood parasites finding five nematode, three cestode, five protozoa, one trypanosome and five *Bartonella* bacteria species in a single population, with individual mice showing simultaneous infections of up to six parasite species at any one time (Knowles *et al.* 2013). Viruses such as cowpox are also known to be common (Telfer *et al.* 2002).

1.4 Methodological approaches

1.4.1 Sampling strategy

The core method of data acquisition for this study centred on a regime of intensive live trapping at three locations on the main island of Hirta (Figures 1.6 & 1.7). Trapping locations were chosen which were geographically distant (within the limits of a rather small island) and broadly representative of the areas of the island in which they were placed. Within these areas, the precise location of trapping sites was informed by the knowledge that the mice preferentially inhabit areas with rock cover, and all contained considerable areas of talus, man-made walls and cleits, or both. Each consisted of a 90m x 90m (0.85ha) grid, with 200 traps placed in pairs every 10 metres. Detailed descriptions and precise locations of the sites can be found in the methods sections of the following three chapters, but in summary they consist of Carn Mor (an extensive and steeply sloping talus field below the sea cliffs on the west of the island, home to a large seabird breeding colony in the summer), Glen Bay (an exposed area of short grass, talus and walls to the north west of the island, and some-time sheep graveyard during the winter) and Village Bay (a mix of short grass, low growing heather and *Sphagnum* bog with little natural talus but an extensive network of walls and cleits, heavily grazed by sheep).

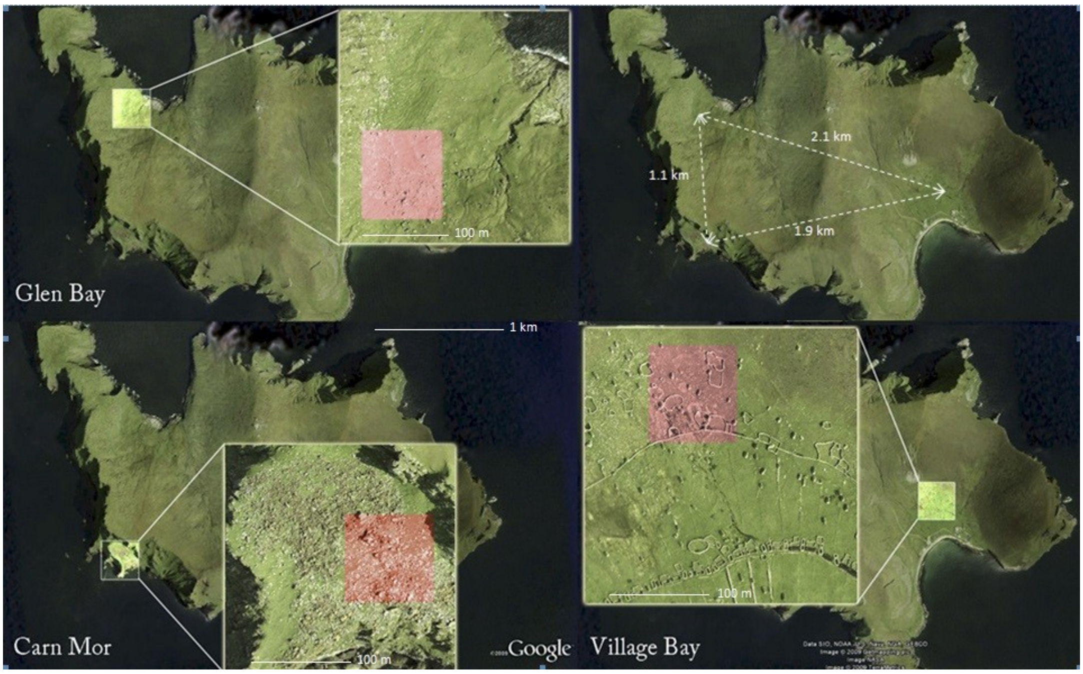

Figure 1.6. The island of Hirta and the locations (blow ups), approximate extents (pink boxes) and approximate distances between the three trapping sites. Images adapted from Google Earth.

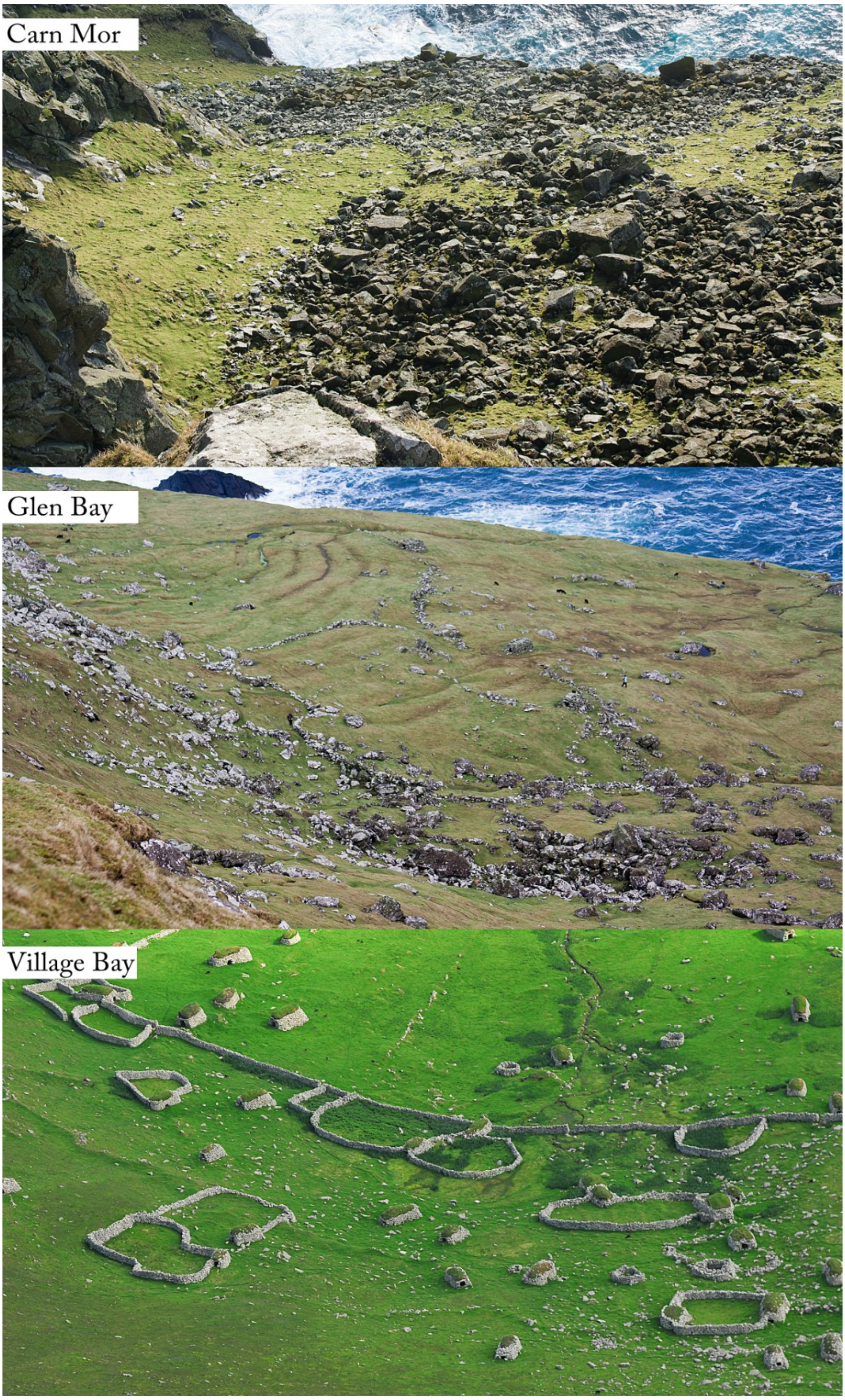

Figure 1.7. Areas containing the three trapping sites, as viewed from vantage points above.

Grids were trapped four times a year from November 2009 until September 2012, totalling 12 sessions, with each session involving trapping for five consecutive nights per grid. The timing of the sessions corresponded broadly with the seasons and were scheduled to capture the anticipated extremes of the population dynamics and breeding phenology. Within a session, sites were trapped sequentially in a random order, as far as logistics and weather conditions allowed. In all, the trapping regime required 14 months of field work across three years and 12 trips.

Such an intensive trapping regime has many advantages. By effectively saturating each area with traps it is possible to catch a high proportion of the populations at each site (around 90%, in this case), ensuring that the sampling process is truly representative and the data set robust. It also provides longitudinal data and samples from the same individuals at multiple points in their life, and is sufficiently frequent to capture, albeit broadly, the annual population cycles typical of temperate small mammals.

1.4.2 Statistical approaches

A trio of statistical modelling approaches have been applied in this study. Chapter 2 considers the morphological and phenological characteristics of the mice and their breeding ecology, for which various linear regression models were employed to test for associations between measurements and various potential explanatory variables. Linear regression models are in widespread use across the sciences and should need little introduction. In particular, linear mixed-effects models (LMMs) were used to examine the relationship between continuous variables (such as weight) with fixed effects (such as age class and sex) whilst controlling for random effects (such as year or individual identity). Similarly, generalised linear models (GLMs) or generalised linear mixed-effects models (GLMMs) were applied when dealing with proportional data such as the number of mice in breeding condition.

Chapter 3 focuses on estimating population densities of the mice. This has traditionally been achieved using probabilistic methods based on mark-recapture data to calculate animal abundance (Pollock *et al.* 1990), but these rely on *ad hoc* methods to calculate an 'effective trapping area' in order to convert those abundance estimates into densities, which are inherently biased by edge effects whereby trap-revealed animal ranges are truncated at the edge of the trapping grid. Recently, alternative likelihood-based spatially-explicit capture recapture (SECR) methods have been developed which integrate capture histories with distance sampling theory to model the declining likelihood of detecting an animal with a particular trap, as the animal's distance from that trap increases. This allows density to be estimated explicitly without needing to calculate an effective trapping area, and the method can be applied to almost any trapping design where the spatial layout of the detectors is known (Efford 2004, Borchers & Efford 2008).

Chapter 4 employs one branch of the complex suite of maximum-likelihood based mark-recapture models which provide estimates for numerous parameters from data on animals which have been marked and then re-encountered at a later date. In particular, this study used Pradel robust design models (Pradel 1996), which estimate detection probabilities over consecutive trap-nights within a session (when the population is assumed to be closed to births, deaths and migration) and then calculate recruitment and apparent survival rates (which together define the population rate of change) for the periods between trapping sessions, when populations are assumed to be open to such processes. Importantly, these models allow the estimated variance to be decomposed into separate sampling and population processes, hence removing bias caused by incomplete population sampling (White *et al.* 2002).

1.5 Chapter aims

The themes and specific questions addressed by the following three data chapters can be summarised thus;

Chapter 2: Body size and breeding ecology

- How large are St Kilda field mice at the present time (specifically weight, body length and tail length)?
- Is there sexual dimorphism in body weight which might provide hints as to the selective pressures that might be driving the evolution of gigantism?
- What is the breeding phenology of the mice, and how does it vary between the sexes and with age, geography and year?

Chapter 3: Spatially explicit capture-recapture estimation of population density

- What is the density of the mouse population on Hirta, and how does this vary through time and between trapping sites?
- What is the home range size of the mice, and does this vary by sex or between trapping sites?

- Does the tendency for a male biased sex ratio in numbers of mice caught reflect a genuine demographical difference, or is it an artefact of different range sizes or capture likelihood between sexes?
- Does SECR analysis provide a suitable framework for future monitoring of mouse populations by The National Trust for Scotland?

Chapter 4: Survival, fecundity and overall population dynamics

- How does the overall rate of population change vary through time, and are there differences between trapping sites?
- How do the separate rates of survival and fecundity contribute to the rate of population change and do these vary between trapping sites?
- Do survival and fecundity estimates support the hypothesis that population dynamics may be driven by marine subsidies?

CHAPTER 2

Body size and breeding ecology of the St Kilda field mouse

2.1.1 General introduction

Having evolved in island isolation from the long-tailed field mouse or wood mouse (*Apodemus sylvaticus*) common across most of Europe, the St Kilda field mouse (*A. sylvaticus hirtensis*) was designated first as a separate species (Barrett-Hamilton 1899) and then subspecies (Barrett-Hamilton 1900) over a century ago, primarily on account of its larger size and different colouration compared to mainland populations of field mice. This endemic subspecies is considered of national importance (Ratcliffe 1977) and is included in and protected under St Kilda's designation as a World Heritage Site. Despite this, relatively little is known about *A. sylvaticus hirtensis*. Further investigation into the core ecology of these mice is a specific objective of the St Kilda management plan (NTS 2003) and essential for informing the future conservation policy of the islands.

Populations that evolve on islands often provide remarkable examples of body size evolution. Among island mammals, the tendency for small species to evolve toward a larger size and large species toward a smaller size is known as the island rule (Van Valen 1973). Various mechanisms have been posited to explain this pattern, with the general belief being that selection favours increased body size in small mammals because it enables them to control more resources and enhances metabolic efficiency, while in large mammals selection favours reduced body size through reduced resource requirements and increased reproductive output. This frequently coincides with release from interspecific competition and/or predation pressure that may otherwise keep body size evolution in check (Meiri *et al.* 2008).

Although examples of island size evolution in both directions are numerous, they are far from consistent and are likely to be governed by the various biotic and abiotic characteristics of individual islands, the biology of the species in question and contingency.

After correcting for phylogeny, fairly strong directional patterns remain in a few clades: carnivores, heteromyid rodents and artiodactyls all typically evolve smaller sizes on islands, whereas murid rodents usually evolve to be larger (Meiri *et al.* 2008).

Interestingly, the two mammal species found on Hirta both belong to one of the aforementioned clades; the already diminutive Soay sheep (*Ovis aries*) found on Soay and Hirta has shown a measurable negative trend in body size over the last 23 years in response to changing environmental conditions (Wilson *et al.* 2007, Ozgul *et al.* 2009) and the St Kilda field mouse is classified as a distinct subspecies on the basis of its large size (Barrett-Hamilton 1899). Similarly, the extinct house mouse was and extant wren subspecies is larger than their mainland counterparts. Previous studies have found that adult male field mice on St Kilda can exceed 50g in weight and females 40g (Harrison 1933, Boyd 1956), which is more than double the mean weight for typical mainland populations (Ernest 2003).

Of course, St Kilda is not unique in being home to *A. sylvaticus* of unusual size; as a species it shows considerable variation in size and many other islands around Scotland, Britain and Europe hold races of field mice that are larger than those on the nearby mainlands (Berry 1969, Angerbjorn 1986), with increased size being most strongly correlated with competitive release from other small rodent species with overlapping niches and with reduced predation (Angerbjorn 1986). Even amongst these giant races, the St Kilda mice are still probably the largest, at least in terms of body length (Angerbjorn 1986).

As well as considerable size variation, *A. sylvaticus* are well known for their variable breeding seasons and litter numbers. Although breeding usually occurs in summer and autumn in temperate climates, field mice may extend reproduction into or even through the winter depending on food availability and population density, even under snow (Smyth 1966). In mainland Britain, *A. sylvaticus* typically breed from March through to October, peaking in the summer months. Females produce anywhere up to 7 litters a year (although 3-4 is more typical) usually of 4-7 young each with gestation taking around 25 days (Harris & Yalden 2008). The young are fully weaned after 18-22 days, and usually start to breed the year after their birth, although individuals born early in the year may breed during the year of birth (Harris & Yalden 2008).

Originally believed to be polygynous or even monogamous on the basis of home range data in some studies (Randolph 1977), more recent paternity analyses using microsatellite data have demonstrated high levels (53-85%) of multiple paternities within litters, with up to three or four fathers per litter, suggesting a polyandrous or promiscuous mating system is more likely (Bartmann & Gerlach 2001, Booth *et al.* 2007, Bryja *et al.* 2008).

Boyd (1969) found that female *A. s. hirtensis* on Hirta were in breeding condition between April and August, with a peak in May/June, although this was inconsistent across years. Juveniles began to enter the trappable population in the second half of June which points to conceptions from late April onwards (assuming normal *A. sylvaticus* gestation and weaning durations). Harrison & Moy-Thomas (1933) did not report age classes, but found that 40% of male and 31% of female field mice caught across Hirta weighed less than 20g (and can hence safely be considered juveniles) in early August of 1931, and a further 36% of males and 26% of females weighed 21-30g, which approximately corresponds with sub adult mice. Therefore, roughly 76% of males and 51% of females caught in August 1931 appear to have been recruits from that year's breeding efforts. In comparison, Boyd (1956) found no juvenile mice in the Village Bay population when trapping in late May of 1955, suggesting that few if any juveniles had been weaned by that point. No conclusions were drawn by previous studies about the number or size of litters, age at first breeding or mating system.

This chapter aims to address the following questions:

- How large are St Kilda field mice at the present time (specifically weight, body length and tail length)?
- Is there sexual dimorphism in body weight which might provide hints as to the selective pressures that might be driving the evolution of gigantism?
- What is the breeding phenology of the mice, and how does it vary between the sexes and with age, geography and year?

Some additional observations on distribution, litter size, birth weight, coat colour, and caching behaviour are also presented.

2.2 Materials & Methods

2.2.1 Study area

Fieldwork was carried out on the island of Hirta, St Kilda, Scotland. St Kilda is a remote archipelago of volcanic origin 64km from the Outer Hebrides and 160km west of the Scottish mainland. Rising as high as 430 metres from the Atlantic, Hirta has an oceanic climate with typically cool temperatures, high rainfall and moderate to strong winds, which have resulted in a treeless landscape of 637 hectares typified by mixed grassland complexes, heather moorlands and peat bogs, bounded by maritime swards and steep-sided sea cliffs (McVean 1961).

Trapping was undertaken at three separate sites (Figure 2.1). **Carn Mor** (57°48'34"N- 8°36'6"W) is located within an extensive and steeply sloping talus field below the sea cliffs on the west side of the island at an altitude of 120-170m. The area within the trapping grid is predominantly (60-70%) rock talus, interspersed with areas of short grass and some larger rock outcrops, and is the nesting site for large numbers of Atlantic puffins (*Fratercula arctica),* northern Fulmars (*Fulmarus glacialis*) and Leach's storm petrel (*Oceanodroma leucorhoa*). Puffin and petrel nests are found in underground burrows or concealed in crevices between the rocks, both of which may also provide shelter for the mice. This site also contains a small number of man-made stone cleits, but they are generally indistinct from the surrounding talus.

Glen Bay (57°49'10"N-8°36'16"W) is located in the north-west corner of the island at an altitude of 70-100m and consists of fairly steep grass and talus slopes on one edge, leading into a predominantly flat area comprised of short, mixed grasslands with ~25% talus coverage and several small stone walls and cleits. The talus areas are used as nest sites by a small number (around 12) of fulmar pairs. The area as a whole is rather exposed and receives little or no direct sunlight during December and January. During winter the cleits and talus often contain carcasses of Soay sheep.

Village Bay (57°48'53"N- 8°34'15"W) is a moderately sloping area approximately 50-80m above sea level in the relatively sheltered south-east corner of the island and consists predominantly of short, mixed grass with a partial transition to low growing heather (*Calluna vulgaris*) on the higher slopes. There are also limited stands of iris and bracken near the lower boundary and a small area of *Sphagnum* bog. Although lacking natural talus, this site does contain an extensive network of stone walls and cleits, a small number of which house fulmar nests in the summer. This area has the highest quality of vegetation for grazing on the island, and hence the highest density of Soay sheep whose carcasses are often found amongst the walls and cleits during overwinter mortality. This is also the only site close to human activity, but is separated from the nearest occupied buildings by 150m of mainly open grassland and is considered free from current human impact.

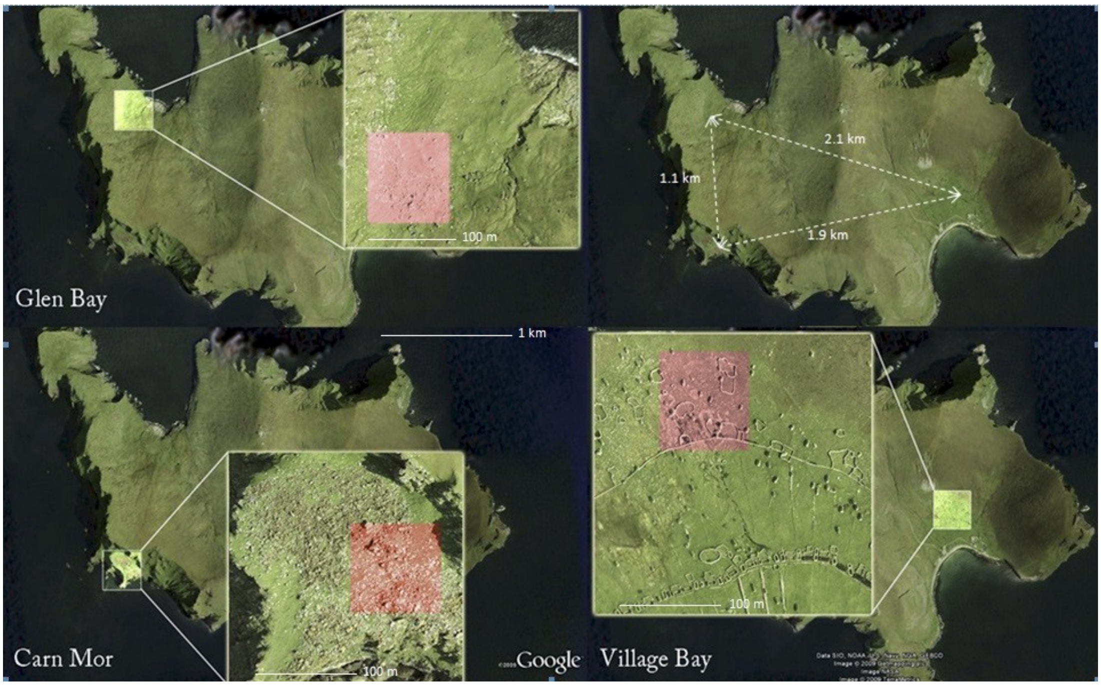

Figure 2:1. The island of Hirta and the locations (blow ups), approximate extents (pink boxes) and approximate distances between the three trapping sites. Images courtesy of Google Earth.

2.2.2 Trapping methods

Twelve primary trapping sessions were carried out on each site over three years between November 2009 and September 2012. Primary sessions took place at around the same time each year, namely in spring (March - early April), early summer (late May - June), early autumn (late August- September) and early winter (November – early December). For ease of reading, sessions will subsequently be referred to simply by their corresponding season throughout the text. Precise trapping dates can be found in Table 2.1. Each primary session consisted of five consecutive nights (occasions, or secondary sessions) per site. Sites were trapped sequentially rather than concomitantly in a random order as far as logistically possible – in particular it was not considered safe to trap at Carn Mor during westerly gales.

Traps were arranged at each site on a grid consisting of 100 trapping stations, with two traps per station totalling 200 traps per grid. Stations were arranged in a 10x10 grid, with 10m between stations, covering a total area of 0.81ha (90m x 90m). The only exceptions to this regime were in the first session on Carn Mor, when adverse weather limited the trapping effort to 90 traps in a 10x9 grid (one trap per station) for four nights instead of five and Glen Bay when all traps were used but only for 4 nights, also in the first session. Traps were positioned within 1m of the notional station, within the cover of rocks, walls or cleits where possible and left in the same spot for the duration of a primary session. Positioning of trapping stations was highly repeatable between sessions. The traps used were 'Longworth' type single catch live traps (Penlon Ltd., Oxford, UK), which were wrapped in bubble wrap to provide insulation and were baited with shelled peanuts and a piece of carrot and stuffed with dried grass for bedding. No pre-baiting or scatter baiting was used, as a previous trial in the summer of 2009 using a small number of traps along the street and ruined houses in Village Bay had achieved high trap success (>80%) without the use of either.

Deployed traps were checked each morning for mice. Newly caught animals were marked using passive integrated transponder (PIT) tags (AVID Plc, Lewes, UK) inserted into the scruff of the neck, or occasionally with individual ear punch patterns. Weather permitting, sex, age class, reproductive condition and body condition scores were recorded for all caught mice. Age classes were defined as Juveniles (pre first moult, still showing early life grey pelage, probably less than 45 days old (Frynta & Zizkova 1992), Sub Adults (post first moult, generally pre-reproductive and yet to over-winter) and Adults which were retrospectively split into two groups; Adult 1 (mice caught in spring which had survived only their first winter) and Adult 2 (mice which had survived to the summer a year after birth or longer). Very few mice survived two winters, so adults caught in the spring were assumed to be Adult 1 unless previous trapping history confirmed they had survived two winters. By the summer all adults were Adult 2 by definition.

Reproductive status was determined by the position of the testes (abdominal or scrotal) in males and by a combination of perforation or non-perforation of the vagina, presence or absence of nipples or nipple 'patches' and evidence of pregnancy or lactation in females. Body condition was determined using palpation of the spinal column (Ullman-Cullere & Foltz 1999). Weights were also recorded to the nearest 0.5g using a Pesola® (Baar, Switzerland) micro-line spring scale, and combined head and body lengths and tail lengths were measured to the nearest 1mm using a metal rule. On initial capture one or more ear tissue punches were taken both to mark the mouse and as a sample, and on the first capture per session a blood sample of ~100 micromols was taken via submandibular venepuncture. Individuals were then released at the point of capture and the traps reset with fresh bait and bedding.

2.2.3 Statistical analysis of morphological characteristics

Individual mice were observed to lose weight when trapped repeatedly within primary sessions, with the exception of juvenile mice which tended to gain weight within a session (Figure 2.2). For this reason, all analyses were carried out on a subset of data limited to measurements taken the first time each individual was caught within a primary session. Initially, the distributions of mouse weights, body lengths (including head) and tail lengths were examined for all individuals across all primary sessions, and simple linear regression models (LMs) were used to model the relationship between weight and body length and tail length in order to determine which metric provided the best proxy for skeletal size. This metric was determined to be body length, which was therefore included in subsequent analysis of body weight to determine if spatial variation in mouse weight was due to a larger skeletal size or improved body condition (i.e. increased weight for a given length).

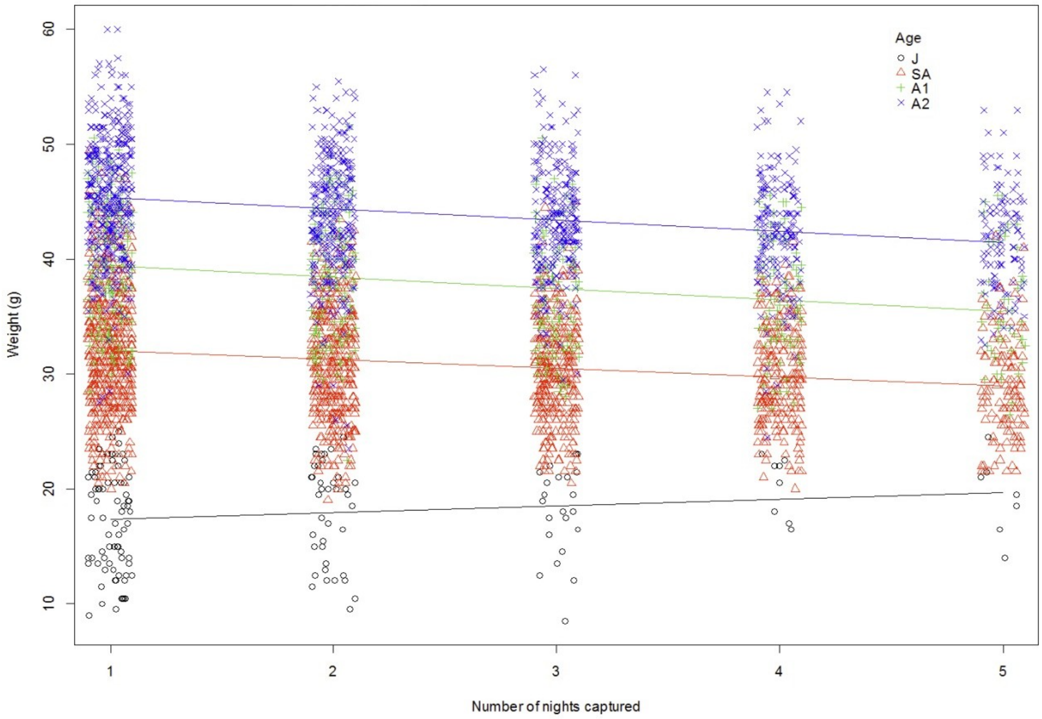

Figure 2.2. Scatterplot of weights for all captures plotted against the number of times mice had been caught within a session, by age class (Juveniles = black, Sub adults = red, Adult 1 = green, Adult 2 = blue). Regression lines calculated from a linear mixed-effects model with age class and number of nights as fixed effects and ID and seasons within years as random effects. Horizontal jitter applied to reduce overlap of data symbols.

Linear mixed-effects models (LMMs) were then used to test for differences in mouse weight between age classes, sexes and the three trapping locations. All three explanatory variables were hence included as fixed effects in the starting models. The longitudinal nature of the study meant that the data set included many repeated measures from individuals over a number of primary sessions spanning multiple seasons and years. Individual identities (ID) were therefore included as a random effect in all models, as were seasons nested within years (see Table 2.1 for the relationship between primary session, season and year). This allowed the models to account for pseudoreplication of measures from the same individual and for potential unexplained temporal environmental variance that could affect mouse weight between seasons and years. Although only three years were present in the data, nesting seasons within years produces 12 factor levels which is considered sufficient for a random effect (J. Hadfield, pers. comm.).

An initial full model with all three fixed effects, all two- and three-way fixed effect interactions and both random effects was fitted and then reduced through backwards elimination of highest level interaction terms, then fixed main effects and then random effects, with models selected on the basis of AIC values. Where models were indistinguishable (ΔAIC < 2) the simpler model was selected on the basis of model parsimony. Models were checked for normality and homogeneity by visual inspection of plots of residuals against fitted values. For the preferred model, means and p values for fixed effects were estimated using Markov chain Monte Carlo (MCMC) sampling. The preferred models were then further investigated by calculating the predicted mean body weight and associated 95% confidence interval for each fixed effect factor level (holding other fixed effects constant at their predicted means) and finally carrying out Tukey's HSD (honestly significant difference) tests on the predicted mean weights for all factor level pairs for each significant fixed effect or interaction.

In order to assess if weight differences between sexes and grids were due to differences in skeletal size or to body condition, the LMM modelling with weight as the response variable was then repeated using the methodology above but with body length included as an additional fixed main effect. Body length was chosen as a proxy for skeletal size as it was found to scale linearly with body weight (Fig. 2.7). It was hypothesised that weight differences due to skeletal size, controlling for age class and sex, would reflect spatial variation in breeding phenology, whilst weight differences independent of body size would reflect spatial variation in food availability or other environmental factors.

2.2.4 Analysis of breeding condition

General linear models (GLMs) or generalised linear mixed-effects models (GLMMs) as appropriate were used to test for sex, year and geographical differences in the proportion of mice in reproductive condition within each age group. Field data on breeding condition was recoded as a binary response variable; animals were considered to be in either breeding condition or not. In males, breeding condition was defined as exhibiting visibly descended testes and in females as showing signs of being pregnant, recently giving birth or suckling offspring.

GLMMs were fitted separately for each age class except juveniles which were excluded as they exhibited no signs of being sexually active. Similarly, data from winter sessions was also excluded as only ten individuals of 442 caught in winter were ever observed to be in breeding condition. This allowed season and year to be fitted as fixed effects where appropriate, which would otherwise have been impossible due to unbalanced nesting of seasons within calendar years during the study period (Table 2.1). The full models for each age class included sex and grid as fixed effects along with year and season when appropriate, an interaction between sex and grid and finally ID as a random effect in the

Adult 2 age class (the other classes did not have repeated measures for individuals). Models were fit using the binomial family (log link) using Laplace approximation. Model reduction, selection and investigation of significant factors was performed as for the morphological characteristics above.

2.2.5 Software

Descriptive statistics, tabulation and graphing were carried out using R versions 2.15.3 and 3.0.0 (RCoreTeam 2014), Minitab 16.1.1 (Minitab 2010) and Excel (Microsoft 2010). LMM and GLMM analyses were carried out using R packages *lme4* (Bates 2014) and *language* (Baayen 2013). Predicted values of response variables for different factor levels of preferred models were calculated using R package *effects* (Fox 2003) and the significance of pair-wise comparisons for factor levels of preferred models were carried out using R package *multcomp* (Hothorn 2008).

2.3 Results

2.3.1 Trapping success

Total trapping success across all sessions and grids amounted to 4462 captures of 787 individuals. The number of mice of each age class caught per session across all grids can be found in Figure 2.3. Per session trapping success by grid, sex and age class is summarised in Table 2.1. The overall sex ratio of mice caught was significantly biased towards males (1.42M:1F, n=783, exact binomial test, $p<0.001$). Two individuals escaped after tagging but before sex was determined, were never re-caught and are hence of unknown sex. Recapture rates were generally high; the mean number of captures per individual within a 5-night primary trapping session was 3.2 (min 1, median 3, max 5), and mean number of primary sessions (seasons) in which an individual was caught was 1.7 (min 1, median 1, max 8). The mean total number of captures per individual was 5.6 (min 1, median 4, max 32).

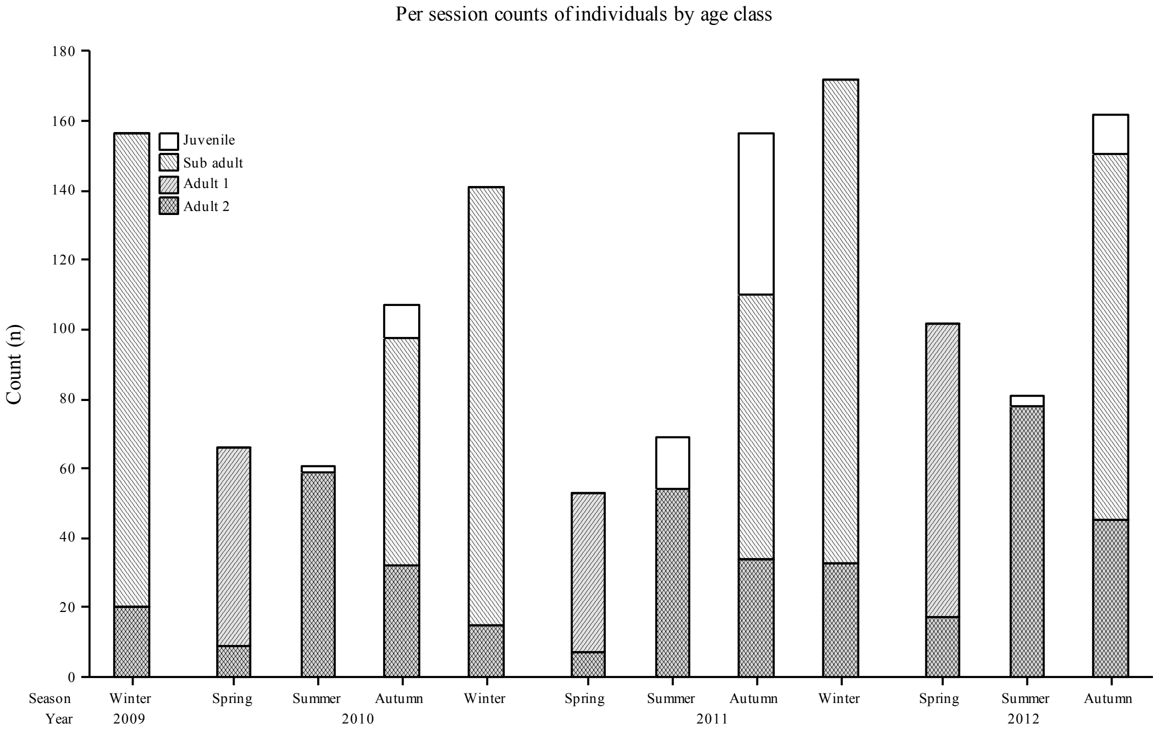

Figure 2.3. Number of individual mice caught in each primary session, by age class.

Table 2.1. Trapping dates and successes for each primary session by grid, sex and age class.

					Males (by age class)				Females (by age class)			
Year	**Session**	**Grid**	**Trapping Dates**	**Total (M/F)**	**J**	**SA**	**A1**	**A2**	**J**	**SA**	**A1**	**A2**
2009	1 Winter	CM	17/11/09 – 20/11/09 *	39 (17/22)	-	13	-	3	-	20	-	2
		GB	26/11/09 – 29/11/09 *	65 (32/32)§	-	28	-	4	-	31	-	1
		VB	08/11/09 – 12/11/09	53 (23/30)	-	14	-	9	-	29	-	1
		Sub Total		**157**	**-**	**55**	**-**	**16**	**-**	**80**	**-**	**4**
2010	2 Spring	CM	30/03/10 – 03/04/10	14 (9/5)	-	-	5	4	-	-	5	-
		GB	21/03/10 – 25/03/10	32 (18/14)	-	-	16	2	-	-	13	1
		VB	13/03/10 – 17/03/10	21 (10/11)	-	-	8	2	-	-	11	-
		Sub Total		**67**	**-**	-	**29**	**8**	**-**	-	**29**	**1**
	3 Summer	CM	15/06/10 – 19/06/10	14 (11/3)	2	-	-	9	-	-	-	3
		GB	30/05/10 – 03/06/10	23 (16/7)	-	-	-	16	-	-	-	7
		VB	07/06/10 – 11/06/10	24 (17/7)	-	-	-	17	-	-	-	7
		Sub Total		**61**	**2**	-	-	**42**	-	-	-	**17**
	4 Autumn	CM	09/09/10 – 13/09/10	52 (29/23)	3	17	**-**	9	3	17	-	3
		GB	25/08/10 – 29/08/10	20 (12/8)	-	3	**-**	9	-	7	-	1
		VB	03/09/10 – 07/09/10	35 (24/11)	2	16	**-**	6	1	6	-	4
		Sub Total		**107**	**5**	**36**	**-**	**24**	**4**	**30**	-	**8**
	5 Winter	CM	13/11/10 – 17/11/10	82 (50/32)	-	43	**-**	7	-	29	-	3
		GB	03/11/10 – 07/11/10	35 (19/16)	-	14	-	5	-	16	-	-
		VB	22/11/10 – 26/11/10	24 (9/15)	-	9	-	-	-	15	-	-
		Sub Total		**141**	**-**	**66**	-	**12**	**-**	**60**	-	**3**
2011	6 Spring	CM	30/03/11 – 03/04/11	29 (22/6)§	-	-	20	2	-	-	6	-
		GB	21/03/11 – 25/03/11	19 (14/5)	-	-	9	5	-	-	5	-
		VB	14/03/11 – 18/03/11	6 (3/3)	-	-	3	-	-	-	3	-
		Sub Total		**54**	**-**	**-**	**32**	**7**	-	-	**14**	-
	7 Summer	CM	17/06/11 – 21/06/11	35 (22/13)	3	-	-	19	6	-	-	7
		GB	10/06/11 – 14/06/11	14 (10/4)	-	-	-	10	-	-	-	4
		VB	31/05/11 – 04/06/11	20 (17/3)	6	-	-	11	-	-	-	3
		Sub Total		**69**	**9**	**-**	-	**40**	**6**	-	-	**14**
	8 Autumn	CM	31/08/11 – 04/09/11	82 (50/32)	18	17	-	15	17	10	-	5
		GB	14/09/11 – 18/09/11	50 (27/23)	7	17	-	3	3	16	-	4
		VB	23/08/11 – 27/08/11	26 (17/9)	2	11	-	4	-	5	-	3
		Sub Total		**158**	**27**	**45**	-	**22**	**20**	**31**	-	**12**
	9 Winter	CM	06/11/11 – 10/11/11	90 (50/40)	-	33	-	17	-	34	-	6
		GB	15/11/11 – 19/11/11	47 (26/21)	-	23	-	3	-	18	-	3
		VB	29/11/11 – 03/12/11	35 (19/16)	-	18	-	1	-	13	-	3
		Sub Total		**172**	-	**74**	-	**21**	-	**65**	-	**12**
2012	10 Spring	CM	01/04/12 – 05/04/12	44 (29/15)	-	-	20	9	-	1	11	3
		GB	24/03/12 – 28/03/12	35 (19/16)	-	-	18	1	-	-	13	3
		VB	12/03/12 – 16/03/12	25 (18/6)	-	-	18	-	-	-	5	1
		Sub Total		**104**	-	-	**56**	**10**	-	**1**	**29**	**7**
	11 Summer	CM	26/05/12 – 30/05/12	35 (23/12)	-	-	-	23	-	-	-	12
		GB	04/06/12 – 08/06/12	25 (16/9)	-	-	-	16	-	-	-	9
		VB	12/06/12 – 16/06/12	18 (12/6)	3	-	-	12	-	-	-	6
		Sub Total		**81**	**3**	-	-	**51**	-	-	-	**27**
	12 Autumn	CM	19/09/12 – 23/09/12	94 (54/40)	6	31	-	17	5	26	-	9
		GB	11/09/12 – 15/09/12	46 (27/19)	-	21	-	6	-	13	-	6
		VB	29/08/12 – 02/09/12	20 (17/3)	-	10	-	7	-	3	-	-
		Sub Total		**160**	**6**	**62**	-	**30**	**5**	**42**	-	**15**

*Trapping limited to 4 nights instead of 5 due to adverse weather conditions.

§ Plus one individual of undetermined sex

2.3.2 Overview of mouse weights, body lengths and tail lengths

Weights of captured mice (Figure 2.4) ranged from 9g (juvenile female) to 60g (adult male). One adult male weighed slightly over 60g but the precise measure was impossible to determine due to exceeding the Pesola® balance scale. Combined head and body lengths (Figure 2.5) ranged from 58mm (juvenile female) to 105mm (adult male). Tail lengths (Figure 2.6) for mice with complete tails ranged from 54mm (juvenile female) to 110mm (adult male). Tail lengths were generally slightly longer than combined head and body lengths, except for ~5% of mice which were missing up to half of their tails, presumably as a result of previous injury. Around one in four mice were also observed to possess a 'white tail tip' – an albino area at the end of the tail up to 16mm long.

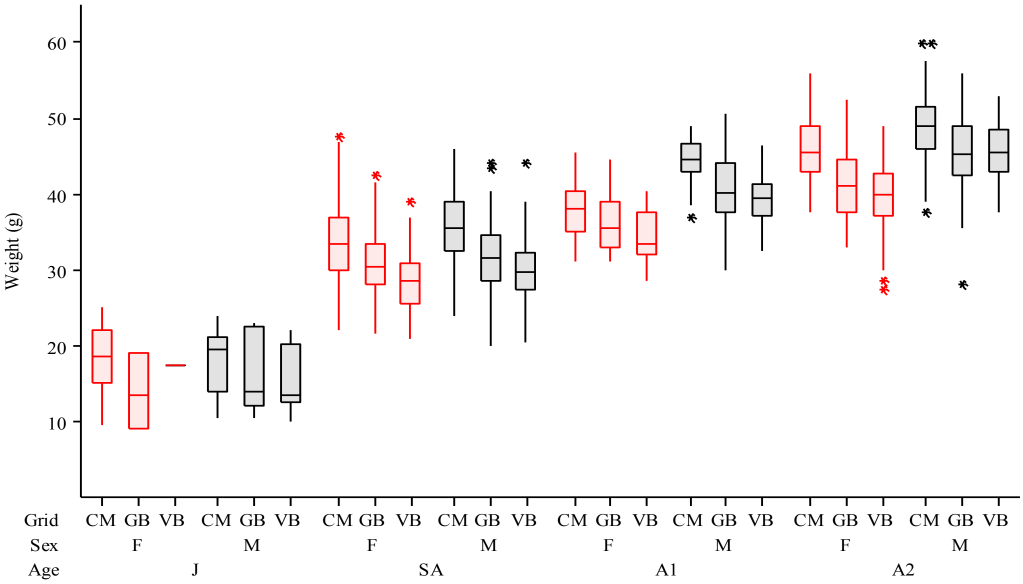

Figure 2.4. Box and whisker plot of mouse weights by age class, sex and grid. Mid-lines indicate medians, boxes upper and lower quartile and whiskers smallest and largest values except for outliers (*) greater than 1.5 times the inter-quartile range.

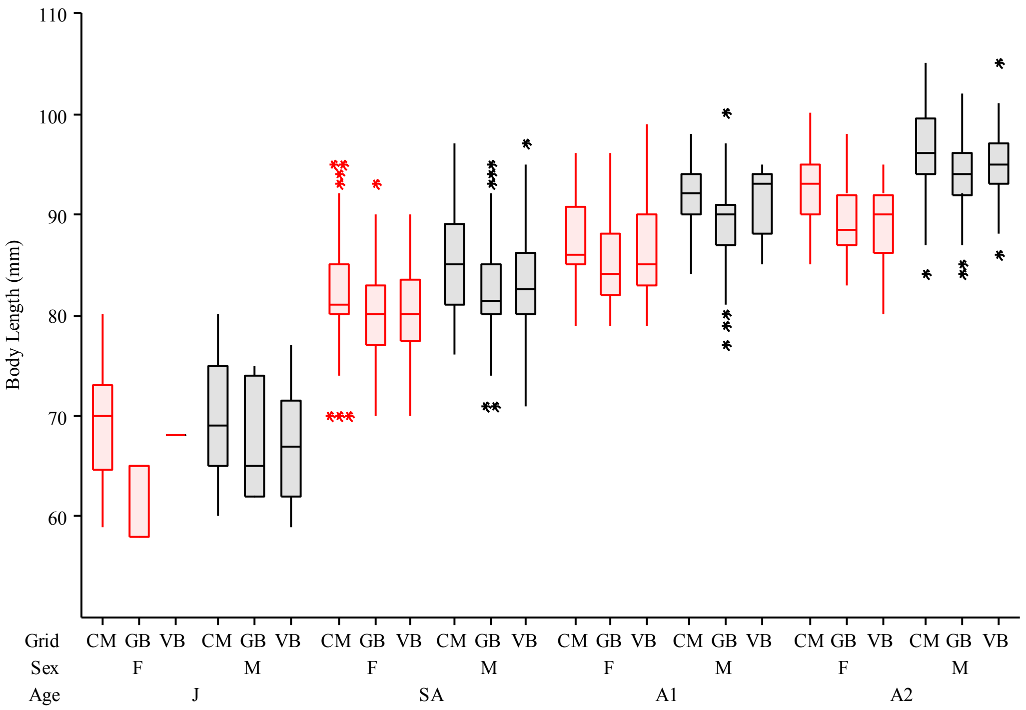

Figure 2.5. Box and whisker plot of mouse body length (including head) by age class, sex and grid. Mid-lines indicate medians, boxes upper and lower quartile and whiskers smallest and largest values except for outliers (*) greater than 1.5 times the inter-quartile range.

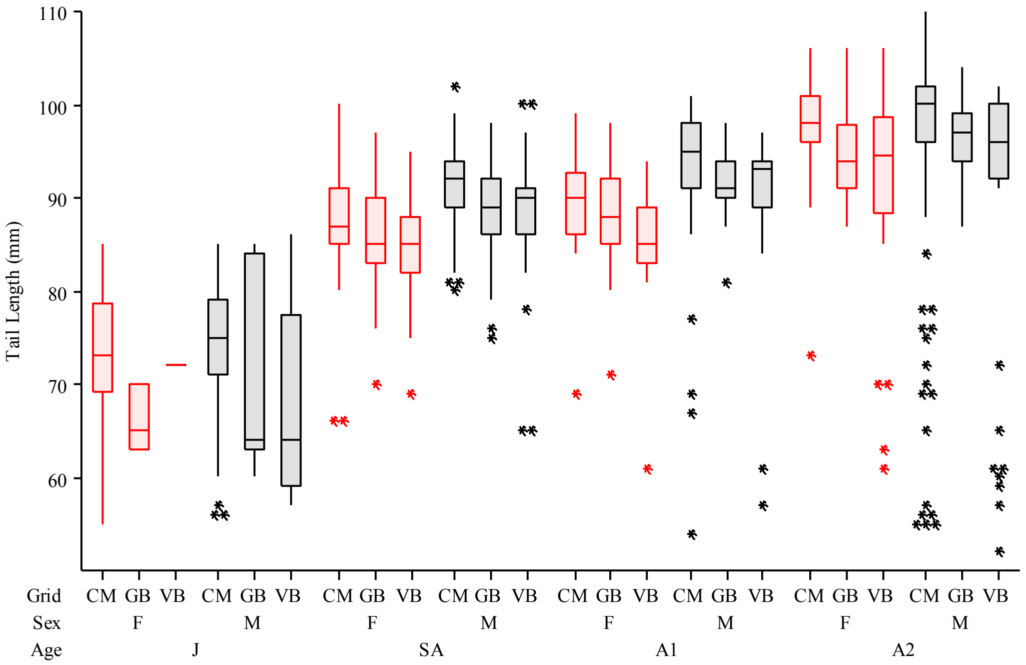

Figure 2.6. Box and whisker plot of mouse tail length (including head) by age class, sex and grid. Mid-lines indicate medians, boxes upper and lower quartile and whiskers smallest and largest values except for outliers (*) greater than 1.5 times the inter-quartile range. The unusually large number of outliers below the whiskers was due to mice with previously damaged tails.

2.3.3 Relationships between weight, body length and tail length

Weight showed a linear relationship with body length and a sigmoid relationship with tail length. Linear regression of weight against body length showed a linear relationship with quite good fit (weight = 0.984 x body length – 48.09, adjusted R^2=0.785, Figure 2.7). The relationship between weight and tail length was slightly more complex and approximately sigmoid, but could be linearised by taking the natural log of the response variable (log(weight) = 0.032 x tail length + 0.670, adjusted R^2=0.772, Figure 10). Mice with damaged tails were excluded from this part of the analysis for obvious reasons.

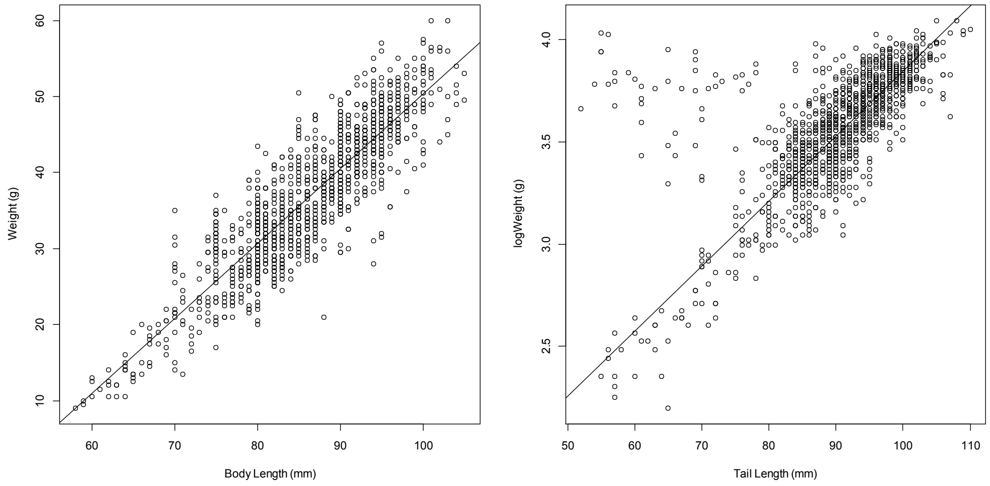

Figure 2.7. Linear regression of weight ~ body length and log(weight) ~ tail length. The large cluster of outliers above the log(weight) ~ tail regression line represent mice with incomplete tails, which were excluded when calculating the regression.

2.3.4 Analysis of body weight using linear mixed-models

Mouse weight varied with age, sex and grid. The preferred model included an age*sex interaction and grid as a main effect (Table 2.2). MCMC estimation of p values for terms in the preferred model (Table 2.3) suggests unsurprisingly that weight increases with each age class, and that there is a significant interaction with sex with males heavier than females in all age classes except for juveniles (Figure 2.8). Grid was significant as a main effect, with mice on all three grids being significantly different from each other (CM>GB>VB, Figure 2.8). The variance of random effects showed that weight differences between groups (age, sex, grid) were considerably greater than those attributable to temporal effects (season, year).

Table 2.2. Results of model selection with mouse weight as response variable. Model selection via AIC. Preferred model in bold. Random effects are in parenthesis. All models also included an intercept term, main fixed effects (Age class, Sex, Grid) and in the case of the three way interaction, all nested 2 way interactions.

LMM model selection with weight as a continuous response

Model	AIC	ΔAIC
Age*Sex + Grid + (1|ID) + (1|Year/Season)	**6934.7**	**0.0**
Age*Sex + Sex*Grid + (1|ID) + (1|Year/Season)	6935.3	0.6
Age*Sex + Sex*Grid + Age*Grid + (1|ID) + (1|Year/Season)	6935.7	1.0
Age*Sex*Grid + (1|ID) + (1|Year/Season)	6939.3	4.6
Age*Sex + Grid + (1|ID)	7066.5	131.8

Table 2.3. Fixed effects, interaction terms and variance components for the preferred weight model, using 1183 observations of 697 individuals. Estimates from linear mixed effect models are listed along with MCMC derived means, 95% confidence intervals and p values. Terms significantly different from the intercept (α=0.05) are highlighted in bold.

Weight ~ Age*Sex + Grid + (1|ID) + (1|Year/Season)

Fixed Effects	Estimate	SE	t value	ICMC mea	95% LCL	95% UCL	p MCMC
Intercept (Juvenile, Female, Carn Mor)	18.67	1.04	17.94	18.93	15.85	21.98	**0.0001**
Age							
- Subadult	14.04	0.77	18.12	14.13	12.49	15.79	**0.0001**
- Adult 1	20.59	1.00	20.62	20.52	18.31	22.64	**0.0001**
- Adult 2	27.10	0.84	32.37	26.82	25.09	28.55	**0.0001**
Sex							
- Male	0.87	0.93	0.93	0.65	-1.30	2.55	0.5102
Grid							
- Glen Bay	-3.42	0.34	-9.98	-3.55	-4.10	-2.97	**0.0001**
- Village Bay	-4.52	0.37	-12.28	-4.78	-5.43	-4.18	**0.0001**
*Age*Sex*							
- Subadult : Male	0.77	0.97	0.80	1.02	-1.01	3.08	0.3318
- Adult 1 : Male	4.32	1.08	3.98	4.57	2.31	6.84	**0.0002**
- Adult 2 : Male	2.92	1.03	2.85	3.43	1.33	5.59	**0.0018**

Random Effects	Variance	Std. Dev
ID (Intercept)	7.29	2.70
Season:Year (Intercept)	1.28	1.13
Year (Intercept)	1.56	1.25
Residual	10.62	3.26

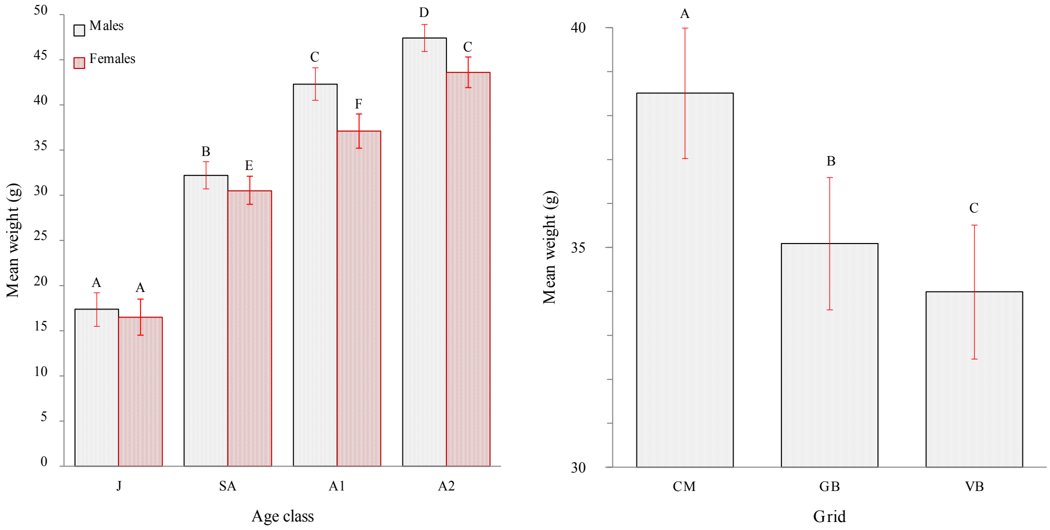

Figure 2.8. Mean mouse body weights as predicted by the preferred model for the interaction between age class and sex (left) and each geographical location (right). Error bars represent 95% confidence intervals. Bars with the same letters are not significantly different (Tukey's HSD, α=0.05).

2.3.7 Analysis of mouse body condition (weight accounting for body length)

Mouse weight varied by age, sex and grid, even when body length was included in the models. Including body length as a main effect in the LMMs resulted in a preferred model including body length as a main effect and age*sex and age*grid interaction terms (Table 2.4). MCMC estimation of p values for terms in the preferred model (Table 2.5) showed a strong correlation between body length and weight. Age class remained significant with an interaction with sex, whereby males were heavier than females but only in the Adult 1 age class (Figure 2.9). There was also a complex interaction between age class and grid, whereby mouse weight varied significantly between all three grids for the Sub Adult and Adult 1 age classes, but showed no differences between grids for juveniles, while in the Adult 2 age class mice on Carn Mor were heavier than those in Village Bay and Glen Bay (Figure 2.9). The variance of random effects showed that differences in body weight between groups (age, sex, grid) after accounting for body length were slightly smaller than those attributable to temporal effects (season, year).

Table 2.4. Results of LMM model selection with mouse weight as response variable, with an additional term for body length. Model selection via AIC. Preferred model in bold. Random effects are in parenthesis. All models also included an intercept term, main fixed effects (Body length, Age class, Sex, Grid) and in the case of the three way interaction, all nested 2 way interactions.

LMM model selection with weight as a continuous response and body length as a fixed effect

Model	AIC	ΔAIC
Body length + Age*Sex + Age*Grid + (1|ID) + (1|Year/Season)	**6109.1**	**0.0**
Body length + Age*Sex + Age*Grid + Sex*Grid + (1|ID) + (1|Year/Season)	6109.3	0.2
Body length + Age*Sex*Grid + (1|ID) + (1|Year/Season)	6117.9	8.8
Body length + Age*Sex + Grid + (1|ID) + (1|Year/Season)	6118.7	9.6
Body length + Age*Sex + Age*Grid + (1|ID)	6335.8	226.7

Table 2.5. Fixed effects, interaction terms and variance components for the preferred weight model (including body length), using 1183 observations of 697 individuals. Estimates from linear mixed effect models are listed along with MCMC derived means, 95% confidence intervals and p values. Terms significantly different from the intercept (α=0.05) are highlighted in bold.

Weight ~ Body length + Age*Sex + Age*Grid + (1|ID) + (1|Year/Season)

Fixed Effects	Estimate	SE	t value	ICMC mea	95% LCL	95% UCL	p MCMC
Intercept (Juvenile, Female, Carn Mor)	-24.52	1.92	-12.75	-26.65	-30.61	-22.36	**0.0001**
Body Length	0.63	0.02	27.77	0.66	0.62	0.71	**0.0001**
Age							
- Subadult	6.08	0.69	8.79	5.67	4.25	7.10	**0.0001**
- Adult 1	9.23	0.95	9.73	8.61	6.67	10.69	**0.0001**
- Adult 2	12.86	0.85	15.11	11.82	10.12	13.51	**0.0001**
Sex							
- Male	-0.09	0.76	-0.12	-0.05	-1.61	1.50	0.9456
Grid							
- Glen Bay	-0.01	1.10	-0.01	0.04	-2.19	2.25	0.9838
- Village Bay	-1.43	1.02	-1.41	-1.42	-3.44	0.61	0.1690
*Age*Sex*							
- Subadult : Male	0.35	0.80	0.44	0.33	-1.37	1.92	0.6920
- Adult 1 : Male	2.94	0.89	3.31	2.81	0.93	4.65	**0.0022**
- Adult 2 : Male	0.88	0.85	1.04	1.06	-0.69	2.76	0.2262
*Age*Grid*							
- Subadult : Glen Bay	-2.00	1.13	-1.77	-2.01	-4.29	0.23	0.0818
- Adult 1: Glen Bay	-1.70	1.22	-1.40	-1.82	-4.36	0.55	0.1510
- Adult 2: Glen Bay	-2.11	1.17	-1.80	-2.17	-4.47	0.19	0.0668
- Subadult : Village Bay	-2.68	1.07	-2.51	-2.79	-4.94	-0.59	**0.0132**
- Adult 1 : Village Bay	-2.62	1.18	-2.23	-3.08	-5.41	-0.62	**0.0132**
- Adult 2 : Village Bay	-0.95	1.10	-0.87	-1.18	-3.48	0.96	0.2910

Random Effects	Variance	Std. Dev
ID (Intercept)	3.08	1.76
Season:Year (Intercept)	0.94	0.97
Year (Intercept)	3.27	1.81
Residual	7.04	2.65

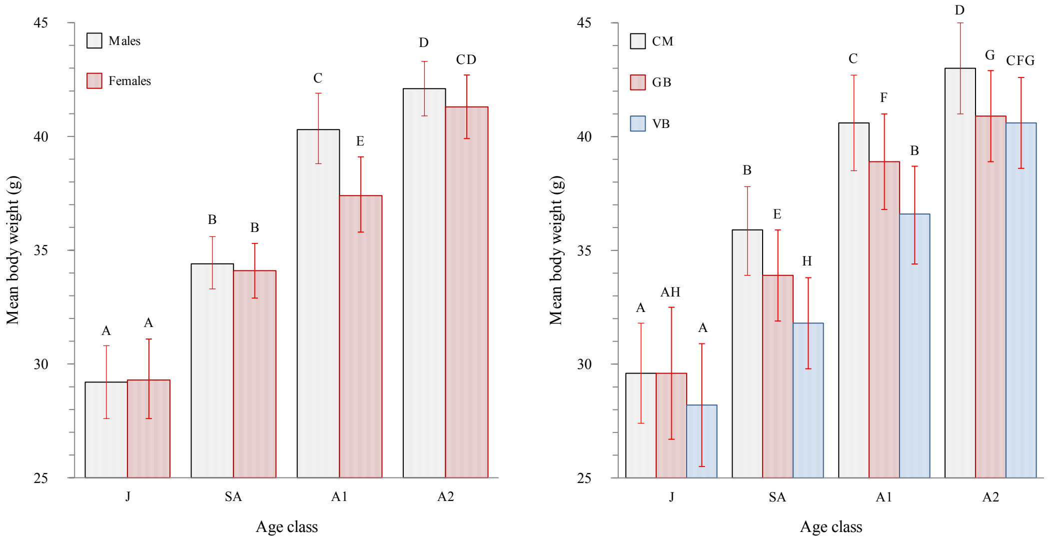

Figure 2.9. Mean mouse body weights as predicted by the preferred model, including body length, for the interaction between age class and sex (left) and the interaction between age class and geographical location (right). Error bars represent 95% confidence intervals. Bars with the same letters are not significantly different (Tukey's HSD , α=0.05).

2.3.8 Breeding phenology

Mice across the island demonstrated distinct breeding and non-breeding seasons (Figure 2.102). Trapping in spring (March and early April) revealed a substantial proportion (0.56-0.97) of male mice from both adult age classes with already descended testes. A relatively smaller proportion (0-0.22) of females from both age classes were recognisably pregnant during the same time period and these always appeared to be in the early stages of pregnancy with no evidence of suckling, suggesting that March generally represents the beginning of the breeding season on St Kilda.

During the summer (late May and June) and autumn (late August and September) trapping sessions, all adult males caught invariably had descended testes, and a high proportion of adult females (0.71-1) were either visibly pregnant, were currently rearing or had recently reared young. In all three years of study the first juvenile mice were caught in mid-June, although the number of juveniles varied considerably (2-15, Table 2.1), as did the weight (and therefore presumably age) of these early juveniles (10-22g). Greater numbers of juveniles were caught in the autumn, although by that point the majority of young mice had already lost their juvenile pelage and were classified as sub adults. Of these sub adults, a small proportion showed signs of descended testes or early pregnancy in the autumn (males

0.06-0.38, females 0.07-0.6), but it is impossible to know if these individuals bred successfully. Certainly no sub adult females ever showed definite signs of suckling.

By each winter trapping session (November to early December) all breeding appeared to have ceased, with only a small proportion (0-0.25) of adult males still exhibiting descended testes, and no pregnant females (although on one occasion a single adult female on Carn Mor did still show signs of recent suckling).

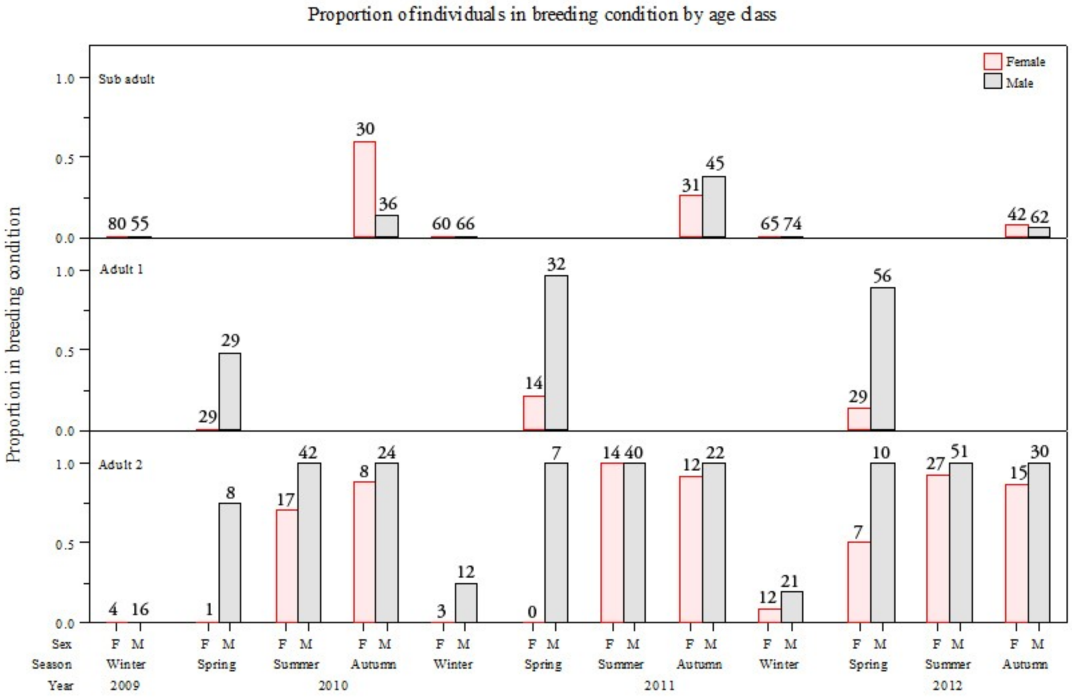

Figure 2.10. Proportion of individuals in breeding condition in each primary session by age class (panels) and sex (females = red bars, males = grey bars). Numbers of individuals upon which each proportion is based are shown above the bars.

2.3.9 GLM/GLMM analysis of the proportion of mice in breeding condition

Adult 2 age class

The proportion of mice in breeding condition in the Adult 2 age class did not vary significantly by sex, grid or year. The preferred model included both year and season as fixed effects (Table 2.6) but *Z*-tests showed that there were no significant differences between individual years and seasons (Table 2.7). Deviance for ID as a random effect was extremely large and probably reflects the unsuitability of the data due to extremely low capture numbers during some trapping sessions.

Table 2.6. Results of GLMM model selection with mouse breeding condition as a binomial response variable for the Adult 2 age class. Model selection via AIC. Preferred models in bold. Random effects are in parenthesis. All models also included an intercept term, main fixed effects as appropriate and in the case of the three way interaction, all nested 2 way interactions.

GLM/GLMM Model selection with breeding condition as a binary response

Adult 2	AIC	ΔAIC
Year + Season + (1|ID)	**70.36**	**0.00**
Sex + Grid + Year + Season + (1|ID)	72.99	2.63
Season + (1|ID)	73.83	3.47
Grid + Year + Season + (1|ID)	74.02	3.66
Sex*Grid + Year + Season + (1|ID)	76.96	6.60
Sex*Grid + Sex*Season + Year + (1|ID)	81.13	10.77
Sex*Grid + Sex*Season + Grid*Season + Year + (1|ID)	86.29	15.93
Year + (1|ID)	91.79	21.43
Sex*Grid*Season + Year + (1|ID)	94.22	23.86

Table 2.7. Fixed effects, interaction terms and variance components for the preferred breeding condition models for the Adult 2 age class. P values calculated using *Z*-tests. Terms significantly different from the intercept (α=0.05) are highlighted in bold.

Adult 2 - Proportion breeding ~ Year + Season + (1|ID)

Fixed Effects	Estimate	SE	z value	p
Intercept (Spring, 2010)	11.88	33.90	0.35	0.726
Season				
- Summer	15.56	36.54	0.43	0.670
- Autumn	1.60	42.24	0.04	0.970
Year				
- 2011	15.52	74.70	0.21	0.835
- 2012	0.81	37.12	0.02	0.983

Random Effects	Deviance	Std. Dev
ID (Intercept)	5395.70	73.45
Residual	58.36	

Adult 1 age class

The proportion of mice in breeding condition in the Adult 1 age class varied by sex, grid and year. The preferred model included sex, grid and year as fixed effects (Table 2.8). *Z*-test derived *p* values (Table 2.9) suggested that males within this age class were significantly more likely to be in breeding condition than females (Figure 2.11, z=7.05, SE=0.69, p<0.0001), that mice on Carn Mor and Glen Bay were significantly more likely to be in breeding condition than those in Village Bay (Figure 2.11, CM: z=2.98, SE=0.73, p=0.0029, GB: z= 2.96, SE=0.71, p=0.0035), and that mice were more likely to be in breeding condition in 2011 and 2012 compared to 2010 (Figure 2.11, 2011: z=4.00, SE=0.84, p<0.0001, 2012: z=4.19,SE=0.64, p<0.0001).

Table 2.8. Results of GLM model selection with mouse breeding condition as a binomial response variable for the Adult 1 age class. Model selection via AIC. Preferred model in bold. All models also included an intercept term and main fixed effects as appropriate.

GLM/GLMM Model selection with breeding condition as a binary response

Adult 1	**AIC**	**ΔAIC**
Sex*Grid + Year	124.89	0.00
Sex + Grid + Year	**125.89**	**1.00**
Sex + Grid	151.12	**26.23**

Table 2.9. Fixed effects, interaction terms and variance components for the preferred breeding condition models for the Adult 1 age class. P values calculated using *Z*-tests. Terms significantly different from the intercept (α=0.05) are highlighted in bold.

Adult 1 - Proportion breeding ~ Sex + Grid + Year

Fixed Effects	**Estimate**	**SE**	**z value**	**p**
Intercept (Female, Carn Mor, 2010)	-4.24	0.83	-5.09	**0.0000**
Sex				
- Male	4.88	0.69	7.05	**0.0000**
Grid				
- Glen Bay	-0.35	0.6	-0.58	0.5600
- Village Bay	-2.18	0.73	-2.98	**0.0029**
Year				
- 2011	3.35	0.84	4	**0.0000**
- 2012	2.71	0.65	4.19	**0.0000**

	Deviance
Residual	113.89

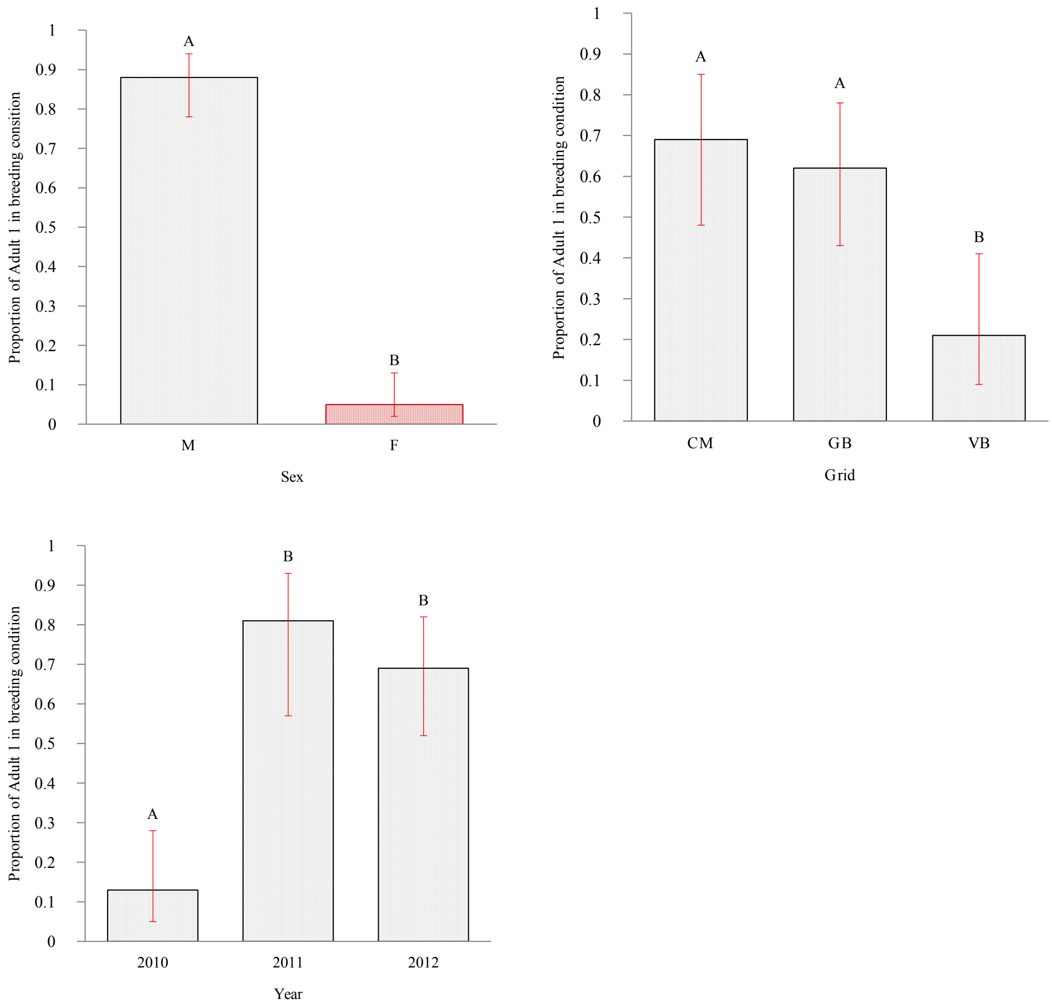

Figure 2.11. Proportion of mice in the Adult 1 age class in breeding condition as predicted by the preferred model by sex (top left), geographical location (top right) and year (bottom). Error bars represent 95% confidence intervals. Bars with the same letters are not significantly different (Tukey's HSD, α=0.05).

Sub adult age class

The proportion of mice in breeding condition in the sub adult age class varied by sex, grid and year. The preferred model (Table 2.10) included sex, grid and year as fixed effects. *Z*-test derived *p* values (Table 2.11) suggested that males within this age class were significantly less likely to be in breeding condition than females (Figure 2.12, z=-2.02, SE=0.69, p<0.0433), that mice on Carn Mor were significantly more likely to be in breeding condition than those in Glen Bay (Figure 2.14, z=2.29, SE=0.43, p=0.0218), and that mice were less likely to be in breeding condition in 2012 than in previous years (Figure 2.12, 2010: z=-1.94, SE=0.48, p=0.0001).

Table 2.10. Results of GLM model selection with mouse breeding condition as a binomial response variable for the sub adult age class. Model selection via AIC with preferred model in bold. All models also included an intercept term and main fixed effects as appropriate.

GLM/GLMM Model selection with breeding condition as a binary response

Sub adult	AIC	ΔAIC
Sex + Grid + Year	**235.85**	**0.00**
Sex*Grid + Year	236.91	1.06
Sex + Year	237.68	1.83
Year	238.92	3.07

Table 2.11. Fixed effects, interaction terms and variance components for the preferred breeding condition models for the sub adult age class. P values calculated using *Z*-tests. Terms significantly different from the intercept (α=0.05) are highlighted in bold.

Sub Adult - Proportion breeding ~ Sex + Grid + Year

Fixed Effects	Estimate	SE	z value	p	
Intercept (Female, Carn Mor, 2010)	-0.08	0.35	-0.22	0.8268	
Sex					
- Male	-0.69	0.34	-2.02	**0.0433**	*
Grid					
- Glen Bay	-0.99	0.43	-2.29	**0.0218**	*
- Village Bay	-0.17	0.41	-0.4	0.6885	
Year					
- 2011	0.19	0.38	0.49	0.6246	
- 2012	-1.94	0.48	-4.02	**0.0001**	***

Random Effects	Deviance
Residual	113.89

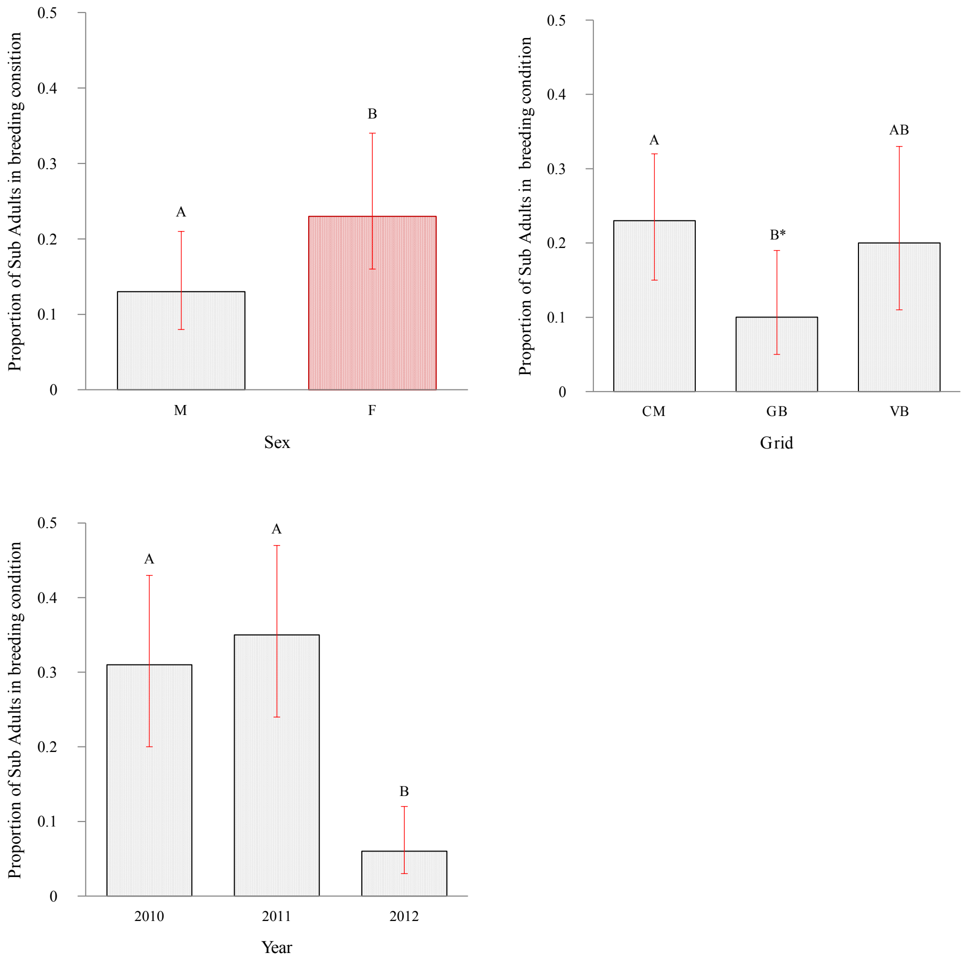

Figure 2.12. Proportion of mice in the Sub Adult age class in breeding condition as predicted by the preferred model by sex (top left), geographical location (top right) and year (bottom). Error bars represent 95% confidence intervals. Bars with the same letters are not significantly different (Tukey's HSD, α=0.05). *Borderline significance; Tukey's HSD test for CM vs GB, p=0.0556.

2.3.10 Additional observations

Distribution

While the bulk of the trapping effort was concentrated on the three grids described, additional opportune trapping sessions were frequently carried out along 'The Street' of mostly ruinous cottages in the Village Bay area of Hirta and for one night in August 2010 in two locations on the neighbouring island of Dun (which is separated from Hirta by a narrow sea channel). All three locations appeared to have large populations of mice. Additionally, anecdotal reports from MOD contractor staff confirmed the presence of mice at radar facilities at the summits of Mullach Sgar (280m) and Mullach Mor (361m) during the period of study.

Litter size and birth weight

Directly observing mouse nests was not possible, but on two occasions litters were born in traps and subsequently abandoned by the female. Litter sizes were 2 and 6 and the pups each weighed between 2.1 and 2.5g.

Coat colour and partial albinism

No attempts were made to record or formally analyse coat colour, but juveniles were observed to have a dark grey pelage typical for *A. sylvaticus*, with a somewhat gradual moult into an a brown adult coat with intermediate individuals often showing brown flanks with a remnant of dark grey down the central dorsal line. The undersides of juveniles were also grey, but various shades of off-white in sub adults, gradually darkening in older adults and with the buff colouration for which the sub species is known becoming more pronounced across the flanks and backs as the mice get older, often extending across the lighter underside, especially down the central ventral line and across the chest.

Three individuals (an adult female and two sub adult males, probably offspring of the female) were caught in close proximity to each other in Glen Bay which had piebald markings, each with one or two areas of white fur across their backs or flanks. Partial albinism such as this is due to recessive mutation of the *Tyrosinase* gene and is normally very rare as expression requires both parents to be heterozygotes or homozygotes and the phenotype is often associated with physiological disorders and higher predation pressure (Lopucki & Mroz 2010). The phenotype is most likely to occur in isolated, inbred or genetically bottlenecked populations due to reduced genetic variability, particularly those on islands where survival tends to be higher and predation lower (Adler & Levins 1994).

Additionally, rates of tail-tip albinism on St Kilda were found to be around 25%. Although tail-tip albinism is more frequently seen than partial coat albinism in rodents, this is still a particularly high rate of incidence, almost ten times greater than reported in previous studies in mainland Britain and Belgium, where incidence was 3.1% and 2.7% respectively (Corbet 1963, Bauchau 1984).

Caching behaviour

Apodemus are well known for caching food supplies, particularly seeds and nuts, for consumption at a later date. No attempt was made to uncover caches during this study, but on numerous occasions the entrances to Longworth traps were completely filled overnight with soil, small rocks, moss and even sheep bones in an attempt to cache the bait contained within. Rarely, the same trap was 'cached' on multiple consecutive nights after being cleared each day, presumably by the same individual.

2.4 Discussion

2.4.1Trapping success and distribution

All three grids were found to contain mouse populations of a reasonable size, supporting previous studies which concluded that field mice were largely ubiquitous across Hirta (Harrison 1933, Boyd 1956, Boyd 1959). The preference of mice for areas of rock cover reported by the same authors was also evident in this study; traps adjacent or close to rock talus, walls and cleits were far more likely to catch animals than those in open grassland, even on very small spatial scales. The importance of trap cover to capture success is discussed further in Chapter 3.

Previous studies disagreed as to whether mice were present at higher altitudes. Harrison & Moy-Thomas (1933) reported only one individual above 500ft (152m) whereas Boyd (1959), using a more efficient trapping technique, caught individuals near the summits of all the major hills except one (Oiseval). This study did not undertake trapping at altitudes above 170m, but anecdotal reports of mice in and around the MOD buildings on two hilltops seems to agree with Boyd's findings. This should be of little surprise given that *A. sylvaticus* are known to live at a wide range of altitudes, including Alpine habitats above 10,000m (Reutter *et al.* 2003). This study can also confirm the presence of mice on the nearby island of Dun. Trapping on Dun was only carried out on one night, but the abundance of mice appeared to be high (18 captures from two ten trap transects at separate locations with traps spaced 10m apart). On the three main grids, the number of individuals present fluctuated seasonally, with combined counts of 54-81 individuals in spring and summer, rising to 107-172 in autumn and winter. Please see the following chapters for detailed analyses and discussion of mouse abundance and densities.

2.4.2 Overview of mouse weight, body length and tail length

The means and distributions of body weight, body length and tail length of *A. sylvaticus hirtensis* are well described by Figures 4-6 for animals of different age classes, sexes and geographic location. Meaningful comparisons with the few previous studies are difficult due to trapping at different times of year and the tendency for results to be presented summarily, with small sample sizes and often without accounting for age, sex or location of capture.

Body weights here are similar to those reported by Boyd (1959), who presents the most useful breakdown of his data, including maximum recorded weights of 56.5g for males and 48.5g for a pregnant female. This study can extend those weight limits to 56g for a pregnant female and in excess of 60g for a male which slightly exceeded the maximum limit of the balance and probably weighed 61-62g. There are some (unreferenced) descriptions in the popular literature of a 70g St Kilda field mouse, but these do not seem to be supported by any published scientific data.

Typical weight ranges for British mainland populations are 13-27g and 13-24g for adult males and females respectively (Flowerdew 1985). Adults in this study were far larger, weighing 23.5-60g for males and 22.5-56g for females. However, no less than 17 out of 27 island populations of *A. sylvaticus* around Scotland and Ireland also display gigantism, often to a similar degree to that of *A. sylvaticus hirtensis*, so large size alone does not set it apart from many of the other insular populations found on islands (Berry 1969, Angerbjorn 1986).

Mean body and tail lengths for ten adult mice are reported by Barret-Hamilton (1906) as 104mm and 100mm respectively, which is considerably greater than the means of 93.8mm and 95.2mm for the same metrics found for adult mice in this study. However, Barret-Hamilton’s measurements were taken from preserved skins rather than live animals so a direct comparison is unwise. It should be noted though that the results for body and tail lengths reported here may be slightly conservative as a result of measuring the mice in a bag in order to protect them from rain and wind as was often present when trapping in winter and spring.

Regression analyses of weight against body and tail length found a linear relationship between weight and body length, and a sigmoidal one between weight and tail length. Body length was hence chosen as a proxy for skeletal size in order to correct for size when analysing weight in order to assess relative body condition. This decision was supported by laboratory studies which have shown that body weight and body length increase at similar rates in *A. sylvaticus* (Frynta & Zizkova 1992).

2.4.3 Analysis of mouse weight

Body weight was found to vary with age, sex and geographical location. Unsurprisingly, model-predicted means for weight increased significantly with consecutive age classes, demonstrating that individuals continue to grow significantly until at least a year after birth. This fits well with laboratory studies of *A. sylvaticus* which have shown that body weight, body length and tail length all show approximately asymptotic growth curves, with growth levelling off at an age of around 300-400 days (Frynta & Zizkova 1992).

Sex differences in weight were also apparent, with the exception of juvenile mice, where there were no significant differences. For mice a year old or more (Adult 2 age class), model-predicted mean weights for males were 8.7% (3.8g) greater than for females. This is somewhat less than has been found in studies of laboratory raised *A. sylvaticus* which found significant sexual dimorphism (controlling for known age) in a number of morphological measures including body weight (males 23% heavier than females at one year old, Frynta & Zizkova 1992) and in wild populations where sexual weight dimorphism varied between 9% and 27% depending on habitat quality (Alcantara & Diaz 1996). The lack of any significant sex differences in juvenile mice is probably due to greater relative age differences between individuals (compared to older age classes) masking any differences between sexes. Sexual dimorphism can sometimes be used as an indicator of breeding system in rodents (Bondrup-Nielsen & Ims 1990), under the assumption that the sex competing most strongly for resources (females for territory vs males for females) will be most strongly selected for size. These findings would therefore be consistent with a polygynous or promiscuous mating system where male breeding success was determined by the number of overlapping female territories. This in turn could be one evolutionary driver behind the gigantism found in the St Kilda population. Simultaneously, the lower degree of sexual dimporphism found here compared to some mainland populations could reflect a lessening in intra-sexual competition between males. Disadvantageous displacement of smaller individuals from ‘safe’ habitats into areas with greater inter-species competition or predation risk may be the outcome of territorial disputes in mainland populations, increasing selection pressure on size amongst males when compared to island populations where these pressures are diminished and aggressive behaviours may be less common (Gray & Hurst 1998).

When including body length as an explanatory variable in the analysis of weight, differences between sexes ceased to be significant for all age classes except Adult 1, suggesting that weight differences reflected variation in skeletal size and were not a consequence of varying body condition between the sexes. Quite why males were heavier than females for a given body length immediately after their first winter is not immediately clear, but it may be linked to the fact that a higher proportion of female sub adult mice were observed to be in breeding condition in the previous autumn, and hence enter winter in a worse overall condition than sub adult males which had not. It is also in keeping with classic observations that male field mice tend to increase in weight and enter breeding condition up to eight weeks earlier than females in the spring. It has been posited that this rapid increase in male spring-time weight may be largely attributable to the growth of the testes, which have been found to be 20 times heavier in summer than in winter Drost & Fellers 1991.

Interestingly, a fairly large and significant geographical trend in all three response variables was also observed. Averaged across all age classes, model-predicted mean weights for mice on Carn Mor were 9.7% (3.4g) heavier than those in Glen Bay and 13.3% (4.5g) heavier than those in Village Bay. For body length, Carn Mor mice were 3.2% (2.6mm) and 1.7% (1.4mm) longer than mice from Glen Bay and Village Bay, respectively. Tail length also showed the same pattern; Carn Mor mice had tails 2.9% (2.6mm) and 3.0% (2.6mm) longer than mice from Glen bay and Village bay. Contrasts between Glen Bay and Village Bay are less consistent, with mice from Glen Bay being significantly heavier (3.2%, 1.1g) but also shorter in the body (1.5%, 1.2mm) and with no difference in tail length compared to those from Village Bay. Mice on Carn Mor were also heavier for a given body length than those elsewhere in all age classes except juveniles, suggesting they are not only larger, but in better condition as well. Mice in Glen Bay were heavier than those in Village Bay for a given body length, but only in Sub Adult and Adult 1 age classes. It should be noted that the variance for temporal random effects on body condition were slightly larger than those for combined grid, sex and age effects, suggesting that seasonal or annual fluctuations in weather or food supply, for example, are at least as important in determining body condition as age, sex or spatial heterogeneity. However, these findings are still consistent with the hypothesis that spatial variation in environmental factors (possibly food supply), rather than differences in the timing of the breeding season are responsible for the observed variation in weight and body condition.

This certainly seems to be a possibility, given the very large numbers of sea birds that use the extensive rock talus on Carn Mor as a breeding site between May and September. It has been suggested that mice on St Kilda may predate or scavenge sea bird eggs (Bicknell 2009) and further work using stable isotope analysis of mouse blood and potential prey samples taken during this study is currently underway to examine the relative importance of different food types (marine-derived sea bird material, dead sheep, invertebrates and plant matter) to the mice on the three grids. Preliminary results show that blood samples from mice on Carn Mor have a strongly marine carbon isotope signature relative to those on the other grids (Bicknell, pers. comm), but further analyses to determine if this is due to differences in mouse diet or a general enrichment of the marine signal throughout the food chain due to bird guano are yet to be completed. Whatever the outcome of that analysis, it is still not difficult to imagine that sea birds might be improving the mouse food supply on Carn Mor, either directly through scavenged or predated eggs and chicks, or indirectly by increasing productivity of plants or invertebrates with deposited guano and carrion. Seabird colonies elsewhere have been shown to increase soil nutrients (Anderson *et* *al.* 1996), primary productivity (Sanchez-Pinero & Polis 2000, Stapp & Polis 2003) and arthropod abundance (Sanchez-Pinero & Polis 2000, Caut *et al.* 2012), as well as providing food for native and introduced rodents directly in the form of carrion, eggs and chicks (Stapp & Polis 2003, Jones *et al.* 2008).

Setting aside Carn Mor, the differences between Glen Bay and Village Bay are somewhat less pronounced, but the mice on Glen Bay are heavier and in better condition for a given body length than those in Village Bay. Potential differences in the quality of the food supply are also more subtle; both sites are predominantly grassland kept short by grazing, with a relatively low and roughly equivalent number of visible seabird nest sites within the grids. Field mice do tend to have broad and adaptable diets but are usually primarily granivorous and grass (seeds and vegetative matter) is reported to form the staple of their diet on St Kilda (Boyd 1959). The wider Village Bay area has the highest quality grazing on the island and hence supports a greater density of sheep than elsewhere. This study took place during a period when the fluctuating sheep population was at an all-time high (until a crash in early 2012). Grazing pressure across the island, but particularly in Village Bay, was intense and it seems possible that the sheep may have impacted the supply of grass seeds and other plant material particularly strongly in Village Bay, reducing the mouse food supply there relative to other sites.

2.4.4 Breeding phenology

The most comprehensive previous account of the breeding season of the St Kilda field mouse comes from Boyd (1959), who over the course of various visits from 1955-58 caught mice in January through to June and in August and December. He found that no males had descended testes between December and March, but that all were partially or fully descended by late April, which agrees well with the findings of this study that 56-97% of males had descended testes in late March or early April, 100% when trapping between May and September, and only 0-25% by November. Boyd found that juvenile mice were first encountered in traps from around the middle of June, which would point to first conceptions typically taking place in late April or early May, assuming a typical *A. sylvaticus* gestation plus weaning period of 6 weeks (Harris & Yalden 2008). This study also caught the first juveniles in mid-June in 2010 and 2012, but as early as the 2nd of June in 2011. Boyd recorded no pregnancies before May, whereas this study encountered small numbers of females that appeared to be in the early stages of pregnancy in early April in two out of three years, so there may be some variation in the precise timing of the onset of the breeding season between years, which is not unsurprising given that *A. sylvaticus*, like many small rodents, shows considerable plasticity in its phenology (Jewell 1966).

Boyd found that female reproduction peaked between May and July, which matches the high proportion of pregnant or recently pregnant females found in May/June in this study, but observed a decline in the number of females in breeding condition in August. However, Boyd failed to distinguish between adult mice and sub adults born earlier in the year of capture (which this study found to be present in large numbers by August), the majority of which are not reproductively active. Boyd's findings therefore probably reflect a normal seasonal shift in the age structure of the population and so do not directly conflict with the finding here that almost all adult mice were still reproductively active in August and September. Pinpointing the precise end of the breeding season is difficult given the length of time between trapping sessions, but the last conceptions probably take place by early-mid August as no juveniles were ever caught in November and the time from conception to post-juvenile moult is generally 9-10 weeks in *A. sylvaticus* (Frynta & Zizkova 1992).

In summary, *Apodemus sylvaticus hirtensis* appear to have a well-defined but relatively short breeding season with pregnancies occurring between early April and early September, peaking between May and July and with the male testicular cycle extending for about a month either side. This is somewhat truncated compared to the breeding season of March to October typically found in mainland *A. sylvaticus* populations, but it is not unusual for a shortening of the season in populations confined to British islands (Harris & Yalden 2008), and insular rodent species often show shortened breeding seasons (Adler & Levins 1994).

GLMM analysis of the proportion of mice in breeding condition did not find any significant differences between sexes, grids, seasons (excluding winter) or years for mice more than a year old (Adult 2), but some variation between sexes, grids and years was found in other age classes. For mice entering their first spring (Adult 1), the vast majority of males were already in breeding condition by April, compared to a very small percentage of females. However, it should be noted that the criteria by which breeding condition was assessed were very different for males and females and reflect different stages of the breeding cycle (preparedness to mate versus successful conception).

Sex differences were also found in sub adults in the autumn of the year in which they were born, whereby female mice were more likely to be in breeding condition than males (although in both cases mice not in breeding condition were in the majority). It appears that some mice of both sexes do attempt to breed in their year of birth, but without pedigree analysis it is impossible to tell if these attempts are successful. No sub adult females were ever caught which showed clear signs of suckling, but it is possible that this was due to the timing of the trapping sessions. Insular rodent populations are often characterised by inhibited sexual maturity (Adler & Levins 1994), so this would not be unusual.

Some geographical differences in the proportion of mice from Sub Adult and Adult 1 age classes in breeding condition were also significant. In particular, mice entering their first spring (Adult 1) were less likely to be in breeding condition in Village Bay compared to the other two grids, and sub adult mice were less likely to be in breeding condition in the autumn of the year in which they were born in Glen Bay compared to Carn Mor, although this difference was of borderline significance and should be accepted with caution.

That said, these findings are broadly consistent with the hypothesis that there may be differences in the quality of food supply between grids. Reproduction in *A. sylvasticus* has been shown to be food limited, with winter food supplementation leading to heavier investment in reproductive effort, larger testes in males and advanced spring breeding in females (Watts 1968). Improved autumn seed supplies have been shown to increase body weight and the length of the breeding season (Hansson 1971). If heavy grazing in Village Bay reduced the availability of seeds (for consumption in autumn or winter through caching), or green vegetative matter which *A. sylvaticus* are known to consume (Hansson 1971, Khammes & Aulagnier 2007), then mice there might be slower to come into breeding condition in the spring. Similarly, a marine-derived increase in food during the summer on Carn Mor might cause more animals to attempt to breed in their first year. However, these hypotheses are presented tentatively as appropriate data to test them are currently unavailable and there may be other biotic or abiotic factors with a role in determining breeding phenology.

Finally, annual differences were also apparent in these two age classes, with significantly fewer male mice in their first spring (Adult 1) exhibiting descended testes in 2010 compared to 2011 and 2012, and a significantly lower proportion of sub adult mice of both sexes were in breeding condition in the autumn following their birth in 2012, compared to 2010 and 2011.

2.5 Conclusion

This study represents the most comprehensive survey of the age structure, core morphological characteristics and breeding phenology of the St Kilda field mouse to date and confirms the widespread distribution of *Apodemus sylvaticus hirtensis* across Hirta and Dun.

Sexual dimorphism was evident in all three morphological measures with males being larger and heavier on average, although mice of the same length tended to weigh the same regardless of sex. Mice tended to grow throughout their lives with marked differences between consecutive age classes, although the rate of growth decreased after around a year. Consistent and significant geographical variation in size and weight was also observed over distances of just 1-2km and may represent the smallest scale geographical variation in *Apodemus* morphology yet recorded. It seems likely that this may be driven at least in part by heterogeneity in the food supply, with the largest differences evident in the sea bird colony at Carn Mor. Male-biased variation in weight between sexes suggests that a promiscuous or polygynous mating system is most likely. Although this was not tested for explicitly it is also supported by much larger range sizes in males during the breeding season (see Chapter 4 for further analysis and discussion). Furthermore, the presence of sexual dimorphism in weight suggests that increased reproductive fitness of larger males may be one evolutionary driver of gigantism amongst the St Kilda mice, despite the magnitude of the dimorphism being lower than in mainland populations.

The mice have a well-defined breeding season between April and early September, somewhat shorter than in mainland British populations but in keeping with their island location. Most individuals do not attempt to breed until their second year, in keeping with patterns of delayed sexual maturation in island rodent populations. Some annual variation in the timing and proportion of younger mice entering breeding condition was observed. Geographical differences in breeding phenology were again noted for some age classes and these may also be driven in part by variation in the food supply. Further analysis of geographical variation in the diet of these mice is currently underway and should provide a clearer picture of the relationship between diet, size and breeding phenology.

Incidental observations of piebald mice and a high incidence of tail-tip albinism are unusual findings that may be symptomatic of reduced genetic variation and founder effects.

CHAPTER 3

Spatially explicit capture-recapture estimation of St Kilda field mouse population densities

3.1. Introduction

3.1.1 General introduction – please see Chapter 2, section 2.1.1

3.1.2 Population dynamics and densities

Numeorus studies of the population dynamics of *A.sylvaticus* have taken place at other locations (e.g Boyd 1956, Bergsted 1965, Tanton 1965, Watts 1969, Hansson 1971, Flowerdew 1972, Green 1979, Erlinge *et al.* 1983, Bengtson *et al.* 1989, Jensen 1996), although care must be taken when making direct due to the use of differing trapping methods and approaches to calculating density or abundance (Ivan *et al.* 2013). However, a synthesis of these along with some consideration of potential bias may provide a relevant framework for general comparison. Northern European populations of *A. sylvaticus* generally undergo seasonal cycles with spring minima and late autumn maxima (Flowerdew 1985, Montgomery 1989,Bengtson *et al.* 1989) and may also exhibit considerable annual fluctuations but not multi-annual cyclic patterns (Montgomery 1989, Gorman & Ahmad 1993). Typical spring minima for mainland British populations vary according to habitat, from 0.5 mice/ha in food-limited sand dune habitats to around 7 mice/ha in deciduous woodland. Typical maxima for the same habitats are 10-12 and 20-55 mice/ha respectively (Flowerdew 1985, Gorman & Ahmad 1993).

Explicit density estimates for *A. sylvaticus* populations on small islands are lacking, but there is a general trend for rodent populations on islands to be both greater and more stable than equivalent mainland populations, although this trend is not always upheld (Adler & Levins 1994), as evidenced in the British Isles by vole populations on Orkney and Skomer (Harris *et al.* 1995) and by *Peromyscus* (which occupy a very similar niche to *Apodemus*) in the Americas (Crowell 1983). Insular populations of *A. sylvaticus* in Iceland have been known to vary dramatically depending on food availability; extremely high densities of 150 mice/ha have been found in habitats with super-abundant autumn food sources (Bengtson *et* *al.* 1989), with more typical maxima of 25-30 mice/ha in woodland and very low maxima (2-3 mice/ha) in grasslands (Unnsteinsdottir & Hersteinsson 2011).

As well as quality and availability of food, climate, predation pressure, inter-specific competition, and disease have also been found to influence population size in small rodents. Variation in *A. sylvaticus* survival in grassland sites in Iceland has been attributed to annual variation in early winter temperature (Unnsteinsdottir & Hersteinsson 2009), and fecundity of Mediterranean populations is known to depend on rainfall leading up to the breeding season (Diaz *et al.* 2010). Reduced or absent predation pressure is commonly correlated with increased density in many insular rodent populations (Adler & Levins 1994), while insular populations of *A. sylvaticus* and the pygmy shrew (*Sorex minutus*) are both depressed by the presence of invasive competitors (*Myodes glareolus* and *Crocidura russula*) in Ireland, although this varies according to habitat (Montgomery *et al.* 2015). Internal parasites are known to play a role in the downward regulation of *Peromyscus* populations, particularly when combined with food shortages – in this case food supplementation and removal of intestinal parasites was sufficient to entirely prevent seasonal population crashes (Pedersen & Greives 2008). Insular rodent populations may harbour a reduced number or richness of diseases (Kuhnen *et al.* 2012) but predicting how this might affect population dynamics is difficult given the complex interactions between parasite communities (Pedersen & Antonovics 2013) and the fact that reduced the reduced genetic variability often found in island populations may increase vulnerability to infectious disease (Obrien & Evermann 1988).

Previous studies on the St Kilda field mice have highlighted their strong affinity for areas of rock talus and man-made drystone structures (buildings, walls and cleits), both of which are widespread across the island, although patchily distributed. The shallow and often waterlogged soils of St Kilda are presumably unsuitable for burrowing and nesting, while the rocky areas provide crevices and perhaps improve drainage (Eagle Clarke 1905, Waterston 1906, Boyd 1956, Boyd 1959). The last major investigation into the distribution of the St Kilda field mice (Boyd 1959) found them to be ubiquitous across Hirta wherever stone structures were present (including near the tops of all major summits) although the mice seemed most abundant in the Village Bay lowlands. Unfortunately, it is difficult to derive any meaningful estimates of abundance from previous studies (Chapter 1, Table 1.1) and they have been rendered unrepeatable due to the construction of a Ministry of Defence base across the line of the main transect (Harrison 1933, Boyd 1956, Boyd 1959). Nor do they provide sufficient information to give an accurate indication of population dynamics, other than the observation that juvenile recruitment into the adult population begins in late June (Boyd 1959).

Indeed, creating unbiased estimates of the density of animal populations remains a major problem for trapping studies in general. Sophisticated techniques for calculating the size of a trappable population do exist (reviewed in Pollock *et al.* 1990, but they rely on *ad hoc* methods for determining the spatial extent of the population (the 'effective trapping area' or ETA) where it extends beyond the limits of the trapping area. Traditionally, population size estimates are converted to a measure of density by dividing by the ETA, which itself is calculated by adding a boundary W to the trapping area based on some measure of animal home range size. However, methods for estimating home range size and W are inherently biased by the truncation of trap-revealed ranges at the edge of the trapping grid (Efford 2004). This bias can be reduced by having a very large trapping area relative to the home ranges of the animals within, but the effort required to conduct trapping on such a scale can quickly become unrealistic.

Recently, several alternative methods for calculating population density from animal trapping data have been developed which integrate trapping with distance sampling theory to model the declining likelihood of detecting an animal as the distance from a trap increases. This allows density ($\widehat{D}$) to be estimated directly without calculating an ETA. These methods include trapping point transects (TPT, Buckland *et al.* 2006), trapping webs (Lukacs *et al.* 2005) and spatially explicit capture-recapture (SECR, Borchers & Efford 2008) TPT and trapping webs require specific trap layouts which are largely incompatible with the trapping methods used in this study, but SECR can be applied to almost any trapping design where the spatial layout of the traps is known and there is a reasonable degree of individual recapture success (Borchers & Efford 2008).

SECR is a likelihood-based method in which the detection process is represented by a mathematical function that describes an animal's declining probability of capture with increasing distance of a trap from its home range centre. Several forms of the detection function are available (see Table 3.1 and Figure 3.1), all of which have the basic parameters *g0* (the intercept; capture probability for a trap placed directly on an animal's home range centre), σ (spatial scale) and $\widehat{D}$ (estimated density of individual home range centres, assumed to follow a homogenous Poisson distribution). Additional non spatial variation in capture probability can be modelled as in conventional capture-recapture (Borchers & Efford 2008).

SECR assumes that individual home range centres are fixed within a trapping session and that the population is closed to births, deaths, immigration and emigration. Traps are also assumed to be able to catch more than one individual, despite the use of single catch traps in this study. Fortunately, simulation studies suggest that multi-catch trap model estimates remain largely unbiased when applied to single catch traps as long as trap saturation is not very high (<85%), as in this study (Efford *et al.* 2009).

In this study, SECR was used to investigate the density of field mice at three different sites on St Kilda in order to quantify seasonal and inter-annual population dynamics and test for spatial variation in population density. The possibility of differing densities or ranging behaviour between sexes is also examined, given that previous studies on St Kilda have always caught considerably more males than females (Harrison 1933, Boyd 1956, Boyd 1959). The final aim was to help assist future monitoring and conservation efforts on St Kilda by firstly identifying a model that could be used by non-specialised personnel to easily and accurately estimate mouse density, and secondly by quantifying mouse home range size in order to inform any potential rat eradication programme of the minimum spacing for poisoned bait stations that would minimise impact on the mice.

3.2 Materials & Methods

Please see sections 2.2.1 and 2.2.2 for details of the study area and trapping methodology.

3.2.1 Accounting for trap cover

Previous studies suggested that mice were heavily associated with rock cover and preliminary trapping outwith the main grids showed that traps in the open tended to catch far fewer mice than those adjacent to walls, cleits or talus. In order to allow rock cover to be included in models, each trapping point on a grid was assigned one of three categorical levels according to a visual assessment of the amount of rock cover present within a 1m radius; Dense (walls, cleits and complex multi-layered talus), Light (shallow surface talus) or Open (no rock cover present). The relative proportion of the three cover types differed between grids and were as follows; Carn Mor (40 Dense, 58 Light, 2 Open), Glen Bay (43 Dense, 51 Light, 6 Open) and Village Bay (37 Dense, 33 Light, 30 Open). All areas of each grid were considered to be viable mouse habitat (and hence no habitat mask was required), as although cover greatly impacted on trap success, very few trapping points failed to catch anything over the course of the study (just 2 in Glen Bay and 4 in Village Bay).

3.2.2 Data Analysis

3.2.2.1 Modeling capture probabilities

Likelihood-based spatially explicit capture recapture (SECR) methods were used to estimate density by modelling the decreasing likelihood of traps catching individual mice as distance from that individual's home rage centre increased**.** Analyses were performed on the entire data set from all grids and sessions, although detection parameters were sometimes allowed to vary temporally and spatially, according to the model being examined.

For numerical integration, the likelihood function was evaluated at each of the 1024 points on a 32x32 point mesh within a square area encompassing the trapping grid and an additional 80m from each edge. This is the area within which the home range centres of individual mice are assumed to fall (according to a homogenous Poisson distribution). Trial models determined this was a sufficiently dense grid and large enough area to avoid bias in parameter estimation.

Models were fitted using the conditional likelihood (likelihood conditioned upon the number of individuals encountered) calculated via the Newton-Raphson nonlinear optimisation method. Initially, three forms of the capture probability submodel (halfnormal, exponential and hazard rate, Table 3.1, Fig. 3.1) were investigated using null models. These were assessed for model fit via corrected Akaike's Information Criteria (AICc) scores and for their effect on density estimation in order to choose a preferred detection function, which was then used for all subsequent models.

A sequential approach to model selection was then adopted, to investigate whether eight further variables (grid, sex, season, year, cover and three different behavioural responses to trapping, Table 3.2) applied to the detection parameters of g0 and sigma improved model fit (again assessed via AICc comparison). Variables were typically fitted to both g0 and sigma singly and in combination, with the exception of cover which was fitted to g0 only because trap-level covariates are difficult to interpret biologically when applied to range size. Initially, the two 'nuisance' variables of behavioural response and trap cover were examined, followed by the other spatial, temporal and sex-based variables both alone and in several biologically plausible additive and interactive combinations (Table 3.4). In total, 37 individual models were tested.

Table 3.1. The three forms of the capture probability submodel investigated (see Fig. 3.1 for the shape of the functions fitted to a null model). d is the distance between an animal's home range centre and any specific trap, *g0* represents the capture probability of a trap placed directly on an animal's home range centre (i.e. the intercept of the function) and *sigma* is a spatial scalar whose magnitude varies between detection functions and is used to describe the radius (in metres) of a circle around an animal's home range centre that includes 95% of the ranging activity of that individual. z describes a distance (in meters) from a home range centre within which the capture probability is constant and does not decay.

Name	**Parameters**	**Function**
Halfnormal	g0, sigma	$g0.exp(\frac{-d^2}{2\sigma^2})$
Hazard rate	g0, sigma, z	$g0.[1 - exp\left\{-\left(\frac{-d}{\sigma}\right)^{-z}\right\}]$
Exponential	g0, sigma	$g0.exp(\frac{-d}{\sigma})$

Table 3.2. Variables used to specify parameter effects. *g0* represents the capture probability of a trap placed directly on an animal's home range centre (i.e. the intercept of the function) and *sigma* is a spatial scalar used to describe the radius (in metres) of a circle around an animal's home range centre that includes 95% of the ranging activity of that individual.

Variable	Type	Applied to	Notes
cover	Trap-level categorical	g0	Three levels: dense, light, open
b	Behavioural learned	g0+sigma	Step change following first capture per session
B	Behavioural transient	g0+sigma	Markovian response dependent on capture on previous occasion only
Bk	Behavioural learned *x* trap response	g0+sigma	As b, but for a particular trap
sex	2 class mixture (h2)	g0+sigma	Finite mixture model with two classes
grid	Separate parameter estimates by grid	g0+sigma	Spatial variation between 3 tap sites
season	Session –level categorical	g0+sigma	Four levels: spring, summer, autumn, winter
year	Session-level categorical	g0+sigma	Four levels: 2009, 2010, 2011, 2012

3.2.2.2 Estimating density

Estimated density ($\widehat{D}$) is a derived parameter from a model fitted by maximizing the conditional likelihood and takes the form of a Horvitz-Thompson-like estimate:

$$\widehat{D} = \sum_{i=1}^{n} \frac{1}{\hat{a}(\hat{\theta}, z_i)}$$

Effective sampling area $\widehat{a_i}(\hat{\theta}, z_i)$ is the estimate of effective sampling area for animal *i* with detection parameter vector θ and a set of individual covariates z (Borchers & Efford 2008). Derived density estimates were calculated for each grid and session combination of the final model and compared using 95% confidence intervals. Density estimates were compared to naïve enumeration by multiplying the number of individuals caught for each grid*session combination by a correction factor of (1/grid area in hectares).

3.2.2.3 Quantification of range size

Spatial and sex-biased range size variation was examined by fitting models where g0 and sigma were allowed to vary by grid and sex and then comparing mean values and confidence intervals of the scale parameter sigma for each grid*sex combination. For the exponential detection function, 4.52 times sigma represents the radius of the circle that includes 95% of the volume of the 2 dimensional figure of rotation formed by the detection function; in other words, 95% of an animal's range falls within a radius of 4.52 times sigma from an individual's home range centre, and 4.52 sigma can hence be used as an indicator of home range size free from trap layout effects.

3.2.2.4 Quantification of sex ratio

Finally, potential sex-biased density variation was investigated by fitting two versions of the null model separately to each grid*session combination; one where the sex ratio was allowed to vary and another where it was fixed at 1:1. As the fixed ratio models are nested within the variable sex ratio models, likelihood ratio (LR) tests could then be performed to determine if models with a fixed sex ratio varied significantly from those where the sex ratio was allowed to vary.

3.2.2.5 Simulation of the effect of trap layout on Village Bay density estimates

In order to assess the accuracy of potential simplified trapping regimes for long-term monitoring of the Village bay population by NTS personnel, simulations were run for three alternative reduced trap layouts (as well as the original 10x10 grid for comparison) for typical parameters of D, g0 and sigma from the Village Bay population, as revealed by the previous SECR analysis. Each simulation worked by automatically generating spatial capture-recapture data sets that fit the specified parameter values (assuming a homogenous distribution of individual home range centres), and then fitting a SECR model to each (Efford 2015).

Trap layouts tested were; the original 10x10 grid with 10m trap spacing (100 trap points), the same grid but including only those traps placed in dense cover (37 trap points), a 5x5 grid in the same location with 20m spacing and all cover types (25 trap points), and a 20 point transect with 20m spacing between trap points along the head dyke (approximated to a straight line), where all traps were assumed to be in dense cover. All simulation used a 64x64 point mask with a conservative 100m buffer around the largest trap layout. Trap layouts were initially simulated for five occasions (consecutive trap nights); two were then taken forward and simulated for 3,4,5,6 and 7 occasions (Table 3.3).

Multiple-year mean real parameter values of D, g0 and sigma for two seasons (Summer; D=5.30, g0= and winter) were calculated from the beta parameter values of the preferred SECR model (Table 3.5) and used as the base detection parameters for simulations (Table 3.3). All three parameters were adjusted for season, while g0 was also adjusted for each trap layout according to the proportion of traps in each level of cover. The exponential detection function was used throughout. Simulations using SECR cannot currently incorporate a trap-specific learned response as was found in the preferred model (Efford

2015), but a simple recapture probability factor can be applied, which was set to 2.30 (calculated from mean capture vs re-capture rates for individuals in Village Bay – see Chapter 4, Figure 4.1).

Table 3.3. Details of potential trapping scenarios investigated using SECR simulation. Four grid layouts of varying design and trap number were investigated, with two being further examined for the effect of varying the number of trapping occasions. Parameter values for simulated populations *D* (density), *g0* (the capture probability of a trap placed directly on an animal's home range centre - i.e. the intercept of the function) and *sigma* (a spatial scalar used to describe the radius (in metres) of a circle around an animal's home range centre that includes 95% of the ranging activity of that individual) were based on typical values from SECR analysis of relevant data sets and were adjusted for season. A constant recapture probability factor of 2.30 was also applied.

Scenario	Number of trapping points	Number of occasions	D		g0		sigma	
			summer	winter	summer	winter	summer	winter
10x10 grid (10m spacing), all traps	100	5	5.30	16.49	0.57	0.77	15.66	9.66
10x10 grid (10m spacing with gaps), dense cover only	37	3,4,5,6,7	5.30	16.49	0.89	0.96	15.66	9.66
5x5 grid (20m spacing) all traps	25	5	5.30	16.49	0.67	0.82	15.66	9.66
20x1 transect (20m spacing) along Head Dyke	20	3,4,5,6,7	5.30	16.49	0.89	0.96	15.66	9.66

500 replicate simulations were run for each of the eight layout*season combinations with 5 trapping sessions (nights). Results summarisation was complicated by a small number of simulations that either did not complete correctly (failed to return standard errors) or produced unreasonably large point estimates and/or standard errors, presumably due to incorrect optimisation of the likelihood function or occasional construction of poor data sets. Such results were difficult to sensor objectively as their distribution overlapped with those that appeared reasonable, which precluded the use of traditional measures of central tendency, dispersion or mean squared error. Therefore (following Ivan *et al.* 2013), all results were retained and presented graphically by calculating the percentage error (PE = predicted density/true density*100) for each simulation, ordering the results by PE and plotting these values against their percentile to form a cumulative distribution plot. Better estimators will have flatter curves closer to zero, with differing curves between estimators representing disparate performance. Again following Ivan *et al.* 2013, the flatness of curves was arbitrarily quantified by calculating the percentage of simulations in which PE was ±20%.

3.2.2 Software

All modelling and density estimation was performed using the SECR 2.9.4 library (Efford 2015) for the R 3.1.2 software package (R Core RCoreTeam 2014) and graphed in R and Microsoft Excel 2010, with the exception of the alternative trapping method simulations, which were carried out using the SECRDESIGN 2.3.0 (Efford 2015) simulation manager for SECR in R 3.1.2.

3.3 Results

3.3.1 Trapping success

Total trapping success across all sessions and grids amounted to 4462 captures of 787 individuals. Numbers of mice caught by date, grid, sex and age class can be found in Chapter 2 (Figure 2.3 and Table 2.1). Recapture rates were generally high; the mean number of captures per individual within a 5-night primary trapping session was 3.2 (min 1, median 3, max 5), and mean number of primary sessions (seasons) in which an individual was caught was 1.7 (min 1, median 1, max 8). The mean total number of captures per individual was 5.6 (min 1, median 4, max 32).

3.3.2 Detection function selection

The three detection functions (halfnormal, hazard rate and exponential; Fig. 3.1) varied considerably in their AICc values, with the hazard rate and exponential functions both improving model fit over the half normal (Table 3.4). The hazard rate and exponential functions were themselves indistinguishable in terms of model fit (ΔAICc < 2) but the hazard rate function includes an extra parameter and the exponential detection function was therefore chosen for all further models on the basis of model parsimony.

Table 3.4. AICc test for the three candidate detection functions (halfnormal, hazard rate and exponential) fitted to null models of the capture data with parameters *g0* (the capture probability of a trap placed directly on an animal's home range centre - i.e. the intercept of the function) and *sigma* (a spatial scalar used to describe the radius (in metres) of a circle around an animal's home range centre that includes 95% of the ranging activity of that individual).

Model parameters			Detection function	No. parameters	AIC	AICc	ΔAICc	AICc weight
g0~1	sigma~1		exponential	3	32968.24	32968.24	0.00	0.64
g0~1	sigma~1	z~1	hazard rate	4	32969.32	32969.35	1.11	0.36
g0~1	**sigma~1**		**half normal**	**3**	**33887.13**	**33887.13**	**918.89**	**0.00**

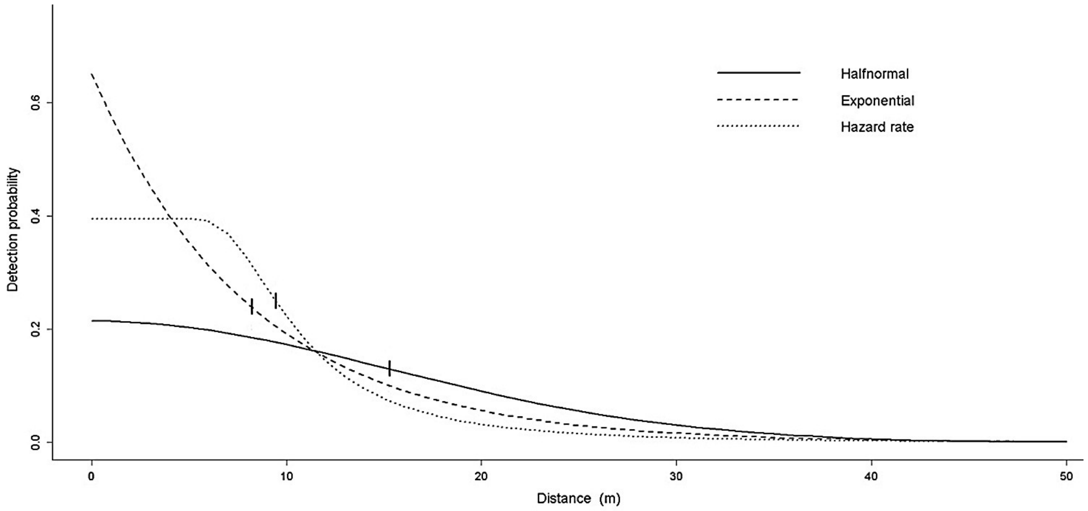

Figure 3.1. Shapes of the three detection functions (halfnormal, hazard rate and exponential) when fitted to null models of the capture data. Capture probability decays for traps further from an individual mouse's home range centre. Vertical bars show values of the spatial scale factor, sigma.

3.3.3 Model fitting

Initially, the nuisance variables of behaviour and cover were examined. Learned (*b*), transient (*B*) and trap-specific learned (*bk*) behavioural responses to trapping on g0 and sigma all greatly improved fit over the null model, as did fitting cover as a trap-level covariate on g0 (Table 3.5). Of the three types of behavioural response *bk* provided the best fit, both when fitted alone and in addition to cover (all cover + behavioural additive combinations on g0 were examined in case the strength of the *bk* model was due to the preference of mice for traps in cover, rather than a true trap-specific behavioural response). Given that the distribution and relative proportion of cover types varied between grids, models containing *bk* + grid and cover additive and interactive effects were also fitted, with the *bk* + grid*cover interaction model providing best fit. Grid was also fit as a singular effect and with *bk*, but these models were not preferred over the *bk* + grid*cover model.

Sex, season and year effects were then fit to both g0 and sigma alone, additively and with season*sex, season*year and season*sex*year interactions. All combinations improved fit over the null model, with season*sex + year being preferred. The difference between the season*sex + year model and the season*sex model (without additive year effect) was relatively small, and both were then included in two final models that also contained the *bk* + grid*cover effects examined previously. The overall preferred model according to AICc ranking was g0~cover*grid + *bk* + season*sex, sigma~grid + *bk* + season*sex (Table 3.5).

Table 3.5 AICc test for 37 SECR models fitted to the capture data. Learned (b), transient (B) and trap-specific learned (bk) behavioural responses, temporal (season and year), spatial (grid) and sex effects, plus plausible interactions, were fitted to g0 (the intercept of the detection function, ie the capture probability for a trap placed precisely at an individual's home range center) and sigma (a spatial scalar, whereby 4.52 times sigma describes the radius of a circle around a home range center that incorporates 95% of ranging behaviour). The effect of rocky cover on g0 was also modelled. Models were ranked and weighted according to AICc.

Model parameters		**Detection function**	**No. parameters**	**AIC**	**AICc**	**ΔAICc**	**AICc weight**
g0~cover*grid + bk + season*sex	sigma~grid + bk +season*sex	exponential	29	31027.03	31028.37	0.00	1.00
g0~cover*grid + bk + season*sex + year	sigma~grid + bk +season*sex + year	exponential	35	31035.71	31038.66	10.29	0.00
g0~cover*grid + bk	sigma~grid + bk	exponential	15	31275.22	31275.59	247.22	0.00
g0~cover + bk	sigma~grid + bk	exponential	9	31312.68	31312.81	284.44	0.00
g0~cover + grid + bk	sigma~grid + bk	exponential	11	31315.75	31315.95	287.58	0.00
g0~cover + bk	sigma~bk	exponential	7	31360.06	31360.15	331.78	0.00
g0~cover + grid + bk	sigma~grid + bk	exponential	9	31361.24	31361.37	333.00	0.00
g0~cover + bk	sigma~bk	exponential	9	31363.94	31364.08	335.71	0.00
g0~cover + b	sigma~b	exponential	7	31587.03	31587.11	558.74	0.00
g0~cover + B	sigma~B	exponential	7	31743.35	31743.43	715.06	0.00
g0~bk	sigma~bk	exponential	5	31960.13	31960.17	931.80	0.00
g0~b	sigma~b	exponential	5	32150.95	32151.00	1122.63	0.00
g0~cover	sigma~1	exponential	5	32245.30	32245.35	1216.98	0.00
g0~cover	sigma~cover	exponential	7	32249.03	32249.12	1220.75	0.00
g0~B	sigma~B	exponential	5	32323.10	32323.15	1294.78	0.00
g0~1	sigma~cover	exponential	5	32422.40	32422.44	1394.07	0.00
g0~season*sex + year	sigma~season*sex + year	exponential	23	32685.26	32686.11	1657.74	0.00
g0~season*sex	sigma~season*sex	exponential	17	32694.41	32694.88	1666.51	0.00
g0~season*sex*year	sigma~season*sex*year	exponential	65	32718.32	32725.14	1696.77	0.00
g0~season + sex + year	sigma~season + sex + year	exponential	17	32724.84	32725.31	1696.94	0.00
g0~season + sex	sigma~season + sex	exponential	11	32734.62	32734.83	1706.46	0.00
g0~season*year + sex	sigma~season*year + sex	exponential	35	32734.85	32736.81	1708.44	0.00
g0~season + year	sigma~season + year	exponential	15	32803.05	32803.42	1775.05	0.00
g0~season*year	sigma~season*year	exponential	33	32811.95	32813.68	1785.31	0.00
g0~season	sigma~season	exponential	9	32817.89	32818.02	1789.65	0.00
g0~sex	sigma~sex	exponential	5	32848.66	32848.70	1820.33	0.00
g0~1	sigma~season	exponential	6	32859.53	32859.59	1831.22	0.00
g0~1	sigma~sex	exponential	4	32898.14	32898.18	1869.81	0.00
g0~grid	sigma~grid	exponential	7	32917.59	32917.68	1889.31	0.00
g0~1	sigma~grid	exponential	5	32920.74	32920.78	1892.41	0.00
g0~year	sigma~year	exponential	9	32931.89	32932.02	1903.65	0.00
g0~year	sigma~1	exponential	6	32948.54	32948.61	1920.24	0.00
g0~grid	sigma~1	exponential	5	32955.77	32955.82	1927.45	0.00
g0~season	sigma~1	exponential	6	32958.57	32958.63	1930.26	0.00
g0~1	sigma~year	exponential	6	32960.54	32960.61	1932.24	0.00
g0~sex	sigma~1	exponential	4	32961.24	32961.27	1932.90	0.00
g0~1	sigma~1	exponential	3	32968.24	32968.24	1939.87	0.00

3.3.4 Density estimates

SECR density estimates (Fig. 3.2) for individual grid*session combinations ranged from 1.87-50.15 mice/ha and showed a strong seasonal effect on mouse density, with a typical pattern of relatively low and stable densities in springs and summers, increasing through the autumns to a winter high. For the two years with data for all seasons, mean winter densities by grid were 1.92 to 8.64 (mean 4.07) times greater that the preceding summer. Apparent total overwinter mortality as assessed by comparing estimated densities between winter and the following spring ranged from 42.2% to 82.8% (mean 65.6%).

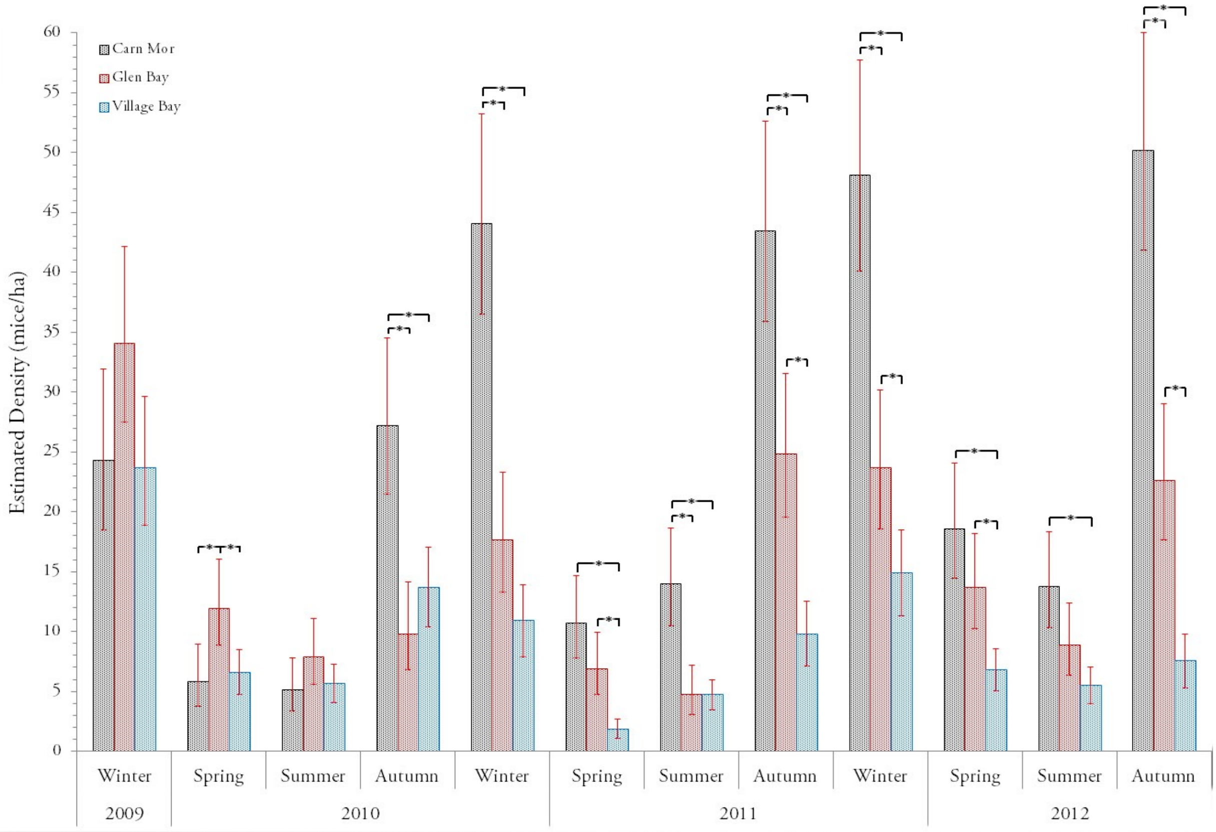

Figure 3.2. SECR estimated densities (bars) and associated 95% confidence intervals (error bars) for the final model (g0~cover*grid + *bk* + season*sex, sigma~grid + *bk* + season*sex) for each of 12 trapping session over three locations; Carn Mor (CM), Glen Bay (GB) and Village Bay (VB). Significant within-session pairwise differences between grids (on the basis of non-overlapping 95% confidence intervals) are denoted with asterisks (including one borderline overlap in spring 2010 where CM and VB CIs overlap by just 0.05mice/ha).

Considerable spatial variation in mouse density was also found (Fig. 3.2), with at least one significant (non-overlapping 95% confidence intervals) pairwise difference between grids for 10 out of 12 trapping sessions. There was a strong overall pattern whereby the highest mouse density tended to be found in Carn Mor and the lowest in Village Bay, although this was not entirely consistent; densities on Carn Mor were significantly greater than Village Bay in 9 of 12 sessions and greater than Glen Bay in 6 sessions, densities in Glen Bay were (borderline) significantly greater than Carn Mor in one session and higher than Village Bay in 6 sessions while densities in Village Bay were never significantly greater than either of the other grids.

3.3.5 Range size

The preferred model (Table 3.5) included effects of grid and a sex*season interaction on sigma. Mean seasonal SECR-estimated home range radiuses (Fig. 3.3) for circles encompassing 95% of the area covered by the detection function of the preferred SECR model revealed significant spatial and sex based variation in mean range sizes. Mean male range sizes were significantly greater than females from the same grid during the spring and summer, but not in autumn and winter. Within grids, male range size was significantly higher in spring and summer than in autumn and winter while female range size for each grid was significantly higher in spring than in winter, but not for any other seasonal pairwise comparisons. Between grids, range size was always largest in Village Bay and smallest on Carn Mor, but this was only significant in autumn and winter and only when comparing Village Bay and Carn Mor, for both sexes.

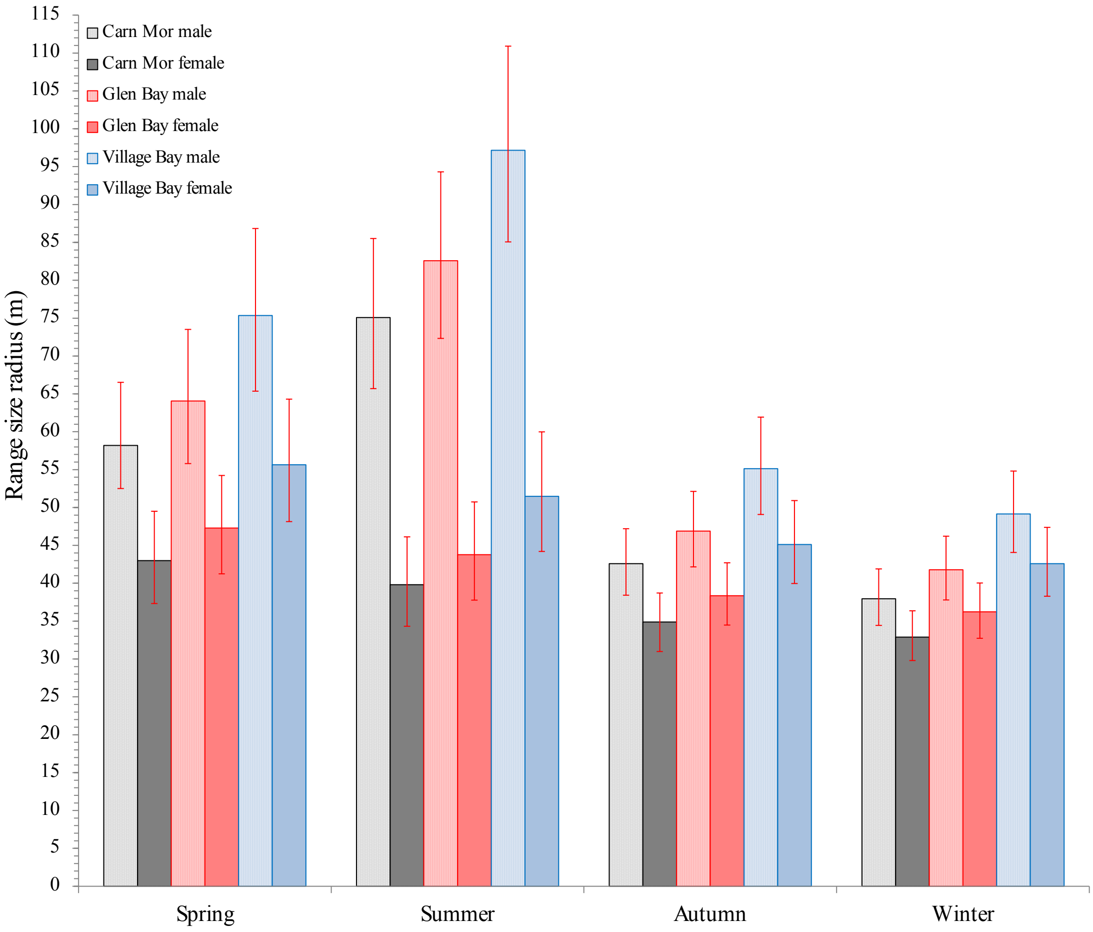

Figure 3.3. Mean seasonal SECR estimated home range radii (for the circle encompassing 95% of the area covered by the detection function) and associated 95% confidence intervals (error bars) by sex and trapping location.

3.3.6 Quantification of sex ratio

The overall sex ratio of individual mice caught was significantly biased towards males (1.42M:1F, n=783, exact binomial test, $p<0.001$). However, likelihood ratio tests for two equivalent SECR models differing only in fixed 1:1 vs free sex ratios for each individual grid*session combination were only significant twice out of 36 tests, which is little more than would be expected at random (Table 3.6).

Table 3.6. Likelihood ratio tests for two SECR models (differing only in having a fixed 1:1 vs free sex ratio) applied separately to each grid*session combination. A trap-specific learned response (*bk*) and sex effects were fitted to both g0 (the intercept of the detection function, i.e. the capture probability for a trap placed precisely at an individual's home range center) and sigma (a spatial scalar, whereby 4.52 times sigma describes the radius of a circle around a home range center that incorporats 95% of ranging behaviour). The effect of cover on g0 was also modelled. All tests were carried out with 1 degree of freedom and significant differences ($p<0.05$) are in bold.

Year		**2009**	**2010**				**2011**				**2012**		
Season		**Winter**	**Spring**	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**
Session		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Carn Mor	**X^2**	1.616	2.252	0.963	1.854	2.530	0.864	0.007	0.987	0.070	2.795	0.460	**4.774**
	p value	0.204	0.134	0.326	0.173	0.112	0.353	0.933	0.321	0.791	0.095	0.498	**0.029**
Glen Bay	**X^2**	0.182	0.327	0.905	0.006	0.000	2.778	0.102	0.126	0.015	0.319	0.227	0.803
	p value	0.670	0.567	0.341	0.936	0.981	0.096	0.750	0.723	0.902	0.572	0.634	0.370
Village Bay	**X^2**	0.515	0.213	0.011	0.547	**6.062**	0.005	**12.187**	2.971	0.427	2.097	0.618	2.481
	p value	0.473	0.644	0.916	0.459	**0.014**	0.944	**0.001**	0.085	0.513	0.148	0.432	0.115

3.3.7 Simulation of varying trapping effort on Village Bay density estimation

For typical model parameters in Village Bay, the default 10x10 grid with 10m trap spacing had 54.8% and 64.4% of density estimates within ±20% of true density in summer and winter respectively. For both seasons, the best performing reduced trapping layout was the 10x10 grid with 10m spacing but only using those trap points in dense cover, scoring 50.2% and 59.4% for summer and winter respectively. The two layouts using both reduced trap number and wider trap spacing performed less well; the 5x5 grid scored 43.2% and 57.2% in summer and winter respectively, and 20x1 head dyke transect scored 47.0% and 51.4% (Figure 3.4). Reduced layouts had a tendency to underestimate density - the median PE values for summer and winter respectively for the four layouts were as follows; 10x10 default grid +0.2% and -0.2%, 10x10 reduced grid +2.3% and -8.0%, 5x5 grid -5.3% and -14.0% and 20x1 transect -6.3% and -12.2%.

The reduced 10x10 grid (best reduced layout overall) and 20x1 transect (best runner up for the summer period when the NTS are most likely to wish to monitor the population due to staff availability) were chosen for further simulation to determine the effect of varying the number of trapping occasions (Figure 3.5). Increasing the number of trapping occasions unsurprisingly improved density estimation in all cases, although the difference was not always large; for the reduced 10x10 grid in summer, 39.2% of estimates were within ±20%

of true density when trapping for three consecutive occasions, rising to 54.4% for seven occasions. In winter the same metrics were 62.2% and 70%. For the 20x1 transect the same metrics were 38.6% and 51.6% in summer and 42.0% and 54.8% in. Median density estimates were close to true density for the reduced 10x10 grid in summer (-0.1% to +1.8% PE) but tended towards underestimation in winter (-2.1% to -9.8% PE). For the 20x1 transect underestimation was more prevalent in both summer (-5.8% to -11.4% PE) and winter (-13.2% to -16.6% PE).

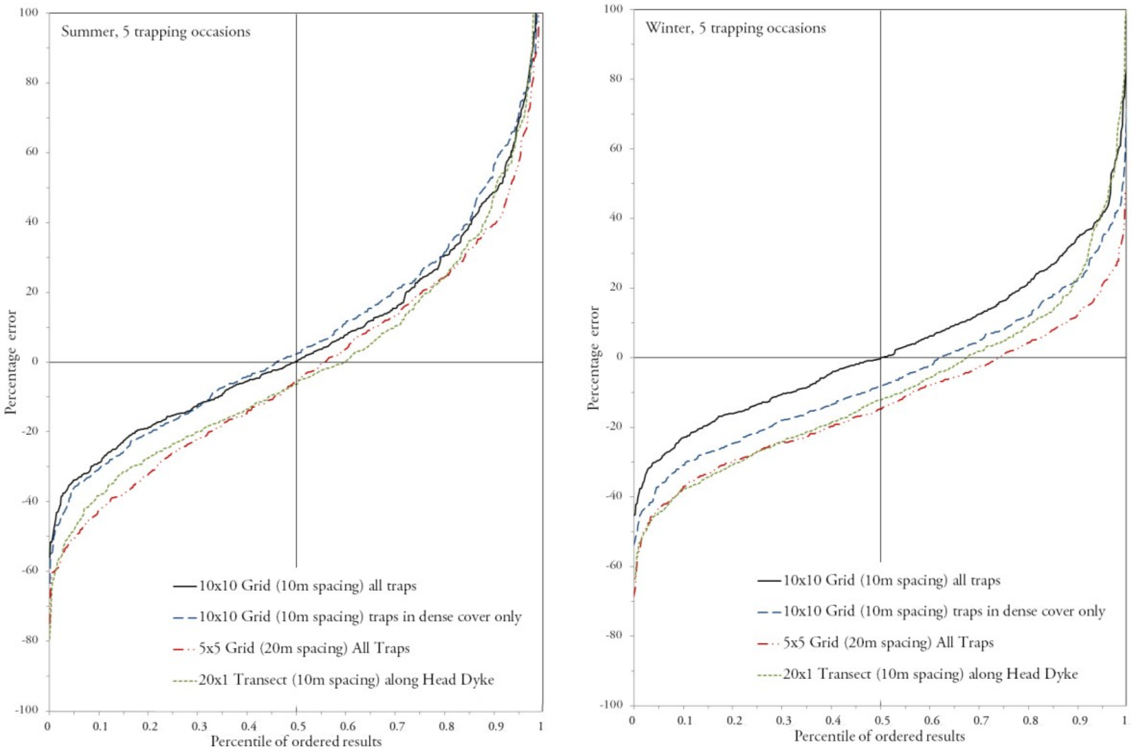

Figure 3.4. Cumulative distribution plots of the percentage error (predicted density/true density*100) of 500 SECR-simulated density point estimates for four alternative trap layouts (the full 10x10 grid with 10m spacing between trap points, a reduced 10x10 grid using only those traps in dense cover, a 5x5 grid with 20m spacing between traps and a 20x1 transect with 20m spacing along the Head Dyke) and two seasons (summer, left, and winter, right). Curves which are flatter and closer to zero PE are considered to provide better fit. Scales are limited to ±100% PE for the sake of clarity, meaning that some extremely high values are not shown.

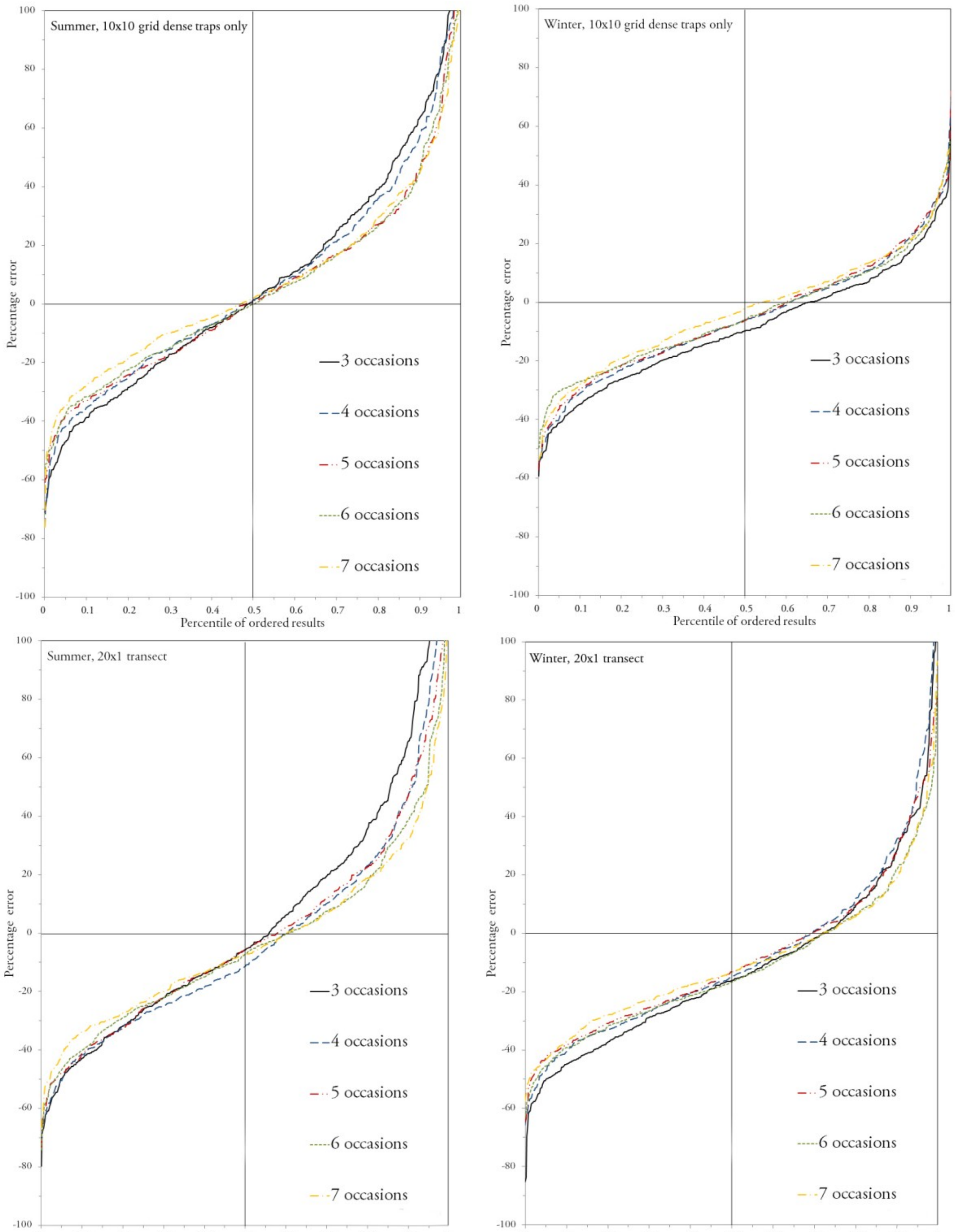

Figure 3.5. Cumulative distribution plots of the percentage error of 500 SECR-simulated density point estimates for each of five different trapping durations across two alternative trap layouts (reduced 10x10 grid with 10m trap spacing using only those traps in dense cover, top, and a 20x1 transect with 20m trap spacing along the Head Dyke, bottom) and two seasons (summer, left, and winter, right). Curves which are flatter and closer to zero PE are considered to provide better fit. Scales are limited to ±100% PE for the sake of clarity, meaning that some extremely high values are not shown.

3.4 Discussion

3.4.1 Model selection

The strongly preferred (ΔAICc >10) model incorporated trap-specific behavioural effects (*bk),* an interaction between grid and trap cover and an interaction between season and sex on g0 and behavioural effects, grid effects and an interaction between season and sex on sigma. SECR derived densities for each grid*session combination were always several times lower (mean 3.14, min 1.98, max 5.24) than naïve counts (Table 2.1, Chapter 2) adjusted for grid size but not incorporating edge effects.

The behavioural responses represent a classic ‘trap happy’ response, whereby mice were more likely to return to an individual trap once they had been caught in it previously in a trapping session, presumably in search of food. This was the preferred behavioural response even when trap cover was also included in models, and so seems to describe a genuine behavioural response rather than a simple artefact of the mice’s preference for rocky cover. The degree of individual trap cover greatly increased the likelihood of trapping success, although this effect was smaller on Carn Mor and greatest in Village Bay, presumably as a reflection of variation in the relative abundances of each cover type between grids. A season*sex interaction was apparent on both g0 and sigma, reflecting large increases in male range size during the breeding season. Between grid variation in g0 and sigma was also apparent – see discussion of home range size below.

Although the preferred model here was reasonably complex and density estimates were computationally demanding, much of that complexity was produced by the need to include seasonal and grid effects in the models due to the design of the trapping regime. A once-yearly monitoring programme in a single location, as might be envisaged by the NTS, would only require a simple model such as g0~cover + bk + sex, sigma~bk + sex, which could be further simplified if all traps were in the same level of cover (see discussion of alternative trapping regime simulations below). Such models can be run in a matter of minutes using simple pre-compiled R scripts, making SECR a suitable tool for long term estimation of mouse densities on St Kilda.

3.4.2 Temporal and spatial density variation

Seasonal variation in mouse density reflected the breeding phenology discussed in Chapter 2, with low and relatively stable population sizes in spring and early summer; within grid differences in density between spring and summer trapping sessions were only significant once (2011, Village Bay) and were caused by movement of novel adult individuals into the grid, which had been at extremely low density. Recruitment of juveniles into the active population began in early or mid-June in all study years and continued into the autumn, probably ending in late September. By November when the winter trapping sessions took place, recruitment had ended but winter mortality was probably not yet severe, so densities then should be representative of annual maxima.

Seasonal fluctuations in density were not extreme, with maxima for each grid 2.2-8.6 times greater than that year's minima (mean 5.2). Absolute density values ranged from 1.9 mice/ha to 50.2 mice/ha. Population densities maxima were an average 2.7 times higher in winter than the preceeding summer, but this varied considerably with a five-fold (1.2-5.9) range in values when looking at individual grid*year combinations. This closely matches findings from a population of *A. sylvaticus* in Iceland with a broadly similar habitat and similar breeding season where population size increased 1.2-7.5 times between March and November (Bengtson *et al.* 1989). Overwinter mortality (between winter and spring trapping sessions) showed considerable variation (between 42-83%), but was typically around 75%, with very few individuals surviving two winters. This again is similar to the Icelandic study, where mortality over the same time period varied between 20% and 72% (Bengtson *et al.* 1989). Other studies in Iceland have shown much lower (by a factor of 10) densities in grassland, but comparable densities in woodland (Unnsteinsdottir & Hersteinsson 2011). Compared to British mainland populations, observed densities were higher than might be expected in relatively impoverished habitats such as sand dunes (Gorman & Ahmad 1993), grassland (Wilson *et al.* 1993) and arable land (Green 1979), instead closely matching those typically found in deciduous woodland (Flowerdew 1985) which is generally seen as the preferred habitat of *A. sylvaticus*. This could be interpreted as evidence that the habitat on St Kilda is somehow superior to similar grassy habitats elsewhere (perhaps due to significant marine trophic subsidies), or as a further example of the frequent observation that island rodent population densities tend to be greater than that of their mainland counterparts (Adler & Levins 1994).

Spatial density variation was marked, with significant differences between grids during all but one session. Although not completely consistent, there was a clear trend for population densities to be highest in Carn Mor and lowest in Village Bay, with Glen Bay falling in between. These differences were most pronounced in the autumn and winter when populations were at their greatest and suggest significant variation in habitat quality across Hirta. Spatial variation in density could be driven by local differences in the food supply. Reproduction in *A. sylvaticus* has been shown to be food limited, with winter food supplementation leading to heavier investment in reproductive effort, larger testes in males and advanced spring breeding in females (Diaz & Alonso 2003). Improved autumn seed supplies have been shown to increase body weight and the length of the breeding season

(Hansson 1971). Artificially altering food supplies have been shown to immediately impact density of *A. sylvaticus* through improving survival (Flowerdew 1972, Bengtson *et al.* 1989), and natural temporal or spatial variation in food supply is often strongly correlated with density (Watts 1969, Hansson 1971, Bengtson *et al.* 1989).

The highest mouse densities were found on Carn Mor, which is used as a breeding site by large numbers of sea birds between May and September. It has been suggested that mice on St Kilda may predate or scavenge sea bird eggs (Bicknell 2009) and further work using stable isotope analysis of mouse blood and potential prey samples taken during this study is currently underway to examine the relative importance of different food types (marine-derived sea bird material, dead sheep, invertebrates and plant matter) to the mice on the three grids. Preliminary results show that blood samples from mice on Carn Mor have a strongly marine carbon isotope signature relative to those on the other grids (Bicknell, pers. comm), but further analyses to determine if this is due to differences in mouse diet or a general enrichment of the marine signal throughout the food chain due to bird guano are yet to be completed. Whatever the outcome of that analysis, it is still not difficult to imagine that sea birds might be improving the mouse food supply on Carn Mor, either directly through scavenged or predated eggs and chicks, or indirectly by increasing productivity of plants or invertebrates with deposited guano and carrion. Seabird colonies elsewhere have been shown to increase soil nutrients (Mizutani & Wada 1988), primary productivity (Anderson & Polis 1999, Garcia *et al.* 2002) and arthropod abundance (Sanchez-Pinero & Polis 2000, Orgeas *et al.* 2003), as well as providing food for native and introduced rodents directly in the form of carrion, eggs and chicks (Stapp 2002, Stapp & Polis 2003).

Setting aside Carn Mor, densities often also varied significantly between Glen Bay and Village Bay, despite both sites having relatively few nesting seabirds. Potential differences in the quality of the food supply do exist, but are perhaps more subtle; both sites are predominantly grassland kept short by grazing, with a relatively low and roughly equivalent number of visible seabird nest sites within the grids. Field mice do tend to have broad and adaptable diets but are usually primarily granivorous and grass (seeds and vegetative matter) is reported to form the staple of their diet on St Kilda (Boyd 1959). The wider Village Bay area has the highest quality grazing on the island and hence supports a greater density of sheep than elsewhere. This study took place during a period when the fluctuating sheep population was at an all-time high (until a crash in early 2012). Grazing pressure across the island, but particularly in Village Bay, was intense and it seems possible that the sheep may have impacted the supply of grass seeds and other plant material particularly strongly in Village Bay, reducing the mouse food supply there relative to other sites. However, the density of the mouse population on the Village Bay grid remained low even after the sheep population crashed, so a grazing-limited hypothesis can offer only a partial explanation for observed differences in density and various other biotic and abiotic factors are also likely to be at work.

3.4.3 Range size

Range size (defined by a circle of radius 4.52 times sigma within which 95% of ranging behaviour occurs) showed significant variation between grids and sexes. Expressed as areas, mean range sizes by grid and sex varied from approximately 0.3ha (females, Carn Mor) to 3.0ha (males, Village Bay). Range sizes were often significantly higher in Village Bay than Carn Mor, for both sexes, and higher in males compared to females on all grids, although this was only significant in spring and summer.

Spatial variation in range size may have been due to differing patterns of rock cover between grids. Carn Mor and Glen Bay both hold a high proportion of natural talus that is spread relatively evenly across the sites, whereas the walls and cleits of Village Bay are for more discrete and patchily distributed, meaning that mice moving from one area of cover to another in search of food or mates may have to travel further. Alternatively, the linear nature of the walls in Village Bay may produce significantly non-circular ranges that would generate relatively large values of sigma (and hence range radius size) relative to actual ranging area. Food supply and density could also affect range size, although these are often correlated (as proposed in this study) and it can therefore be difficult to disentangle social from ecological effects. Supplemental feeding has been shown to reduce range size in *A. sylvaticus* living in poor quality sand dune habitat (Akbar & Gorman 1993), while in *A. flavicollis* females have been known to reduce intra-sexual territoriality and increase range size when food is scarce, in turn driving an increase in male range size in order to maintain range overlap with as many females as possible during the breeding season (Stradiotto *et al.* 2009).

Sex differences in range size are known to occur in other *A. sylvaticus* populations and, as shown here, tend to be larger in males (Attuquayefio *et al.* 1986, Korn 1986, Rogers & Gorman 1995), particularly during the spring and summer. This is usually attributed to a combination of different behaviour during the breeding season (females tend to defend a small territory whilst males travel relatively large distances to improve their chances of encountering females in oestrus) and possibly a more general increase in foraging range in males in order to sustain a larger body mass (Attuquayefio *et al.* 1986). Knowledge of the seasonal variations in range size shown here are important considerations for the planning of potential poison or trap-based rat eradication programmes.

3.4.4 Sex ratios

The overall male to female sex ratio of individuals caught in this study was heavily male biased, but this seems to be an artefact of the larger male range sizes resulting in more captures. Once sex differences in capture probabilities and range sizes were included in the models there was no significant evidence for biased sex ratios. This suggests that the tendency for trapping higher numbers of males than females in this study and previous studies of mice on St Kilda do not reflect genuine imbalances in the sex ratio of the population.

3.4.4 Simulation of varying trapping effort on Village Bay density estimation

The methods used in this study involved setting 200 Longworth traps at 100 trapping points, repeated over three grids. This represents considerable effort and expense that is unlikely to be considered by the NTS as a viable long term monitoring programme. Therefore, several alternative trapping scenarios were assessed for accuracy using simulation. Effort and expense could most easily be limited by monitoring at just one site, and at just one time of year. NTS staff are typically only present on the island during the summer months when the mouse population is low, so this is the most likely period for monitoring to take place, although winter trapping was also examined as it provides additional information with regard to breeding success during the summer.

Cumulative distribution plots of density estimates from the full trapping regime used in this study were compared to those generated using three alternative reduced trapping regimes. All three tended to underestimate mouse density during winter conditions, but the original 10x10 grid censored to only include those trap positions in dense cover (using 37 trapping points out of 100) performed very closely in the summer, and was the least prone to underestimation in the winter. The 5x5 grid with 20m spacing (25 trapping points) performed worst overall, while the 20x1 transect with 20m spacing (20 trapping points) along the Head Dyke performed slightly better and would be considerably easier to set up by novice personnel.

Varying the number of consecutive days on which the 10x10 dense cover-only grid and 20x1 transect were carried out during each trapping session showed a general pattern of relatively poor accuracy with 3 days, approximately similar accuracy for 4-6 days and noticeably improved accuracy with 7 days, although all still produced considerable underestimation of density in the case of the 20x1 transect in winter.

Although assessment metric are somewhat arbitrary, overall the reduced 10x10 grid using only traps in dense cover run for 4 nights trapping seems to provide good accuracy for the effort required and could be run in the summer with only one trap at each location (37 traps total) without being concerned about trap saturation exceeding the 85% saturation threshold for using SECR analysis with single catch traps without generating bias. Dense cover in Village Bay is heavily associated with man-made walls and cleits which are already mapped, so a simple map of trap locations could be generated which would make setting out the traps very simple for new staff.

3.5 Conclusion

This study presents the first robust quantification of the population densities of *Apodemus sylvaticus hirtensis* and demonstrates the suitability of SECR as a tool for future monitoring of the mouse population as part of the St Kilda action plan (NTS, 2003). Overall the mouse population densities fell within normal ranges for *Apodemus sylvaticus*, closely matching the density of mice found in woodland and other favourable habitat in Great Britain and elsewhere. Temporal variation typical of temperate small mammal populations was found, with low densities in spring and early summer, increasing through the breeding season and reaching a highpoint at the beginning of winter. Geographical density variation was also present and often of an equal magnitude to temporal variation. There was a strong pattern across multiple years of population densities being highest in Carn Mor and lowest in Village Bay. These differences were most pronounced in autumn and winter and seem likely to be driven at least in part by variation in the food supply.

Significant differences in mean range size were found between sexes, seasons and grids, with males having larger home ranges than females, particularly during the spring and summer breeding season and range sizes for both sexes were larger in Village Bay than elsewhere. Large ranges in males are typical for *Apodemus* and many other small mammals and probably reflect behavioural differences between sexes during the breeding season. Spatial variation in range size may reflect differences in the distribution of rock cover, food availability, density-mediated social effects or a combination of the three. SECR estimated sex ratios were not significantly biased towards males as suggested by count data in this and previous studies.

CHAPTER 4

Survival and fecundity of the St Kilda field mouse, as revealed by capture-mark-recapture

4.1 Introduction

4.1.1 General introduction - Please see Chapter 2, section 2.1.1

4.1.2 Survival and fecundity

Elsewhere, population dynamics of *A. sylvaticus* generally show increases between summer and winter and decreases during winter and spring, in line with the breeding season (Flowerdew 1985, Montgomery 1989). Densities are thought to be locally food limited (Montgomery & Montgomery 1990, Gorman *et al.* 1993, Unnsteinsdottir & Hersteinsson 2011) and may include density-dependent effects on population regulation during periods of increase, but not decrease (Montgomery 1989, Mallorie & Flowerdew 1994), perhaps as a result of female territoriality, although this may be overridden by a super-abundance of food (Smyth 1966). Various other non-cyclic rodents are known to exhibit negative density-dependent effects on fecundity (Reed & Slade 2008).

The population dynamics of this island population are presumably governed largely by some combination of food availability, disease and the climatic conditions. Previous analyses (Chapter 3) have demonstrated significant differences in population densities between different geographical locations, with the hypothesis that these are driven at least in part by differences in the food supply.

This study aims to expand on the previous findings by using mark-recapture models to separate and quantify the processes of survival and recruitment which together define the population rate of change. Importantly, these models allow the estimated variance to be decomposed into separate sampling and population processes, hence removing bias caused by incomplete population sampling (White *et al.* 2002). The Pradel models used here (Pradel 1996) allow estimation of survival, fecundity and overall rate of population change without needing to estimate abundance, which reduces parameterisation of models and is therefore relatively robust when using data that is sometimes sparse due to low numbers of alive animals, as in this study.

As well as simply quantifying survival, fecundity and overall rates of population change, this study aims to determine if there is spatial variation in survival and fecundity which could explain the observed differences in density between trapping sites. Previous chapters have discussed in depth the potential differences in the food supply between grids as an explanatory hypothesis for the observed differences in size, condition and density of mice across the island. In particular, the summertime presence of a large seabird breeding colony at Carn Mor seems likely to play a role in governing the increased size and abundance of mice there, and the intense grazing pressure of the large sheep population in Village Bay may have the opposite effect. Seasonal seabird colonies elsewhere have been shown to increase soil nutrients (Mizutani & Wada 1988), primary productivity (Anderson & Polis 1999,Garcia *et al.* 2002) and arthropod abundance (Sanchez-Pinero & Polis 2000, Orgeas *et al.* 2003), all of which could continue to improve the food supply relative to the other sites outwith the bird breeding season, especially given the known caching behaviour of *Apodemus*. Additionally, an improved food supply is likely to be at least partly responsible for mice on Carn Mor being in better condition (heavier for a given body length) than elsewhere (Chapter 2, Fig. 2.9). Specifically, models were constructed that included interactions between grid and season, allowing testing of the hypotheses that survival and/or summer fecundity are greater on Carn Mor than elsewhere, either during the summer period alone or year round. Explicitly, these are defined as follows; (1) that the presence of seabirds on Carn Mor between summer and autumn increases population growth rates through increased summer-autumn survival and/or fecundity relative to other sites, but the effect is temporal and survival therefore decreases on Carn Mor relative to other sites outwith the seabird breeding season as a result of increased population densities without additional marine subsidies; (2) that the presence of seabirds on Carn Mor between summer and autumn increases population growth rates through increased summer-autumn survival and/or fecundity relative to other sites, and that survival rates continue to be greater than or equal to other grids outwith the summer-autumn period despite the increased density due to long term enrichment of the food web by marine subsidies. Both hypotheses necessarily assume that the differences in the population dynamics of the mice between sites are predominantly food driven.

4.2 Materials & Methods

Please see Chapter 2, sections 2.2.1 and 2.2.2 for a description of trapping sites and methodologies.

4.2.1 Data Analysis

Mark-recapture data was analysed using the Pradel robust design recruitment model (Pradel 1996) for closed populations with Huggins' abundance estimation. This model estimates apparent survival rate (φ, including survival and emigration rates, hereafter simply called survival) and fecundity (*f*, the number of new animals at time *i* as a proportion of animals present at time *i-1*). Apparent survival is defined as the probability that an animal that has not emigrated from the population is alive at time *i+1*, given that it was alive at time *i* and hence is conditioned upon releases at earlier time intervals. In contrast, fecundity is calculated by reversing the capture history such that an animal's prior capture at time *i* is conditioned upon it being present at time *i+1* in order to directly determine the probability of an animal entering the population (Pradel 1996). The observed rate of population change between sessions ($\hat{\lambda}$) is not estimated directly but can be derived simply as f + φ for a given time. To reduce the number of parameters fitted to each model, the conditional (rather than full-likelihood) form of the models were used, in which abundance ($\hat{N}$) is a derived parameter conditioned on the number of animals detected (Huggins 1989). Finally, models also include the 'nuisance' parameters of capture probability (p) and recapture probability (c).

Robust design models assume that populations are closed to mortality, migration and recruitment within a trapping session, but that gaps between sessions are long enough for these open population processes to take place. Individual trapping sessions lasted for only 5 nights for each grid and the mouse populations are assumed to be closed for this brief period. Closure tests (Stanley & Burnham 1999) are available to test this assumption but were not carried out as they are known to be unsuitable for data where animals exhibit strong behavioural responses to trapping, as in this study (White 1982). Capture histories for both sexes and all three grids were concatenated with site and sex incorporated as grouping variables. Dummy trapping occasions with survival fixed at 1 and recruitment and capture/recapture probabilities fixed at 0 were added to the capture histories to account for nights where trapping was elsewhere than the grid in question, in order to allow precise time lengths between trapping sessions to be specified separately for each grid. Between-session lengths were calculated as days but converted to monthly units (days/30) to prevent issues with numerical convergence which can occur if, for example, daily survival rates are close to 1.

4.2.2 Model specification and selection

Initially, capture and recapture probabilities were examined using models with constant survival and fecundity rates. Null models (constant and equal p and c) and models with behavioural effects (constant but non-equal p and c) were tested, followed by models where p and c varied by grid and sex and as an interaction between the two. Within session time effects were not examined as they were considered unsuitable given the structure of the trapping regime (due to requiring a very large number of additional parameters) and models incorporating between-session time variation on p and c produced highly unrealistic parameter estimates due to data limitations and were discarded. Selection via AICc values produced a preferred model with behavioural and grid effects on c and a grid*sex interaction on p, which was then used as the basis for all subsequent models.

Survival and fecundity were hypothesised to vary with time, grid and population density. Density was defined as that present on each grid at the beginning of each inter-session period, using estimates obtained from previous analyses (Chapter 3, section 3.3.4). Sex and age were not included as a variable on φ as previous analysis had demonstrated no significant difference in the sex ratio of mice caught (see Chapter 3, section 3.3.6) so survival rates were presumed to be similar, and Pradel models are not able to incorporate the age of individuals. Initially we examined whether season and year improved model fit on φ and *f*, individually, additively and as an interaction. Models including a season*year interaction on either φ or *f* produced extremely large standard errors and had to be discarded. Of the remaining models, two were indistinguishable (ΔAICc = 0.24) and so the simpler model with seasonal effects on φ and *f* but no year effects was chosen as the basis for more complex models incorporating season, grid and density. Given that three way interactions between these variables were biologically plausible, and that these interactions may be acting differently on survival and fecundity, a top down approach to model selection was adopted in order to limit the number of models considered. The initial model featured a full season*grid*density interaction on both φ and *f*, but failed to produce reasonable estimates or standard errors due to data limitations. Therefore, all combinations of two-way interactions plus a third additive effect for both φ and *f* were considered, all of which returned reasonable estimates and standard errors. Any further attempts at simplification of high ranking models, either by dropping additive effects or removing interactions, resulted in significantly worse model fit (ΔAICc > 2) and so model simplification was halted after this point. All models were ranked according to AICc and model-averaged estimates for φ and *f* were then calculated.

It should be noted that estimates of fecundity for the periods between the autumn and winter trapping sessions are somewhat difficult to interpret biologically, as they are skewed by the presence of large numbers of non-breeding young of the year (see Chapter 2), and Pradel models are unable to incorporate age. To overcome this, a second set of analyses were carried out as described above, but with the autumn trapping data from 2010 and 2011 censored from the data. The small number of juvenile mice caught in the summer sessions were also censored. These should provide relatively unbiased estimates of net fecundity between the summer and winter sessions (which bookend the periods of juvenile recruitment), although unavoidably these fecundity estimates still include immigration.

4.2.3 Software

All analyses were carried out using the RMark 2.1.6-1 (Laake 2013) for the R 3.0.1 statistical software package (R Core RCoreTeam 2014) to construct models, which were then passed to and run by the MARK 7.1 (White 2014) software package. Graphs were plotted using Microsoft Excel 2010.

4.3 Results

4.3.1 Trapping success

Total trapping success across all sessions and grids amounted to 4462 captures of 787 individuals. Numbers of mice caught by date, grid, sex and age class can be found in Chapter 2 (Figure 2.3 and Table 2.1). Recapture rates were generally high; the mean number of captures per individual within a 5-night primary trapping session was 3.2 (min 1, median 3, max 5), and mean number of primary sessions (seasons) in which an individual was caught was 1.7 (min 1, median 1, max 8). The mean total number of captures per individual was 5.6 (min 1, median 4, max 32). As with previous studies, mice were heavily associated with rock cover and traps in the open tended to catch far fewer mice than those adjacent to walls, cleits or talus.

4.3.2 Capture probability models

Capture probability models (Table 4.1) showed a strong increase in fit when including a within session behavioural effect, and mice were roughly twice as likely to enter traps once they had already been caught in a session (Fig. 4.1). Allowing p to vary according to an interaction between grids and sexes both improved model fit, as did allowing c to vary between grids, but models including sex effects on c were not preferred. Mean daily capture probabilities (Fig. 4.1) equated to an overall mean capture probability per individual of 90.3% per typical 5-day trapping session. Capture probabilities differed slightly between grids and sex, being slightly higher overall for females, and slightly lower for females on Carn Mor and males in Village Bay compared to elsewhere, although not always significantly. Recapture rates were slightly but significantly lower on Carn Mor than elsewhere.

Table 4.1. AICc test for the five capture (p) and recapture (c) models, with constant survival (Phi) and fecundity (*f*) rates. The preferred model (p~grid, c~grid, bold) was selected on the basis of AICc and was used as the basis for all subsequent models.

Parameters				No. parameters	AICc	ΔAICc	Deviance
Phi~1	***f*~1**	**p~grid*sex**	**c~grid**	**11**	**12210.73**	**0.00**	**12188.67**
Phi~1	*f*~1	p~grid*sex	c~grid*sex	14	12214.44	3.71	12186.34
Phi~1	*f*~1	p~grid + sex	c~grid + sex	10	12220.56	9.83	12200.51
Phi~1	*f*~1	p~grid + sex	c~grid	9	12220.86	10.13	12202.82
Phi~1	*f*~1	p~grid	c~grid	8	12222.45	11.72	12206.41
Phi~1	*f*~1	p~1	c~grid + sex	7	12225.10	14.37	12211.07
Phi~1	*f*~1	p~1	c~grid	6	12225.40	14.67	12213.38
Phi~1	*f*~1	p~1	c~grid*sex	9	12229.09	18.36	12211.05
Phi~1	*f*~1	p~grid	c~1	6	12256.89	46.16	12244.87
Phi~1	*f*~1	p~sex	c~sex	6	12257.13	46.40	12245.11
Phi~1	*f*~1	p~sex	c~1	5	12258.30	47.57	12248.29
Phi~1	*f*~1	p~1	c~sex	5	12258.68	47.95	12248.66
Phi~1	*f*~1	p~1	c~1	4	12259.85	49.12	12251.84
Phi~1	*f*~1	p~1	c=p	3	13575.67	1364.94	13569.67

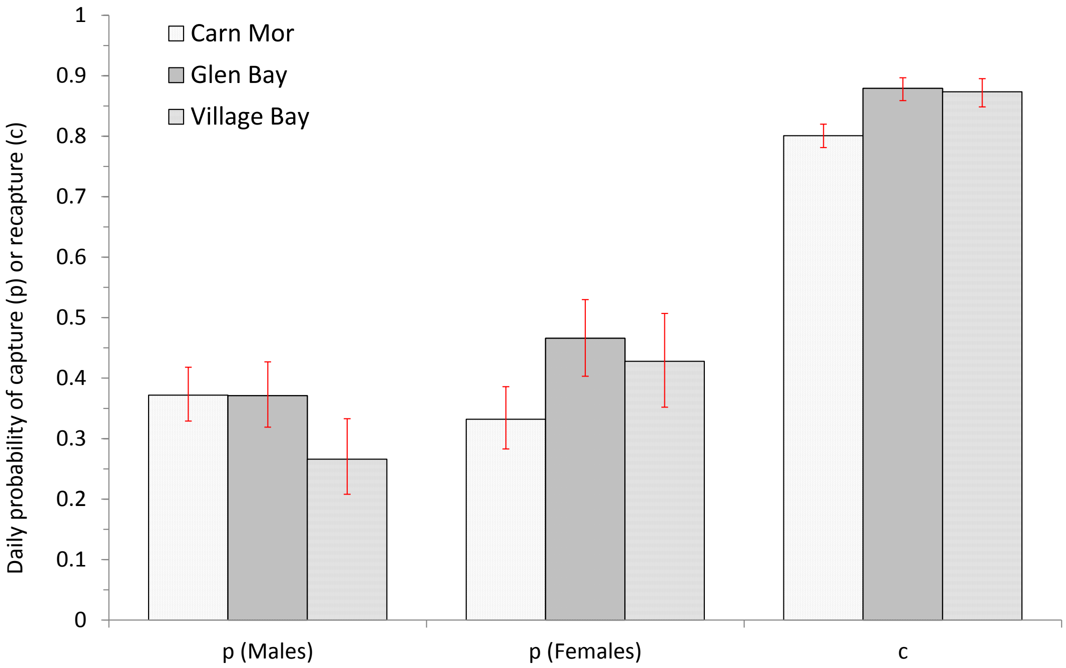

Figure 4.1. Estimated mean daily capture probabilities (p) by sex and recapture probabilities (c) (bars) and associated 95% confidence intervals (error bars) for each of the three trapping sites for the preferred model (p~grid*sex, c~grid).

4.3.3 Survival and fecundity

When ranked according to AICc (Table 4.2), two models were indistinguishable (ΔAICc < 2). These both included a season*grid interaction plus density effect on φ, and either a density*grid or season*grid interaction plus season or density, respectively, on *f*. Estimates of φ varied considerably between grids and trapping intervals with mean monthly inter-seasonal survival rates (Fig. 4.2) of between 0.67 and 1.00.

Table 4.2. AICc rankings for Pradel survival and fecundity models. Preferred models are in bold, and all AICc weights used in model averaging of estimates are shown.

Parameters				No. param.	AICc	ΔAICc	AICc weight	Deviance
Phi~density + season*grid	***f*~density*grid + season**	**p~grid*sex**	**c~grid**	**31**	**11830.65**	**0.00**	**0.4170**	**11768.19**
Phi~density + season*grid	***f*~density + season*grid**	**p~grid*sex**	**c~grid**	**35**	**11830.84**	**0.19**	**0.3790**	**11760.26**
Phi~density + season*grid	*f*~density*season + grid	p~grid*sex	c~grid	32	11833.39	2.75	0.1058	11768.90
Phi~season*grid	*f*~density + season*grid	p~grid*sex	c~grid	34	11834.18	3.53	0.0720	11765.62
Phi~season*grid	*f*~density*season + grid	p~grid*sex	c~grid	31	11836.22	5.58	0.0257	11773.76
Phi~density*season + grid	*f*~density + season*grid	p~grid*sex	c~grid	32	11844.99	14.34	0.0003	11780.50
Phi~density*season + grid	*f*~density + grid + season	p~grid*sex	c~grid	26	11847.30	16.65	0.0001	11794.97
Phi~density*grid + season	*f*~density + season*grid	p~grid*sex	c~grid	31	11847.55	16.90	0.0001	11785.09
Phi~density*season + grid	*f*~density*grid + season	p~grid*sex	c~grid	28	11847.63	16.98	0.0001	11791.25
Phi~density + grid + season	*f*~density + season*grid	p~grid*sex	c~grid	29	11847.96	17.31	0.0001	11789.55
Phi~density*grid + season	*f*~density*grid + season	p~grid*sex	c~grid	27	11848.28	17.63	0.0001	11793.92
Phi~density + season*grid	*f*~density*season	p~grid*sex	c~grid	30	11848.31	17.66	0.0001	11787.88
Phi~density*season + grid	*f*~density*season + grid	p~grid*sex	c~grid	29	11849.20	18.55	0.0000	11790.80
Phi~season + grid	*f*~density*season + grid	p~grid*sex	c~grid	25	11850.83	20.18	0.0000	11800.53
Phi~density*grid + season	*f*~density + grid + season	p~grid*sex	c~grid	25	11850.88	20.21	0.0000	11800.56
Phi~season + grid	*f*~density*grid + season	p~grid*sex	c~grid	24	11850.86	20.23	0.0000	11802.60
Phi~density + grid + season	*f*~density + grid + season	p~grid*sex	c~grid	23	11851.31	20.66	0.0000	11805.06
Phi~density*grid + season	*f*~density*season + grid	p~grid*sex	c~grid	28	11851.86	21.21	0.0000	11795.49
Phi~density + grid + season	*f*~density*season + grid	p~grid*sex	c~grid	26	11852.26	21.61	0.0000	11799.93
Phi~density + grid + season	*f*~density*grid + season	p~grid*sex	c~grid	25	11852.55	21.90	0.0000	11802.25
Phi~season*grid	*f*~density*grid + season	p~grid*sex	c~grid	30	11855.83	25.18	0.0000	11795.40
Phi~density + season*grid	*f*~density + grid + season	p~grid*sex	c~grid	29	11857.42	26.77	0.0000	11799.02
Phi~season*grid	*f*~density + grid + season	p~grid*sex	c~grid	28	11857.93	27.28	0.0000	11801.55
Phi~density + season*grid	*f*~season*grid	p~grid*sex	c~grid	34	11882.86	52.21	0.0000	11814.30

Within-season between-grid pairwise comparisons (Figure 4.2) showed a general pattern of significantly higher survival on Carn Mor compared to Village Bay during the summer (and one autumn), but few other significant differences barring low survival on Carn Mor in the winter of 2009 and significantly higher survival in Village Bay between spring and summer 2011, when all 6 individuals in Village Bay survived to the following trapping session and survival was therefore fixed at 1. Regarding fecundity, although grid effects improved model fit on *f*, within-season between-grid pairwise comparisons were only significant in 2 out of 33 Figure 4.3). Between seasons, fecundity was highest between summer and autumn across all grids as expected, usually significantly (Figures 4.4). Patterns of seasonal effects on survival were complex and differed between grids (Figures 4.4); on Carn Mor survival was significantly lower in winter than all other seasons, in Glen Bay there was no significant seasonal variation in survival, whilst in Village Bay survival tended to be lowest in summer, although not always significantly.

Density was positively correlated with survival, although this effect was small at 0.016 on the logit scale for the highest ranking model (equivalent to an increase in monthly survival rate of 0.037 between densities of 1 and 20 mice/ha). Conversely, density had a significant negative effect on fecundity, the magnitude of which varied between grids. The highest ranking model included a density*grid interaction on *f*, whereby increasing density from 1 to 20 mice/ha resulted in a cross-season average drop in fecundity from 0.42 to 0.26 on Carn Mor, from 0.37 to 0.16 in Glen Bay and from 0.41 to 0.08 in Village Bay.

Rates of population change (λ) between trapping sessions (Fig. 4.5) were generally negative (<1) between winter and spring, stable (~1) or slightly negative between spring and summer, and stable or positive (>1) between summer and autumn and autumn and winter. Seven out of eleven intervals included significant differences between grids although this was quite chaotic with little obvious trend other than for significantly higher rates of population increase on Carn Mor than elsewhere between summer and autumn.

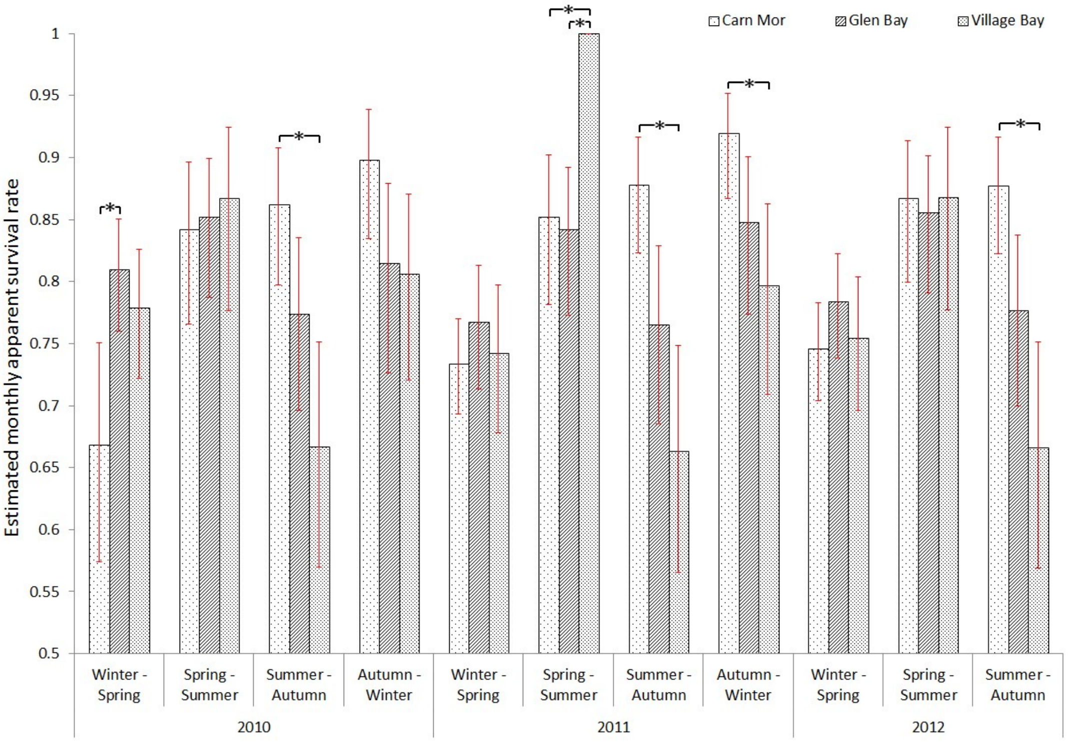

Figure 4.2. Estimated model-averaged monthly apparent survival rates φ (bars) and associated 95% confidence intervals (error bars) for the intervals between trapping sessions for each of the three trapping sites. The φ value for Spring-Summer 2011 in Village Bay was fixed to 1 to prevent numerical convergence issues (and hence has no associated error bars).

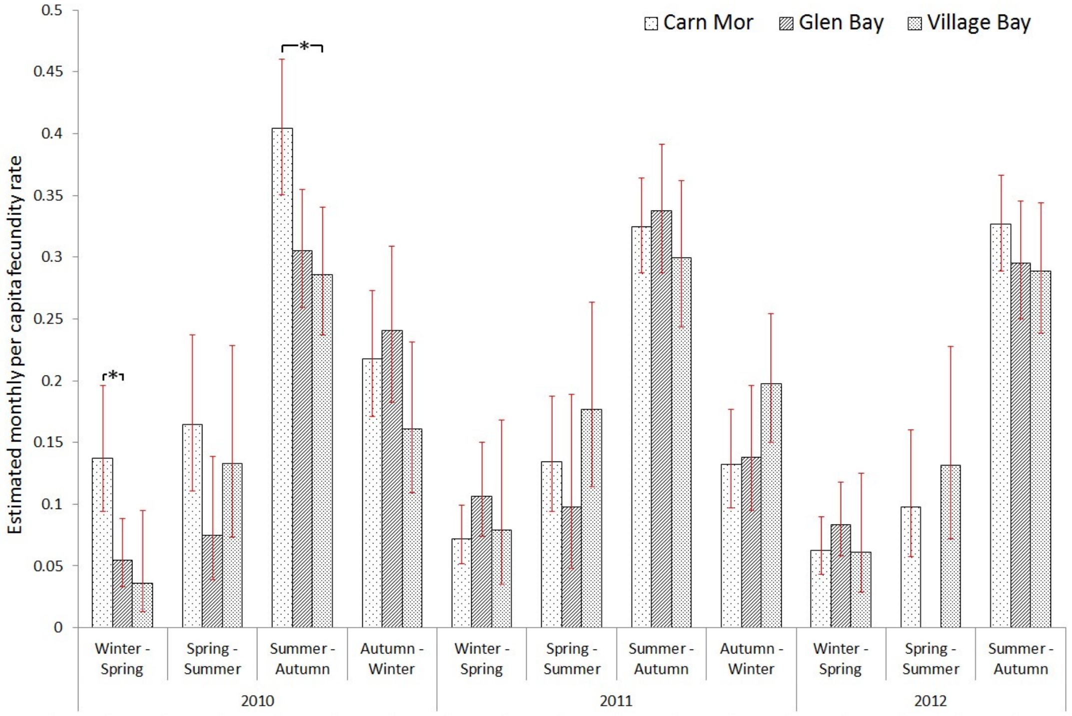

Figure 4.3. Estimated model-averaged monthly net fecundity rates (bars) and associated 95% confidence intervals (error bars) for each of the three trapping sites. The *f* value for Spring-Summer 2011 in Glen Bay was fixed to 0 to prevent numerical convergence issues (and hence has no associated error bars).

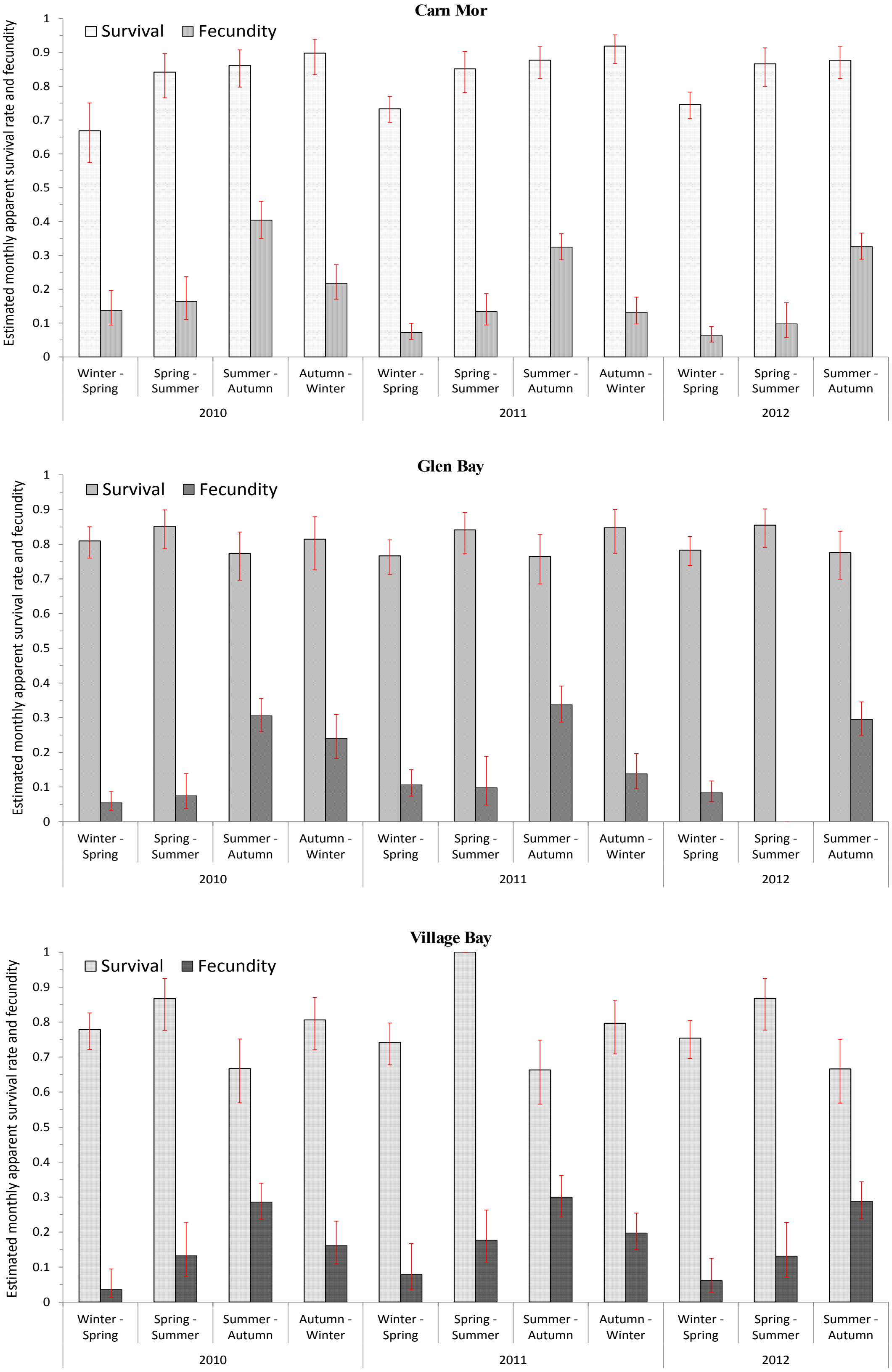

Figure 4.4. Estimated model-averaged survival and fecundity rates (bars) and associated 95% confidence intervals (error bars) for each of the three trapping sites. Two estimates have no associated error bars as they were restrained to either 1 or 0 to prevent numerical convergence issues.

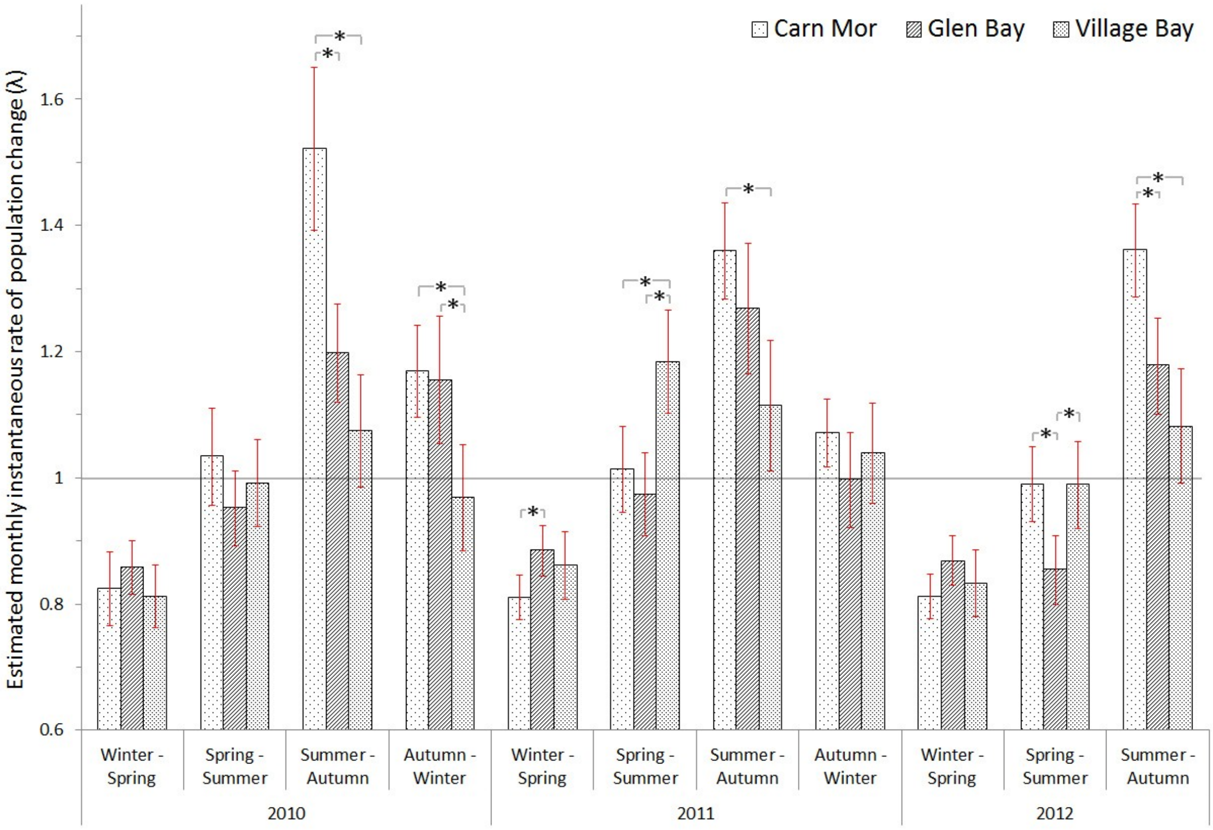

Figure 4.5. Estimated model-averaged rate of population change λ (bars) and associated 95% confidence intervals (error bars) for the intervals between trapping sessions for each of the three trapping sites. Significant pairwise differences between grids for a given interval are marked with an asterisk (*).

4.3.4 Net fecundity across breeding seasons

As for the full data set, model selection (Table 4.3) for a reduced data set omitting autumn trapping sessions and censoring juveniles caught in the summer also produced a preferred model that included a season*grid interaction plus density effect on φ, and season*grid interaction plus density on *f*. Monthly fecundity rates across the entire breeding season (Fig. 4.6) were significantly higher on Carn Mor than Glen Bay for 2010, but there were no other significant differences between grids within years or between years for a given grid.

Table 4.3. AICc test for Pradel models with autumn trapping data and juveniles removed from the data in order to obtain less biased estimates for fecundity during the breeding season. Preferred model in bold, and AICc weights used to calculate parameter estimates are also shown.

Parameters				No. param.	AICc	ΔAICc	AICc weight	Deviance
Phi~density + season*grid	**f~density + season*grid**	**p~grid**	**c~grid**	**26**	**9154.19**	**0.00**	**0.8076**	**9101.79**
Phi~density + season*grid	f~density*grid + season	p~grid	c~grid	24	9157.31	3.12	0.1701	9108.96
Phi~density + season*grid	f~density + grid + season	p~grid	c~grid	22	9162.79	8.60	0.0110	9118.49
Phi~density + season*grid	f~density*season + grid	p~grid	c~grid	24	9164.09	9.90	0.0057	9115.74
Phi~season*grid	f~density + season*grid	p~grid	c~grid	25	9165.62	11.43	0.0027	9115.25
Phi~density + season*grid	f~density + season	p~grid	c~grid	20	9167.80	13.61	0.0009	9127.56
Phi~season*grid	f~density*grid + season	p~grid	c~grid	23	9167.80	13.61	0.0009	9121.48
Phi~season*grid	f~density + grid + season	p~grid	c~grid	21	9168.41	14.21	0.0007	9126.14
Phi~density + season*grid	f~density*season	p~grid	c~grid	22	9170.19	16.00	0.0003	9125.90
Phi~season*grid	f~density*season + grid	p~grid	c~grid	23	9171.90	17.72	0.0001	9125.50
Phi~density + season*grid	f~season*grid	p~grid	c~grid	25	9175.46	21.26	0.0000	9125.08
Phi~density + season*grid	f~ grid + season	p~grid	c~grid	21	9175.84	21.64	0.0000	9133.57
Phi~density*season + grid	f~density + season*grid	p~grid	c~grid	24	9180.50	26.31	0.0000	9132.15
Phi~density*grid + season	f~density + season*grid	p~grid	c~grid	24	9183.55	29.36	0.0000	9135.21
Phi~density*season + grid	f~density + grid + season	p~grid	c~grid	20	9186.40	32.21	0.0000	9146.16
Phi~density + grid + season	f~density + season*grid	p~grid	c~grid	22	9186.62	32.43	0.0000	9142.33
Phi~density*season + grid	f~density*grid + season	p~grid	c~grid	22	9188.63	34.43	0.0000	9144.33
Phi~density*season + grid	f~density*season + grid	p~grid	c~grid	22	9188.91	34.72	0.0000	9144.62
Phi~density*grid + season	f~density*grid + season	p~grid	c~grid	22	9189.45	35.25	0.0000	9145.15
Phi~density*grid + season	f~density + grid + season	p~grid	c~grid	20	9190.09	35.82	0.0000	9149.80
Phi~density*grid + season	f~density*season + grid	p~grid	c~grid	22	9192.60	38.41	0.0000	9148.31
Phi~density + grid + season	f~density + grid + season	p~grid	c~grid	18	9193.87	39.68	0.0000	9157.68
Phi~density + grid + season	f~density*season + grid	p~grid	c~grid	20	9196.04	41.85	0.0000	9155.80
Phi~density + grid + season	f~density*grid + season	p~grid	c~grid	20	9197.49	43.30	0.0000	9157.25
Phi~density + season*grid	f~density*grid	p~grid	c~grid	22	9217.16	63.26	0.0000	9173.16
Phi~density + season*grid	f~density + grid	p~grid	c~grid	20	9227.27	73.08	0.0000	9187.03

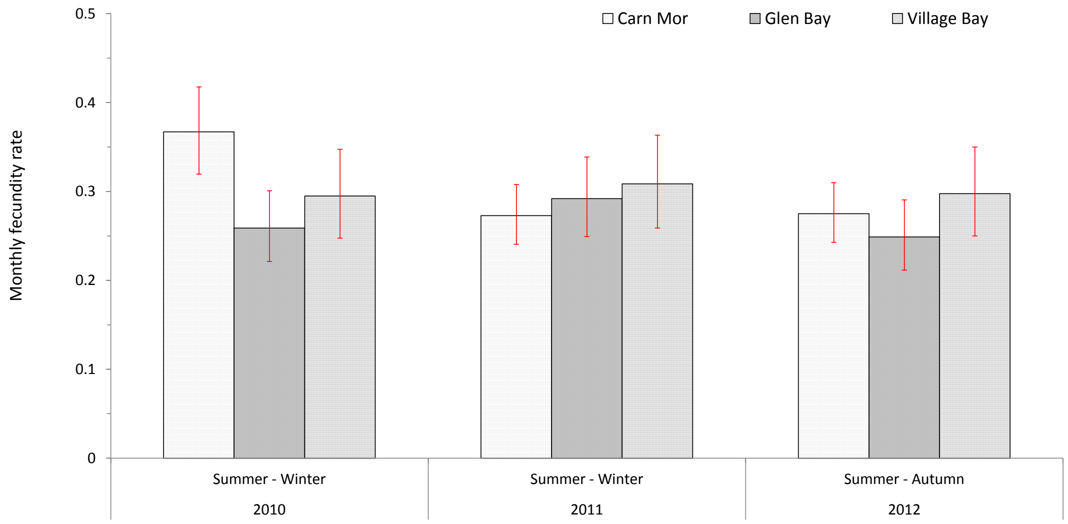

Figure 4.6. Estimated model-averaged monthly net fecundity rates (bars) and associated 95% confidence intervals (error bars) for each of the three trapping sites for the 2010 and 2011 Summer-Winter periods and the 2012 Summer-Autumn period. Estimates for intervals outside of the breeding season are not shown.

4.4 Discussion

4.4.1 Capture rates

Capture probability models demonstrated a considerable short term behavioural response to trapping, whereby mice were more than twice as likely to enter traps once they had been caught once within a trapping session. This supports the findings of Chapter 3, where a corresponding ‘trap happy’ effect was found in spatially explicit analysis of the capture histories. Similar responses to trapping have been seen in other *A. sylvaticus* populations (Gurnell 1982), so this is not unusual. There was a slight variation in capture rates between grids and sexes but these did not follow any obvious pattern, and mice on Carn Mor of both sexes had slightly lower probabilities of recapture, perhaps due to a slightly weaker behavioural response or as an artefact of the greater proportion of dense cover found there. Daily capture rates across all grids and sessions indicate that a mean of 90% of the trappable population will have been caught in any particular five day trapping session, suggesting that in general the data set should provide a good representation of the populations sampled and that the results presented in previous chapters are robust.

4.4.2 Survival and fecundity

Spatial and temporal variation in survival and fecundity of the mice is inevitably complex and with only three years of data any conclusions are tentative, but even so some observations can be made. Survival rates in Glen Bay were the least variable of the three grids, with no significant differences between any time intervals, while the Carn Mor population showed reduced overwinter survival rates compared to other time periods in those years, and in Village Bay survival rates were lowest in summer. Mean survival rates were 83% on Carn Mor, 81% in Glen Bay and 78% in Village Bay, which exceed or are towards the upper end of typical 70-80% ranges for *A. sylvaticus* in favourable habitat (Bengtson *et al.* 1989, Gorman *et al.* 1993, Wilson *et al.* 1993) and considerably higher than observed in resource limited grasslands in Iceland (Unnsteinsdottir & Hersteinsson 2011). Survival rates were relatively stable between grids and through time, despite frequently large (up to a factor of seven) differences in the density of mice on the different grids. Density was positively correlated with survival although the effect was small and is likely to reflect the fact that the model selection process was not able to include a three way interaction between density, season and grid, with strongly weighted models including density as an additive effect only. As in previous studies on other *A. sylvaticus* populations (Mallorie & Flowerdew 1994, Unnsteinsdottir & Hersteinsson 2009), survival rates do not therefore seem to be strongly linked to absolute population densities, either between grids or within grids over time. Instead, survival appears to be governed by variable environmental factors such as food supply, disease, or the impact of the prevailing weather (although these may also interact with density).

With regards to fecundity, the greatest variation was between seasons, with a large increase in fecundity between summer and autumn and a smaller increase between autumn and winter as expect, together capturing the bulk of the breeding season. Fecundity rates outside of this window exclusively reflect immigration into the grid area. Although grid effects did improve model fit there was little evidence for any significant pattern in fecundity estimates between grid, either throughout the year or during the breeding season. There was, however, evidence of a negative effect of density on fecundity, which seems to be widespread in small mammal populations (Reed & Slade 2008). This effect varied considerably between grids, being strongest in Village Bay and weakest on Carn Mor, perhaps due to less competition for food or between females for nest sites.

Overall instantaneous rates of population change (λ) closely matched the findings for survival, in that there was a clear pattern of spatial variation in the rate of population increase during the summer, this being greatest in Carn Mor and lowest in Village Bay. Taking these results together, it seems the observed differences in mouse densities between grids are therefore primarily driven by differential survival rates during the summer and perhaps autumn, which are highest in Carn Mor and lowest in Village Bay, but usually very similar outside of this period. This is consistent with the previously described hypothesis (2) that marine derived trophic subsidies play a role in governing mouse densities both during the summer-autumn breeding period and when the birds are no longer present. This hypothesis is also consistent with the earlier observation that increasing density suppressed fecundity most strongly in Village Bay and least strongly on Carn Mor.

It should be re-emphasised that a current limitation of Pradel models is that recruitment due to breeding is indistinguishable from immigration from outside the trappable population, and similarly permanent emigration cannot be distinguished from mortality. Therefore it is impossible within this analysis to account for potential source-sink dynamics, whereby large scale seasonal movements between different parts of the island could alter densities and skew estimates of survival and fecundity. Given that *Apodemus* are sometimes known to disperse considerable distances (Gliwicz 1988, Zhang & Usher 1991), this is a potentially major source of bias, although analysis of genetic structuring of the St Kilda population has shown limited genetic differentiation between sites (individuals from Carn Mor are genetically differentiated from those in Glen Bay and Village Bay, (Robertson

2011). Either way, knowledge of source-sink habitats is of importance for conservation planning, where effort can be best spent on protecting or managing more productive source habitats, so this is a prime avenue for further study.

4.5 Conclusion

This study represents the first quantification of the survival and fecundity rates of *Apodemus sylvaticus hirtensis*. The derived capture probabilities demonstrated that a very high proportion of the trappable population within the grids was sampled. Density dependence on survival was present but negligible, but negative effects of density on fecundity were of a greater magnitude and appeared to be mediated by availability of spatially heterogeneous resources, possibly food or nest sites. Survival rates were high overall, matching or exceeding those found in favourable habitats in mainland Britain, in keeping with the tendency for island rodent populations to show elevated survival rates but reduced or delayed fecundity (Adler & Levins 1994).

Differences in densities between sites appear to be driven primarily by variable survival (and hence instantaneous rates of population increase) during the summer and perhaps autumn, but not during other time periods, which supports the hypothesis that marine derived trophic subsidies vary spatially, being greatest on Carn Mor and least in Village Bay, both during the months when seabirds come ashore to breed and with a lasting effect afterwards. There was little evidence for spatial variation in survival or fecundity outside of this period although densities often still varied significantly, suggesting that any marine subsidies may continue after the seabirds have left, given that Carn Mor continues to support greater densities of mice throughout much of the year.

CHAPTER 5

Discussion

The aim of this study was to investigate and quantify some of the core ecology of *Apodemus sylvaticus hirtensis*. To that end, this thesis presents data on i) the basic morphological traits of weight, body length and tail length and examines how these vary with age, sex and geographical location, ii) breeding phenology and how this varies with age, sex and location, iii) population densities, free from edge effect bias, and how they vary temporally, geographically and between sexes and iv) population rates of change and the component processes of survival and fecundity and how these vary temporally, geographically and between sexes. Specific findings have been discussed in detail in the relevant chapters, but there are some broader themes which have emerged during the course of the study which are discussed here, as well as possible implications for the future management of the mice and ideas for further work.

5.1 Geographical variation and inter-species interactions

Substantial and frequently significant geographical variation was observed in some aspect of every biological metric examined in this study, including body weight and condition of adult and sub-adult mice, breeding phenology of the Adult 1 age class, overall population densities and survival rates and associated rates of population change during the breeding season. Although all three sites were not always clearly separated and differences were not always consistent through time, there was strong overall pattern whereby mice tended to be larger, in better condition, more numerous and showed higher survival on Carn Mor than elsewhere, with the inverse true of Village Bay, while Glen Bay tended to occupying a middle ground. Taken together, these differences point to a substantial difference in habitat quality between the three sites.

Although a number of factors such as microclimate and quality of nesting sites could be involved, it seems likely that the primary driver for these differences is the quality of the food supply, and work is underway to quantify these differences (see section 5.4, below). Regardless of whether or not the mice directly predate seabirds, it seems highly probable that marine trophic subsidies, due to the summer presence of the seabird colony on Carn Mor but with effects persisting throughout the year, have a considerable impact on the fitness of mice living there and the population carrying capacity of the environment. The morphological and population level characteristics of Glen Bay and Village Bay tended to be less distinct, and potential differences in diet between these two sites are less clear. Both sites host only small numbers of sea birds and consist mainly of short grass cropped low by sheep. However, the sheep have a strong tendency for non-random dispersal in favour of higher quality grazing (Jones *et al.* 2006) which are most common in the Village Bay area, and the grass supply there is under intense grazing pressure. It is possible that this could reduce the supply of grass seeds, which are known to form an important part of the mouse diet (Harrison 1933), relative to other sites. Grazing pressure has also been found to increase silica levels in plant material which were inversely correlated with population growth in a study of voles (Massey *et al.* 2008). Either of these mechanisms could play some role in suppressing the population growth in Village Bay.

The interaction between these two species may be more complex than this, however, as sheep corpses across the island were frequently found to show signs of being eaten by mice, particularly the fleshy areas of the head and mouth, and the tendons at the back of the heel (pers. obs). As sheep mortality tends to be heaviest between February and April, it is conceivable that cadavers may form an important localised and seasonal food resource for some mice towards the end of winter. The crash in the sheep population in the spring of 2012 did not coincide with any change in mouse survival however. Neither was there any subsequent change in fecundity in the summer. It is a shame that data collection ended in September of 2012, because if grazing does impact seed production then reduced sheep numbers could potentially affect mouse fecundity or survival later in the year, or even in the following year.

5.2 Insular traits

Across the various metrics considered in this study, a consistent pattern emerges of traits typical of the island syndrome in rodents. As well as their famed gigantism, the mice demonstrate reduced sexual dimorphism compared to mainland populations. This may be due to reduced male-male competition either as a result of the breakdown of territoriality in the face of high population densities or smaller consequences to fitness from the competitive exclusion of smaller males from prime habitats when interspecies competition and predation is lacking. Although not extreme compared to some example of island rodent populations, densities equalled or exceeded those found in favourable habitat such as woodland in mainland Britain. High densities may drive changes in life history strategy by reducing reproductive output (as seen here in the shortened breeding season and tendency to delay reproduction until the second year of life), which in turn drives selection for greater body size and survival in both sexes (also seen in this study). Additionally, the high incidence of tail tip albinism and the presence of some piebald individuals points towards a population with low genetic diversity and high inbreeding or founder effects.

Although this study does not explicitly examine the validity of the sub-species status of *A. sylvaticus hirtensis*, these traits taken together with certainly point towards the mice on St Kilda being highly isolated from outside gene flow and strongly adapted as an island ecotype.

5.3 Management and conservation considerations

Overall, the outlook for the field mice on St Kilda appears positive. They are distributed widely across Hirta and Dun, as they were half a century or more ago, and show population densities that are similar to favourable habitats elsewhere in Britain and Europe. They appear to have retained the generalist tendencies of *Apodemus* elsewhere, making the most of the limited habitats and food resources available on the islands and undergoing rapid population increases when conditions are favourable. There seems little immediate cause for concern for this subspecies, assuming maintenance of the *status quo*.

However, three years of data is far too little to observe any long term trends in population size, and The National Trust for Scotland may wish to consider regular monitoring of the populations. A minimal approach to such monitoring might consist of a single line of traps along a linear feature such as the head dyke at a reasonable distance (~100m or more) from human habitation (perhaps centred on the location of the trapping grid in this study). Twenty traps spaced 10m apart and set for five consecutive nights, with mice marked individually (ear punches are a cheap method which works well for relatively small numbers of mice and requires little training) should provide simple count data that would be comparable between years. Trapping before juvenile recruitment begins in earnest in June would provide a manageable number of mice for inexperienced personnel to handle and give a measure of the minimal annual population size at the locality.

A more comprehensive approach would be to explicitly estimate density at one or more sites. SECR modelling appears to provide a robust method for quantifying and comparing population densities in the face of large variation in range sizes between sites, seasons and sexes. The advantage of a SECR approach, providing that the spatial layout of the traps is known and that the traps are not highly saturated with mice, is that the results should be relatively unbiased by variation in grid size or the number of traps. Simulations presented in Chapter 4 show that accurate estimation of mouse density around the Village Bay grid could be achieved with just 37 traps set for 4 nights, and mildly downwardly biased estimates with as few as 20 traps along the Head Dyke.

Should rats or other predators ever become established and require a poison based eradication campaign, then the range size data presented in Chapter 3 will prove useful in deciding the spacing of bait stations. It is a slightly unhappy coincidence that the area where rats are most likely to come ashore (Village Bay) is also where poisoning would have the greatest impact on the mouse population, due to a greater range size there compared to the other grids, but as long as island-wide extinction was avoided then the area should eventually re-populate and in a worst case scenario mice from Dun could be used to repopulate Hirta. During the successful Canna rat eradication programme (Bell *et al.* 2011) poison bait was distributed at distances of 50m and 100m across the entire island and enough field mice (also of a giant strain) survived to apparently repopulate quickly. Mice on St Kilda appear somewhat more susceptible to 100m poison spacing given than SECR revealed range diameters of almost 200m for males in Village Bay in summer (ranges were smaller for females and in other locations and seasons) so potential spacing may need to be revised upwards depending on season and location.

5.4 Further work

5.4.1 Dietary analysis

Of primary interest, given the findings discussed, is the continuing stable isotope analysis of mouse blood samples and prey items collected during this study, with the aim of assessing population and individual level dietary niches. In particular, this work aims to assess the influence of dietary niche on ecology and phenotype by correlating differences in morphology, density and population dynamics between the three study grids with dietary variation.

Carbon and nitrogen isotope values have been obtained for 588 mouse blood plasma samples and 339 dietary items, spread across the three years and three sites, and preliminary results (Tony Bicknell, unpublished data) indicate significant variation in both carbon and nitrogen isotope ratios between grids, with a strong marine carbon signature in mice on Carn Mor compared with elsewhere, whilst nitrogen signatures suggest an elevated trophic level of mice on both Carn Mor and Village Bay grids compared to the Glen Bay grid, although there also appears to be a strong grid*season interaction in play in both carbon and nitrogen signatures. Isotope mixing models need to be performed to ascertain the precise components of mouse diet and determine if these differences are due to genuine dietary variation or simply local variation in prey isotope signatures due to environmental factors such as, for example, a broad marine signature enrichment of the Carn Mor food chain due to bird guano. Nevertheless, once this analysis is complete, it should provide a much clearer understanding of the preferred diet of the mice and how diet is correlated with mouse morphology and population dynamics, and perhaps allow many of the conclusions discussed elsewhere in this thesis to be stated more strongly. Furthermore, if the dietary analysis strongly suggests direct consumption of bird material by mice at Carn Mor, then, since the birds are also of high conservation concern, more intensive studies of the true extent of live predation versus scavenging by the mice should be instigated, probably through the use of camera monitoring of petrel and puffin burrows.

If the isotope analyses confirm dietary differences between grids, and given that generalist small mammal species such as *A. sylvaticus* typically exhibit higher plasticity than specialists (Bozinovic *et al.* 2011), particularly in climatically variable temperate habitats (Naya *et al.* 2008), then the mice of St Kilda could potentially make an interesting study organism for investigating plasticity in natural populations at small spatial scales. Numerous behavioural and physiological differences have been observed in small mammals in response to variability in food supply (Jacobs 1996, Ehrhardt *et al.* 2005, Gutman *et al.* 2007, Zhao *et al.* 2009) but the majority of these tend to be either laboratory studies or focused on differences over large latitudinal or attitudinal ranges, whereas St Kilda could potentially provide quantifiable differences between populations within 1-2km of each other, or less. However, such studies may not sit easily with the current focus on conservation on the islands.

5.4.2 Genetics

A large number of ear tissue samples are available from the mice caught during this study, which could from the basis of a number of potential genetic investigations. Firstly, it would be interesting to apply modern phylogenetic techniques to determine the genetic origin of the St Kilda population, a question which is of considerable interest to the public that visit the islands. Secondly, there is scope for investigation of genetic diversity and structure amongst the sub-populations on Hirta and on Dun. Initial investigation of a suite of 8 microsatellite markers suggest there is some degree of genetic structuring between the two islands and possibly within Hirta (Robertson 2011). However, this data needs expanding with an increased number of individuals and markers (some have already been identified) in order to strengthen the conclusions. Thirdly, if sufficient additional microsatellite markers could be identified to compensate for the low allelic diversity, then pedigrees could potentially be constructed in order to examine the reproductive success of individuals and the factors that may affect reproductive fitness in *A.s. hirtensis*. Finally, there is scope for examining whether or not the gigantism of the mice on St Kilda has a genetic component. Common garden experiments could test differences in growth between mice from St Kilda and the mainland, and between mice from different locations on Hirta. Single Nucleotide Polymorphism (SNP) sequencing is currently being used to identify loci involved in controlling body weight in laboratory mice and islands populations of house mice that exhibit gigantism (Chan *et al.* 2012), and should be adaptable for use with *Apodemus*.

5.4.3 Distribution elsewhere in the archipelago

There is a continuing nagging question as to whether or not mice are present on the other islands and sea stacs of the archipelago which are generally very inaccessible. The historical references tend to be vague and in some cases contradictory about the presence or otherwise of mice on Soay, Boreray and the two large stacs – Stac Lee and Stac an Armin. On the balance of probabilities, and given the lack of any sightings by seabird and sheep researchers, archaeologists or wardens (despite some baiting on Soay and Boreray), it seems unlikely. However, there is no record of anyone attempting to place traps during the occasional rare overnight trip to these locations. It would therefore be useful if some traps could be stored in the NTS facilities on Hirta, and an effort made to disseminate them to any future overnight trippers to the other islands, even if just to confirm their absence.

5.4.4 Parasite survey

As well as competition or predation from introduced rodents, disease introduction is increasingly considered a major risk for island species which can suppress population fitness or even directly contribute to extinction events (e.g. Wyatt *et al.* 2008). It would be of considerable strategic benefit to create a snapshot of diseases found in the mouse population prior to potential introduction. Methods such as salt flotation and PCR-based diagnostic are well established for surveying mouse diseases (e.g. Henderson *et al.* 2013) and have been successfully applied to wild populations of *Apodemus sylvaticus* (Knowles *et al.* 2013). A one-off collection effort of blood and faecal samples would be sufficient for a snapshot and would only need to be repeated in response to an accidental introduction or suspected disease outbreak.

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