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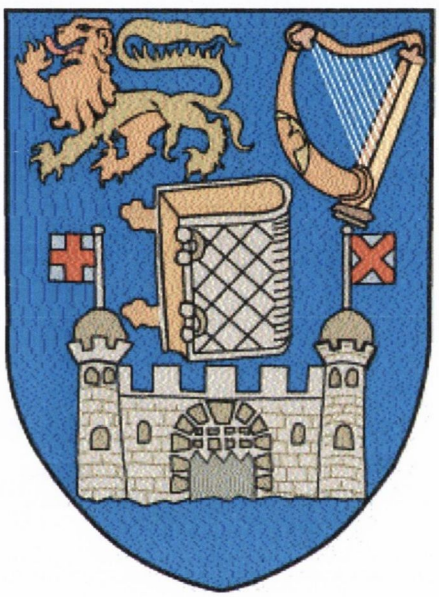
Parasites in a host species' invasion: a unique small mammal model system

Karen Loxton



A thesis submitted in the fulfilment for the Degree of Doctor of Philosophy to the University of Dublin, Trinity College.

January 2015

DECLARATION

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SUMMARY

It is becoming increasingly evident that biological invasions result in altered disease dynamics in invaded ecosystems, with knock-on effects for native host communities. Invasive species may acquire native parasites, acting as reservoirs of infection (spillback) or interfere with native parasite transmission, resulting in reduced risk to native hosts (dilution). Invasive species may also transmit novel parasites to native hosts (spillover). Furthermore, through various means, invaders lose a proportion of their parasite fauna resulting in regulatory release and improved performance in the new habitat (Enemy Release Hypothesis). The present study investigated disease dynamics in an invaded ecosystem, using the helminth communities of the native wood mouse (*Apodemus sylvaticus*) and the invasive bank vole (*Myodes glareolus*) in Ireland.

Native wood mice were collected over 2 years from four sites in Ireland; 2 sites where bank voles are present and 2 sites where the bank vole has not yet invaded. Quantitative analyses revealed significant spatial and temporal variation in the helminth communities of wood mice. Results also showed that wood mice in uninvaded locations have significantly higher burdens of the dominant gastrointestinal nematode *Syphacia stroma.*

In parallel, bank voles were collected over 2 years from 2 sites in Ireland. A survey of their helminth parasites revealed that the introduced bank vole has lost much of its helminth fauna. Three helminth species were recovered from bank voles. Two species, *Aonchotheca murissylvatici* and *Mesocestoides spp.* were most likely acquired in Ireland while the third species, *Aspiculuris tetraptera* likely co-invaded along with the bank vole. Despite the acquisition of native parasites, the invasive bank vole in Ireland has a much lower helminth species richness compared to bank voles in indigenous ranges.

Within bank vole invaded sites, quantitative comparisons of the helminth communities of bank voles and wood mice showed wood mice were significantly more parasitised in terms of helminth species richness, prevalence and abundance of infection. Wood mice and bank voles shared two helminth species; *A. murissylvatici* and *Mesocestoides spp*. Prevalence and abundance of both helminths was greater in bank voles. Moreover, prevalence and abundance of *A. murissylvatici* was greater in wood mice in the presence of voles and *Mesocestoides spp*. was only found in wood mice in invaded sites.

The major finding of this thesis is that there are significant differences in helminth parasitism between the introduced bank voles in Ireland and bank vole populations in indigenous ranges, as well as between introduced bank voles and native wood mouse.

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CHAPTER 1

General Introduction

1.1 Parasites in Ecology

In 1880 Ray Lankester lamented the parasitic lifestyle as the degeneration of the "..active, highly-gifted crab, insect, or annelid" to a "...mere sac, absorbing nourishment and laying eggs" (Lankester 1880: p. 33). While parasites will never be afforded the charismatic status of their free-living hosts, over a century's worth of research has revealed parasites are far more than the passive degenerates envisioned by Lankester. Today parasites are recognised as major drivers of evolution and as important components of ecological communities (Hudson *et al.* 2006; Schmid-Hempel 2009; Tompkins *et al.* 2011; Hatcher and Dunn 2011). Though small, parasites are abundant; their biomass reaching levels comparable to top predators in certain estuarine systems (Kuris *et al.* 2008). Incorporating this parasitic biomass into food webs has revealed parasites significantly affect food web topology, influencing energy flow, connectance and food web links (Lafferty *et al.* 2006; 2008). By affecting the outcome of competition between hosts, parasites act as keystone species, structuring free-living communities (Hatcher and Dunn 2011). So integral is the role of parasites in ecosystems and community structure, that Hudson *et al.* (2006) considered parasite diversity a sign of ecosystem health.

Parasites are defined broadly as organisms which exploit other organisms (the host) as a habitat and for nutrition and in doing so cause some degree of harm (Anderson and May 1978). By this definition parasitism is probably the most common life-style on earth (Windsor 1998). Parasitic organisms are divided into two broad categories according to the relationship they establish with the host. Microparasites are small, have short generation times with direct multiplication within the host and induce durable immunity. Viruses, bacteria, fungi and protozoa are included in this category. Macroparasites are larger, tend to have longer generation times than mircroparasites and do not

induce long term immunity. Macroparasites rarely multiply directly within the definitive host, though asexual multiplication does occur in intermediate hosts such as in many trematode miracidia and some species of cestode in the family Taeniidae (Whitfield and Evans 1983). Macroparasites include helminths, parasitic arthropods and other metazoan parasites (Anderson and May 1978). The following literature review will focus mainly on macroparasites, discussing microparasites where appropriate.

1.2 Parasite Assemblages

A central aim in community ecology is the search for the determinants of patterns of species distributions, abundances and interactions (Poulin 2007a; Mittelbach 2012). Parasites and the communities they form have a number of features which make them particularly useful in investigating ecological communities at different scales. Parasite communities within hosts are discrete, comparable replicates that are replicable in time and space, allowing for rigorous statistical analyses.

Margolis *et al.* (1982) and Bush *et al.* (1997) defined the terms to be used when discussing parasite communities, identifying three levels:

- Infracommunity - a community of parasite infrapopulations within a single host. An infrapopulation is all the individuals of a single species of parasite within an individual host, or specific organ, at a particular time. Infracommunities are short lived, lasting only as long as the lifetime of the host. They are also dynamic with constant recruitment and death of parasites.
- Component community - all infrapopulations of parasites associated with some subset of a host population (e.g. within a defined geographical location). Unlike infracommunities where the host defines the boundaries of the community, component communities have no discrete boundaries. As such they are artificial constructs determined by the researcher.

- Compound community - all potential parasites of a host species, including free-living stages.

Combes (2001) proposed a concept of ecological and biological filters which determine the structure of parasite communities at these various scales. Encounter filters exclude hosts that a parasite will not encounter because of ecological or geographic reasons. Compatibility filters excludes hosts in which a parasite cannot survive or develop for morphological, physiological or immunological reasons. These two core processes determine the distribution and abundance of parasites within and across host populations (Fig. 1.1).

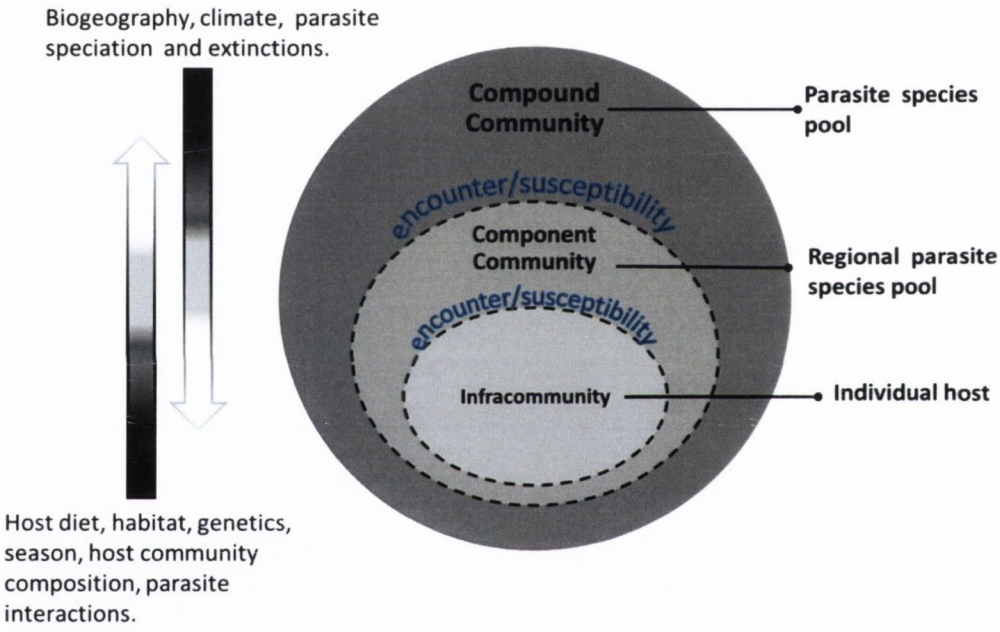


Figure 1.1 The hierarchical structure of parasite communities and the importance of factors affecting community structure at the various scales. Adapted from Coombes (2001).

1.2.1 The Compound Community

Traditionally, studies in parasitology have emphasized the importance of local factors in shaping parasite communities (Guégan *et al.* 2005). However, as these communities represent a subset of the parasite species available, the mechanisms shaping diversity of the compound community of a host species ultimately determine component and infracommunities. The compound communities of modern species have been inherited from ancestral species and modified over their phylogenetic

history (Poulin 2007b). Phylogeny may therefore be one of the most important determinates of a host species parasite richness (Poulin *et al.* 2011a). New species are added to the parasite fauna in two ways; through speciation within a host lineage creating congeneric species (Kennedy and Bush 1992) and host switching (Hoberg and Klassen 2002). Vertebrates appear to differ in the rates of within-host speciation and parasite host switching. While mammals have greater rates of within-host speciation, bird and fish parasite communities are formed predominately by host-switching events. This may be due in part to large mammalian herbivores, whose size and restricted diets provide many similar niches, while reducing the acquisition of novel food borne parasites (Mouillot and Poulin 2004). Different modes and rates of parasite diversification may be part of the explanation for differences in parasite diversity among vertebrates such as birds and fish (Kennedy *et al.* 1986). Parasites are lost from the fauna through extinction of a species in all host communities.

Parasite communities are more similar across populations of the same host species than between different host species (Bordes and Morand 2008) suggesting host species traits influence parasite diversity. Combes (2001) reviewed sixteen different hypotheses to explore why parasite diversity differs among host species. While many of these remain to be tested, of those that have, none have emerged as strong, exclusive predictors of parasite diversity (Bordes *et al.* 2010). Often the direction of the relationships found between predictors and diversity is inconsistent among studies, and the predictive power of the significant studies is low (Poulin 1997; 2004). When corrections for phylogeny and sampling bias are made, many of the relationships either become weaker or disappear altogether (Poulin 1997). However, a recent meta-analyse controlling for phylogeny and sampling bias found the best predictors of macroparasite species richness in animal, plant and fungal hosts were host body size, size of host range and host density (Kamiya *et al.* 2013).

1.2.2 Component Communities

Component communities are subsets of the parasite fauna and are assembled over evolutionary time, formed by species invasions, speciation, extinctions, colonisations and hosts switching (Poulin

2007b). While the overall species richness of parasite communities appears to be a host species characteristic, the composition of component communities varies within populations of the same host species (Poulin 2007b; Kennedy 2009). This variability may be because component communities are truly random assemblages of the available parasite species pool, or as a result of host traits and environmental characteristics. The patterns observed in the composition of component communities and possible mechanisms are discussed below.

1.2.2.1 Decay of similarity with geographical distance

How similar biological communities are to each other can be predicted by their proximity to each other. This concept, known as distance decay, is a commonly observed pattern in free-living communities (Nekola and White 1999; Soininen *et al.* 2007) and may occur by three mechanisms (Soininen *et al.* 2007)

1) Organisms have limited dispersal capabilities and similarity will decay even in homogenous environments.
2) Barriers to the dispersal of organisms exist in the environment.
3) Decreasing similarity in climatic and physiochemical variables will exclude some species and suit others.

Geographical distance *per se* is not the cause of dissimilarity, but rather a surrogate for these non-mutually exclusive processes.

A similar pattern has been found in parasite component communities. The farther apart a population of hosts are, the more dissimilar their component communities. (Poulin and Morand 1999; Poulin 2003; Poulin and Krasnov 2010). Parasites have limited ability to spread over geographical distances, being reliant on their most vagile host. Therefore host vagility may influence similarity and richness of component communities. The component communities of species with limited dispersal capabilities, such as freshwater fish and amphibians, are more distinct from each other than species in continuous environments such as marine fish, birds and mammals (Poulin

1997; Oliva and González 2005; Poulin and Krasnov 2010). Isolated communities, even if adjacent to each other, will have limited opportunities for exchange of parasite species, and may develop different communities due to stochastic events. However, similarity between communities can be increased if a number of parasite species have complex life cycles involving vagile hosts, such as birds, which are able to move freely between habitats (Esch *et al.* 1988).

In studies that have investigated distance decay at larger scales, decreases in community similarity may be explained by environmental changes in climatic and biotic gradients that determine species establishment (Nekola and White 1999; Soininen *et al.* 2007). For many helminths, the physical and chemical aspects of the environment influence free-living stages and intermediate hosts, and may override patterns of distance decay. Stickleback parasite communities showed significant decay in similarity with distance across the stickleback geographic range, though similarity was greater between communities that shared similar habitats independent of distance. How closely habitats resembled each other (based on salinity) was as important for component community similarity as the geographical distance between populations (Poulin *et al.* 2011b).

1.2.2.2 Environmental Factors

Local abiotic and biotic conditions account for the variation between communities by modifying transmission success. Free-living stages of helminths are exposed to varying degrees of temperature, salinity, pH and oxygen, but have species specific limitations to what they can tolerate (Pietrock and Marcogliese 2003). Hatching and the development of larvae in faeces is primarily dependent on temperature and moisture (Stromberg 1997) and changes in temperature stimulate trematode cercarial release in snails (Poulin 2006). The significance of climate variables on host-parasite interactions is evidenced by changes in the exposure of hosts to parasite infections that is presently occurring due to global climate change (Harvell *et al.* 2009; Hernandez *et al.* 2013).

The diversity of other organisms in the environment can also affect transmission rates. Predation on parasite infected prey is very common in certain food webs (Lafferty *et al.* 2006). While trophic

transmission is used by some helminths (Johnson *et al.* 2010) infective stages that are consumed by a non-host species will be lost from the local pool. Predation may be particularly high in communities with large numbers of generalist predators such as estuarine habitats (Lafferty *et al.* 2006). Animals will also consume free-living stages indirectly; dung beetles (Scarabaeinae) significantly reduce the abundance and availability of helminth eggs spread by animal faeces (Nichols *et al.* 2008). Predation on parasites is therefore an important mechanism of the dilution effect (a reduction in parasite transmission with increasing community diversity) (Johnson *et al.* 2010).

1.2.2.3 Host Density and Size

One of the core concepts of mathematical models used to explore parasite transmission is the density of the host populations (Anderson and May 1978, May and Anderson 1978). In these models, encounter rates between host and parasite is a function of either the density of infected hosts (density-dependent) or the proportion of the population infected (frequency-dependent). Parasites that are directly-transmitted or those with free-living stages are modelled as having density-dependent encounter rates, while systems where the number of contacts made between individual hosts does not increase with density, such as sexually transmitted diseases, use frequency-dependent models (McCallum *et al.* 2001; Begon *et al.* 2002).

Parasites with density-dependent transmission require a minimum host density for the establishment, spread and persistence of a parasite. Below this threshold, contact rates between susceptible hosts and infectious propagules become too few to maintain infection or allow establishment (Anderson and May 1992). Epidemiological modelling also makes use of the basic reproductive rate of the parasite (R_0) to determine whether a parasite will establish and persist within a host population. For macroparasites, R_0 is defined as number of successful progeny produced by a single female parasite introduced into a new population. If $R_0 > 1$, the parasite will be able to invade and persist in a host population (Poulin 2004). In contrast, parasites with frequency-

dependent transmission do not require a minimum threshold and rates of transmission and are not dependent on host density.

Theory therefore implies that hosts at high population densities will be able to support a greater diversity of parasite species. There is some empirical evidence for this: host density positively correlates with parasite richness across host species (Morand and Poulin 1998; Arneberg 2002; Nunn *et al.* 2003; Poulin and Mouillot 2004a) though the relationship is not universal (Morand and Harvey 2000). Across populations of the same host species the relationship between host abundance and parasite transmission can be obscured by a number of factors including climate and parasite life history and transmission mode. Therefore studies on wild hosts often provide a limited or even negative association between parasite prevalence/abundance and host density (Montgomery and Montgomery 1988; Haukisalmi and Henttonen 1990; Winternitz *et al.* 2012). For directly-transmitted helminths at least, host density has been shown to correlate strongly with parasite species richness and abundance (Arneberg *et al.* 1998; Arneberg 2002). Host density also emerges as one of the strongest drivers of parasite species richness in Bordes and Morand's (2011) meta-analysis.

1.2.3 Infracommunities

Infracommunities are subsets of the parasite species making up component communities, existing within a single host. These communities are more dynamic and shorter lived than component communities, with large rates of species turnover and are assembled over ecological time (Poulin 1997). A number of patterns have been identified in infracommunities.

1.2.3.1 Local and Regional Richness

Species richness at a local scale can be strongly related to regional diversity, or, local community richness can be independent of the number of species found regionally and structured by local processes (Cornell and Lawton 1992; Srivastava 1999). Local-regional plots have been used to determine the importance of local versus regional processes in structuring species assemblages (Srivastava 1999). A curve-linear relationship between local and regional richness suggests

communities are strongly structured by local processes, such as species interactions (Cornell and Lawton 1992). These communities are said to be saturated and interactive, and increases in regional richness have little impact on species composition (Srivastava 1999). A linear relationship indicates that local communities are non-interactive/isolationist and unsaturated, so that richer local communities are found in areas of high regional richness. Regional processes such as long distance dispersal and speciation will therefore determine the upper limit to the number of species in these communities (Cornell and Lawton 1992; Srivastava 1999).

For most free-living communities, a linear relationship has been found, and local communities do not appear to be saturated (Gaston 2000). In contrast, Kennedy and Guegan (1996) found a curvilinear relationship between maximal infracommunity richness and component community richness for helminth parasites of eels in Britain. The authors suggested that processes acting within the infracommunity limited species richness. However the generality of this relationship in parasite communities has been called into question (Poulin 2007b). Norton *et al.* (2003) investigated eels in Britain as well as Europe, which has higher helminth component richness than Britain. In contrast to the findings of Kennedy and Guegan (1996), the authors found a linear relationship between infracommunity and component community richness in eels

Indeed, saturation of helminth communities appears to be rare. Across birds and mammals the relationship between maximum infracommunity richness and component community richness is linear (Poulin 2007b). The absence of saturation suggests that infracommunities are random assemblages of the species available from the component community (Norton *et al.* 2003; Poulin 2007b).

1.2.3.2 Interactions between parasite species

Interactions between species are an important force structuring free-living communities (Bonsall and Hassell 1997). As most animals in natural populations are infected with more than one parasite

species (Behnke *et al.* 2001a; Cox 2001; Lello *et al.* 2004; Bordes and Morand 2011), intraspecific parasite interactions potentially structure parasite communities.

There is convincing evidence from laboratory studies that interactions between parasite species occur (Behnke *et al.* 1978; Behnke *et al.* 2001a; Cox 2001). These interactions may be direct and/or indirect. Direct interactions include competition for resources, space and attachment sites that lead to changes in resource use by affected helminths (functional response) (Poulin 2001).The now classic studies by Holmes (1961; 1962) showed shifts in preferential site attachment and reduced growth in the cestode *Hymenolepis diminuta* when it co-occurred with the acanthocephalan *Moniliformis dubius*.

Indirect interactions are host-mediated, whereby parasites alter the host environment via the host immune system. Immune-mediated interactions may result in synergistic interactions (apparent facilitation), as when the immunosuppressive activities of one parasite species benefit co-infecting species. For example, infection with *Heligosomoides bakeri* reduces the acute response to a second nematode, *Trichinella spiralis*, in mice (Behnke *et al.* 1978). Antagonistic interactions (apparent competition) occur between antigenically similar species which elicit cross-immunity decreasing the success of other parasite species (Behnke *et al.* 2001a; Pedersen and Fenton 2007).

Though laboratory studies clearly show interactions between helminths under experimental conditions, studies in wild populations have had mixed outcomes (Kennedy 2009). Strong interactions have been found in species-rich helminth communities of birds (Bush and Holmes 1986), while other studies have concluded parasites communities are weakly interacting (Haukisalmi and Henttonen 1993; Poulin 2001; Behnke *et al.* 2005). There are a number of methodological issues that can obscure the presence of parasite species interactions. Most studies are cross-sectional, giving data from a single time point where the sequence of parasites acquisition cannot be determined. The 'priority effect' (Poulin 2001) occurs when the interactions between helminths depends on the order of establishment of species. Karvonen *et al.* (2009) showed how positive associations, based

on correlative data sets, could break down in infection experiments. Infection by one parasite species effectively immunised the host to infections by other species, however the effect depended on the sequence of infection.

Fenton *et al.* (2010) argued that the way in which parasite data is analysed generates much of the lack of consensus on the role of parasite interactions in wild hosts. Studies seeking interspecific interactions have generally been observational, undertaken at the level of the host population using two broad approaches; presence and absence data is used to test species co-occurrences against null models, or abundance data is used to test for pairwise associations between parasite species (Pedersen and Fenton 2007). Using mathematically generated parasitological data Fenton *et al.* (2010) concluded that these standard statistical approaches used to detect interactions in observational data, particularly correlation-based ones, were unreliable. Recently Fenton *et al.* (2014) tested the standard statistical approaches against real parasitological data generated from perturbation experiments in small animal communities where the interactions between parasite species were known. The authors confirmed that standard approaches were unreliable for detecting intraspecific parasite interactions in wild populations.

The behaviour and ecology of the host and/or parasite can result in species co-occurring, rather than associations resulting from interspecific parasite interactions (Behnke *et al.* 2001a). Johnson and Buller (2011) found a consistent positive correlation between co-occurring trematodes from field data at the landscape level due to the ecological similarity of the parasites. Positive correlations were also found at the within-host scale due to differences in host exposure and immunity. However, using experimental infections, the authors found negative interactions between the trematodes, likely due to apparent competition as a result of cross-immunity.

The aggregated nature of parasite distributions (Shaw and Dobson 1995, see section 1.3) makes the likelihood of species encountering each other too low for competitive interactions to occur in nature (Poulin 2001). Aggregation can also cause certain sub-groups of hosts to be more prone to

combinations of parasites. Helminth species that are otherwise rare in Finnish Lapland reach a prevalence of up to 50% in old and post breeding female voles in late summer (Haukisalmi *et al.* 1988). Studies therefore need to include sufficient numbers of each host functional group in order to detect interactions.

Species rich parasite communities might be expected to be more interactive than species poor ones due to the increased likelihood of co-infections. Holmes and Price (1986) viewed parasite communities as existing along a continuum from isolationist to interactive, so that the structuring effects of interspecific interactions ranged in importance. Compared to birds, helminth communities of fish are depauperate (Kennedy *et al.* 1986). The relatively more diverse and abundant parasite communities of birds and mammals should then be more interactive than fish. However marine fish parasite communities range from isolationist to interactive (Poulin and Luque 2003) and no evidence of interactivity was found in the species rich parasite communities of opossums (Ellis *et al.* 1999). The majority of parasite communities of vertebrates appear to isolationist (Poulin 1997) and how important interactions are in structuring communities is still an open question.

1.3 Aggregation

The distribution of parasites in hosts is most often characterised by an aggregated pattern: a few hosts have many parasites and most carry few or no parasites (Shaw and Dobson 1995; Shaw *et al.* 1998). This pattern of parasite distribution is so pervasive that Crofton (1971) proposed it as a defining feature of parasitism and Poulin (2007a) has described it as a general law of parasitology. Parasite aggregation can be quantified as the ratio of the variance to the mean number of parasites per host. If the mean number of parasites per host equals the variance, the distribution is said to be random. As the ratio increases the distribution moves away from randomness toward aggregation, becoming more aggregated as the variance-to-mean ratio increases (Poulin 2007b). Determining how parasites are distributed in hosts, and the mechanisms driving distributions, is fundamental to

the wider understanding of epidemiology and disease dynamics. The most heavily infected individuals may be the hosts spreading infectious stages and maintaining disease persistence.

Shaw and Dobson (1995) regressed log variance against log mean number of parasites per host across 250 wildlife populations. They found most of the variation in log-variance (87%) was explained by log-mean burden. The small amount of variability in parasite aggregation not explained by mean burden is thought to be due to differences in host exposure (extrinsic factors) and host susceptibility (intrinsic factors) to parasites.

1.3.1 Extrinsic Factors

1.3.1.1 Seasonal variation

Seasonal changes in the prevalence and abundance of helminths in hosts are well established (Tenora *et al.* 1979; Abu-Madi *et al.* 2000; Cattadori *et al.* 2005). Seasonal fluctuations in infection are caused by a combination of factors, including changes in parasite rates of development, changes in host behaviour, physiology and population structure. These factors interact resulting in changes in both the exposure and susceptibility of hosts to parasites throughout the year (Montgomery and Montgomery 1988; Dowell 2001; Altizer *et al.* 2006). Transmission of helminths with intermediate hosts will be restricted to times when such hosts are available. Invertebrates in particular are strongly regulated by seasonal changes in abundance (Wolda 1988) and will be available as hosts and prey to differing degrees throughout the year.

Seasonal changes also affect hosts in ways that modify parasite transmission. Birds and mammals show seasonal changes in immune activity, upregulating their immune activity in response to winter stressors such as low temperatures and reduced food availability (Nelson 2004; Martin *et al.* 2008). During spring and summer conditions are more favourable to growth and reproduction, however less energy is available for immune responses (Sheldon and Verhulst 1996; Martin *et al.* 2008). Reproduction and lactation are energetically demanding (Speakman 2008) and are associated with greater helminth intensities (Festa-Bianchet 1989; Cattadori *et al.* 2005). Males also suffer a

reduction in immune function during the breeding season as stressors such as energetic courtship displays and aggressive territorial encounters result in decreased resistance to parasites in several species (Klein 2000).

Changes in host population age structure occur throughout the year. Seasonal breeding occurs in many higher vertebrates. Summer declines in helminth burdens are due to the influx of new hosts during breeding seasons, which causes a dilution effect and corresponding decline in helminth burdens (Bajer *et al.* 2005). The rest of the year the host population consists of individuals with immunological experience to parasites (Cattadori *et al.* 2005).

1.3.1.2 Spatial variation

Parasite propagules are unlikely to be evenly distributed in the environment as microhabitat environmental conditions affect both the distribution and transmission of parasite stages. For example, vegetation cover providing shaded and moist microclimates has been associated with greater abundances of *Toxocara* eggs in soil samples (Ruiz *et al.* 2001). This clumped spatial distribution can translate into aggregated distribution in hosts. Under experimental conditions the spatial distribution of cestode eggs (*Hymenolepis diminuta*) was found to influence the distribution of infection in the host beetle *Tribolium confusum*. The more aggregated the dispersal of eggs, the more aggregated pattern of infection found in the host population (Keymer and Anderson 1979).

In helminths with complex life cycles, habitats suitable for parasite, intermediate host and definitive host must intersect for transmission to be completed. Such habitats may be patchy in the wider environment resulting in areas of high transmission risk. Prevalence of the cestode *Echinococcus multilocularis* in foxes appears to depend on the habitat suitability for the intermediate host as well as for survival of helminth eggs. Spatial modelling showed that variation in environmental suitability for *E. multilocularis* eggs was the best explanation for aggregated infection in vole intermediate host (Hansen *et al.* 2004). Foxes whose territories include areas suitable for *E. multilocularis* egg

development will therefore have increased probability of encountering infected intermediate hosts as prey items

1.3.2 Intrinsic Factors

1.3.2.1 Sex

Differences between males and female hosts are also postulated to lead to differences in parasite burdens and species composition. Meta-analyses have found a greater intensity and prevalence of parasites in males, particularly in the higher vertebrates (Poulin 1996a; Schalk and Forbes 1997; Moore and Wilson 2002; Zuk 2009). The trend is by no means universal and there are many examples of parasites to which female hosts are more susceptible (Morales-Montor *et al.* 2004). However, a male-bias to parasitism is dominant in laboratory experiments (Zuk and McKean 1996; Schalk and Forbes 1997) so that the majority of hypotheses explaining sex differences deal with male bias.

According to the immunocompetence handicap hypothesis (ICHH), the male immune system is handicapped due to higher levels of androgens (Folstad and Karter 1992). Testosterone is required for expression of secondary sexual traits in mammals while simultaneously having an immunosuppressive effect. Testosterone-dependent traits are therefore hypothesised to provide an honest signal of a male's immune function (Folstad and Karter 1992). The ICHH provides a mechanism for parasite mediated sexual selection whereby females choose males by the evaluation of secondary sexual traits (e.g. feather brightness) as a proxy for parasite resistant genes (Hamilton and Zuk 1982). However, meta-analyses show only weak and inconsistent links between testosterone and immune function (Roberts *et al.* 2004).

An alternative hypothesis omits hormones and explains differences in immunocompetence with differences in life history and investment in immune function. This is based on Batemans Principle (Bateman 1948), and fitness related differences between the sexes. Females increase fitness through reproductive success by investing in longevity and immunity to improve future breeding

opportunities. Males invest in present breeding opportunities, enhanced growth or secondary sex traits at the expense of body condition and immune function (Rolff 2002; Moore and Wilson 2002; Zuk 2009). When it the female host who increase investment in growth over future breeding then they have been found to suffer the greater parasite burdens (Moore and Wilson 2002). As sex differences occur in insects and other invertebrates that lack testosterone (Zuk and McKean 1996), life history strategy may be a more inclusive theory for sex differences in parasite burden.

Other factors also cause sex differences in parasitism. Sexual size dimorphism (SSD) is common among animals, with male-biased SSD predominating in birds and mammals (Fairbairn 1997). A larger animal is able to host more parasites and more likely to be encountered by parasites through increased food intake and time spent foraging (Arneberg 2002; Moore and Wilson 2002). Dispersal rates also differ between sexes; in mammals it is often the male with the larger home range (Greenwood 1980, Pusey 1987). Having a large home range increases the opportunities for over lapping territories and exchange of parasites with other hosts (Wilson *et al.* 2003; Krasnov *et al.* 2012).

Determining if there is a sex bias to parasitism is an important part of understanding disease dynamics, though traditional parasite surveys may not always reveal the full story. Ferrari *et al.* (2004) showed that even where no sex bias in parasite burden was observed, males were responsible for driving parasite population dynamics. In the study, wild yellow-necked mice (*Apodemus flavicollis*) were treated with anthelmintics. Reducing parasite burden in males caused a reduction of the nematode *Heligmosomoides polygyrus* intensity in females, but similar treatment of females did not significantly reduce parasites in males. A later study showed *H. polygyrus* worms from breeding males were more fecund (Luong *et al.* 2010). Thus, even in systems where no sex bias in parasite burdens is found, one sex may still be responsible for driving infection rates.

1.3.2.2 Host Age

Changes in parasite intensity with age are frequently seen in studies of wild host populations (Montgomery and Montgomery 1988; Behnke *et al.* 1999; Bajer *et al.* 2005). The mechanisms underlying these changes are complex as host exposure and susceptibility to infection changes with age. In addition there is the uncertainty of the role of acquired immunity in wild populations (Woolhouse 1998; Duerr *et al.* 2003; Raffel *et al.* 2011).

The relationship between host age and parasite intensity has been used to explore changes in infection intensity with age. These generally take 3 main patterns; a linear increase in mean parasite intensity with age (Type I), an asymptotic increase toward a gradual levelling off (Type II) and a decline in intensity after an initial rise (Type III) (Fig. 1.2).

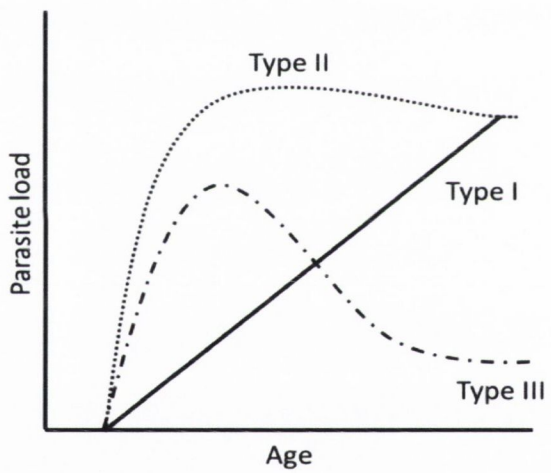


Figure 1.2 Three general patterns of age intensity curves. Type 1 (solid line), Type II (dotted line), Type III (dashed line). Adapted from Wilson *et al.* (2002).

These patterns have been found to be specific to the host-parasite system studied, and can vary between populations of the same host (Wilson *et al.* 2002). A Type I profile is a function of increased exposure to parasites over time. Type II will occur due to a balance between constant rates of parasite acquisition and parasite death. Both occur in the absence of an effective immune response (Wilson *et al.* 2002). The type III convex profile can be generated by a number of mechanisms

including parasite mediated host mortality (Anderson and Gordon 1982) and age-related changes in exposure (Boag *et al.* 2001).

Convexity (type III) in age-parasite intensity profiles may also be driven by adaptive immunity. The host immune response is generally density-dependent for macroparasites and cumulative exposure with age will result in a convex profile if adaptive immunity occurs (Anderson and May 1985). Evidence for adaptive immunity comes from patterns in age-intensity profiles known as peak shift. Woolhouse (1998) showed the age-intensity/prevalence profiles of several parasites and pathogens in human and animal populations depended on the transmission pressure. When transmission rates were low, infection rates increased slowly and infection peaked in older individuals. At high transmission rates, more individuals are exposed early, and infection intensity peaked in younger hosts. While acquired immunity to macroparasites is difficult to demonstrate conclusively in studies on wild hosts, longitudinal studies and those combining modelling and experimental infections have shown that acquired immunity is important in shaping host age-parasite intensity profiles (Cattadori *et al.* 2005; Tinsley *et al.* 2012).

1.3.2.3 Genetic and Immune differences

Individual hosts will vary in their ability to resist the parasites they encounter. This heterogeneity is highlighted by infection experiments that remove differences in exposure by subjecting individuals to identical infection protocols. Such experiments often result in variation in parasite loads between individuals of similar genetic strains suggesting variation in individual immune resistance which is under genetic control (Tanguay and Scott 1992; Dold *et al.* 2011). In wild animals the effect of living in a variable and unpredictable environment will result in even greater inter-individual variation in immune responses (Abolins *et al.* 2011). Immune responses are energetic and trade-offs required between immune responses and other processes such as growth or reproduction may require a host to down regulate immune-function (Martin *et al.* 2011). The magnitude of these trade-offs will differ between individuals as well as between populations of hosts living under different conditions.

1.3.2.4 Parasite traits

It is also important to consider intrinsic traits of parasites themselves when determining causes of aggregation in hosts. Parasite mode of transmission influences aggregation in hosts with trophically transmitted helminths having higher levels of aggregation (Shaw and Dobson 1995). Intermediate hosts as prey items transmit parasite infections as packets, so that patterns of aggregation in intermediate hosts can be transferred and even amplified in the definitive host (Vickery and Poulin 2002).

1.4 Costs associated with parasitic infections

Generally, parasitism is considered an exploitative interaction in which the parasite causes some degree of harm to the hosts (Bush *et al.* 2001). Macroparasites have been shown to reduce the survival and fecundity of their hosts (Pedersen and Greives 2008; Watson 2013). The detrimental effects on survival and/or reproduction associated with parasitism may be due to the physiological and metabolic damage caused by parasites, or the cost of generating and maintaining an immune response (Viney 2002). The direct costs associated with maintaining an immune system are difficult to measure, but observations that immune suppression occurs when food energy is restricted and that immune responses to infections require high levels of glucose and glutamine are suggestive (Lochmiller and Deerenberg 2000). The immune system is one of many competing physiological processes to which resources need to be allocated. Lactating bighorn ewes (*Ovis canadensis*), and ewes that had produced young early in life, show a decreased resistance to pathogens and parasites (Festa-Bianchet 1989) suggesting a trade-off between immune function and reproduction. While there is a need for more studies in wild populations to determine the magnitude of the costs parasites pose to hosts, the literature of parasites in livestock suggests costs of parasitism can be substantial (Lochmiller and Deerenberg 2000).

Through their effects on host fecundity and survival, parasites have the potential to regulate host populations. Anderson and May modelled the conditions under which macroparasites would

regulate hosts (Anderson and May 1978; May and Anderson 1978). The models incorporated two important features: the aggregated distribution of parasites and parasite effects on survival and reproduction. The models demonstrated that parasites having a moderate virulence, and which have a low degree of aggregation within the host population, are more likely to regulate hosts. Parasites with no impact on host population growth cannot regulate hosts, while parasites causing host mortality will reduce opportunities for transmission to other hosts (Anderson and May 1978; May and Anderson 1978).

Empirically demonstrating that parasites regulate wild populations has been more difficult. To begin with, a distinction needs to be made between true regulation and compensatory regulation. If parasites disproportionately affect those hosts already suffering reduced fitness unrelated to parasitism (e.g. due to competition, predation and resource limitation) parasites are said to act in a compensatory rather than regulatory manner (Holmes 1982). To demonstrate that parasites actually regulate host populations, changes in host population density need to be related to changes in parasite burdens (Wilson *et al.* 2002). Performing such experiments in wild populations is challenging, however a few large scale manipulations have been undertaken.

Hudson *et al.* (1998) were able to show that the cyclical population crashes seen in red grouse (*Lagopus lagopus scoticus)* could be reduced if the birds were treated for a gastrointestinal parasite. Grouse are infected with a caecal nematode that reduce condition and fecundity, which together with the low degree of parasite aggregation in grouse generated population instability (Dobson and Hudson 1992; Hudson *et al.* 1992). However, treatment of the nematode infection lessened, but did not eliminate, fluctuations in grouse population density, suggesting the parasite amplified the population cycles, but other factors were involved in driving them (Lambin *et al.* 1999). Pedersen and Greives (2008) demonstrated population crashes in white-footed mouse (*Peromyscus leucopus*) were intensified by intestinal parasite infection, but acorn masting was proposed as the main driver of the mice population cycles. Thus, much of the evidence on the role of parasites in host population

regulation suggests that parasites impact on regularly fluctuating populations in combination with other factors (Tompkins *et al.* 2011).

1.5 Parasites and Invasive Species

The breakdown of biogeographic barriers, either as unintended consequences of human activities or through deliberate introductions, has facilitated the global spread of species (Kolar and Lodge 2001; Taraschewski 2006). These biological invasions are now recognised as a major threat to biodiversity and ecosystem functioning (Sala *et al.* 2000). There is an increasing recognition that parasites are important in mediating the success of invasions by altering disease dynamics (Daszak *et al.* 2000; Prenter *et al.* 2004; Hatcher and Dunn 2011; Fig 1.3).

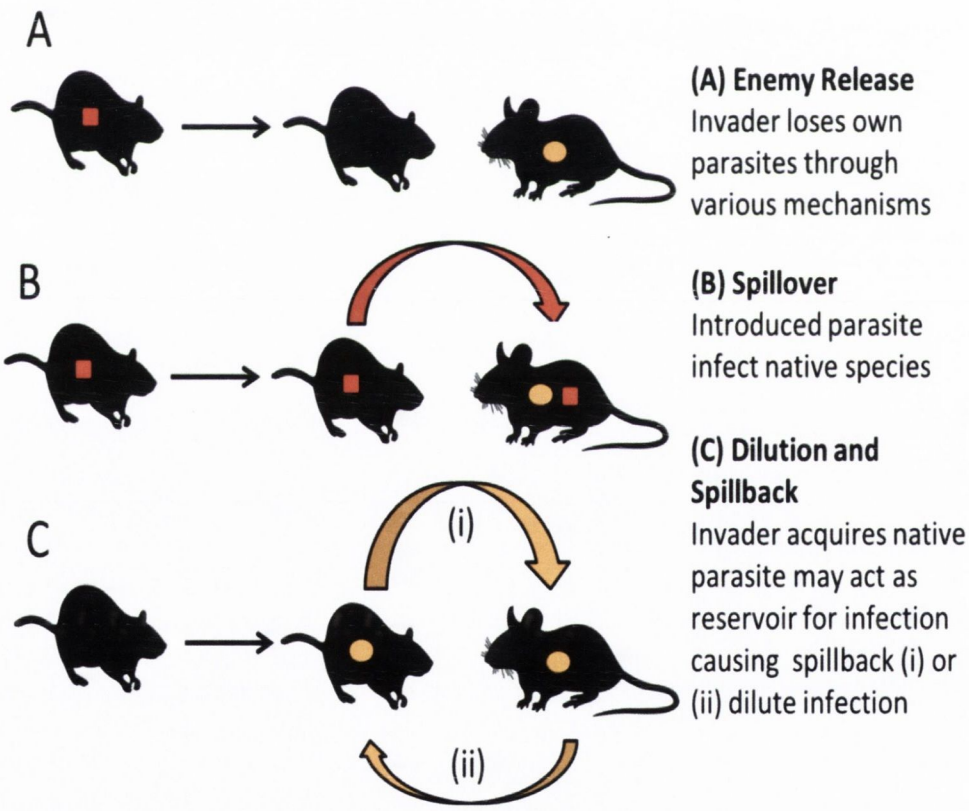


Figure 1.3 Altered disease dynamics in an invaded system. Adapted from Hatcher and Dunn (2011).

1.5.1. Parasite Lost and Parasite Regained

Studies across a range of plant and animal taxa have found that invasive species are less parasitised than conspecifics in indigenous ranges (Mitchell and Power 2003; Torchin *et al.* 2003; Torchin and Mitchell 2004). Parasites may be absent from introduced host population or go extinct due to low host densities or unsuitable conditions in the new habitat (Torchin *et al.* 2001; Mitchell and Power 2003; Torchin *et al.* 2003). The Enemy Release Hypothesis (ERH) proposes that the loss of co-evolved parasites during invasion releases invaders from the negative effects of parasitism, allowing hosts to reach higher population densities than in the indigenous range (Keane and Crawley 2002).

The loss of parasite in introduced hosts may allow for regulatory release and compensatory release. Regulatory release will occur when the host has low resistance to a parasite and is strongly regulated by it. Loss of the parasites results in direct changes to survivorship, fecundity, biomass or other demographic parameters. Compensatory release occurs when the host is well defended and loss of the parasite allows reallocation of resources from defence to other metabolic functions. Compensatory release will occur over evolutionary time as genotypes for costly defence are selected out of the population. These two pathways are not mutually exclusive and both may occur in an invasive population (Colautti *et al.* 2004).

Over time, invasive species will acquire new parasites from the native parasite species pool. However, these replacements on average make up less than a third of the parasites that have been lost by invaders (Torchin *et al.* 2003). The longer an introduced species inhabits its new range the more parasites it will accumulate (Cornell and Hawkins 1993) though the rate of accumulation varies. Torchin *et al.* (2001) reported an accumulation rate of 1 parasite taxon every hundred years in introduced green crab populations while Gendron *et al.* (2012) found a doubling of parasite richness in the invasive goby (*Neogobius melanostomus*) in 15 years. Poulin and Mouillot (2003) used the taxonomic distinctness of parasites, rather than species richness, and found introduced salmonids rapidly accumulate helminth communities as diverse as those in their original ranges.

1.5.2 Spillover

Those parasites that are introduced along with invasive hosts have the potential to spill over and infect native hosts (Fig. 1.3B). The spillover of novel parasites has been implicated in facilitating certain invasions, as appears to be the case in the spread of grey squirrels (*Sciurus carolinensis*) and replacement of native reds squirrels (*Sciurus vulgaris*) in the United Kingdom. Grey squirrels carry squirrelpox virus which is largely benign to them but causes high mortality in reds (Tompkins *et al.* 2002). As a result, empirical and modelling studies indicate that replacement of red squirrels by grey squirrels can be up to 25 times faster than in areas where the disease is present (Tompkins *et al.* 2003; Rushton *et al.* 2006). The high mortality in reds means that the virus would likely burn out in red squirrel populations, however the grey squirrels act as a reservoir for successive infection (Gurnell *et al.* 2006).

1.5.3 Spillback

Introduced species that acquire native parasites can potentially increase the total number of infective stages that native hosts are exposed to (Fig 1.3Bi). While spillback has received less attention in the invasion literature it is likely a common cause of altered diseases dynamics in invaded systems. A review by Kelly *et al.* (2009a) found that introduced hosts acquired a mean of 6.3 endemic parasites, with native parasites making up 67% of the parasite fauna of introduced species. Spillback of native parasites onto native hosts will depend on the competence of the introduced species as a host. In some of these new host-parasite associations the introduced species have proved to be extremely competent hosts with native parasites achieving higher prevalence, abundance and fecundity in introduced, compared to native hosts (Kennedy *et al.* 1991; Rauque *et al.* 2003).

1.5.4 Dilution

Where an introduced species acquires a native parasite but has low competence, it can act as a sink, reducing transmission and decreasing infection prevalence in the native host, creating a dilution

effect (Fig. 1.3Bii) (Norman *et al.* 1999; Holt *et al.* 2003; Thieltges *et al.* 2009). A number of different mechanisms are thought to result in dilution (Keesing *et al.* 2006), but the majority of empirical studies suggests dilution results from a decrease in encounter rates between susceptible hosts and parasites. Reduced encounter rates occur either indirectly through a reduction in density of hosts (susceptible host regulation) or directly through reduced encounter rates by density independent means (encounter reduction) (Keesing *et al.* 2006; Johnson and Thieltges 2010).

Many helminths have complex life cycles and rely on free living infectious stages. They therefore have the potential to be strongly affected by changes in community diversity and composition caused by species introductions (Johnson and Thieltges 2010). Under experimental conditions Kopp and Jokela (2007) recorded up to a 30% decrease in trematode infections in native fresh-water snails (*Potamopyrgus antipodarum*) when exposed together with the introduced snail *Lymnaea stagnalis*. Using field data, Kelly *et al.* (2009b) also found the abundance of introduced brown trout (*Salmo trutta*) in streams was significantly correlated with a reduction of helminth infections in native fish.

1.6 The study system: Helminth parasites of the native Irish wood mouse (*Apodemus sylvaticus*) and invasive bank vole (*Myodes glareolus*).

The helminth communities of small rodents in Europe, Britain and Ireland have been the subject of numerous studies (Table 1.1 and 1.2).

Table 1.1 Parasitological surveys of *Apodemus sylvaticus* in Ireland, Britain and Europe that include intestinal helminths.

Location	Species richness[1]	Study Type	Factors affecting parasite community structure/species composition	Reference
Ireland	7	Cross sectional	Season, host sex, host diet.	Langley and Fairly (1982)
Ireland	9	Cross sectional	Season, host diet.	O'Sullivan *et al.* (1984)
Northern Ireland	8	Cross sectional	Annual changes in host population , age, diet and season, site	Montgomery and Montgomery (1988; 1989; 1990)
Mediterranean and Continental Europe	17	Meta-analyses	Size of geographic area surveyed, parasite life-cycle.	Feliu *et al.* (1997)
Southern England	8	Cross sectional	Host age, between year variations.	Behnke *et al.* (1999)
Southern England	5	Cross sectional	Site, season.	Abu-Madi *et al.* (2000)
Various Mediterranean Sites	13	Cross sectional	Site, parasite life cycle, size of geographic area surveyed, mammal diversity.	Goüy de Bellocq *et al.* (2003)
Iberian Peninsula	5	Manipulation- food supplementation	Food supplementation lowered prevalence of short lived nematodes, host sex differences.	Díaz and Alonso (2003)
Spain	16	Cross sectional	Host population dynamics related to environmental perturbation (fire), parasite life cycles.	Fuentes *et al.* (2004)
Portugal	9	Cross sectional	Host age and sex, site (habitat), season, and year.	Eira *et al.* (2006)
Germany	9	Cross sectional	Phylogenetic relatedness of hosts.	Klimpel *et al.* (2007a)
Portugal, England		Meta-analyses	Co-infection and helminth species interactions.	Behnke *et al.* (2009)

Location	Species richness[1]	Study Type	Factors affecting parasite community structure/species composition	Reference
Spain	17	Cross sectional	Host population dynamics related to environmental perturbation (fire), parasite life cycles.	Fuentes *et al.* (2010)
Southern Italy	5	Cross sectional	Host age, habitat.	Milazzo *et al.* (2011)
Mediterranean	28	Cross sectional	Host sex differences in helminth resistance and tolerance.	Bordes *et al.* (2012)
Spain	14	Cross sectional	Environmental perturbation (fire) reduced risk depending on parasite life cycle.	Torre *et al.* (2013)
England	8*	Longitudinal, drug-based perturbation of nematodes.	Parasite community stability with rapid return to pre-perturbation levels.	Knowles *et al.* (2013)
Spain	14	Cross sectional	Host age, sex and season.	Debenedetti *et al.* (2014)

[1]Species richness included juvenile and adult cestodes associated with the intestine, body cavity and surface of the liver.
*Only intestine examined.

Table 1.2 Parasitological surveys of *Myodes glareolus* in Ireland, Britain and Europe that include intestinal helminths.

Location	Species richness[1]	Study Type	Risk factors/ study conclusions	Reference
Norway	8	Cross sectional	Season, host age	Tenora *et al.* (1979)
Ireland	3	Cross sectional	Season, host diet	O'Sullivan *et al.* (1984)
Finnish	11	Cross sectional	Season, host immunological mechanisms , host density,	Haukisalmi *et al.* (1988)
Finland	6	Cross sectional	Host density, climate	Haukisalmi and Henttonen (1990)
Finland	6	Cross sectional	Evolution of competitive ability favoured in rare parasites	Haukisalmi and Henttonen (1999)
Poland	11	Cross sectional	Site, host age	Behnke *et al.* (2001b)
Poland	11	Cross sectional	Host sex differences in immunity trade-offs	Barnard *et al.* (2002)
Poland	11	Cross sectional	Site	Barnard *et al.* (2003)
Southern Italy	7	Cross sectional	Host sample size, composition of mammalian definitive hosts.	Milazzo *et al.* 2003.
Poland	15	Cross sectional	Season, host age, age *season interaction	Bajer *et al.* (2005)
Poland	13	Cross sectional	Year - variation at the level of regional and component fauna	Behnke *et al.* (2008a)
Poland	13	Cross sectional	Host age, site*year interaction, medium-term stability at infracommunity level	Behnke *et al.* (2008b)
France	6*	Cross sectional	Phylogenetic relatedness of hosts	Pisanu *et al.* (2009)
Spain and France	14	Cross sectional	Season, host sex	Ribas *et al.* (2009).
Poland	7*	Cross sectional	Intermediate MHC allelic diversity associated with lowest intensity of common nematode	Kloch *et al.* (2010)

[1]Species richness included juvenile and adult cestodes associated with the intestine, body cavity and surface of the liver.
*Only intestine examined.

The best studied species belong to the Murinae genus *Apodemus* (mice) and Arvicolinae genus *Myodes* (voles). Both are widespread throughout Europe (Temple and Terry 2007) and are often the dominant woodland rodent species (Stenseth *et al.* 2002). In Ireland however, the coexistence of Murinae and Arvicolinae rodents has only occurred very recently. The rodent fauna of Ireland is extremely depauperate compared to Britain and mainland Europe. Murinae rodents in Ireland include the brown rat *Rattus norvegicus* and house mouse *Mus musculus* and one native non-commensal woodland species, the wood mouse *Apodemus sylvaticus* (Marnell *et al.* 2009). No Arvicolinae rodents occurred prior to the introduction of the bank vole *Myodes glareolus* (formerly *Clethrionomys glareolus*).

The bank vole was first recorded in Ireland near Listowel, Co. Kerry, in 1964 (Claassens and O'Gorman 1965). Smal and Fairley (1984), estimating the rate of spread, proposed the bank vole was introduced to Ireland around 1940. Stuart *et al.* (2007) using mitochondrial (mt) cytochrome *b* gene sequences found a close genetic relationship between Irish and German bank voles. From this information they suggested that a small population of bank voles was transported to Ireland along with earth moving equipment for the River Shannon hydroelectric scheme at Ardnacrusha. This pushed the date of introduction back to 1926 and narrowed the point of introduction to Foynes, Co Limerick. The bank vole now occupies approximately one-third of the south-west of Ireland (Fig 1.4) and is continuing to expand its range at a rate of between 1.79 to 2.5 km/year (Montgomery *et al.* 2012; White *et al.* 2012).

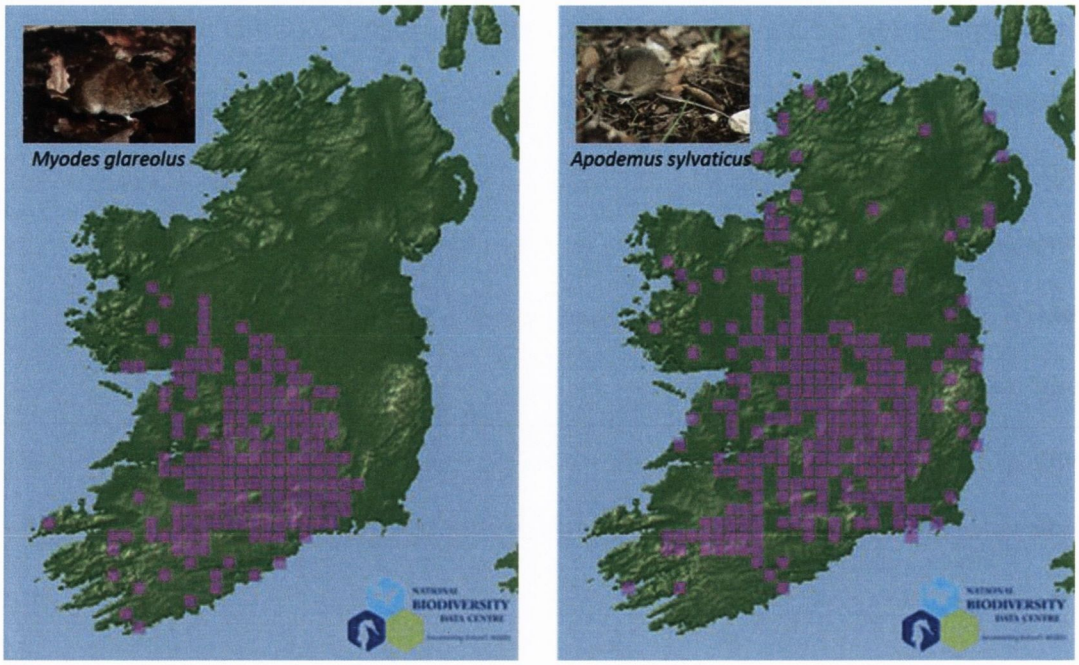


Figure 1.4 Species distribution maps (2010-2015) for *Myodes glareolus* and *Apodemus sylvaticus* in Ireland (National Biodiversity Data Centre). Species photos: *M. glareolus* (James 2010) and *A. sylvaticus* (Hillewaert 2010). It should be noted that while the distribution map of *M. glareolus* is accurate, the distribution of *A. sylvaticus* is underrepresented, particularly in Northern Ireland.

1.6.1 Do wood mice and bank voles compete?

The co-occurrence of wood mice and bank voles throughout Europe and Britain is likely facilitated by niche segregation in diet, temporal activity and habitat selection. Wood mice are mainly granivorous - green plant and animal material (insects, molluscs, annelids) making up a larger proportion of the diet when seed is scarce in late spring and early summer (Watts 1968; Smal and Fairley 1980). Bank voles are less dependent on seeds, consuming greater proportions of green plants in the spring and summer and tree leaves and fungi in autumn. Animal material is taken but makes up a minor part of the diet (Watts 1968; Smal and Fairley 1980). During heavy seed fall, however seeds are eaten in abundance by bank voles (Drozdz 1966).

The bank vole can be trapped at various times but appears to be mainly diurnal and crepuscular while the wood mouse shows little diurnal activity (Canova 1993). Wood mice are mainly sylvatic though can be found in many habitats including hedgerows, urban forests, gardens and parks, sand

dunes, blanket bog and wet heath providing the landscape is not flooded (Dickman and Doncaster 1987; Montgomery and Dowie 1993; Gurnell and Flowerdew 2006; Flowerdew and Tattersall 2008). They are common on agricultural land, invading cereal crops during the summer, returning to nearby woods following the autumn harvest (Baker *et al.* 2003). The bank vole occupies similar habitats to the wood mouse but prefers areas of cover and is not found on farmland (Fairley and Jones 1976; Van Apeldoorn *et al.* 1992).

Despite temporal and spatial segregation, intraspecific competition between wood mice and bank voles does occur at high population densities and is often asymmetrical, though the direction of competition can differ. Flowerdew (1985) found the combined densities of wood mice and voles had a negative effect on the over-wintering success on wood mice, but not on bank voles, when food was limiting. This may be explained by the differences in diet. While bank vole and wood mice diets overlap, bank voles can also take advantage of a wider variety of vegetable matter, including consuming large quantities of dead tree litter (Watts 1968). Such dietary plasticity may give bank voles a competitive advantage over wood mice when other food is in short supply. In a long term removal experiment by Fasola and Canova (2000), removal of wood mice strongly affected the densities of bank voles but only a slight effect of removal of bank voles on wood mice density was observed.

In Ireland where wood mice occur both allopatrically and sympatrically with bank voles (Fig. 1.4) a comparison of the habitat preferences of wood mice can be made. Wood mice show a preference for more ground cover when they occur in a habitat without bank voles, but increase their use of open ground in mixed communities (Fairley 1966; Fairley and Jones 1976; Montgomery and Bell 1981). Greenwood (1978) found that wood mice and bank voles in Britain were usually intolerant of each other when they came into contact. The timing of bank vole visits to feeding stations was determined by the activity of the nocturnal wood mouse. This interspecific intolerance appears to result in increasing diurnal activity of bank voles in the presence of wood mice in order to reduce

interspecific encounters (Greenwood 1978; Canova 1993). Such changes in behaviour and habitat preference are suggestive of interference competition

1.7 Aims and Objectives

The objective of the present thesis was to investigate disease dynamics in an invaded ecosystem using the helminth communities of the invasive bank vole (*Myodes glareolus*) and native wood mouse (*Apodemus sylvaticus*) in Ireland.

Field collections of bank voles and wood mice were undertaken to fulfil the following aims:

- To quantitatively analyse the helminth communities of wood mice within a community ecology framework. Wood mice were collected from 4 sites over 2 years to investigate both the temporal and spatial variation within their helminth communities. To determine the impact of the invasive bank vole on native host-parasite dynamics in the wood mice, sites were divided between locations invaded by bank voles (2 sites) and locations beyond the invasion front (2 sites) (Chapter 3).

- To investigate the helminth communities of the invasive bank vole from two sites in Ireland over a two year-period. From the data collected the invasive bank vole can be analysed within a biogeographical context, by comparing patterns of helminth infection in Irish bank voles with published studies of bank voles in their indigenous ranges (Chapter 4).

- To investigate helminth parasitism in the invasive bank vole in a community context through quantitative comparisons of the helminth communities of the invasive bank vole and native wood mouse from shared sites in Ireland (Chapter 5).

CHAPTER 2

Material and Methods

2.1. Trapping

Fieldwork was carried out over 2 years (2011-2012), during autumn (October- November). Rodents were trapped using standard Longworth live mammal traps. Each trap was bedded with dry straw and baited with peanuts. Traps were placed in pairs, ten meters apart along straight line transect, camouflaged with foliage and left in situ overnight. Sites were initially trapped for three consecutive nights and then revisited as needed. Relative population size for each year and site was calculated as the number of successful trappings during the first 3 day trapping session, divided by the number of traps laid out.

2.2 Sites

Four sites were chosen in Ireland, two located in vole invaded areas and two in uninvaded areas. Vole invaded sites (henceforth referred to as mice-vole sites) were located in County Galway and uninvaded sites (mice-only sites) were located in the Counties Dublin and Wicklow. Two sites (Coole and Knocksink) covered an area large enough to make sub-sampling of the site feasible. Ordnance Survey Ireland coordinates (X, Y) are given for each site and sub-site.

2.2.1 Mice-Vole Sites

Coole (A) and (B)

- The site referred to as Coole was located in the Coole nature reserve Co. Galway, which is part of the Coole-Garryland complex special area of conservation. Vegetation was comprised of mixed deciduous forest, mainly oak (*Quercus*), ash (*Fraxinus*) and hazel (*Corylus*). Two sub-sites were sampled within Coole, referred to as Coole (A) (X- 143710, Y- 205120) and Cool (B) (X- 144060, Y- 205000) (Fig 2.1). Coole (A) and Coole (B) differed in the amount of ground cover. Coole (A) had patches of conifer stands and so ground cover was scarce. In comparison Coole (B) had a dense ground cover layer of ground ivy (*Hedera*).

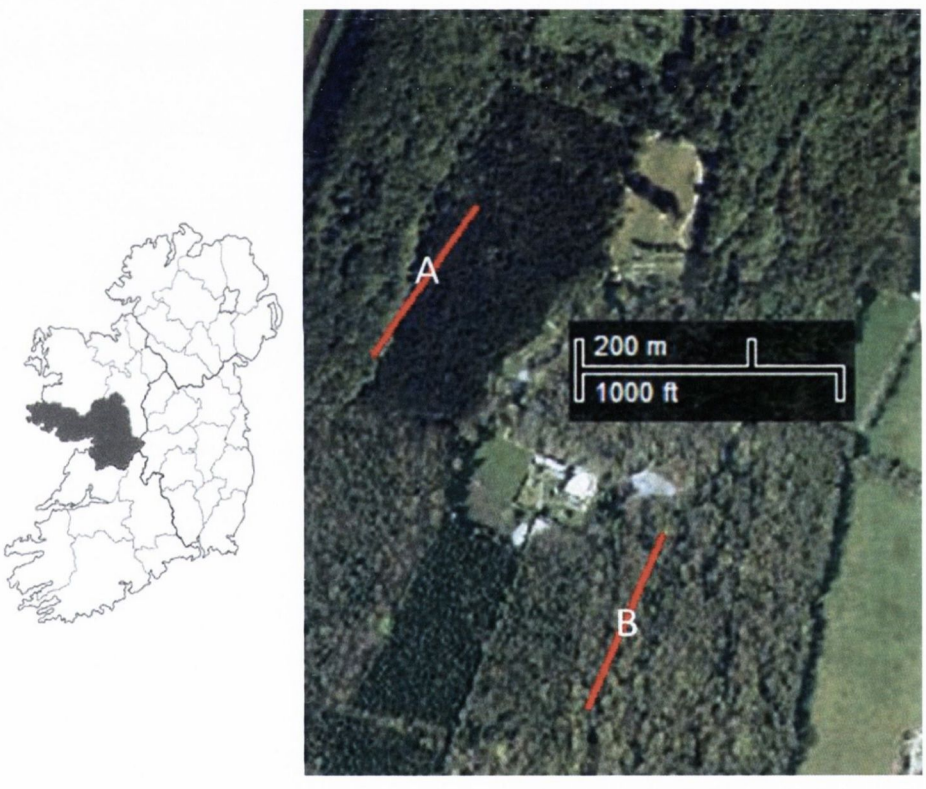


Figure 2.1 Satellite image of site Coole (A) and Coole (B) in County Galway. Sub-sites are indicated by red lines. (Source: Ordnance Survey Ireland). Location of County in which trapping took place is indicated by the shaded area on Map of Ireland.

Merlin

- Merlin Park Woodland is an urban woodland situated on the eastern edge of Galway City. The woodland was similar to Coole Woods consisting of native oak-ash-hazel woodland, mixed broadleaved woodland and conifer woodland. Dense ground cover of bracken (*Rubus*), and ivy covered all of the area trapped. A single line of traps was set in Merlin (X-134180, Y- 225300) (Fig. 2.2).

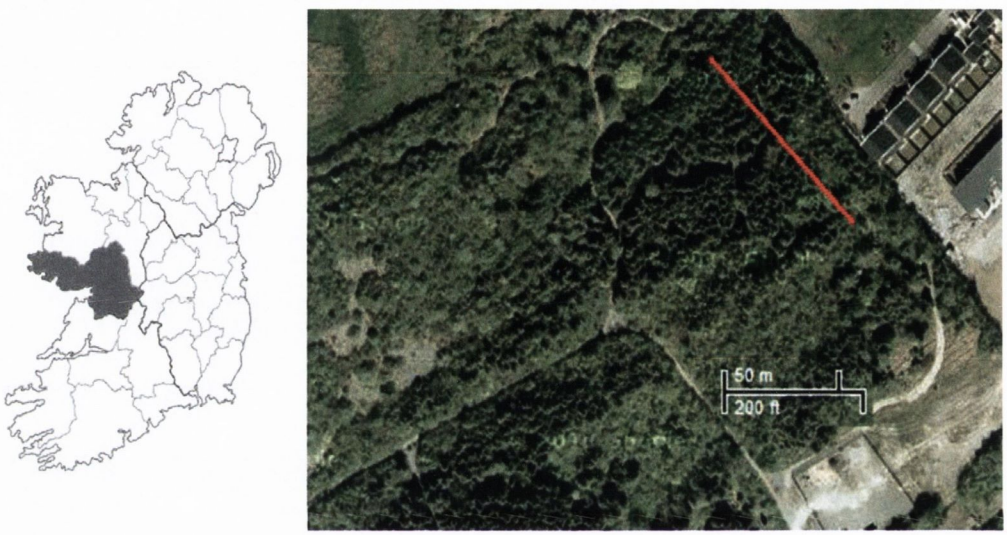


Figure 2.2 Satellite image of Merlin Park Woodlands in County Galway showing single trap line. (Source: Ordnance Survey Ireland).

2.2.2 Mice-only Sites

Knocksink (A) and (B)

- Knocksink Wood Nature Reserve (operated by the National Parks and Wildlife Service) is located in the Glencullen River Valley just North of Enniskerry, Co. Wicklow. The woods consisted of mixed deciduous trees, oak being the most abundant with ground cover of bracken, brambles and herbaceous plants. Two sub-sites were sampled within Knocksink Woods, referred to as Knocksink (A) (X- 321838 , Y- 217954) and Knocksink (B) (X- 321412 , Y-218122) (Fig. 2.3).

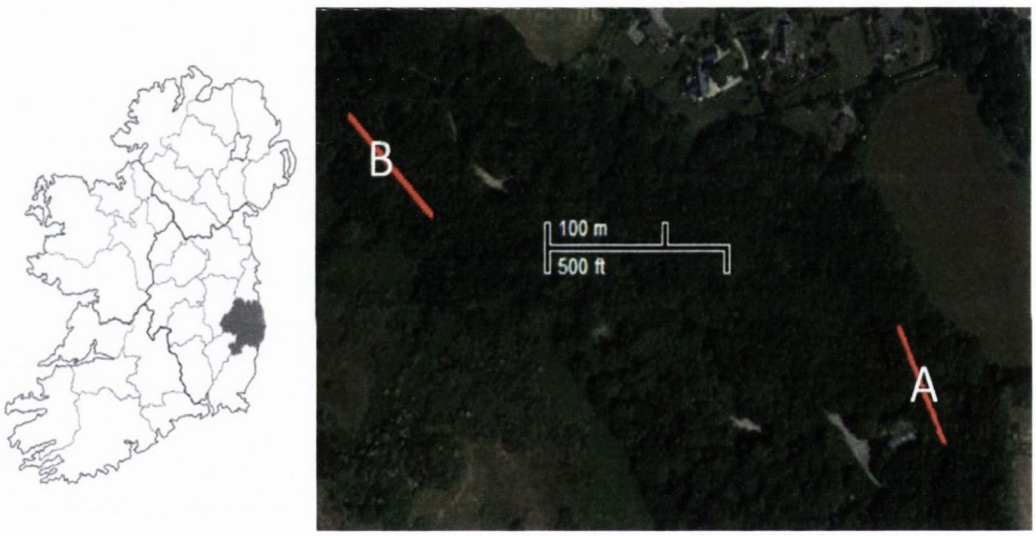


Figure 2.3 Satellite image of site Knocksink (A) and Knocksink (B) in County Wicklow. Sub-sites indicated by red lines. (Source: Google Earth).

Santry

- Santry Woods is a small patch of woodland in Santry, Co. Dublin, located on the periphery of Trinity University Dublin playing grounds and adjacent to a public park. The periphery of the wooded area was overgrown with nettles (*Urtica*) and brambles (*Rubus*) while the interior of the wooded area was comprised of mixed deciduous trees, mainly chestnut (*Aesculus*), and sycamore (*Acer*) with ground cover consisting mostly of brambles, ground ivy and nettles (*Urtica*). Two shorter trapping lines were used as a single long line ran into a section of the woods that flooded regularly. The two lines were combined in any analyses and not considered as sub-sites (X- 316468, Y- 240187) (Fig. 2.4).

Figure 2.4 Satellite image of Santry Woods in County Dublin showing two trap lines. (Source: Google Earth).

2.3 Laboratory Procedure

Closed taps were collect each morning and removed to the laboratory. Animals were deeply anesthetised with Isoflurane and euthanized by cervical dislocation. Each individual was weighed to the nearest 0.1 gram. Body measures were taken with callipers to the nearest millimetre. Body measures taken included; head length, head width, hind foot length and the length between nose and anus. Sex was determined based on the distance between the anus and urethra opening and confirmed on examination of internal sex organs.

Visually assessments of maturity were made based on reproductive status including signs of lactation, pregnancy, uterine scars, perforation status of vaginal opening in females and presence of external testis in males. In wood mice maturity was also determined based on pelt coloration and condition, with a brown patch on the upper torso indicating adult individuals (Gurnell and Flowerdew 2006).

The entire intestinal tract from oesophagus to anus was removed and stored in 70% alcohol until examination. The surface of the liver and body cavity were checked and any adult or juvenile helminths removed. Both eyes were dissected out and stored in 10% formalin for at least 3 months. After this time lenses were removed, washed in deionised water and dried in a fan assisted oven at 60° for 48 hours. The weight of both lenses was recorded the nearest 0.0001g. If one lens in a pair was damaged, the weight of the single lens was doubled.

2.4 Species Identification

At the end of each sampling session, intestines were divided into stomach, small intestine, caecum and colon. Each part was washed out with saline, gently scraped and the content examined under a under a dissecting microscope. All helminths were counted and stored in 70% ethanol.

Helminths were identified using the following literature; Harvey and Channon (1956); Tenora *et al.* (1983); Montgomery *et al.* 1987; Justine and Roguin (1990); Khalil *et al.* (1994), Khalil *et al.* (1994); Khalil *et al.* (2014).

Glossary of terms used to describe helminth life-history stages

- **Metacestode**. Developmental stage of a cestode in the intermediate host; juvenile cestodes.
- **Tetrathyridium.** Metacestode form of the tapeworm cyclophyllidean genus *Mesocestoides.*
- **Strobilocercus.** Metacestode form of the tapeworm *Hydatigera taeniaeformis* (previously *Taenia taeniaeformis*, see Nakao *et al.* 2013).
- **Monoxenous.** Living within a single host during the parasites life-cycle.

2.5 Statistical Analyses

2.5.1 Age and Principal Component Analyses

Relating age to body mass or other morphometric measurements is complicated by variability in growth rate due to difference in the nutritional status of animals. The growth of the eye lens is less dependent on nutritional status (Morris 1972) and was chosen as the primary measurement on which to assign rodents to age groups. A spearman rank correlation analyses showed that 2 morphometric measures, body weight and nose to anus length correlated significantly with eye lens weight (Table 2.1). These three morphometric measures were fitted to a Principal Component Analyses. Principal component 1 was then used to order the mice and allocate them to three age classes: juvenile, adult and mature. Visual assessments of maturity were used to help allocate mice at the limits at each category (Behnke *et al.* 2001b).

Table 2.1 Correlation matrix for morphometric measures used to determine age classes for wood mouse and bank voles.

	Body weight		**Body length**	
	Wood mouse	***Bank vole***	***Wood mouse***	***Bank vole***
Eye lens weight	r=0.77, P<0.005	r=0.75, P<0.005	r=0.61, P<0.005	r=0.70, P=0.005
Body weight	-	-	r=0.72, P<0.005	r=67 P<0.005

2.5.2 Measures of Helminth Community Structure

Helminth community structure was statistically analysed at two hierarchical levels: the component community and infracommunity (Bush *et al.* 1997).

Community structure was measured following methods described by Kennedy and Hartvigsen (2000) and Behnke *et al.* (2001b).

Measures of component community structure are:

- Total number of helminth species.

- The Berger-Parker Dominance Index. This index measures the proportion of the sample made up by the dominant species. The dominant species is the species showing the highest proportion in each data set The index is calculated as $d= \frac{N_{max}}{N}$ where N_{max} is the number of individuals in the most abundant species and N is the total of all individuals in the sample.
- Simpson's Index of Diversity calculated as $D= \frac{\sum i\, n_i(n_i-1)}{N(N-1)}$ where n_i is the total number of individuals of the ith a particular species and N =the total number of individuals of all species. This index measures the probability that two individuals selected randomly from the sample will belong to the same species. As D and diversity are negatively related, Simpson's index was expressed as the reciprocal form, 1/D.

Measures of infracommunity structure are:

- Mean species richness – the average number of parasite species per host (Montgomery and Montgomery 1989).
- Maximum number of species per host.
- Infracommunity diversity was measured by the mean and max Brillouin's Index, appropriate for fully censured communities (Pielou 1966). The index was calculated per host (infected and uninfected) as $HB=\frac{\ln(N!)-\sum \ln(ni!)}{N}$, where N is the total number of individuals in the sample, *ni* is the number of individuals of species *i*, ln(x) refers to the natural logarithm of x.
- Mean abundance - the total number of helminths of a particular species divided by the total number of hosts, both infected and uninfected (Bush *et al.* 1997).
- Prevalence of individual helminth species. Prevalence is defined as the number of hosts infected with one or more helminth species divided by the number of hosts examined (Bush *et al.* 1997).

2.5.2 Modelling

Log-transforming count data fails when parasites are highly aggregated which can result in the transformed data being bimodal if there is an excess of zeroes. This increases the likelihood of Type I and Type II errors (Wilson and Grenfell 1997). Log-transformation also lowers the power of the analyses (O'Hara and Kotze 2010). Generalized linear models are generalizations of classical linear models which allow for the error structure to be specifically defined. Wilson and Grenfell (1997) found that GLMs produced fewer type I and II errors compared to linear regression models using log-linear transformation and that standard parametric tests were less precise when the data is log-transformed. Thus GLMs with the error structure specified as negative binomial or quasi-poisson is recommended for the analyses of aggregated parasite data (Wilson and Grenfell 1997; O'Hara and Kotze 2010).

All statistical analyses were performed in the R statistical computing environment (R Development Core Team 2010) version 3.0.2 with additional tools from statistical packages cited in text. Full factorial models incorporated all factors and all interactions between factors. Factors included the intrinsic measures of age, 3 levels (juvenile, adult, mature) and sex, 2 levels (male, female) and the extrinsic factors of year, 2 levels (2011 and 2012) and site, 4 levels (Knocksink, Santry, Coole , Merlin). For the purposes of modelling, due to low sample sizes in some host functional groups, sub-sites were combined (Coole A and B= Coole; Knocksink A and B= Knocksink).

GLM models were simplified using the step procedure to derive the minimal sufficient model. Residual deviance of the simplified model was used to perform a goodness of fit test for the overall model. Models were said to fit reasonably well when the goodness-of-fit χ^2 test was not statistically significant. The significance of the remaining terms was determined by removing them from the model and testing for changes in deviance with chi-squared (χ^2) test for Poisson and binomial, likelihood ratio tests (*LR*) for negative binomial errors and *F* test for Gaussian and quasi-poisson errors. When satisfactory models could not be generated by GLM (as tested by χ^2), non-parametric

tests were used to examine each of the main effects in turn. Mann-Whitney U test was used for 2 group comparisons and Kruskal-Wallis test for more than 2 groups.

Abundance was analysed with the modified negative binomial GLM from the MASS package (Venables and Ripley 2002), which provides an estimate of the aggregation parameter, *k*, and log-ratio link function (McCullagh and Nelder 1989). Prevalence data (percentage of animals infected) were calculated with the Clopper-Pearson exact 95% confidence intervals using the function "exactci" in the R package PropCIs (Scherer 2010). The degree of aggregation in the data was calculated using the index of dispersion (I, variance to mean ratio) and the negative binomial exponent (*k*) using maximum likelihood method in MASS package (Venables and Ripley 2002). Smaller values of *k* indicate higher levels of aggregation. When *k* is above 20 the distribution approaches a random distribution, described by Poisson distribution. Frequency distributions of individual taxa were also tested for goodness of fit to negative binomial, positive binomial quasi-poisson and poisson models by χ^2 test using the "fitdistrplus" package (Delignette-Muller *et al.* 2012).

A Bray-Curtis similarity index of was performed for component community similarity following log(n+1) transformation of mean abundance for each helminth species by site and year. A hierarchical cluster diagram of group-average linking based on Bray-Curtis community similarity values for 4 sites in 2 years was generated with the "vegan" package (Oksanen *et al.* 2007).

CHAPTER 3

Helminth Communities of Wood Mice

3.1 Introduction

Since Holmes' (1961; 1962) benchmark publications introduced a quantitative approach to the study of parasite communities, there has been a growing appreciation for the use of parasites as model systems in community ecology (Poulin 1995). The overall aim of community ecology is not only to detect patterns in species abundance and occurrence, but to determine the mechanistic processes underlying these patterns. However, the scale (spatial and temporal) at which communities and other natural processes are studied can constrain our understanding of the mechanisms shaping patterns (Levin 1992). The hierarchical nature of parasite communities make then ideally suited to investigations of community structure and richness across multiple scales. Parasite communities are organised into different levels from infracommunities within a single host to component communities of a host population to the sum of component communities across a host species range. As such, the composition of parasite communities allow for the factors determining community structure, stability and variability to be studied at multiple spatial and temporal scales (Poulin 1997; 1999).

The ubiquitous nature and large population sizes of wild rodents have made them popular study systems for parasitologists resulting in a number of valuable insights into the processes structuring parasite communities (see Table 1.1, Chapter 1 for a list of references). Changes in the prevalence and abundance of helminths are known to occur seasonally due to changes in the transmission strength of helminths and/or changes in host susceptibility (Montgomery and Montgomery 1990; Bajer *et al.* 2005) Across Europe, differences in peak abundances of helminths can be attributed to regional climatic conditions, particularly the severity of winter. In regions experiencing harsh winter conditions, parasite transmission is reduced so burdens are low in spring and increase through to

autumn (Bajer *et al.* 2005). Regions with milder winters allow for greater parasite transmission during the cold season and parasite burdens peak in winter and spring as helminths accumulate through winter (Abu-Madi *et al.* 2000).

Within the same climatic zone, composition and abundance of helminth communities vary considerably, even between sites of similar habitat quality or relatively close proximity (Montgomery and Montgomery 1990; Abu-Madi *et al.* 2000; Behnke *et al.* 2001b; Barnard *et al.* 2003) suggesting local factors play a large role in structuring helminth communities of small rodents. Haukisalmi and Henttonen (1999) concluded that aggregation of helminth parasites of bank voles (*Myodes glareolus*) was primarily determined within sites rather than between them. At the smallest scale, the level of the host, studies have also revealed significant variation in helminth infracommunities, suggesting that once extrinsic factors have been taken into account, host characteristics also play a role in structuring communities. Intrinsic factors important in structuring infracommunities of wood mice include age (Abu-Madi *et al.* 1998; Behnke *et al.* 1999), diet (Montgomery and Montgomery 1990) and sex (Eira *et al.* 2006).

Another potentially important structuring force at the level of the infracommunity is interactions between parasite species. Traditionally, studies have focused on single parasite species in host-parasite interactions, however there is growing evidence that interspecific parasite interactions can influence parasite transmission, host pathology and susceptibility to future infections (Cox 2001; Graham *et al.* 2007; Ezenwa *et al.* 2010). Despite evidence for parasite interactions in laboratory studies (Behnke *et al.* 1978; Behnke *et al.* 2001b; Cox 2001), evidence from the field has been mixed. Studies from wild population have reported evidence of strong interspecific interactions (Bush and Holmes 1986; Lello *et al.* 2004) while other studies have found little evidence that interactions structure parasite communities (Poulin 2001; Poulin 1996b; Behnke *et al.* 2005; Behnke 2008).

A potential structuring force rarely considered in parasite community studies is the diversity and nature of the species making up the free-living community of the target host. One important

hypothesis to consider the effects of diversity on disease risk is the dilution effect, which proposes that the net effects of biodiversity reduce the risk of disease to certain focal hosts (Keesing *et al.* 2006). Prior to the introduction of the bank vole (*Myodes glareolus*) in the 1920s (Stuart *et al.* 2007), the wood mouse was Ireland's only small woodland rodent. The introduction of the bank vole has essentially doubled the diversity of small woodland rodents, with potential impacts on disease transmission for the native wood mouse. For example, Telfer *et al.* (2005) found that the presence of the invasive bank vole in Ireland was correlated with a reduction of infection of two species of the flea-transmitted pathogen *Bartonella* in native wood mice. The dilution effect was caused by bank voles reducing the contact rate between the flea vector and the most competent parasite reservoir, the wood mouse.

In order to investigate the processes structuring the helminth communities of wood mice in Ireland, mice were collected from 4 sites over 2 years and their helminth communities quantitatively analysed. Analyses of helminth communities over a number of sites and years allows for the investigation of both the temporal and spatial variation within communities. To determine any impact of the invasive bank vole on host-parasite dynamics of the wood mice, sites were divided between locations invaded by bank voles (2 sites) and locations beyond the invasion front (2 sites).

3.2 Results

3.2.1 Host Population Structure

3.2.1.1 Host Sample Size

A total of 389 wood mice were collected and analysed over 2 years of sampling. Table 3.1 summarises the population structure by year, site and sex. The sex ratio was close to 1 with 52.7% males and 47.3% females (χ^2_1 = 1.13, P>0.05). Significantly more wood mice (64.8% of total sample) were caught in 2011 (χ^2_1 = 34.0, P<0.001).

Table 3.1 Numbers of wood mice examined by site, year and sex.

Site		Year	Female	Male	Total
Mice-only Sites	Knocksink(A)*	2011	27	22	49
	Knocksink(B)*		30	19	49
	Santry		25	21	46
		Combined	**82**	**62**	**144**
Mice-Vole Sites	Coole(A)*	2011	16	27	43
	Coole(B)*		14	20	34
	Merlin		14	17	31
		Combined	**44**	**64**	**108**
		2011 Total	**126**	**126**	**252**
Mice-only Sites	Knocksink(A)	2012	11	14	25
	Knocksink(B)		15	10	25
	Santry		17	26	43
		Combined	**43**	**50**	**93**
Mice-Vole Sites	Coole(A)	2012	3	15	18
	Coole(B)		8	7	15
	Merlin		4	7	11
		Combined	**15**	**29**	**44**
		2012 Total	**58**	**79**	**137**
				Grand Total	**389**

*See Chp.2 Materials and Methods for explanation of sub-sites A and B.

3.2.1.2 Age Classes

To ensure that morphometric measures chosen to determine age increased through the assigned age classes, 2-way GLM models were fitted with each morphometric measure as the dependent variable and age class and sex as explanatory variables (Behnke *et al.* 2001b). All models showed a

highly significant main effect of age class: mean body weight ($F_{2, 387}$ =239.2 P<0.001, Fig. 3.1A), mean body length ($F_{2, 387}$ =38.1, P<0.001, Fig 3.1B) and eye lens ($F_{2, 389}$ =431.73, P<0.001, Fig. 3.1C). In all cases morphometric measures increased through the age classes. For body weight, there was also a significant main effect of sex ($F_{1, 387}$ =21.6, P<0.001), males (19.1g ±0.26) being heavier than females (17.9g ±0.25, Fig. 3.1A).

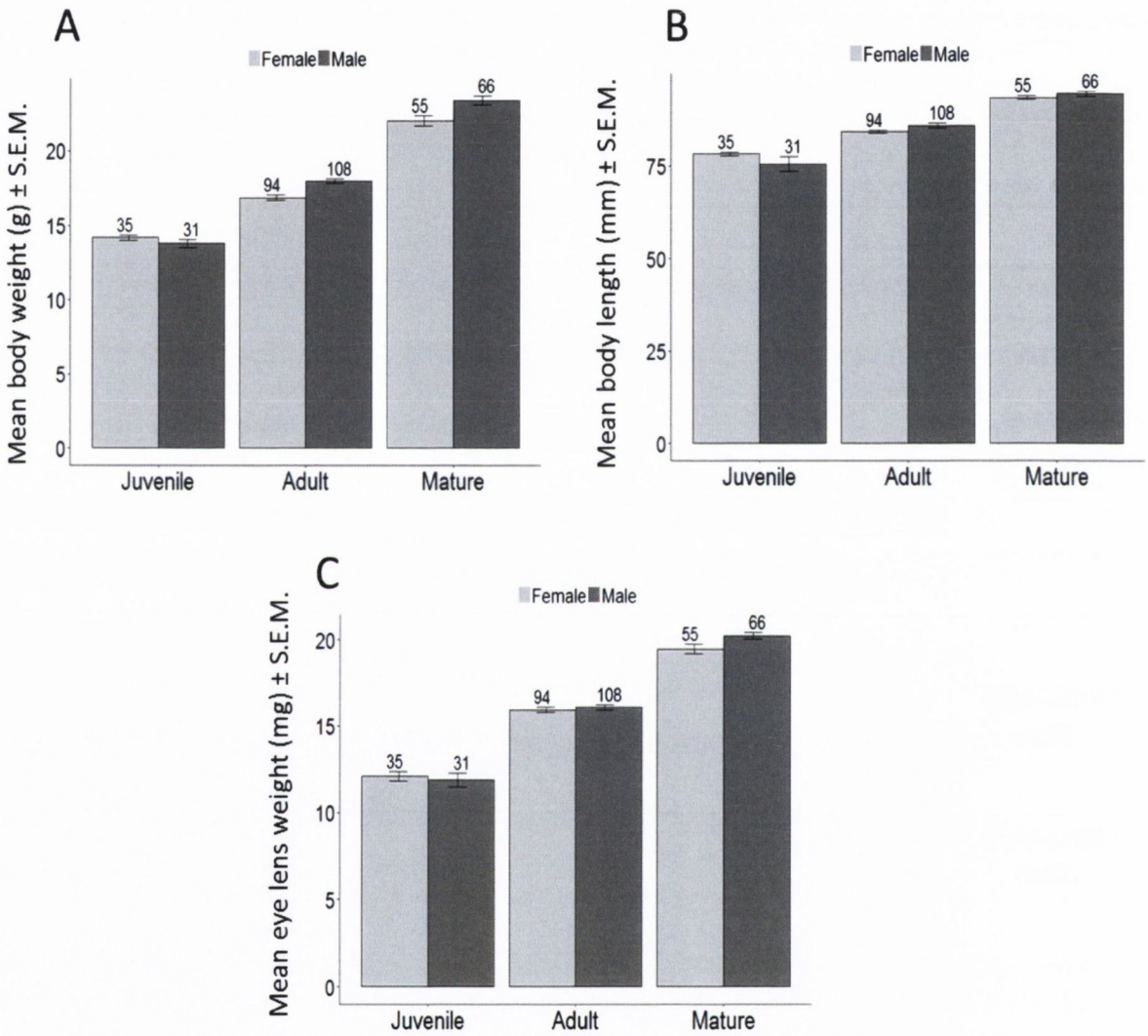


Figure 3.1 Morphometric measures in relation to age class for total sample of wood mice. Confidence intervals are indicated by error bars and sample size is shown above error bars. Body weight (A), body length (B) and eye lens weight (C).

Approximate range of values for each morphometric measure assigned to the age classes are given in Table 3.2.

Table 3.2 Approximate ranges of morphometric measures used to assign wood mice to three age classes.

Factor	Juvenile	Adult	Mature
Eye lens (mg)	7-12	12-19	>19
Weight (g)	8-14	14-22	>22
Nose to anus length (mm)	18-77	77-95	>95

The majority of wood mice were classed as adult (51.9%), mature mice making up 31.1% of the samples and juveniles 17.0%. There was some variation between sites; in Merlin in 2011 juveniles made up the majority of wood mice sampled in this site, and in Knocksink (B) in 2012 wood mice classed as mature were more abundant (Table 3.3). Between mice-only and mice-vole sites there was a difference in the proportion of the sample made up by adult wood mice. In mice-only sites 57.0% of wood mice were classed as adult while in mice-vole sites the proportion was 44.1%. There was a slight decrease in the proportion of adult wood mice from 2011 (52.4%) to 2012 (51.1%).

Table 3.3 Allocation of wood mice to three age classes by site and year.

Site		Year	Juvenile	Adult	Mature	Total
Mice Sites	Knocksink(A)	2011	9	25	15	49
	Knocksink(B)		6	36	7	49
	Santry		5	26	15	46
		Combined	**20**	**87**	**37**	**144**
Mice-vole	Coole(A)	2011	11	12	20	43
Sites	Coole(B)		3	20	11	34
	Merlin		15	13	3	31
		Combined	**29**	**45**	**34**	**108**
Mice Sites	Knocksink(A)	2012	2	12	11	25
	Knocksink(B)		4	10	11	25
	Santry		5	26	12	43
		Combined	**11**	**48**	**34**	**93**
Mice-vole	Coole(A)	2012	0	6	12	18
Sites	Coole(B)		4	8	3	15
	Merlin		2	8	1	11
		Grand Total				**389**

3.2.2 Helminth Community Structure

3.2.2.1 Helminth Fauna of Wood Mice in Ireland

Ten helminth species were recovered from wood mice in this study (Table 3.4). These included 8 intestinal helminths species, 4 nematodes, 2 cestodes and 2 trematodes. A further 2 species of larval cestode were recovered - the larval strobilocercus of *Hydatigera taeniaeformis* and the tetrathyridium form of the cestode *Mesocestoides spp*. All the helminth species found in the present study have been recorded in previous Irish studies except for *Mesocestoides spp.* (Appendix Table 1A). Helminth species found over the course of the study are listed in Table 3.4, along with the taxa to which they belong and whether the life-cycle is direct or indirect. The number of helminth species recorded at sites ranged from 4 to 8 species. All 8 were only recorded in Knocksink as this was the only site that *Heligosomoides polygyrus* was recovered from.

Table 3.4 Helminth species recovered from wood mice by taxon.

Taxon	Species	Location	Life-cycle
Nematoda	*Syphacia stroma*	SI, LI	Direct
	Aonchotheca murissylvatici *(previously Capillaria murissylvatici)*	SI	Direct
	Trichuris muris	C	Direct
	Heligosomoides polygyrus *(previously Nematospiroides dubius)*	SI	Direct
Cestoda	*Hymenolepis hibernia*	SI	Indirect
	Skrjabinotaenia lobata *(previously Catenotaenia lobata)*	SI	Indirect
	Mesocestoides spp.	BC	Indirect
	Hydatigera taeniaeformis *(previously Taenia taeniaeformis)*	L	Indirect
Trematoda	*Corrigia vitta*	PL	Indirect
	Brachylaemus recurvum	SI	Indirect

Locations within the host are indicated by SI – small intestine, LI – Large intestine, C – Caecum, BC- body cavity, PL - Pancreatic lobes and L – Liver.

A total of 110,927 helminths were recovered, 52,932 in 2011 and 57,995 in 2012. The vast majority were nematodes, accounting for 97% of all helminths. Cestodes made up 0.85% of the total sample and trematodes 2.1% (Table 3.5). The sum total of all helminth taxa increased by 9.57% in 2012,

despite a 1.8 fold decrease in host sample size. Nematodes increased by 7.24%, trematodes by 77.7% and the largest increase was in cestodes, which increased by 423.7%.

The helminth species composition at each site was very similar between years. Differences were due to the appearance of *Aonchotheca murissylvatici* in Santry and Knocksink A and B in 2012 and the disappearance of *A. murissylvatici* and *Hymenolepis hibernia* from Merlin in 2012, possibly due to the smaller sample size of wood mice collected in 2012. Slightly more variation in species composition was observed when replicated sites were not combined. For instance *Trichuris muris* was absent from Knocksink (A) in 2011 but present in 2012 while it was present in both years at Knocksink (B). The majority of helminths were recovered from Knocksink (55.6%) with the sub-sampled site Knocksink (B) having the highest sum total of helminths over all. Percentage distribution of helminths in the remaining sites was as follows: Santry, 34.2%, Coole 9.32% and Merlin 0.91% (Table 3.5).

Table 3.5 Percentage (%)* distribution of all helminth species of wood mice by year and site with confidence intervals given in brackets.

Species	Year	Knock(A)	Knock(B)	Santry	Coole(A)	Coole(B)	Merlin	Total
All Helminths	2011	15.3 (15.1-15.5)	15.9 (15.7-16.1)	12.6 (12.4-12.8)	1.19 (1.12-1.25)	1.93 (1.85-2.01)	0.8 (0.75-0.85)	47.7 (47.4-48.0)
	2012	7.87 (7.71-8.03)	16.5 (16.3-16.7)	21.6 (21.4-21.8)	4.32 (4.20-4.44)	1.89 (1.81-1.97)	0.11 (0.09-0.13)	52.3 (52.0-52.6)
	Total	**23.1 (22.9-23.4)**	**32.4 (32.1-32.7)**	**34.2 (33.9-34.5)**	**5.5 (5.37-5.64)**	**3.82 (3.71-3.93)**	**0.92 (0.86-0.97)**	**100**
Nematodes	2011	14.9 (14.7-15.1)	15.7 (15.5-15.9)	12.4 (12.3-12.6)	1.09 (1.02-1.15)	1.91 (1.83-1.99)	0.73 (0.68-0.78)	46.8 (46.5-47.1)
	2012	7.48 (7.33-7.64)	15.9 (15.7-16.1)	20.8 (20.6-21.1)	4.19 (4.07-4.31)	1.77 (1.70-1.85)	0.05 (0.03-0.06)	50.2 (49.9-50.5)
	Total	**22.4 (22.2-22.7)**	**31.6 (31.3-31.9)**	**33.3 (33.0-33.6)**	**5.27 (5.14-5.41)**	**3.68 (3.57-3.79)**	**0.77 (0.72-0.82)**	**97.0 (96.9-97.1)**
Cestodes	2011	0.03 (0.02-0.05)	0.04 (0.03-0.05)	0.02 (0.01-0.03)	0.02 (0.01-0.03)	0.02 (0.01-0.03)	0.01 (0.01-0.02)	0.14 (0.12-0.16)
	2012	0.1 (0.08-0.12)	0.26 (0.23-0.29)	0.12 (0.10-0.15)	0.13 (0.11-0.15)	0.08 (0.06-0.10)	0.02 (0.02-0.04)	0.72 (0.67-0.77)
	Total	**0.14 (0.11-0.16)**	**0.3 (0.27-0.34)**	**0.14 (0.12-0.17)**	**0.14 (0.12-0.17)**	**0.1 (0.08-0.12)**	**0.04 (0.03-0.05)**	**0.85 (0.80-0.91)**
Trematodes	2011	0.3 (0.27-0.34)	0.18 (0.15-0.20)	0.14 (0.12-0.16)	0.08 (0.07-0.01)	0.01 (0.00-0.01)	0.06 (0.05-0.08)	0.77 (0.72-0.82)
	2012	0.28 (0.25-0.32)	0.34 (0.31-0.37)	0.66 (0.61-0.71)	0.01 (0.00-0.01)	0.04 (0.03-0.05)	0.04 (0.03-0.06)	1.36 (1.30-1.43)

Species	Year	Knock(A)	Knock(B)	Santry	Coole(A)	Coole(B)	Merlin	Total
S. stroma	2011	14.2 (14.0-14.4)	15.2 (15.0-15.5)	12.4 (12.3-12.6)	1.05 (0.99-1.11)	1.75 (1.68-1.83)	0.72 (0.68-0.78)	45.4 (45.1-45.7)
	2012	6.94 (6.79-7.09)	15.4 (15.2-15.6)	20.8 (20.5-21.0)	4.18 (4.06-4.30)	1.72 (1.65-1.80)	0.05 (0.03-0.06)	49 (48.8-49.3)
	Total	**21.1 (20.9-21.3)**	**30.6 (30.4-30.9)**	**33.2 (32.9-33.5)**	**5.23 (5.10-5.36)**	**3.47 (3.37-3.58)**	**0.77 (0.72-0.82)**	**94.4 (94.3-94.6)**
H. polygyrus	2011	0.77 (0.72-0.83)	0.47 (0.43-0.51)	-	-	-	-	
	2012	0.54 (0.50-0.58)	0.48 (0.44-0.52)	-	-	-	-	
	Total	**1.31 (1.25-1.38)**	**0.95 (0.89-1.00)**	**-**	**-**	**-**	**-**	**2.26 (2.17-2.35)**
T. muris	2011	0 (0-0.003)	0.004 (0-0.01)	0.002 (0-0.01)	0.009 (0-0.02)	0.01 (0-02)	0 (0-0.003)	0.03 (0.02-0.04)
	2012	0.005 (0-0.01)	0.002 (0-0.01)	0.03 (0.02-0.04)	0.003 (0-0.01)	0.007 (0-0.01)	0 (0-0.003)	0.05 (0.03-0.06)
	Total	**0.004 (0-0.01)**	**0.006 (0-0.01)**	**0.03 (0.02-0.04)**	**0.01 (0-0.02)**	**0.02 (0.01-0.03)**	**0 (0-0.003)**	**0.07 (0.06-0.09)**
A murissylvatici	2011	0 (0-0.003)	0 (0-0.003)	0 (0-0.003)	0.03 (0.02-0.04)	0.14 (0.12-0.17)	0.001 (0-0.006)	0.17 (0.15-0.20)
	2012	0.0009 (0-0.005)	0.02 (0.01-0.03)	0.02 (0.01-0.04)	0.006 (0-0.01)	0.04 (0.03-0.06)	0 (0-0.003)	0.09 (0.08-0.11)
	Total	**0.0009 (0-0.005)**	**0.02 (0.01-0.03)**	**0.02 (0.01-0.04)**	**0.03 (0.02-0.06)**	**0.19 (0.16-0.21)**	**0.002 (0-0.006)**	**0.26 (0.23-0.30)**

Species	Year	Knock(A)	Knock(B)	Santry	Coole(A)	Coole(B)	Merlin	Total
H. hibernia	2011	0.01 (0-0.02)	0.03 (0.02-0.04)	0.01 (0-0.02)	0.0009 (0-0.005)	0 (0-0.003)	0.002 (0-0.007)	0.06 (0.04-0.07)
	2012	0.08 (0.07-0.01)	0.26 (0.23-0.29)	0.03 (0.02-0.04)	0 (0-0.003)	0.05 (0.04-0.07)	0 (0-0.003)	0.42 (0.38-0.46)
	Total	**0.1 (0.08-0.12)**	**0.3 (0.26-0.32)**	**0.04 (0.03-0.05)**	**0.0009 (0-0.005)**	**0.05 (0.04-0.07)**	**0.002 (0-0.007)**	**0.48 (0.44-0.52)**
C. lobata	2011	0.02 (0.01-0.03)	0.01 (0-02)	0.004 (0-0.001)	0.01 (0-0.02)	0.02 (0.01-0.03)	0.01 (0-0.02)	0.07 (0.06-0.09)
	2012	0.02 (0.01-0.03)	0 (0-0.003)	0.09 (0.08-0.11)	0.13 (0.12-0.15)	0.03 (0.02-0.04)	0.02 (0.01-0.03)	0.29 (0.26-0.33)
	Total	**0.04 (0.02-0.05)**	**0.009 (0-0.01)**	**0.1 (0.08-0.12)**	**0.14 (0.12-0.17)**	**0.05 (0.03-0.06)**	**0.03 (0.02-0.05)**	**0.36 (0.33-0.40)**
C. vitta	2011	0.3 (0.27-0.34)	0.17 (0.15-0.20)	0.14 (0.12-0.16)	0.07 (0.06-0.09)	0 (0-0.003)	0.06 (0.05-0.08)	0.75 (0.70-0.80)
	2012	0.21 (0.18-0.24)	0.33 (0.30-0.37)	0.61 (0.57-0.66)	0.002 (0-0.006)	0.002 (0-0.006)	0.41 (0.03-0.06)	1.2 (1.14-1.26)
	Total	**0.51 (0.47-0.56)**	**0.5 (0.46-0.55)**	**0.75 (0.70-0.80)**	**0.08 (0.06-0.09)**	**0.002 (0-0.006)**	**0.1 (0.08-0.12)**	**1.95 (1.86-2.03)**
B. recurvum	2011	0 (0-0.003)	0.005 (0-0.01)	0 (0-0.003)	0.008 (0-0.02)	0.005 (0-0.01)	0.003 (0-0.007)	0.02 (0.01-0.03)
	2012	0.07 (0.06-0.09)	0.006 (0-0.01)	0.05 (0.03-0.06)	0.004 (0-0.009)	0.03 (0.02-0.05)	0.002 (0-0.007)	0.17 (0.14-0.19)
	Total	**0.07 (0.06-0.09)**	**0.01 (0-0.02)**	**0.05 (0.03-0.06)**	**0.01 (0-0.02)**	**0.04 (0.03-0.05)**	**0.005 (0-0.01)**	**0.18 (0.16-0.21)**

Species	Year	Knock(A)	Knock(B)	Santry	Coole(A)	Coole(B)	Merlin	Total
Mesocestoides. spp.	2011	0 (0-0.003)	0 (0-0.003)	0 (0-0.003)	0.009 (0-0.02)	0.009 (0-0.02)	0 (0-0.003)	0.002 (0-0.007)
	2012	0 (0-0.003)	0 (0-0.003)	0 (0-0.003)	0 (0-0.003)	0.009 (0-0.02)	0 (0-0.003)	0.009 (0-0.02)
	Total	**0 (0-0.003)**	**0 (0-0.003)**	**0 (0-0.003)**	**0.009 (0-0.02)**	**0.009 (0-0.02)**	**0 (0-0.003)**	**0.003 (0-0.008)**
H. taeniaeformis	2011	0.004 (0-0.01)	0.001 (0-0.005)	0.003 (0-0.008)	0 (0-0.003)	0 (0-0.003)	0 (0-0.003)	0.007 (0-0.01)
	2012	0 (0-0.003)	0 (0-0.003)	0.002 (0-0.007)	0 (0-0.003)	0 (0-0.003)	0 (0-0.003)	0.002 (0-0.001)
	Total	**0.004 (0-0.009)**	**0.009 (0-0.01)**	**0.005 (0-0.01)**	**0 (0-0.003)**	**0 (0-0.003)**	**0 (0-0.003)**	**0.009 (0-0.02)**

Percentage distribution of helminths is given for the entire sample across sites and years.

3.2.2.2 Component Community Structure of Helminths of Wood Mice

Syphacia stroma was the dominant species at all sites in both years. The Berger-Parker Dominance Index was above 0.8 for all sites except Merlin where *S. stroma* only made up 40% of the total helminth sample recovered in 2012 (Table 3.6). The dominance of *S. stroma* is reflected in measures of Simpson's Index of Diversity. The Simpson's increased in Knocksink and Santry in 2012 as the proportion of the sample made up of *S. stroma* decreased. In Coole (A) Simpson's Index decreased in 2012 and *S. stroma* made up a greater proportion of total helminths recovered. The proportion of *S. stroma* was the same in Coole (B) in 2011 and 2012, as was Simpson's. Only at Merlin was there a decrease in the proportion of *S. stroma* in 2012 and a decrease in Simpson's. This was due to the absence of 2 helminth species in Merlin in 2012.

Table 3.6 Helminth component community measures in wood mice by year and site based on intestinal species only.

	Year	Knocksink(A)	Knocksink(B)	Santry	Coole(A)	Coole(B)	Merlin
Total Species	2011	5	7	5	7	5	6
	2012	8	7	7	6	7	4
Berger-Parker	2011	0.93	0.95	0.99	0.88	0.91	0.91
	2012	0.88	0.93	0.96	0.97	0.91	0.40
Dominant Species	2011	*S. stroma*	*S. stroma*	*S.stroma*	*S.stroma*	*S.stroma*	*S.stroma*
	2012	*S. stroma*	*S. stroma*	*S.stroma*	*S.stroma*	*S.stroma*	*S.stroma*
Simpson's Index	2011	1.11	1.09	1.00	1.27	1.20	1.20
	2012	1.27	1.10	1.08	1.07	1.20	1.12

There was a marked increase in the number of species carried by wood mice in 2012, as evidenced by the change in the shape of the frequency distribution of species richness (Fig 3.2). The majority of mice in both years were infected with more than one helminth species with co-infections increasing from 60.7% in 2011 to 86.7% in 2012. The number of wood mice that were helminth-free decreased from 5.2% (13) to only a single wood mouse (0.75%) in 2012.

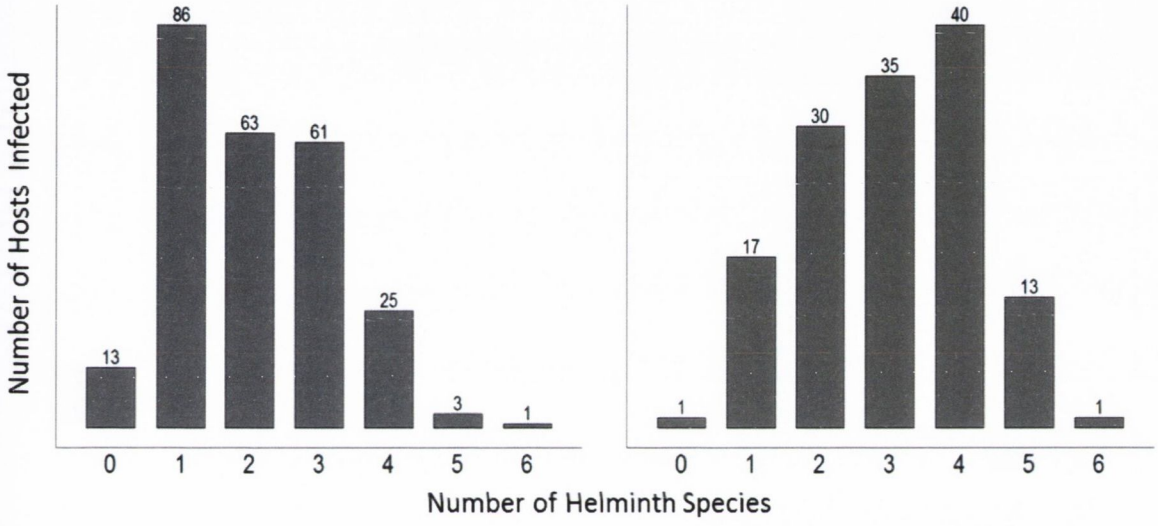


Figure 3.2 Frequency distribution of intestinal helminth species richness in wood mice in 2011 (A) and 2012 (B). Host sample size is indicated above the bars.

Component community similarity for all sites in both years was analysed by means of the Bray-Curtis Dissimilarity Index (Fig. 3.3). Analyses revealed a clear dissimilarity between mice-vole and mice-only sites in 2011. Merlin in 2012 clustered with 2011 mice-vole sites , however Coole in 2012 clustered with mice-only sites, being most similar to Santry in 2012. Knocksink was the only site that that showed a strong similartity between the two years sampled.

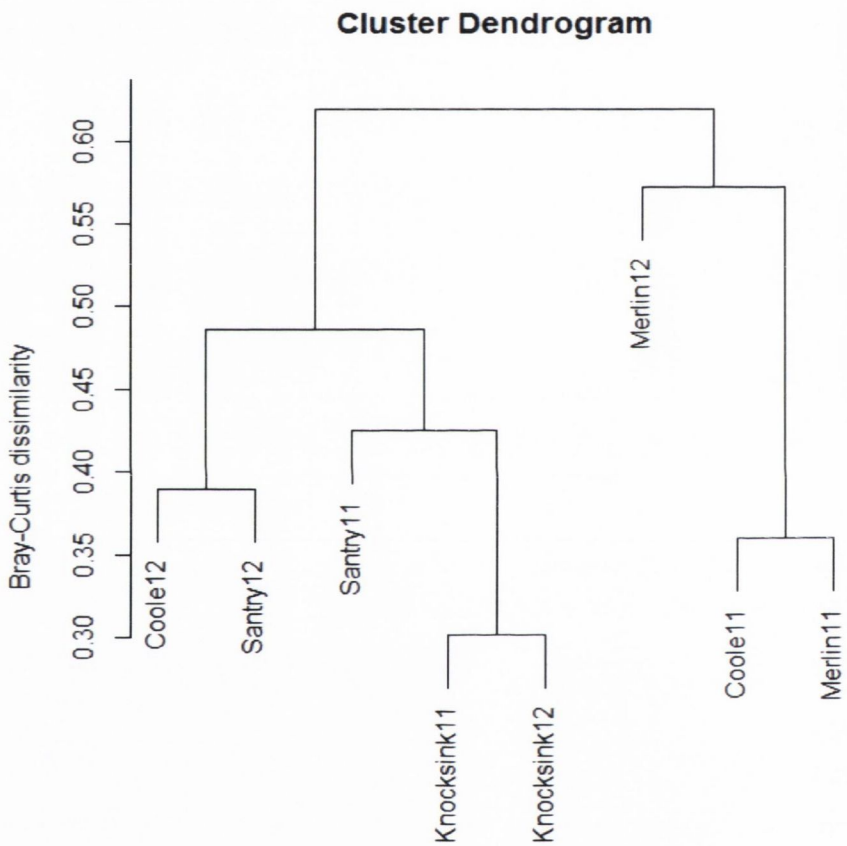


Figure 3.3 Bray-Curtis Dissimilarity dendrogram for wood mice at all sites in 2011 and 2012. Sub-sites have been combined for analyses. Coole11 = Coole (A) 2011 and Coole (B) 2011; Merlin11 = Merlin 2011; Knocksink11 = Knocksink (A) 2011 and Knocksink (B) 2011; Santry11 = Santry 2011. Coole12 = Coole (A) 2012 and Coole (B) 2012; Merlin12 = Merlin 2012; Knocksink12 = Knocksink (A) 2012 and Knocksink (B) 2012; Santry12 = Santry 2012

3.2.2.3 Infracommunity Structure of Helminths of Wood Mice

The maximum number of helminth species infecting wood mice was 6 which occurred in one wood mouse in Santry in 2012 and in Coole B in 2001. In both years in Merlin helminth co-infection in wood mice did not reach above 3 species (Table 3.7). Nematodes made up the bulk of infracommunities overall (276.6 ±24.3), followed by trematodes (6.07 ±0.60) and cestodes (2.44 ±0.05). The mean number of helminths recovered from wood mice increased in 2012 by 101.4%. The increase occurred at all sites except Merlin. The biggest increase in mean abundance was in the cestodes, which increased by 866.7% in 2012. Overall wood mouse infracommunities with the greatest mean number of nematodes and cestodes were found at Knocksink (B), while for trematodes the greatest mean abundances were recovered from Santry. Parasite species showed an aggregated distribution in wood mice (Appendix1, Table 4A).

Table 3.7 Measures of helminth infracommunity structure in wood mice by year and site.

	Year	Knocksink (A)	Knocksink (B)	Santry	Coole(A)	Coole(B)	Merlin	Total Sample
Mean Species	2011	3.02 ±0.11	3.00 ±0.15	1.60 ±0.10	1.37 ±0.15	1.76 ±0.16	1.00 ±0.14	2.05± 0.07
	2012	3.60 ±0.22	3.72 ±0.20	3.09 ±0.17	2.11 ±0.20	2.60 ±0.36	1.81 ±0.26	3.01 ±0.11
	Total	**3.22 ±0.11**	**3.24 ±0.12**	**2.30 ±0.13**	**1.59 ±0.13**	**2.00 ±0.16**	**1.21 ±0.13**	**2.37 ±0.06**
Max Species	2011	4	5	3	6	4	3	6
	2012	5	5	6	4	5	3	6
Mean Helminths	2011	345.6 ±46.2	360.6 ±68.4	303.9 ±60.4	30.6 ±5.83	62.9 ±27.15	28.61 ±7.50	210 ±21.8
	2012	349.0 ±116.5	731.5 ± 155.4	557.4 ± 110.2	266.1 ±130.6	139.7 ±35.6	11.4 ±2.99	423.3 ±55.2
	Total	**346.7 ±49.3**	**485.9 ±71.7**	**426.4 ±62.8**	**100.1 ±40.4**	**86.1 ±22.2**	**24.1 ±5.67**	**285.1 ±24.5**
Mean Nematodes	2011	338.0 ±46.0	355.7± 68.6	300.2 ±60.4	28.0 ±5.89	62.2 ±27.2	26.0 ±7.64	206.1 ±21.8
	2012	332.0± 115.2	704.9 ±154.1	537.3 ±109.7	257.9 ±131.1	131.2 ±32.4	4.55 ±2.79	406.5 ±54.8
	Total	**336.0 ±48.9**	**473.7 ±71.1**	**414.8 ±62.5**	**95.7 ±40.5**	**83.3 ±21.6**	**20.4 ±5.85**	**276.6 ±24.3**
Mean Cestodes	2011	0.69 ±0.25	0.90 ±0.28	0.37 ±0.21	0.40 ±0.26	0.52 ±0.19	0.39 ±0.18	0.56 ±0.1
	2012	4.48 ±1.63	11.6 ±6.70	3.14 ±1.20	7.83 ±1.97	5.87 ±3.56	2.45 ±0.79	5.79 ±1.4
	Total	**2.02 ±0.60**	**4.53 ±2.32**	**1.76 ±0.59**	**2.61 ±0.74**	**2.20 ±1.13**	**0.93 ±0.28**	**2.44 ±0.51**
Mean Trematodes	2011	6.86 ±1.10	4.00 ±0.99	3.30 ±1.20	2.15 ±1.11	0.17 ±0.12	2.22 ±1.07	3.38 ±0.4
	2012	12.6 ±2.45	15.0 ±3.04	16.9 ±3.36	0.33 ±0.20	2.60 ±2.54	4.36 ±1.72	11.03 ±1.4
	Total	**8.78 ±1.14**	**7.73 ±1.35**	**9.90 ±1.88**	**1.61 ±0.79**	**0.92 ±0.70**	**2.79 ±0.91**	**6.07 ±0.60**
Mean Brillouin's Index	2011	0.37 ±0.04	0.33 ±0.04	0.10 ±0.03	0.13 ±0.04	0.21 ±0.05	0.06 ±0.02	0.21 ±0.02
	2012	0.51 ±0.07	0.40 ±0.06	0.26 ±0.04	0.26 ±0.06	0.28 ±0.06	0.29 ±0.09	0.34 ±0.03
	Total	**0.42 ±0.04**	**0.35 ±0.03**	**0.18 ±0.03**	**0.16 ±0.03**	**0.23 ±0.04**	**0.12 ±0.03**	**0.25 ±0.01**
Max Brillouin's Index	2011	0.98	1.04	0.71	1.19	0.81	0.54	1.19
	2012	1.03	1.10	0.92	0.79	0.79	0.80	1.10

Species Richness

Over the two years of the study, mean species richness in wood mice was 2.37 ±0.06 (Table 3.7). Species richness was greater in mice-only sites (2.88 ±0.08) compared to mice-vole sites (1.62 ±0.09) and was greatest at the mice-only site of Knocksink (B) (3.24 ±0.12). There was little difference in mean species richness between the sub-sampled sites Knocksink (A) and (B). Mean species richness increased in 2012 and this increase was observed at all sites.

Site was the most important factor determining differences in species richness (GLM, family= Poisson, site: $\chi^2_3 = 72.7$, $P < 0.001$, Fig. 3.4A). There was an increase in species richness in 2012 (GLM, family= Poisson, year: $\chi^2_1 = 7.18$, $P < 0.01$), this occurred at all sites, but the rate of increase varied (GLM, family= Poisson, site:year: $\chi^2_3 = 10.6$, P=0.05, Fig. 3.4C). Santry had the largest increase in mean species richness (97.6%) while the smallest increase was at Knocksink (21.6%).

Intrinsic factors also had an influence on species richness with richness increasing through the age classes (GLM, family= Poisson, age class: $\chi^2_2 = 14.0$, $P < 0.001$, Fig. 3.4B).

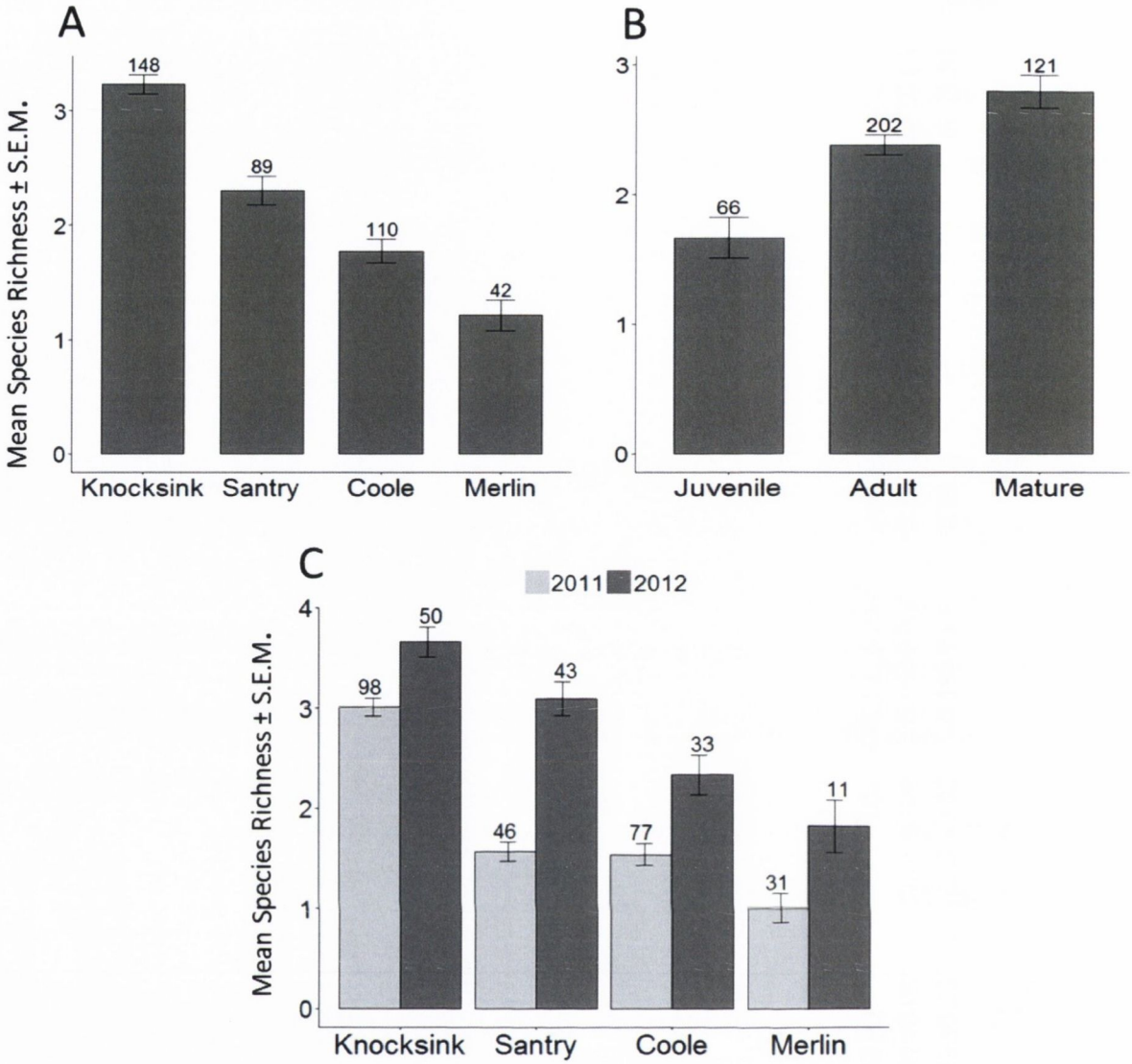


Figure 3.4 Mean helminth species richness in wood mice. Species richness by site (A), age class (B) and site and year (C).

Brillouin's Index of Diversity

Brillouin's Index of diversity for wood mice over the entire study was greater in mice-only sites (0.31 ±0.02) than in mice-vole sites (0.17 ±0.02). Knocksink had the highest measure with sub-sites combined (0.38 ±0.02). The sub-sampled site Knocksink (B) in 2012 had the highest measure of Brillouin's overall (Table 3.7). There was a significant influence of age, Brillouin's increasing from juveniles to mature wood mice (GLM, family = quasi-poisson, age class: $F_{2, 385}$ =25.6, P<0.001 P <0.001, Fig. 3.5A) but no significant effect of sex (sex: $F_{1, 385}$ =2.3, P =0.13). Site was significant, Brillouin's in Knocksink being significantly greater, while differences between the remaining sites varied less (GLM, family = quasi-poisson, site: $F_{3, 385}$ =18.4 P <0.001, Fig. 3.5B). Brillouin's also increased significantly in 2012 (GLM, family = quasi-poisson, year: $F_{1, 385}$ = 15.3, P <0.001, Fig. 3.5C).

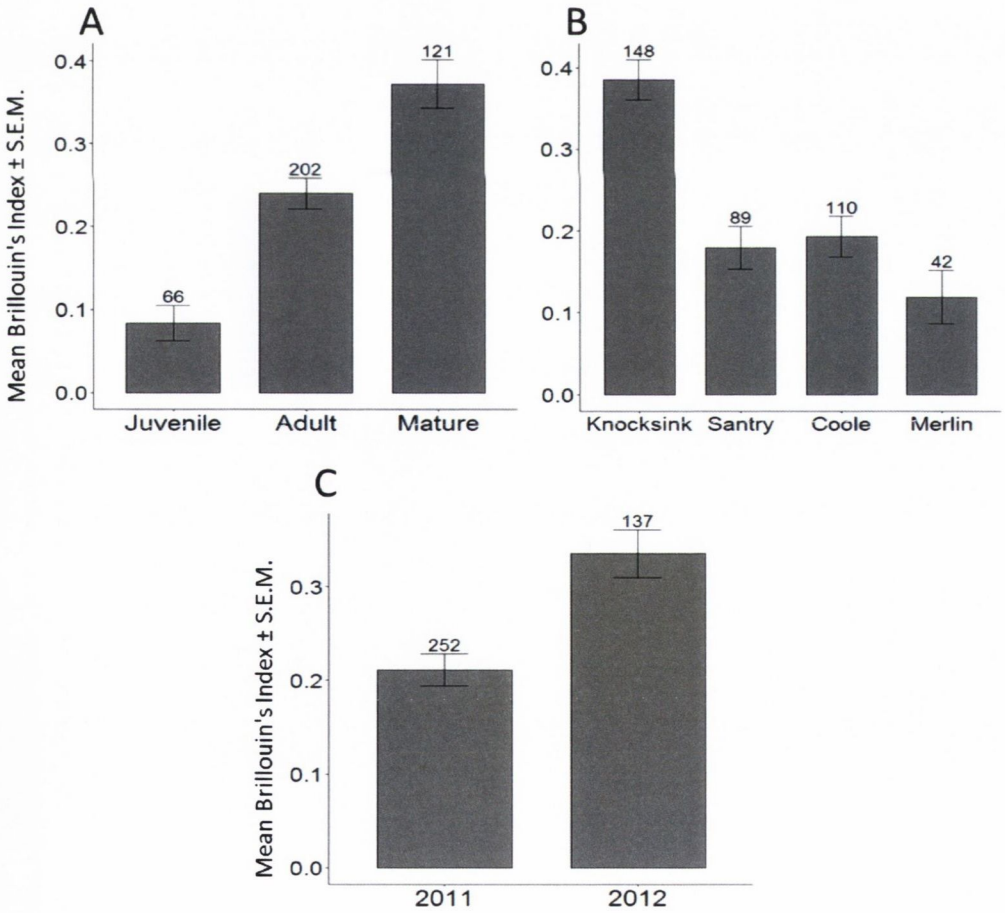


Figure 3.5 Brillouin's Index of Diversity (S.E.M) for wood mice. Brillouin's by age class (A) site (B) and year (C).

Prevalence and Abundance of Individual Helminth Species

The prevalence and abundance of all helminth species recorded in wood mice in this study is summarised in Table 3.8.

Table 3.8 Prevalence (%) with 95% Clopper–Pearson confidence intervals and mean abundance ±standard error of all helminth species of wood mice by year and site.

Species	Year	Knock(A)	Knock(B)	Santry	Coole(A)	Coole(B)	Merlin	Total Sample
S. stroma	2011	98.0(89.1-99.9)^{P} 320.5 ±46.0^{A}	98(89.1-99.9)^{P} 345.0 ±68.7^{A}	93.5(82.1-98.6)^{P} 300.2 ±60.4^{A}	81.4(66.0-92.0)^{P} 27.1 ±6.0^{A}	88(72.5.-96.7)^{P} 57.1 ±27.2^{A}	47.6(30.2-63.6)^{P} 25.9 ±7.7^{A}	86.9(82.1-90.8)^{P} 199.7 ±21.7^{A}
	2012	92.0(74.0-100)^{P} 307.7 ±112^{A}	96.0(79.6-100)^{P} 682.7 ±153.4^{A}	97.7(87.799.9)^{P} 535.9 ±109.8^{A}	83.0(58.6-96.4)^{P} 257.4 ±131.2^{A}	93.3(68.1-99.8)^{P} 127.4 ±32.3^{A}	45.5(16.7-76.6)^{P} 4.5 ±2.8^{A}	89.8(83.4-94.3)^{P} 397.1 ±54.4^{A}
	Total	**95.9(88.6-99.2)^{P} 316.2 ±48.2^{A}**	**97.3-(90.6-99.7)^{P} 459.1 ±70.9^{A}**	**95.5(88.9-98.8)^{P} 414.1 ±62.6^{A}**	**82.0(70.0-90.6)^{P} 95.0 ±40.5^{A}**	**89.8(77-96.6)^{P} 78.7 ±21.6^{A}**	**47.6(32.0-63.6)^{P} 20.3 ±5.85^{A}**	**87.9(84.3-91.0$^{)P}$ 269.2 24.2^{A}**
*H. polygyrus**	2011	93.9(83.1-98.7) 17.5 ±3.91	91.8(80.4-97.7) 10.6 ±1.37	- -	- -	- -	- -	92.9(85.8-97.1) 14.1 ±2.09
	2012	88.8(68.0-97.5) 23.8 ±6.07	100(86.3-100) 21.3 ±3.3	- -	- -	- -	- -	94(83.5-98.7) 22.6 ±3.4
	Total	**91.9(83.2-97.0) 19.7 ±3.3**	**94.6(86.7-98.5) 14.2 ±1.55**	**- -**	**- -**	**- -**	**- -**	**93.2(87.9-96.7) 16.9 ±1.83**
T. muris	2011	0(0-7.3) 0	8.2(2.3-19.6) 0.08 ±0.04	4.34(0.53-14.8) 0.04 ±0.03	14.0(5.3-27.9) 0.26 ±0.12	26.5(12.9-44.4) 0.44 ±0.16	0(0-0.11) 0	8.3(5.2-12.5) 0.13 ±0.03
	2012	8.0(1.0-26.0) 0.20 ±0.16	8.0(1.0-26.0) 0.12 ±0.09	32.6(19.1-48.5) 0.74 ±0.22	11.1(1.4-34.7) 0.17 ±0.12	26.7(7.8-55.1) 0.53 ±0.26	0(0-0.28) 0	17.5(11.6-24.9) 0.37 ±0.09
	Total	**2.7(0.32-9.42) 0.07 ±0.06**	**8.11(3.03-16.8) 0.09 ±0.04**	**18.0(10.6-27.5) 0.38 ±0.11**	**13.1(5.8-24.2) 0.22 ±0.09**	**26.6(14.9-41.1) 0.47 ±0.13**	**0(0-8.4) 0**	**11.6(8.56-15.2) 0.08 ±0.03**

Species	Year	Knock(A)	Knock(B)	Santry	Coole(A)	Coole(B)	Merlin	Total Sample
A. murissylvatici	2011	0(0-7.3) 0	0(0-7.3) 0	0(0-7.7) 0	9.3(2.6-22.1) 0.70 ±0.56	26.5(12.9-44.4) 4.62 ±3.84	3.2(1.0-16.7) 0.06 ±0.06	5.6(3.1-9.1) 0.75 ±0.53
	2012	4.0(0.1-20.4) 0.04 ±0.04	12.0(2.5-31.2) 0.76 ±0.68	23.3(11.8-38.6) 0.63 ±0.26	22.2(6.4-47.6) 0.39 ±0.20	40.0(16.3-67.7) 3.27 ±1.57	0(0-28.5) 0	17.5(11.6-24.9) 0.75 ±0.24
	Total	**1.35(0.03-7.30) 0.01 ±0.01**	**4.05(0.84-11.4) 0.26 ±0.23**	**11.2(5.52-19.7) 0.30 ±0.13**	**13.1(5.83-24.2) 0.61 ±0.40**	**30.6(18.3-45.4) 4.2 ±2.69**	**2.31(0.06-12.6) 0.04 ±0.05**	**9.77(7.01-13.2) 0.75 ±0.35**
H. hibernia	2011	18.4(8.8-32.0) 0.31 ±0.11	32.7(19.9-47.5) 0.67 ±0.18	10.9(3.6-23.6) 0.28 ±0.20	2.3(0.1-12.3) 0.02 ±0.02	0(0-10.3) 0	3.2(0.1-16.7) 0.06 ±0.06	12.7(8.9-17.5) 0.25 ±0.06
	2012	32.0(14.9-53.5) 3.64 ±1.64	64.0(42.5-82.0) 11.6 ±6.70	23.3(11.8-38.6) 0.70 ±0.33	0(0-18.5) 0	13.3(1.7-40.5) 3.73 ±3.66	0(0-28.5) 0	26.3(19.1-34.5) 3.41 ±1.35
	Total	**23.0(14.0-34.2) 1.43 ±2.32**	**43.2(31.8-55.3) 0.05 ±0.05**	**16.9(9.75-26.3) 0.48 ±0.19**	**1.63(0.04-8.78) 0.020.02**	**2.04(0.05-10.8) 1.141.12**	**2.4(0.06-12.6) 0.050.05**	**17.5(13.8-21.6) 1.37 ±0.48**
S. lobata	2011	10.2(3.4-22.2) 0.39 ±0.23	2.0(0.1-10.9) 0.22 ±0.22	2.2(0.1-11.5) 0.09 ±0.09	11.6(3.9-25.1) 0.37 ±0.26	23.5(10.7-41.2) 0.53 ±0.19	16.1(5.5-33.7) 0.32 ±0.18	9.9(6.5-14.3) 0.31 ±0.09
	2012	28.0(12.1-49.4) 0.84 ±0.34	0 (0-13.7) 0	20.9(10.0-36.0) 2.44 ±1.14	77.8(52.4-93.6) 7.83 ±1.97	66.7(38.4-88.2) 2.13 ±0.58	63.6(30.8-89.1) 2.45 ±0.79	34.3(26.4-42.9) 2.38 ±0.49
	Total	**16.2(8.67-26.6) 0.54 ±0.20**	**1.35 (0.03-7.30) 0.15 ±0.15**	**11.2(5.52-19.7) 1.22 ±0.56**	**31.1(19.9-44.3) 2.57 ±0.74**	**36.7(23.4-51.7) 1.02 ±0.24**	**28.6(15.7-44.6) 0.88 ±0.28**	**18.5(14.8-22.7) 1.04 ±0.19**
C. vitta	2011	81.4(66.6-91.6) 6.86 ±1.10	59.2(44.2-73.0) 3.90 ±0.97	45.7(30.9-61.0) 3.30 ±1.20	11.6(3.9-25.1) 1.93 ±1.08	0(0-10.3) 0	22.6(9.59-41.1) 2.13 ±1.00	40.5(34.4-46.8) 3.29 ±0.44
	2012	76.0(54.9-90.6) 9.28 ±1.77	76.0(54.9-90.6) 14.8 ±3.03	79.1(64.0-90.0) 15.8 ±3.38	5.6(0.1-27.3) 0.11 ±0.11	6.78(0.17-31.9) 0.13 ±0.13	63.6(30.8-89.1) 4.18 ±1.76	59.1(50.4-67.4) 9.71 ±1.35
	Total	**79.7(68.8-88.2) 7.67 ±0.91**	**64.9(52.9-75.6) 7.57 ±1.33**	**61.8(50.9-71.9) 9.34 ±1.86**	**9.84(3.70-20.2) 1.39 ±0.77**	**2.04(0.05-10.8) 0.04 ±0.04**	**33.3(19.6-49.5) 2.67 ±0.87**	**47.0(42.0-52.1) 5.55 ±0.57**

Species	Year	Knock(A)	Knock(B)	Santry	Coole(A)	Coole(B)	Merlin	Total Sample
	2011	0(0-7.3) 0	8.2(2.3-19.6) 0.10 ±0.05	0(0-7.7) 0	7.0(1.5-19.1) 0.21 ±0.15	8.8(1.9-23.7) 0.18 ±0.12	6.5(0.8-21.4) 0.10 ±0.07	4.8(2.5-8.2) 0.09 ±0.03
B. recurvum	2012	32.0(14.9-53.5) 3.28 ±1.72	16.0(4.5-36.1) 0.28 ±0.15	32.6(19.1-48.5) 1.16 ±0.40	11.1(1.4-34.7) 0.22 ±0.17	13.3(1.7-40.5) 2.47 ±2.26	9.1(0.2-41.3) 0.18 ±0.18	22.6(15.9-30.6) 1.33 ±0.42
	Total	**10.8(4.78-20.2) 1.11 ±0.60**	**10.8(4.78-20.2) 0.16 ±0.06**	**15.7(8.88-25.0) 0.56 ±0.20**	**8.20(2.72-18.1) 0.21 ±0.11**	**10.2(3.39-22.2) 0.88 ±0.70**	**7.14(1.50-19.5) 0.12 ±0.07**	**11.1(8.12-14.6) 0.53 ±0.15**
	2011	10.2(3.40-22.2) 0.20 ±0.12	2.04(0.05-10.9) 0.20± 0.12	6.52(1.37-17.9) 0.65 ±0.04	0(0-822) 0	0(0-10.3) 0	0(0-11.2) 0	3.57(1.65-6.67) 0.06 ±0.03
H. taeniaeformis	2012	0(0-13.7) 0	0(0-13.7) 0	4.65(0.57-15.8) 0.04 ±0.03	0 (0-18.5) 0	0(0-21.8) 0	0(0-28.5) 0	1.46(0.18-5.17) 0.01 ±0.01
	Total	**6.76(2.23-15.1) 0.14 ±0.08**	**1.35(0.03-7.30) 0.01 ±0.01**	**5.62(1.85-12.6) 0.06 ±0.02**	**0(0-5.87) 0**	**0(0-7.25) 0**	**0(0-8.41) 0**	**2.83(1.42-5.00) 0.04 ±0.02**
	2011	0(0-7.25) 0	0(0-7.25) 0	0(0-7.71) 0	2.33(0.06-12.3) 0.07 ±0.07	2.94(0.07-15.3) 0.03 ±0.03	0(0-11.2) 0	0.79(0.10-2.84) 0.02 ±0.01
Mesocestoides. spp.	2012	0(0-13.7) 0	0(0-13.7) 0	0(0-8.22) 0	0(0-18.5) 0	13.3(1.66) 1.07 ±0.73	0(0-28.5) 0	1.46(0.18-5.17) 0.12± 0.08
	Total	**0(0-4.86) 0**	**0(0-4.86) 0**	**0(0-4.06) 0**	**1.64(0.04-8.80) 0.05 0.05**	**6.12(1.28-16.9) 0.35 0.23**	**0(0-8.41) 0**	**1.03(0.28-2.61) 0.05 0.03**

[P] Prevalence (%) with 95% confidence intervals

[A] Abundance ± standard error of the mean

*Analysed for populations from Knocksink sites only

Syphacia stroma

S. stroma was the most prevalent and abundant helminth at all sites (Table 3.8). Overall 342 (87.9% CI: 84.3-91.0) wood mice were infected with *S. stroma*. Prevalence was 86.9% (CI: 82.0-90.81) in 2011 which increased to 89.8% (CI: 83.4-94.3) in 2012 (Table 3.8). Site was the main factor affecting prevalence (GLM family=binomial, site: $\chi^2_3 = 18.9$, $P < 0.001$, Fig. 3.6A). Knocksink and Santry had a similar prevalence but prevalence dropped in Coole and was lowest in Merlin (Table 3.8). There was a main effect of age (GLM family=binomial, age class: $\chi^2_2 = 11.3$, $P < 0.01$), with prevalence increasing from juvenile to adult and deceasing again in the mature class (Fig. 3.6B).

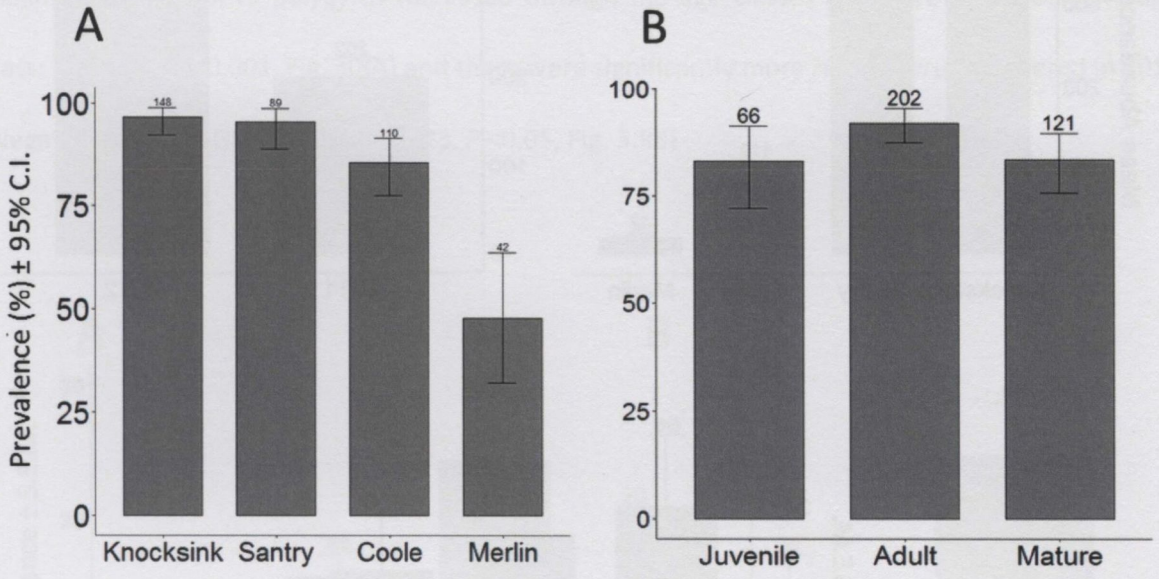


Figure 3.6 Prevalence (%) of *Syphacia stroma spp.* in wood mice. Prevalence by site (A) and age class (B).

Full factorial abundance models could not be fitted for *S. stroma,* nor could simpler models without interaction terms and so non-parametric tests were used. The mean abundance of *S. stroma* infracommunities in wood mice was significantly higher in Santry and Knocksink, decreasing substantially in Coole and reaching the lowest level in Merlin (Kruskal-Wallis test, site: $\chi^2_3 = 137.17$, $P < 0.001$, Fig 3.7A). Santry and Knocksink accounted for 90% of all *S. stroma* recovered. Mean abundance increased from 2011 to 2012 (Mann-Whitney *U* test, year: $z = -4.16$, $P < 0.001$, Fig. 3.7B).

The increase in mean abundance was seen at all sites except Merlin. The effect of age was also significant (Kruskal-Wallis test, age class: $\chi^2_2 = 9.11$, $P < 0.05$, Fig. 3.7C), mean abundance was highest in juveniles decreasing in adult and mature wood mice. The average burden of *S. stroma* was higher in males (295.2 ±38.1) than females (240.2 ±28.5), but not significantly so (Mann-Whitney U test, sex: z= 0.02, P=0.98).

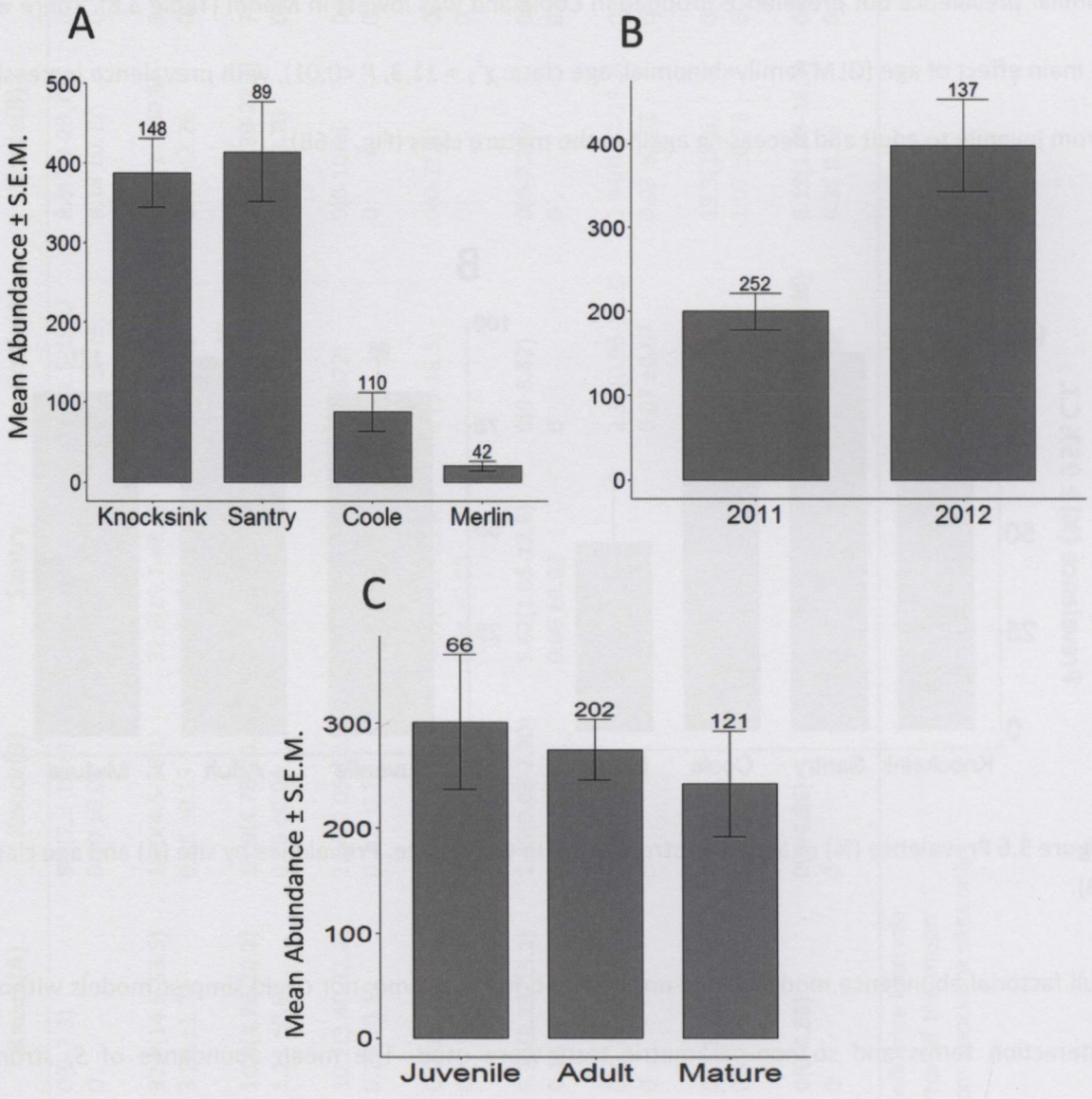


Figure 3.7 Mean abundance of *Syphacia stroma* in wood mice. Abundance by site (A), year (B) and age class.

Heligosomoides polygyrus

H. polygyrus was found only at Knocksink and analyses are limited to this site. Out of 148 wood mice at Knocksink, 138 (93% CI: 87.9-96.7) were infected. Models for prevalence could not be fitted so non-parametric statistics were used. No significant differences in prevalence were found in the data though prevalence was higher in 2012 compared to 2011 (Table 3.8) and higher in female wood mice (females: 95.2% CI: 88.1-98.6; males: 90.7% CI: 81-96.5). Prevalence was lowest in juvenile wood mice age classes (85.7% CI: 63.6-96.9), increased in in adults (96.4% CI: 89.8-99.2) and decreasing again in mature wood mice (90.9% CI: 78.3-97.5).

Mean abundance of *H. polygyrus* increased through the age classes (Negative binomial GLM, age class: LR_2=22.9, P <0.001, Fig. 3.8A) and there were significantly more *H. polygyrus* recovered in 2012 (Negative binomial GLM, year: LR_1=5.23, P <0.05, Fig. 3.8B)

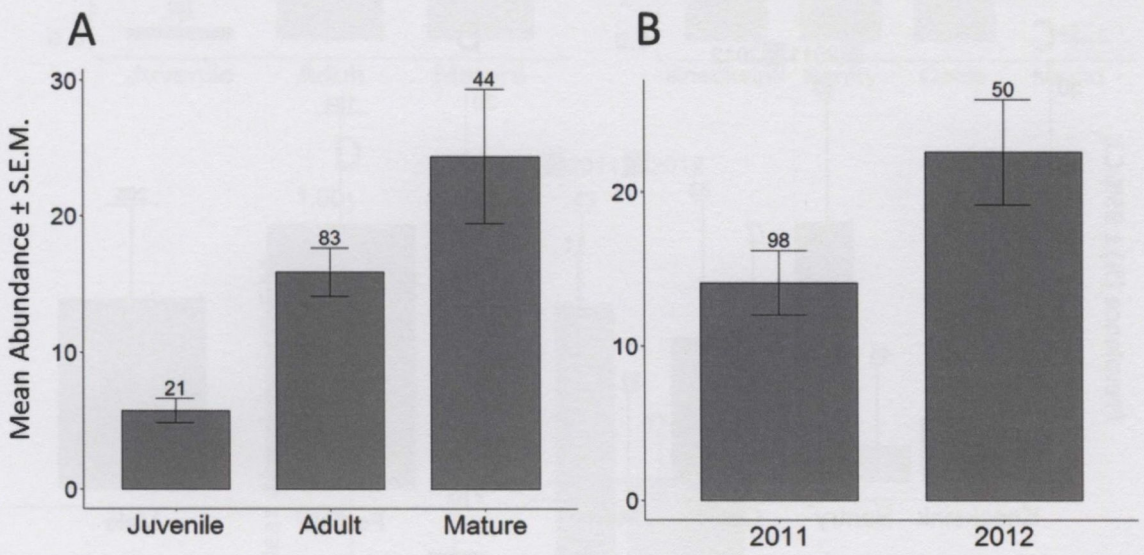


Figure 3.8 Mean abundance of *Heligosomoides polygyrus* in wood mice. Abundance by age class (A) and year (B).

Trichuris muris

Prevalence of *T. muris* was 11.6% (CI: 9.56-15.2, Table 3.8) with 45 wood mice infected. Age class accounted for most of the deviance in both prevalence (GLM family=binomial, age class: $\chi^2_2 = 19.6$, $P < 0.001$, Fig. 3.9A) and abundance (Negative binomial GLM, age class: $LR_2 = 20.7$, $P < 0.001$, Fig. 3.10A), increasing significantly from juvenile to mature wood mice.

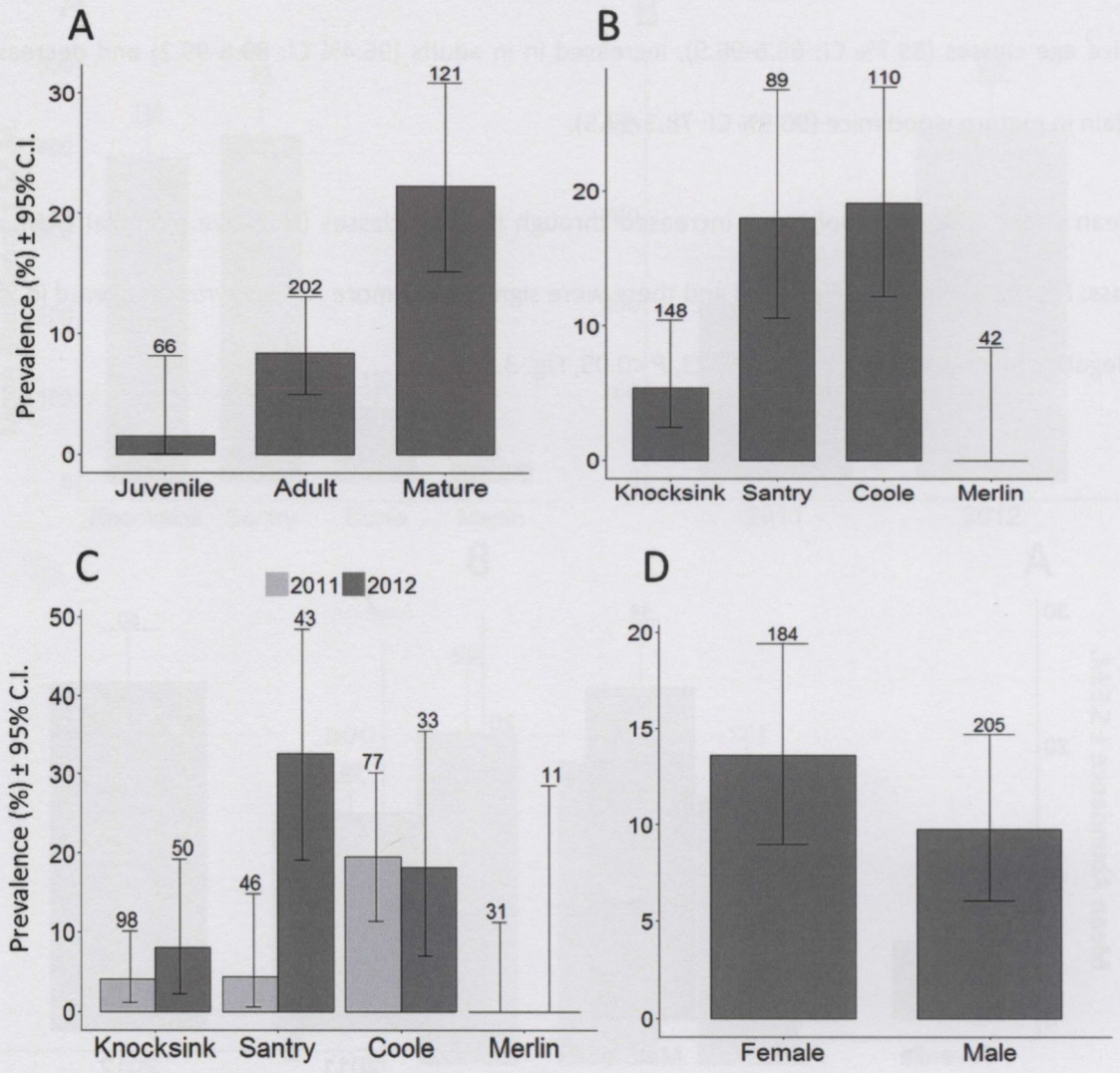


Figure 3.9 Prevalence (%) of *Trichuris muris* in wood mice. Prevalence by age class (A), site (B), site and year (C) and sex (D).

Site significantly affected both prevalence and abundance. *T. muris* was absent from Merlin and prevalence and abundance were lowest in Knocksink. Prevalence was highest in Coole (GLM family=binomial, site: $\chi^2_3 = 15.6$, $P < 0.001$, Fig. 3.9B) but abundance was greatest in Santry (Negative

binomial GLM, site: LR_3=14.3, P <0.05, Fig. 3.10B). A significant site:year interaction revealed a large increase in prevalence (GLM family=binomial, site:year χ^2_3 = 10.6, P <0.05, Fig. 3.9C) and abundance (Negative binomial GLM, site:year: LR_3=4.92, P <0.05, Fig. 3.10C) in Santry in 2012. Prevalence and abundance increased in both Knocksink and Santry and decreased slightly in Coole in 2012. Prevalence was significantly higher in female wood mice (GLM family=binomial, sex: χ^2_1 = 5.3, P <0.05, Fig. 3.9D).

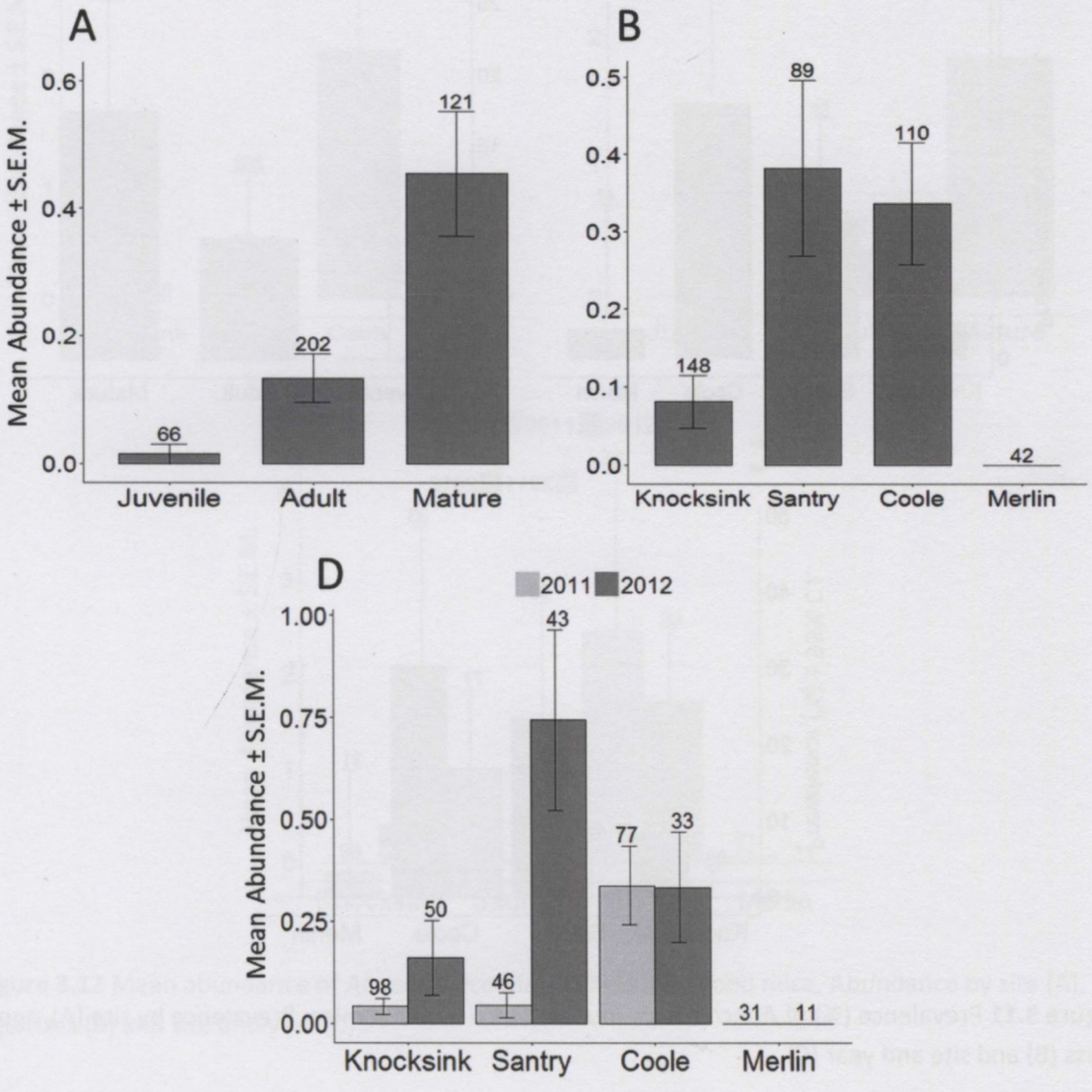


Figure 3.10 Mean abundance of *Trichuris muris* in wood mice. Abundance by age class (A), site (B) and site and year (C).

Aonchotheca murissylvatici

A. murissylvatici was the nematode with the lowest prevalence in wood mice with 38 wood mice infected (9.77% CI: 7.00-13.2). The majority of infected wood mice were found in Coole A and B (Table 3.8) and there was a significant main effect of site (GLM family=binomial, site: $\chi^2_3 = 28.1$, $P < 0.001$, Fig. 3.11A).

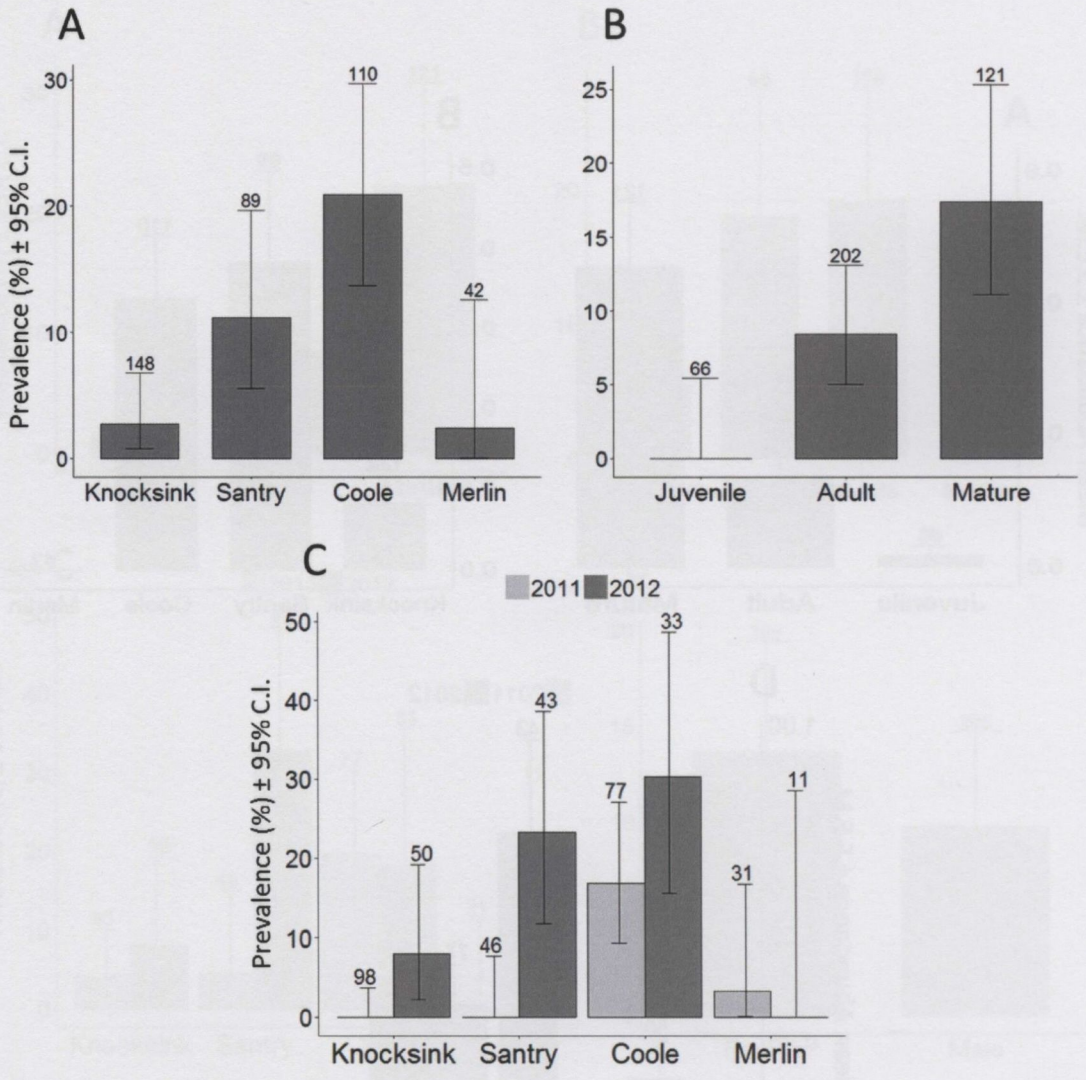


Figure 3.11 Prevalence (%) of *Aonchotheca murissylvatici* in wood mice. Prevalence by site (A), age class (B) and site and year (C).

No juvenile wood mice were found with infections and prevalence increased from adult to mature wood mice (GLM family=binomial, age class: $\chi^2_2 = 16.6$, $P < 0.001$, Fig. 3.11B). Modelling revealed a

significant interaction between year and site; *A. murissylvatici* was absent from Knocksink and Santry in 2011, appearing in wood mice in 2012, while disappearing from Merlin in 2012 (GLM family=binomial, site:year: $\chi^2_3 = 13.1$, $P < 0.05$, Fig. 3.11C).

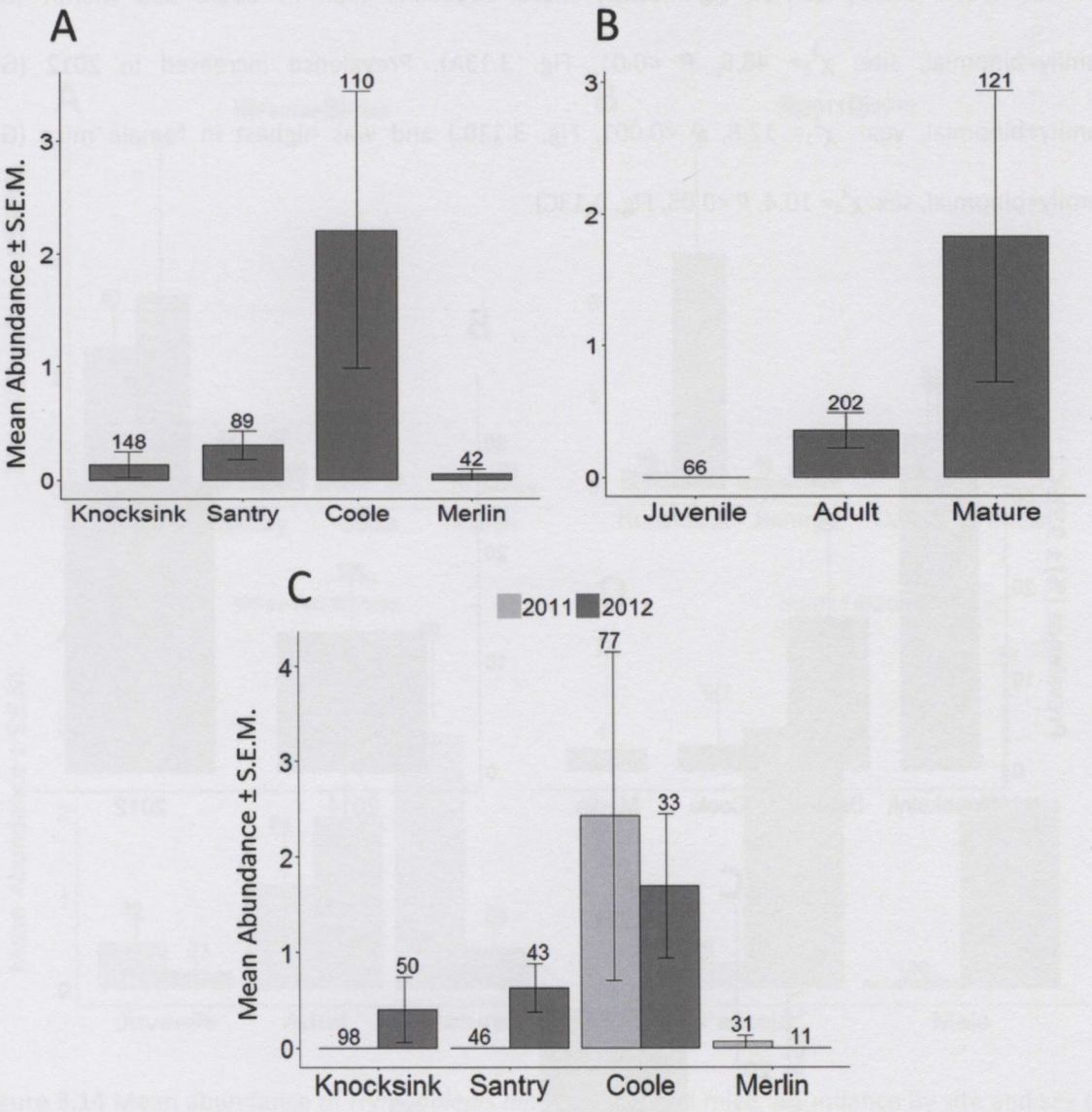


Figure 3.12 Mean abundance of *Aonchotheca murissylvatici* in wood mice. Abundance by site (A), age class (B) and site and year (C).

Mean abundance of *A. murissylvatici* was significantly affected by site, age class and an interaction between site and year. Mean abundance was highest in Coole (Negative binomial GLM, site: LR_3=30.9, $P < 0.001$, Fig. 3.12A) and increased from juvenile to mature wood mice (Negative binomial

GLM, age class: LR_1=5.23, P <0.05, Fig. 3.12B). Abundance increased in Knocksink and Santry in 2012 but decreased in Coole and Merlin (Negative binomial GLM, site:year: LR_3=14.5, P <0.01, Fig. 3.12C).

Hymenolepis hibernia

Sixty-eight wood mice (17.5 CI: 13.8-21.6) were infected with *H. hibernia* (Table 3.8). Wood mice in Knocksink and Santry carried significantly more infections than in Coole and Merlin (GLM family=binomial, site: χ^2_3= 48.5, P <0.01, Fig. 3.13A). Prevalence increased in 2012 (GLM family=binomial, year: χ^2_1= 12.8, P <0.001, Fig. 3.13B,) and was highest in female mice (GLM family=binomial, sex: χ^2_1= 10.4, P <0.05, Fig. 3.13C).

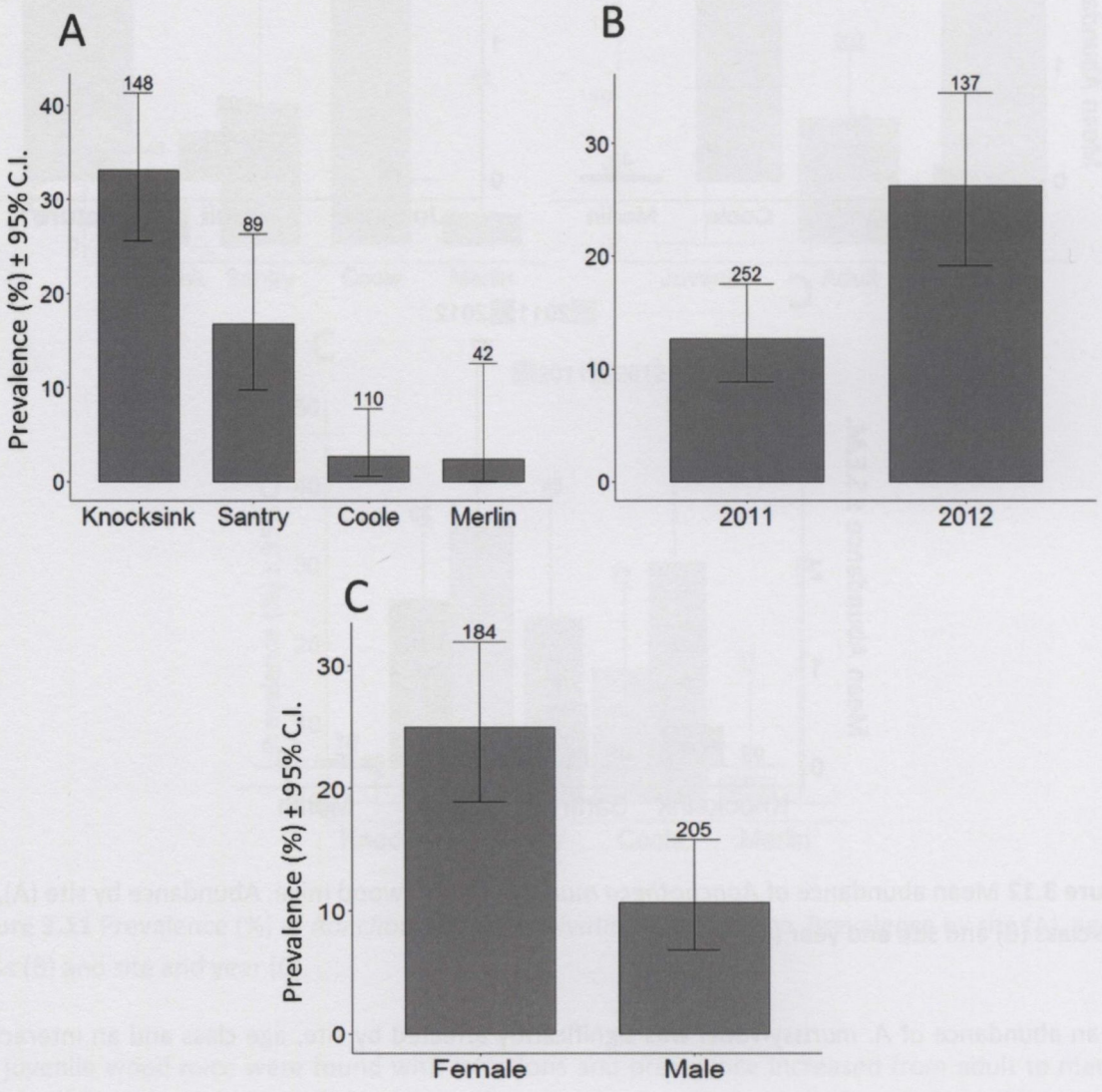


Figure 3.13 Prevalence (%) of Hymenolepis hibernia in wood mice. Prevalence by site (A), year (B) and sex (C).

The model for abundance was complicated by a number of significant main effects and interactions. Female wood mice (1.5 ±0.5) were more heavily infected than males (1.2 ±0.8) (Negative binomial GLM, sex: LR_1=24.5, P <0.001) but this differed between sites. In Knocksink and Merlin, males carried heavier infections while females were slightly more heavily infected in Santry and no males carried infections in Coole (Negative binomial GLM, site:sex: LR_3=28.6, P<0.001, Fig. 3.14A).

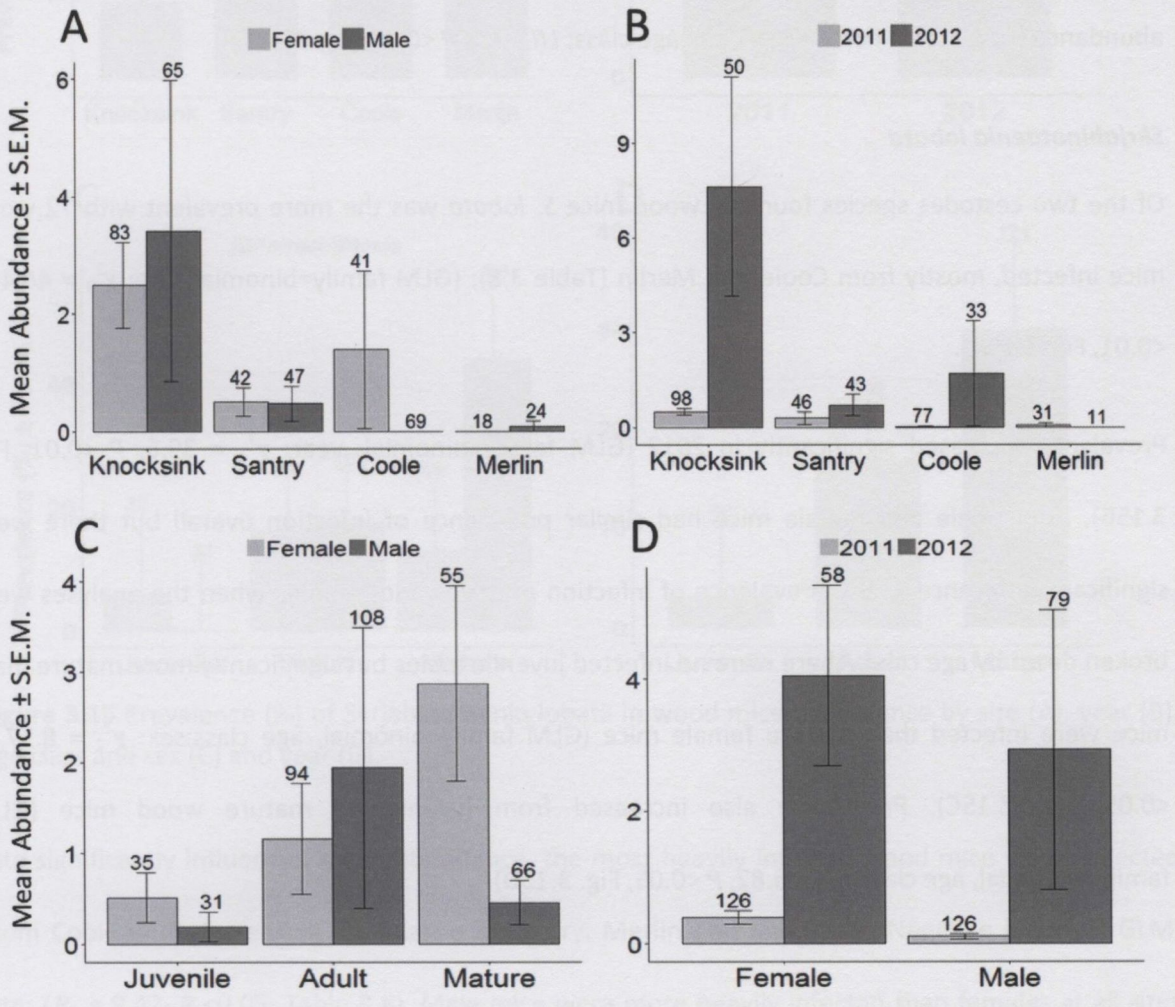


Figure 3.14 Mean abundance of *Hymenolepis hibernia* in wood mice. Abundance by site and sex (A), site and year (B), age class and sex (C) and sex and year (D).

Abundance increased in 2012 overall (Negative binomial GLM, year: LR_1=25.7, P <0.001, Table 3.8) with a significantly greater rate of increase in Knocksink compared to the other sites (Negative binomial GLM, site:year: LR_3=18.6, P <0.001, Fig. 3.14B). Mean abundance increased in 2012 (Negative binomial GLM, year LR_1=25.7, P <0.001, Table 3.8) and the rate of increase was greater in females (Negative binomial GLM, sex:year LR_1= 5.02, P <0.05, Fig. 3.14D). An interaction between sex and age class revealed that mature female wood mice were driving much of the female bias in mean abundance (Negative binomial GLM, sex:age class: LR_2=7.5, P <0.05, Fig. 3.14C).

Skrjabinotaenia lobata

Of the two cestodes species found in wood mice *S. lobata* was the more prevalent with 72 wood mice infected, mostly from Coole and Merlin (Table 3.8); (GLM family=binomial, site: χ^2_3 = 44.4, P <0.01, Fig. 3.15A).

Prevalence increased significantly in 2012 (GLM family=binomial, year: χ^2_1 = 39.6, P <0.01, Fig. 3.15B). Adult male and female mice had similar prevalence of infection overall but there were significant difference in the prevalence of infection in males and females when the analyses were broken down by age class. There were no infected juvenile males but significantly more mature male mice were infected than mature female mice (GLM family=binomial, age class:sex: χ^2_2 = 8.57, P <0.05, Fig. 3.15C). Prevalence also increased from juvenile to mature wood mice (GLM family=binomial, age class: χ^2_2 = 6.82, P <0.05, Fig. 3.15D).

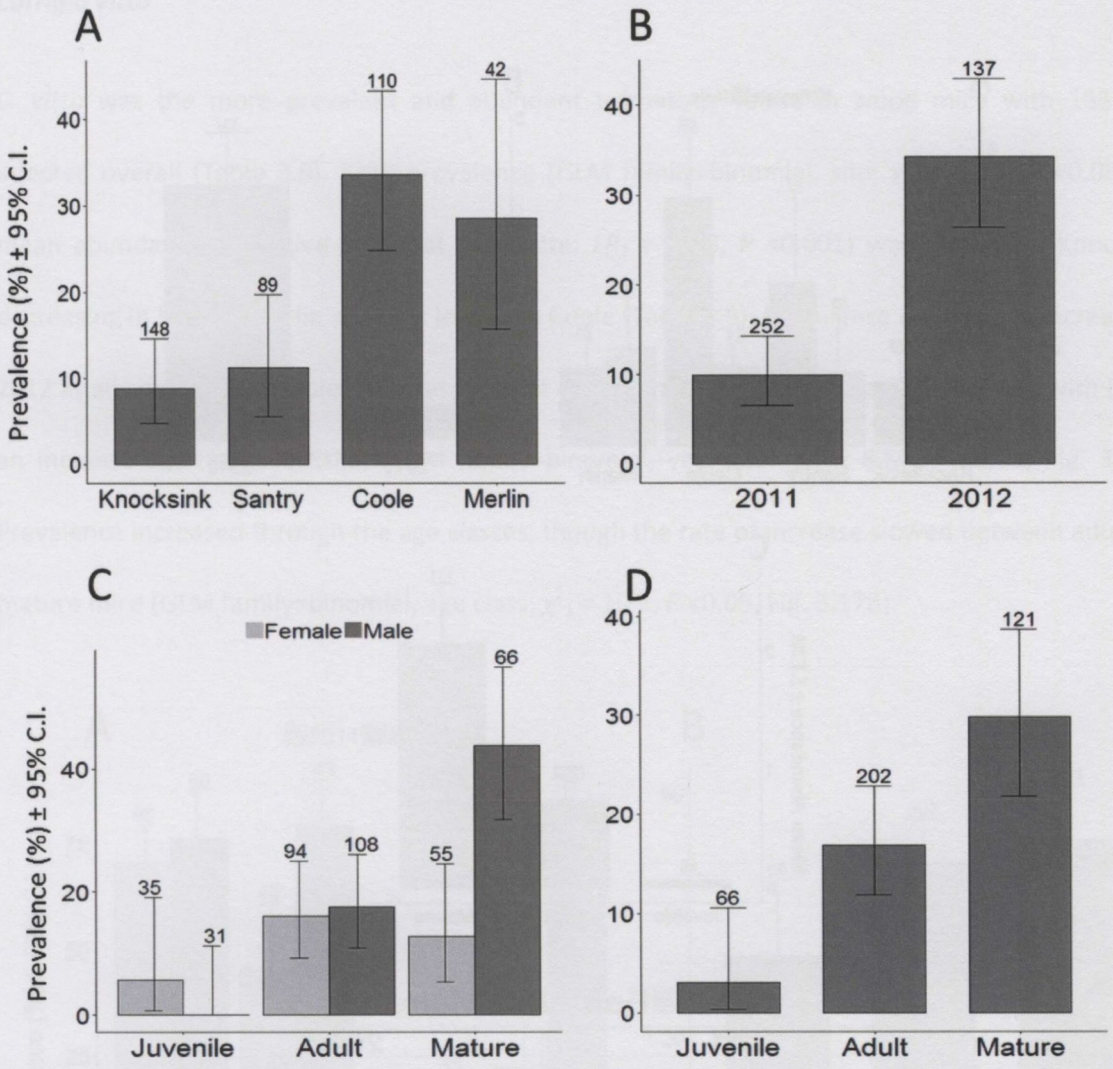


Figure 3.15 Prevalence (%) of Skrjabinotaenia lobata in wood mice. Prevalence by site (A), year (B), age class and sex (C) and year (D).

Site significantly influenced mean abundance, the most heavily infected wood mice were collected from Coole with decreasing abundance in Santry, Merlin and Knocksink (Negative binomial GLM, site: $LR_3 = 9.42$, $P < 0.05$, Table 3.8). Male mice were more heavily infected than females at all sites except Merlin and the difference between males and females was greatest in Coole (Negative binomial GLM, site:sex $LR_3 = 15.8$, $P < 0.001$, Fig. 3.16A). Mean abundance increased in 2012 (Negative binomial GLM, year: $LR_1 = 8.75$, $P < 0.05$, Fig. 3.16B) and through the age classes (Negative binomial GLM, age class: $LR_2 = 8.57$, $P < 0.05$, Fig. 3.16C). There was also a significant three way interaction between sex, year and site (Negative binomial GLM, site:year:sex: $LR_3 = 7.94$, $P < 0.05$, Fig. 3.16D).

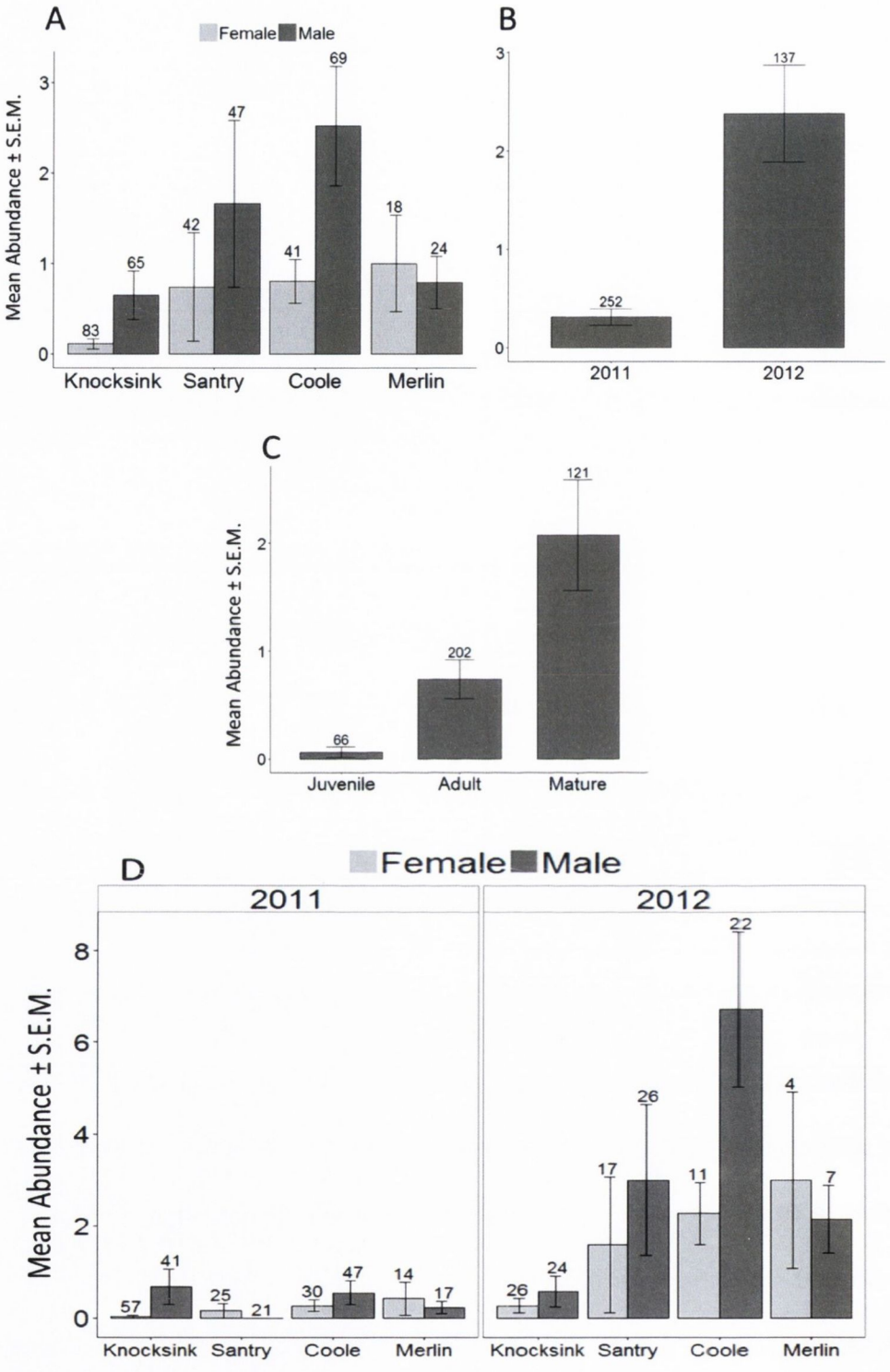


Figure 3.16 Mean abundance of *Skrjabinotaenia lobata* in wood mice. Abundance by site and sex (A year (B), age class (C) and site, year and sex (D).

Corrigia vitta

C. vitta was the more prevalent and abundant trematode found in wood mice with 183 mice infected overall (Table 3.8). Both prevalence (GLM family=binomial, site: χ^2_3 = 91.4, P <0.05) and mean abundance (Negative binomial GLM, site: LR_2 = 22.8, P <0.001) was highest in Knocksink, decreasing in Santry, Merlin and was lowest in Coole (Table 3.8). Prevalence of infection increased in 2012 at all sites except Coole with the greatest rate of increase in Merlin and Santry but with less of an increase seen at Knocksink (GLM family=binomial, year:site: χ^2_1 = 8.57, P <0.05, Fig. 3.17A). Prevalence increased through the age classes, though the rate of increase slowed between adult and mature mice (GLM family=binomial, age class: χ^2_1 = 10.1, P <0.05, Fig. 3.17B).

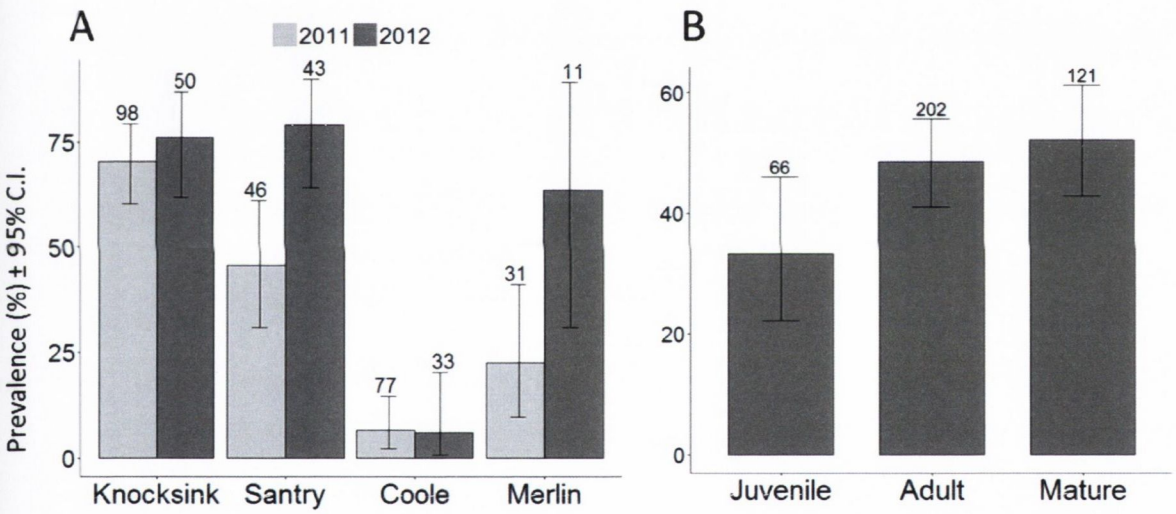


Figure 3.17 Prevalence (%) of *Corrigia vitta* in wood mice. Prevalence by site and year (A) and age class (B).

Mean abundance increased in 2012 (Table 3.8) and this increase occurred at all sites except Coole and was significantly greater in Santry and Knocksink (Negative binomial GLM: site:year: LR_3 =30.2, P <0.001, Fig. 3.18A). Females were more heavily infected at all sites except Merlin (Negative binomial GLM: site:sex: LR_3 =14.4, P <0.05, Fig. 3.18B). Abundance increased through the age classes (Negative binomial GLM: age class: LR_2 =9.62, P <0.05) though the rate of increase differed between site (Negative binomial GLM: site:age class LR_6 = 9.4, P <0.05, Fig. 3.18C).

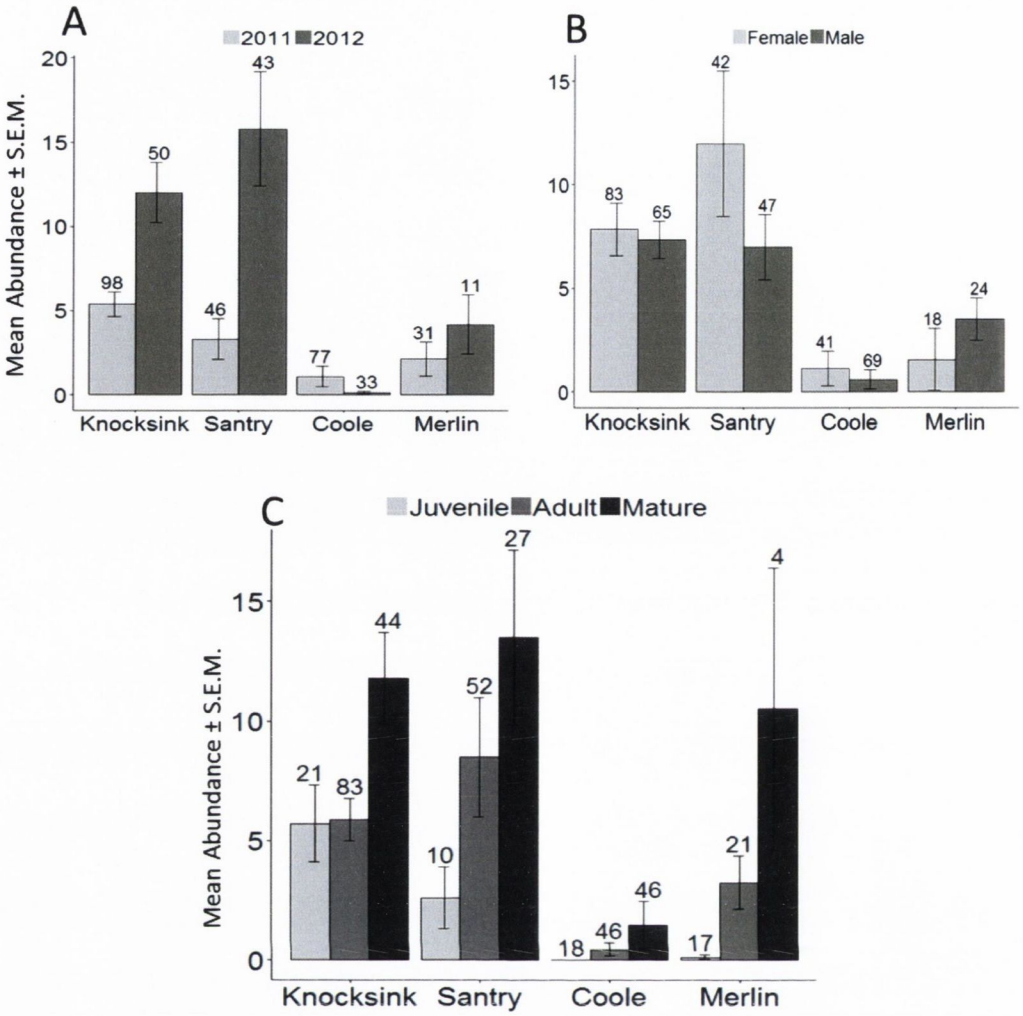


Figure 3.18 Mean abundance of *Corrigia vitta* in wood mice. Abundance by site and year (A), site and sex (B) and site and age class (C).

Brachylaemus recurvum

A total of 43 wood mice carried *B. recurvum* infections (4.8% in 2011 and 23% in 2012, Table 3.8). Prevalence was highest in mature wood mice, increasing at a slower rate between juveniles and adults (GLM family=binomial, age class: χ^2_1= 12.4, P <0.05, Fig. 3.19A). Prevalence increased significantly in Santry and Knocksink in 2012 with a much lower rate of increase in Coole and Merlin from 2011 to 2012 (GLM family=binomial, site:year χ^2_3= 12.3, P <0.05, Fig. 3.19B).

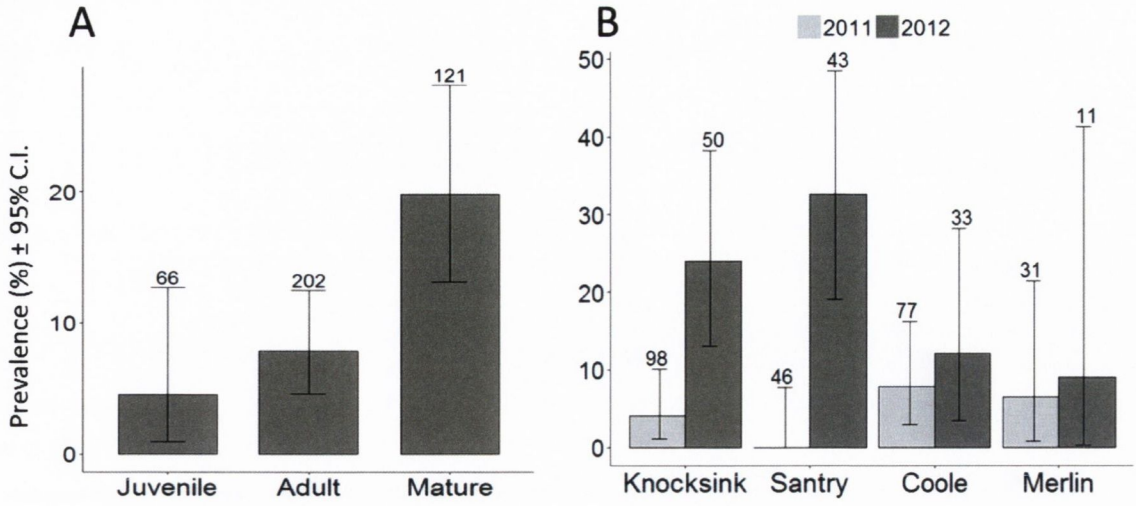


Figure 3.19 Prevalence (%) of *Brachylaemus recurvum* in wood mice. Prevalence by age class (A) and site and year (B).

Mean abundance was significantly lower in Coole compared to the other sites (Negative binomial GLM, site: $LR_3 = 10.6$, $P < 0.05$, Table 3.8). The rate of increase varied between age classes according to site (Negative binomial GLM: site:age class: $LR_6 = 14.7$, $P < 0.05$, Fig. 3.20A).

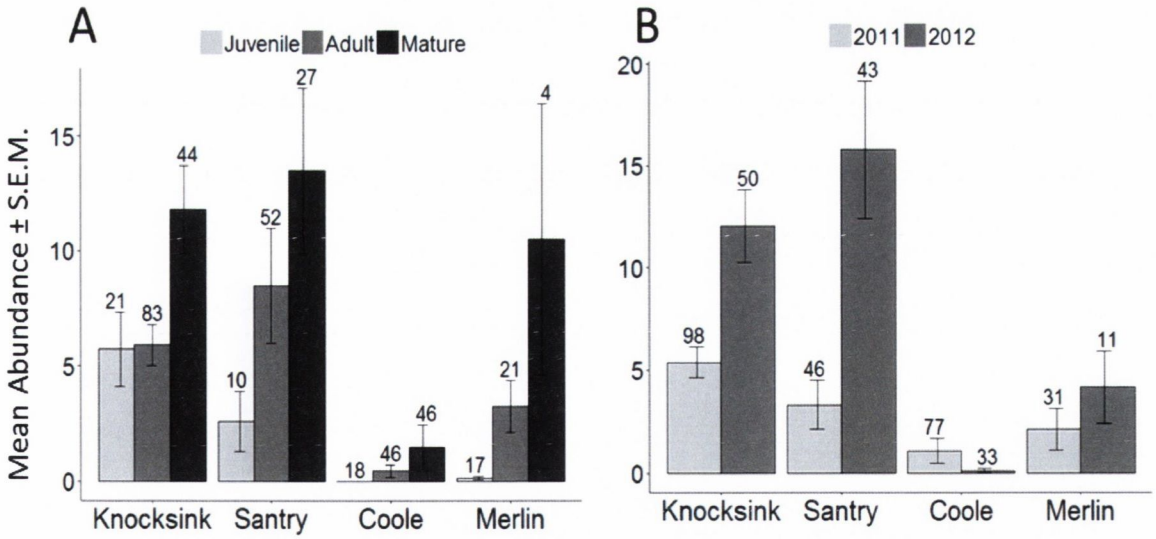


Figure 3.20 Mean abundance of *Brachylaemus recurvum* in wood mice. Abundance by site and age class (A) and site and year (B).

The rate of increase in abundance in 2012 also varied between sites. Mean abundance did not increase in 2012 in Coole. While an increase in mean abundance was seen in Merlin in 2012, this was

significantly less than increase recorded in Knocksink and Santry (Negative binomial GLM, site:year: $LR_3 = 12.3$, $P < 0.01$, Fig. 3.20B).

3.2.3 Infracommunity measures of helminths of wood mice by region

Overall the prevalence and mean abundance of nematodes, cestodes and trematodes were greater in mice-only sites (Table 3.9).

Table 3.9 Prevalence (%) with 95% Clopper–Pearson confidence intervals and mean abundance ±standard error of all helminth species excluding *H. polygyrus* in mice-only and mice-vole sites.

Species	Year	Mice-Only Sites		Mice-Vole Sites	
		Prevalence	Mean Abundance*	Prevalence	Mean Abundance*
Total Helminths	2011	98.6 (95.1-99.8)	337.4±33.9	89.8 (82.5-94.8)	40.2 ±9.14
	2012	100 (96.1-100)	548.9±73.6	97.7 (88.0-99.9)	159.3 ±56.0
	Total	**99.2 (97.0-99.9)**	**420.1±36.0**	**92.1 (86.6-95.8)**	**74.7 ±17.9**
Nematodes	2011	97.2 (93.0-99.2)	332.0±33.9	81.5 (72.9-88.3)	38.2 ±9.18
	2012	98.9(94.2-100)	527.2±73.1	79.5 (64.7-90.2)	151.4 ±56.0
	Total	**90.5 (86.2-93.8)**	**408.6±35.8**	**93.7 (87.0-96.4)**	**71.0 ±17.8**
Cestodes	2011	25.7 (18.8-33.6)	0.72 ±0.15	18.5 (11.7-27.1)	0.45 ±0.13
	2012	49.4 (38.9-60.0)	5.80 ±1.94	72.7 (57.2-84.0)	5.84 ±1.48
	Total	**35.0 (29.0-41.5)**	**2.71 ±0.78**	**34.2 (26.7-42.3)**	**2.01 ±0.48**
Trematodes	2011	63.2 (54.8-71.1)	4.75 ±0.64	15.7 (9.46-24.0)	1.54 ±0.54
	2012	81.7 (72.4-89.0)	15.3 ±1.87	31.8 (18.6-47.6)	2.11 ±0.90
	Total	**70.5 (64.2-76.2)**	**8.87 ±0.89**	**20.4 (14.3-27.7)**	**1.71 ±0.46**
S. stroma	2011	96.5 (92.1-98.8)	322.3±33.9	74.1 (64.7-82.0)	36.2 ±9.1
	2012	95.7 (89.3-98.8)	514.1±72.7	77.3 (62.2-88.5)	149.8 ±56.0
	Total	**96.2 (92.9-98.2)**	**397.6±35.6**	**75.0 (67.3-81.7)**	**69.1 ±17.8**

Species	Year	Mice-Only Sites		Mice-Vole Sites	
		Prevalence	Mean Abundance*	Prevalence	Mean Abundance*
T. muris	2011	4.17 (1.54-8.84)	0.04 ±0.02	13.9 (7.99-21.9)	0.24 ±0.07
	2012	19.4 (11.9-28.9)	0.43 ±0.12	13.6 (5.17-27.4)	0.25 ±0.10
	Total	**10.1 (6.60-14.7)**	**0.19 ±0.05**	**13.8 (8.76-20.3)**	**0.24 ±0.06**
A. murissylvatici	2011	0 (0-2.3)	0	13.0 (7.27-20.8)	1.75 1.23
	2012	15.1 (8.48-24.0)	0.51 ±0.22	22.7 (11.5-37.8)	1.27 0.57
	Total	**5.91 (3.27-9.71)**	**0.20 ±0.09**	**15.8 (10.4-22.6)**	**1.61 0.89**
H. hibernia	2011	20.9 (14.5-28.4)	0.42 ±0.10	1.85 (0.22-6.53)	0.03 ±0.02
	2012	36.6 (26.8-47.2)	4.42 ±1.89	4.55 (0.56-15.5)	1.27 ±1.25
	Total	**27.0 (21.5-33.1)**	**1.99 ±0.75**	**2.63 (0.72-6.60)**	**0.39 ±0.36**
S. lobata	2011	4.8 (1.98-9.76)	0.24 ±0.11	16.7 (10.2-25.1)	0.41 ±0.13
	2012	17.2 (10.2-26.4)	1.35 ±0.54	70.5 (54.8-83.2)	4.54 ±0.94
	Total	**9.70 (6.25-14.2)**	**0.68 0.23**	**32.2 (24.9-40.3)**	**1.61 ±0.32**
C. vitta	2011	62.5 (54.1-70.4)	4.72 ±0.64	11.1 (5.87-18.6)	1.37 ±0.52
	2012	77.4 (67.6-85.4)	13.8 ±1.83	20.5 (9.8-35.3)	1.14 ±0.51
	Total	**68.3 (62.0-74.2)**	**8.27 ±0.87**	**13.8 (8.76-20.3)**	**1.31 ±0.40**
B. recurvum	2011	2.78 (0.76-6.96)	0.03 ±0.02	7.41 (3.25-14.1)	0.17 ±0.07
	2012	27.9 (19.1-38.2)	1.49 ±0.51	11.4 (3.79)	0.98 ±0.78
	Total	**12.6 (8.71-17.6)**	**0.61 ±0.20**	**8.56 (4.63-14.2)**	**0.40 ±0.23**
Mesocestoides	2011	0 (0-2.50)	0	1.85 (0.23-6.53)	0.04 ±0.03
	2012	0 (0-3.89)	0	4.55 (0.56-15.5)	0.36 ±0.25
	Total	**0 (0-1.54)**	**0**	**2.63 (0.72-6.60)**	**0.13 ±0.08**

*Mean abundance calculated from raw data.

For nematodes and trematodes prevalence and abundance was greater in mice-only sites in both years. However for cestodes, prevalence and abundance was greater in in mice-vole sites in 2012. This was due to *S. lobata*, which was more prevalent and abundant in mice-vole sites, particularly in 2012. Other helminth species that had a greater prevalence and abundance in mice-vole sites were *T. muris* in 2011 and overall; *B. recurvum* in 2011 and *A. murissylvatici* and *Mesocestoides spp.* in both years.

3.2.4 Helminth Species Interactions

Pairwise associations were performed between helminth species excluding wood mice that did not harbour at least one of the two species in a pair (Table 3.10). Negative interactions between pairwise species associations were most common. Twelve interactions were significant but no pairwise interaction was significant at all sites in both years.

Table 3.10 Spearman Rank Pairwise species associations between the intensity of infection of the five most common helminths in wood mice by region and year.

	Year		*H. polygyrus*	*H. hibernia*	*C. lobata*	*C. vitta*
Mice-Only Sites	2011	***S. stroma***	-0.14 (96)	-0.11(140)	-0.04(140)	-0.03(139)
		H.polygyrus[1]		-0.13(91)	-0.11(92)	0.12(93)
		H. hibernia			-0.71**(37)	-0.05(98)
		C. lobata				-0.07(93)
Mice-Vole Sites	2011	***S. stroma***	-	-0.27*(82)	-0.34**(83)	-0.50** (88)
		H. hibernia			-0.55*(20)	-0.05(13)
		C. lobata				-0.47*(26)
Mice-Only Sites	2012	***S. stroma***	0.10 (49)	-0.27*(82)	-0.09 (89)	0.24*(90)
		H.polygyrus[1]		-0.08(57)	-0.06(48)	0.06(49)
		H. hibernia			-0.69**(46)	-0.10(78)
		C. lobata				-0.27*(73)
Mice-Vole Sites	2012	***S. stroma***	-	0.31(31)	-0.18 (41)	-0.53**(42)
		H. hibernia			-0.24(32)	-0.68*(11)
		C. lobata				-0.54**(35)

Double zeros (wood mice free from both helminth species in a pair) were excluded; sample sizes are shown in brackets.
*$P<0.05$
**$P<0.005$
[1]Analysed for Knocksink only

3.3 Discussion

As with other studies of wood mice in both Ireland and Britain, the intestinal helminth communities of wood mice were dominated by monoxenous nematodes both at the component and infracommunity level (Montgomery and Montgomery 1988, 1990; Abu-Madi *et al.* 2000; Behnke *et al.* 2004). *S. stroma* dominated diversity indices; only at Merlin in 2012 did *S. stroma* make up less than 80% of all helminths recovered. *Heligosomoides polygyrus*, while one of the dominant helminths where it was present, has a patchy distribution in Ireland (Montgomery and Montgomery 1990) and was only found at one site - Knocksink. The L3 larvae are free-living and feed on bacteria in the faecal material (Fahmy 1956; Bryant 1973). This stage is therefore particularly vulnerable to extrinsic factors such as soil acidity, which has been shown to affect larval survival (Abu-Madi *et al.* 1998).

Mean species richness for the total sample of wood mice sampled varied between 2 and 3 species per wood mouse. Lowest species richness was found in juveniles, increasing in adult and more slowly in mature animals. While some of the helminths such as *S. stroma* can be acquired by very young mice, the majority will be encountered over time as foraging and diet breadth increases, particularly as very young wood mice eat little animal food and therefore few invertebrate intermediate hosts (Watts 1968).

Montgomery and Montgomery (1990) found helminth communities of wood mice in Ireland varied greatly in species composition and relative abundance over a 5 year period, while other communities remained much the same. Even over the 2 year period of the present study helminth communities varied greatly. Species composition was only constant at Coole, at all other sites helminth species appeared and disappeared between years. The greatest change between years was in Merlin where 2 helminth species disappeared in 2012 and in Santry where 2 more species were recorded in 2012. These 2 sites however were not sub-sampled as Coole and Knocksink were, and the sample size at Merlin in 2012 was particularly low. If the sub-sampled sites are taken into

consideration there appears to be much more instability in the species diversity of intestinal helminths of wood mice. It is well established that increasing the area sampled and sample size of the host will increase the species of parasites found (Morand and Poulin 1998) and examining too small a sample size over a limited area may suggest more temporal and spatial instability of parasite species diversity than actually exists.

One of the strongest patterns to emerge from the data was an increase in parasite species richness and mean abundance in 2012 which occurred at all sites, though the relative ranking of sites with regard to these measures remained almost identical in both years. Mean species richness was greatest at Knocksink decreasing in Santry, Coole and lowest in Merlin. Knocksink had the greatest mean abundance in 2011, this changed to Santry in 2012 and Coole and Merlin remained at 3rd and last respectively.

The increase in mean species richness and abundance across all sites suggests that the factors increasing helminth transmission success were widespread in 2012. While site specific conditions will influence parasite dynamics at the very local scale (Abu-Madi *et al.* 1998), widespread factors such as climate will also determine fluctuations. The sites used, though widely separated, are on roughly the same latitude and as such definitive hosts, intermediate hosts and helminths are subject to very similar fluctuations in weather. For instance, both mice-only and mice-vole sites saw an increase in rainfall over the summer months in 2012, though the amount of rainfall received differed between sites (Appendix, Table 3A). Montgomery and Montgomery (1989) found density of wood mice had a positive effect on species richness; however the effect was delayed by 4-7 months. The relative population size of wood mice was roughly the same between years, except at Merlin where there was the largest reduction in trapping success in 2012, though species richness still increased in Merlin in 2012 (Appendix, Table 2A). While there appears to be no direct correlation between mouse density and species richness in this study, the results of Montgomery and Montgomery (1989) suggest that differences in host density between the years cannot be ruled out as a factor.

Intestinal helminth species richness in wood mice is also positively associated with the quantity of animal food in the diets of mice (Langley and Fairley 1982; Montgomery and Montgomery 1989). The increase in species richness seen in 2012 may be partly due to an increase in animal material in the diets of wood mice in 2012. This is supported by the finding that the proportion of the sample made up by Cestodes and Trematodes, all indirectly transmitted, increased in 2012. Seed is typically in short supply in spring and summer and wood mice will concentrate on feeding on invertebrates (Watts 1968; Smal and Fairley 1980). However a good seed fall in the autumn can provide food into the following summer (Smal and Fairley 1980). O'Sullivan *et al.* (1984) did not find a peak in trematode infections in summer in wood mice in Ireland, which they ascribed to a good seed crop the previous autumn. In Ireland, 2010 was a mast year for oak acorns (pers. comm. C. Lawton). If the mast was large enough wood mice would have needed to rely less on invertebrate food during the summer months of 2011, but by summer 2012 invertebrate food appeared to become more important, as reflected in the increase in helminths with intermediate hosts, particularly trematodes. As mast events are synchronised across large areas (Shibata *et al.* 2002), the change in diet would have affected wood mice at all sites.

Transmission of helminths is also positively associated with increased average rainfall in the summer months. Trematode sporocyst infections have been found to increase after wet summers (Morley and Lewis 2008) and high summer rainfall also resulted in high levels of infection of the cestode *Catenotaenia sp.* in a vole population during the autumn (Haukisalmi and Henttonen 1990). Summer rainfall levels were also found to explain much of the year-to-year variation in nematode egg counts from grouse, likely due to increased recruitment in wetter summer months (Moss *et al.* 1993). Average summer rain fall was higher in 2012 across Ireland (Appendix, Table 3A) which likely contributed to increase in mean helminth species diversity and overall increases in helminth prevalence and mean abundance seen in 2012.

There were also significant local effects on the transmission of indirectly transmitted nematodes. Conditions at Coole do not appear to be conducive to the transmission of *Corrigia vitta*. Of the two trematodes recovered, *C. vitta* is typically the more common in wood mice in the United Kingdom and Ireland, *Brachylaemus recurvum* occurring more rarely (Montgomery and Montgomery 1990; Behnke *et al.* 1999; Abu-Madi *et al.* 2000). In all sites except Coole, *C. vitta* reached an overall prevalence of 20%. The low prevalence and abundance at Coole appears to be widespread in this site, as the sub-sites had similar measures. The effect was not seen across mice-vole sites and despite the low wood mice sample at Merlin, prevalence and abundance of *C. vitta* was closer to values obtained in mice-only sites. The life-cycle of *C. vitta* is unknown but other dicrocoeliid trematodes have 2 intermediate hosts, a snail as first intermediate and arthropods as second intermediate hosts (Manga-González *et al.* 2001; Morley and Lewis 2008). There is the possibility that some, as yet unknown, environmental factor at Coole is unsuitable for one or both intermediate hosts.

One of the few indirectly transmitted helminths to have greater prevalence and abundance in vole-mice than mice-only sites in both years was *S. lobata*. As with other anoplocephalid cestodes, oribatid mites probably serve as intermediate hosts (Gleason and Buckner 1979). The mice-vole sites occur in the west of Ireland which has a higher annual rainfall than the east (Appendix, Table 3A). Soil moisture is positively related to mite density and diversity (Tsiafouli *et al.* 2005) and may account for the higher prevalence of *C. lobata* at Merlin and Coole.

Mean species richness increased through the age classes, which is common in parasitological studies of wood mice (Montgomery and Montgomery 1989; Behnke *et al.* 1999; Fuentes *et al.* 2004). Species richness will increase simply as a function of increased exposure as wood mice increase exploration and home range with age. Other factors include developmental time and life-cycles of helminths. *T. muris* has a very low prevalence and abundance in younger age classes as this parasite takes 5 weeks to become adult (Behnke *et al.* 1984). Older wood mice also consume more animal

material than younger cohorts and will also be exposed to more species with indirect life-cycles (Watts 1968).

The observation that most individual parasites had highest prevalence and abundance in mature animals suggests infection pressure is low in the environment and wood mice become exposed to more parasites over time. *S. stroma* was the exception, this nematode showing a significant convex parasite age-intensity curve (Type III) with mean abundance greatest in juvenile mice and decreasing in the older age classes. The direct life-cycle of *S. stroma* lends itself to the rapid build-up helminth numbers among closely associated infected individuals. Female *S. stroma* migrate to the anus and lay eggs on the perianal region. Eggs are embryonated and are infective within hours with mice acquiring infections through self- and allogrooming, as well as from infected bedding. Retro-infection, where hatched larvae migrate from the anal region back into the colon can also occur (Taffs 1976). The high prevalence and abundance of *S. stroma* in juveniles suggests young wood mice are regularly infected in the nest (Lewis 1968).

Decreasing infection intensity with age can indicate the effects of acquired immunity (Wilson *et al.* 2002), and laboratory mice have been found to produce an antibody response to *S. obvelata* (Sato *et al.* 1995). Other investigations in wild wood mice have found the intensity of *S. stroma* infections to increase in older animals (Behnke *et al.* 1999) although prevalence of infection in the youngest age class was much lower than in this study. The high levels of exposure of juvenile mice to *S. stroma* in the present study may result in the development of resistance, as host immune response to helminths is dependent on cumulative exposure to infection (Quinnell *et al.* 1990). Alternatively when young mice move away from the nest, they are no longer exposed to high levels of reinfection. As young mice move out from the nest population level exposure to *S. stroma* is increased, as seen in the increase in prevalence of infection in adult mice, but the force of infection decreases as contact between heavily infected individuals becomes less frequent and mean abundance of infection decreases.

Behnke *et al.* (1999) found prevalence and abundance of *S. stroma* was higher in males, which the authors attribute to differences in either exposure or immunocompetence. There was no significant effect of sex in the present study, though prevalence and abundance was higher in males. Wood mice in the sites investigated were infected early and prevalence was high in all age groups. The finding of no significant difference between males and females under these conditions suggests that differences in exposure may be more important for generating heterogeneities in *S. stroma* infections between sexes, rather than differences in immuncompetence. Males maintain larger home ranges than females and an individual male's home range may overlap several other males. As a result males will occasionally share burrows, potentially exposing then more frequently to *S. stroma* propagules (Tew and Macdonald 1994).

Non-random helminth associations may suggest that species interactions have a role in structuring infracommunities. Co-occurrences of helminth species can be the product of local conditions and so evidence of species interactions should be replicated in independent host samples (Poulin and Valtonen 2002; Behnke *et al.* 2005). By dividing the sample between years and between mice-only and mice-vole sites, significant helminth associations could be validated in comparable host communities across time and space and the effects of local stochastic processes determined.

The nematode *H. polygyrus* is known to have immunosuppressive abilities (Maizels *et al.* 2012) and infection with *H. polygyrus* is associated with enhanced establishment and survival of other helminths (Behnke *et al.* 1978; 2001a; 2005). No significant positive pairwise association between *H. polygyrus* and other helminths was found in this study, but due to the restricted distribution of *H. polygyrus*, associations could only be tested at Knocksink. Infection with *H. polygyrus* is also positively associated with the species richness of helminth infracommunities (Behnke *et al.* 2005) and may explain why mean species richness was greatest overall at Knocksink. When analyses of mean species richness were limited to the helminths found at all sites (i.e. excluding *H. polygyrus*) mean species richness in Santry in 2012 was greater than in Knocksink. This suggests local factors at

Santry, at least in 2012, positively affected helminth transmission to a greater degree than any positive effects of co-infection with *H. polygyrus*.

One of the strongest pairwise associations found was a negative association between the two cestodes *H. hibernia* and *S. lobata*, which occurred in mice-only sites in both years and in mice-vole sites in 1 year. It was personally observed that cestodes could reach sizes that completely filled the small intestine of wood mice, leaving little space for the growth of a second cestode of either the same or different species. Therefore direct competitive interactions between the two cestodes are likely to occur. However local effects may be generating this pattern as mean prevalence and abundance of *H. hibernia* was greatest in mice-sites, while in mice-vole sites *S. lobata* was more abundant and prevalent. Therefore while negative associations were found across sites, the identity of the negatively affected cestode depended on the site examined.

The second pairwise association that was found in 3 out 4 of the sub-samples was a negative association between *C. vitta* and *S. lobata*. As *C. vitta* occupies the pancreatic lobes and *S. lobata* the small intestine, direct competitive interactions are unlikely to occur. It is not known precisely the intermediate host used by these helminths but both are thought to use arthropods at one stage. Pairwise association can be transferred to definitive hosts via intermediate hosts (Lotz *et al.* 1995) so the occurrence of interactions in intermediate hosts could account for the associations observed here.

In general, evidence using helminth burdens suggest helminth interactions play little to no role in the structuring of helminth communities in rodents (Behnke *et al.* 2005; Behnke 2008). In the present data set there was some consistency in the sign of the association, most associations were negative and remained negative across sites and years, however no association was significant in all four sites in both years. Further subgrouping data by sex and age would likely further weaken associations (Behnke *et al.* 2005).

Wood mice in mice-only sites carried heavier parasite burdens than wood mice in mice-vole sites. Several processes may underlie the observation of a dilution in disease risk with increasing biodiversity (Keesing *et al.* 2006). Dilution due to the removal of parasite propagules by incompetent hosts has been demonstrated in aquatic systems (Thieltges *et al.* 2009). In these systems parasite propagules are diffuse within the environment and invasive species that are filter feeders can remove a large numbers of parasites, resulting in 'encounter reduction' for the focal host (Keesing *et al.* 2006). While many of the helminth species had a lower prevalence and mean abundance in wood mice in mice-vole sites, it would be difficult to determine if bank voles were removing enough helminth propagules to cause an encounter reduction dilution effect. In contrast to aquatic systems, in terrestrial systems parasite propagules will be aggregated in areas used by the focal host. Predation on intermediate hosts by bank voles is probably insignificant as bank voles typically consume more green plant and less animal matter than wood mice (Butet and Delettre 2011).

The dilution effect can also occur if the density of susceptible hosts is reduced (susceptible host regulation) (Keesing *et al.* 2006). When parasite transmission is density-dependent, increasing biodiversity will decrease disease risk if the added species reduce the abundance of the main host, so long as intraspecific transmission is greater than interspecific transmission (Dobson 2004; Rudolf and Antonovics 2005). According the findings of Montgomery *et al.* (2012) the bank vole in Ireland is having a negative effect on the population number of wood mice. There is some support of this finding in the present study-: both mice-vole sites had lower relative population sizes than mice-only sites. If voles are reducing the density of wood mice, this will have an indirect effect on helminths with density-dependent transmission.

The relationship between host densities and parasite abundance and prevalence however can be obscured by a number of factors in wild populations. For indirectly-transmitted helminths, the population densities of intermediate hosts may obscure any link between density of definitive hosts and infection prevalence and abundance. The link between host density and infection is more robust

for directly-transmitted helminths (Arneberg *et al.* 1997). Even for these helminths, those with free living stages are subject to climatic or site conditions. In contrast, the life-cycle characteristics of *S. stroma* make it the most useful helminth in this system to explore the consequences of differences in host density.

S. stroma is transmitted by host-to-host contact as well as infected bedding and food and should therefore track host density closely (Lewis 1968; Taffs 1976). The life expectancy of both adults and free-living stages is short and eggs are not very resistant to environmental conditions (Müller-Graf *et al.* 1999), so that frequent infections and reinfections are needed to maintain the high infrapopulations seen in this study. Montgomery and Montgomery (1988) found *S. stroma* to be particularly sensitive to low wood mice densities. Dilution effects may only be detectable where introduced species have close to zero competencies for a parasite, as in most examples of the dilution effect the introduced hosts investigated do not transmit the parasites (Telfer and Brown 2012). The bank vole in Ireland appears to have no reservoir competence for *S. stroma* (see Chapter 4). Moreover, both the prevalence and abundance of *S. stroma* was consistently lower in wood mice in mice-vole sites and relative population sizes of wood mice were lowest in mice-vole sites (Appendix, Table 2A).

Within mice-only sites Knocksink had a higher relative population than Santry, although the highest mean abundance of *S. stroma* was found in Santry, which suggests that the correlation between host population size and *S. stroma* infection is not consistent. However Santry is a small wooded site surrounded by sports playing fields and an urban landscape. Wood mice are likely concentrated within the more favourable wooded habitat, resulting in increased wood mouse encounters and *S. stroma* transmission. This phenomenon is also seen in wood mice in other semi-isolated habitats, such as hedgerows in between arable land (Abu-Madi *et al.* 2000)

In contrast to the variation in helminth community structure observed at the infra and component scale, at the regional scale, total helminth species richness has remained relatively stable. Of the 12

species recorded in previous Irish studies (Appendix, Table 1A), 9 were found in this investigation Based on molecular data, Montgomery *et al.* (1987), have suggested *H. diminuta* found in Irish wood mice is a separate species, *H. hibernia*. Missing from all sites investigated was *Plagiorchis elegans* which has been found in wood mice in Ireland, though at a low prevalence (Langley and Fairley 1982; Montgomery and Montgomery 1988). This trematode is normally a parasite of birds and is more abundant in June, declining by August (Langley and Fairley 1982). It is therefore possible that surveys later in the year would miss the parasite at low abundance and prevalence. *Ganguleterakis spumosa* was found in a single study by Langley and Fairley (1982), a nematode of rats, its presence in wood mice is likely an accidental infection. *T. muris* was completely absent from Merlin Woods, interestingly Langley and Fairley (1982) did not record this nematode from the same area either. Tetrathyridia of the cestode *Mesocestoides spp.* were recovered from the body cavities of wood mice in mice-vole sites and have not been recorded in wood mice in Ireland previously (Appendix 1, Table 1A)

CHAPTER 4

Helminth Communities of the Invasive Bank Vole

4.1 Introduction

Biological invasions are a major cause of biodiversity loss and biotic homogenisation as well as causing environmental damage and economic losses (Pimentel *et al.* 2001; Simberloff 2011). The damage caused by invasive species is due in part to the large population densities and body size that successful invaders reach in invaded habitats (Torchin *et al.* 2003). Understanding the mechanisms that allow invasive species to invest in increased population and body growth is therefore a vital step toward predicting and mitigating impacts of invasions. One of the most intuitively appealing explanations for the demographic release observed in successful invaders comes from the Enemy Release Hypothesis (ERH), which relates the success and impact of invasive species to the loss of regulation by co-evolved natural enemies, such as parasites, in the invaded range (Keane and Crawley 2002; Torchin *et al.* 2002; 2003).

A combination of parasite life-history traits and ecological characteristics mean that introduced hosts lose parasites at every stage of invasion; though translocation, establishment and spread (MacLeod *et al.* 2010). The initial translocated group (founder population) of plants or animals is usually small, consisting of only a few individuals. As host sample size is correlated with parasite species richness, and due to the overdispersed nature of parasites, small founder populations will only host a proportion of the parasites found in the indigenous component community (Walther *et al.* 1995; Shaw *et al.* 1998). These may simply be a random collection of the parasites available, though certain species will have a higher likelihood of being sampled. Typically these will include parasites with a higher prevalence in the indigenous range (mean prevalence of 30% and more) as common species are often less aggregated in host populations (Haukisalmi *et al.* 1988; Torchin *et al.* 2003).

Repeated introductions of a species will provide more opportunities for parasites from their indigenous range to establish. Repeated introductions of the black rat (*Rattus rattus*) accounts for the high percentage of black rats' indigenous parasites recovered from introduced populations, one of the highest values in a study of 26 invasive species (Torchin *et al.* 2003).

During the translocation of introduced species further parasite species loss may occur. Virulent parasites will be lost if the stresses of translocation and establishment result in the death of heavily parasitised hosts (Møller 2005). If heavily parasitised hosts are disproportionately affected by the stresses of translocation, hosts with lower parasite burdens will be selected for, which may ultimately result in a founder population made up of resistant host genotypes (Colautti *et al.* 2004).

Parasites that are translocated along with the host could still be lost during the establishment and range expansion phases of species invasions. As stated previously, founder populations are usually small and there can be considerable time lags before these populations grow to become invasive (Simberloff 2009). Epidemiological models suggest there is a host threshold density below which a parasite cannot sustain itself (Anderson and May 1978) and many introduced parasites will go extinct before the required threshold densities for parasite maintenance can be reached (Torchin *et al.* 2003; Colautti *et al.* 2004). However, if there are competent alternative native hosts in the invaded environment, the overall population density of susceptible hosts may be high enough to maintain the parasite. This is likely part of the reason why Kennedy and Bush (1994) found that introduced fish escape more readily from specialist parasites that infect a restricted range of host species.

The number of hosts a parasite requires to complete its life-cycle is an important determinant of whether it establishes along with an introduced host. Parasites with direct life-cycles establish more often compared to those with indirect life cycles (Lymbery *et al.* 2014). Those with indirect life-cycles will be lost if intermediate or definitive hosts are missing in the invaded habitat, or if environmental conditions are unsuitable for free-living stages (Torchin and Mitchell 2004; Thieltges *et al.* 2008).

Avian malaria was repeatedly introduced to the Hawaiian Islands, but it was not until the introduction of the mosquito vector that transmission and establishment occurred (Van Riper *et al.* 1986). Similarly, the introduction of the sibling vole (*Microtus rossiaemeridionalis*), in the 1960s and 70s to the Svalbard region of Norway probably facilitated the establishment of the cestode *Echinococcus multilocularis*. Infected Artic foxes migrating between Svalbard and Siberia over winter pack ice are the likely source of the transmission stages, but local establishment of the parasite only occurred after introduction of the vole which acts as intermediate host (Henttonen *et al.* 2001).

While invasive species may lose many of their original parasites, they will encounter new parasite species in the invaded range. The number of parasites that invaders acquire will depend in large part on the composition of the native host community. Parasites typically have greater infection success in closely related hosts as these share similar physiological and immunological characteristics (Kennedy and Bush 1994; Perlman and Jaenike 2003; Poulin and Mouillot 2003; Poulin and Keeney 2008). There will therefore be greater opportunities for parasite switching if there are a number of native species that are closely related to the invader.

The number of parasite species acquired in invaded ranges will also depend on the degree of parasite specialisation (Woolhouse *et al.* 2001). Native parasites that are highly host specific, infecting one host species, are less likely to be acquired and establish in introduced populations. In general, invasive species tend to acquire generalist native parasites to a greater degree than specialist native parasites (Kennedy and Bush 1994; Poulin and Mouillot 2003; Kelly *et al.* 2009b; Mastitsky *et al.* 2010). However, experimental investigations suggest that host specificity can break down when new hosts and parasites are brought together (Perlman and Jaenike 2003; Poulin and Keeney 2008).

The bank vole (*Myodes glareolus*) was introduced to Ireland from Germany in the late 1920s, expanding its range at an estimated 1.79 km/year (Stuart *et al.* 2007, Montgomery *et al.* 2012). From the discussion above a few predictions on the general composition of the intestinal helminth

community of the invasive bank vole in Ireland can be made. We can predict that any helminths to have co-invaded along with the bank vole are likely to be species with a simple life-cycle, have high transmission rates and low host species specificity. The haplotype diversity of Irish bank voles indicates that the founder population was small, or that it went through a population bottleneck during range expansion (Stuart *et al.* 2007). Any parasites requiring a high host density for transmission would have been lost from the bank vole while populations were small. Ireland has a species poor mammal fauna, particularly of rodents and smaller bodied animals dependent on woodland and forest ecosystems. Of small ground dwelling rodents Ireland has three species, the brown rat (*Rattus norvegicus*), wood mouse (*Apodemus sylvaticus*) and house mouse (*Mus musculus*) (Marnell *et al.* 2009; Montgomery *et al.* 2014). Therefore, not only are there few phylogenetically closely related species, but Ireland is also lacking the sorts of host species that would be ecologically similar to bank voles. Acquisition of helminths by bank voles in Ireland will probably be low, resulting in a species poor community made up mainly of broad generalists.

In order to investigate the helminth fauna of the invasive bank vole in Ireland, bank voles were collected from two sites over a two-year period. Bank vole parasitism could then be analysed within biogeographical context by comparing patterns of helminth infection in Irish bank voles with published parasitological studies of bank voles in their indigenous ranges.

4.2 Results

4.2.1 Host Population Structure

4.2.1.1 Host Sample Size

A total of 177 bank voles were collected and analysed over 2 years of sampling. Table 4.1 summarises the population structure by year, site and sex. Though not significant, more male bank voles (55.9%) were trapped than females (44.1%), (χ^2_1 = 2.49, P>0.05) and overall more bank voles were trapped in 2011 (55.9%; 2012 44.1%, (χ^2_1 = 2.49, P>0.05).

Table 4.1 Numbers of bank voles examined by site, year and sex.

Site	Year	Female	Male	Total
Coole (A)*		9	16	25
Coole (B)*	2011	23	29	52
Merlin		10	12	22
	Total	**42**	**57**	**99**
Coole (A)	2012	13	5	18
Coole (B)		8	20	28
Merlin		15	17	32
	Total	**36**	**42**	**78**
	Grand Total		**177**	

*See Chp.2 Materials and Methods for explanation of sub-sites A and B.

4.2.1.2 Age Class

Statistical models for age class were calculated as described in Chp.3. All models showed a highly significant main effect of host age class: mean body weight ($F_{2,174}$ =94.4 P<0.001, Fig. 4.1A), mean body length ($F_{2,174}$ =120.8, P<0.001, Fig. 4.1B) and eye lens ($F_{2,174}$ =129.3, P<0.001, Fig. 4.1C). In all cases morphometric measures increased through the age classes.

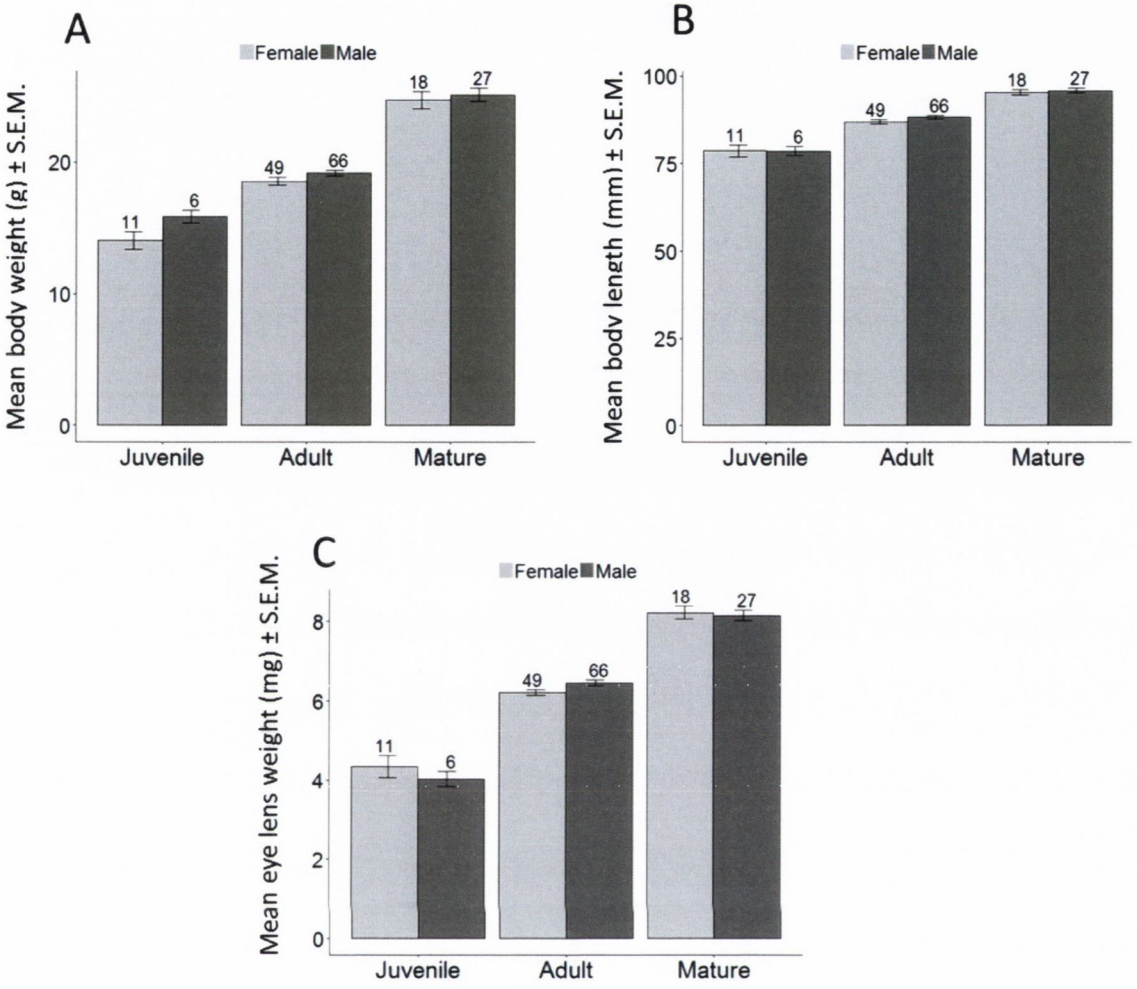


Figure 4.1 Morphometric measures in relation to age class for total sample of bank voles. Confidence intervals are indicated by error bars and sample size is shown above error bars. Body weight (A), body length (B) and eye lens weight (C).

Approximate range of values for each measure assigned to the age classes are given in Table 4.2.

Table 4.2 Approximate ranges of morphometric measures used to assign wood mice to three age classes.

Factor	Juvenile	Adult	Mature
Eye lens (mg)	2-5	4-7	>6
Weight (g)	8-17	14-23	>20
Nose to anus length (mm)	66-85	75-100	>85

There was a significant difference in the numbers of bank voles from each age class (χ^2_2= 86.4, p < 0.001). The majority of bank voles were classed as adult (87.6%), mature voles making up 25.4% of the samples and juveniles 9.60% (Table 4.3). More bank voles were caught in 2011, but not significantly so (χ^2_1 = 2.49, p > 0.05). The proportion of mature bank voles in the sample increased by 4.55% in 2012.

Table 4.3 Allocation of bank voles to three age classes by year and site.

Site	Year	Juvenile	Adult	Mature	Total
Coole(A)	2011	2	18	5	25
Coole(B)		3	41	8	52
Merlin		6	7	9	22
	Total	**11**	**66**	**22**	**99**
Coole(A)	2012	0	12	6	18
Coole(B)		2	15	11	28
Merlin		4	22	6	32
	Total	**6**	**49**	**23**	**78**
Grand Total			**177**		

4.2.2 Helminth Community Structure

Three helminth species were recovered from bank voles in County Galway (Table 4.4). These included 2 intestinal nematode species *Aonchotheca murissylvatici* and *Aspiculuris tetraptera* and the tetrathyridia form of the cestode *Mesocestoides spp.* recovered from the body cavity of bank voles. All three helminth species were recovered at all sites and in both years.

Table 4.4 Helminth species recovered from bank voles by taxon.

Taxon	Species	Location	Life Cycle
Nematoda	*Aspiculuris tetraptera*	LI	Direct
	Aonchotheca murissylvatici	SI	Direct
Cestoda	*Mesocestoides spp.*	BC	Indirect

Locations within the host are indicated by SI – small intestine, LI – Large intestine and BC- body cavity.

A total of 4188 helminths were recovered, 1523 in 2011 and 2665 in 2012. Thus 75% more helminths were recovered in 2012 despite a 21.1% decrease in host sample size. The vast majority were Nematodes, accounting for 92.9% of all helminths. Cestodes made up 7.12% of the total sample (Table 4.5).

Table 4.5 Percentage (%) distribution of all helminth species of bank voles by year and site with confidence intervals given in brackets.

Species	Year	Coole(A)	Coole(B)	Merlin	Total
All Helminths	2011	7.45 (6.67-8.29)	25 (23.7-26.4)	3.87 (3.30-4.50)	36.4 (34.9-37.8)
	2012	3.49 (2.95-4.09)	33.9 (32.5-35.5)	26.2 (24.9-27.6)	66.6 (62.2-65.1)
	Total	**10.94 (10.0-11.9)**	**59.0 (57.5-60.5)**	**30.1 (28.7-31.5)**	**100**
Nematodes	2011	7.45 (6.67-8.29)	24.2 (22.9-25.6)	3.22 (2.71-3.80)	34.9 (33.5-36.4)
	2012	2.44 (1.99-2.95)	32.8 (31.4-34.2)	22.8 (21.5-24.1)	56 (56.5-59.5)
	Total	**9.89 (9.0-10.8)**	**57 (55.5-58.5)**	**26 (24.7-27.3)**	**92.9 (92.1-93.6)**
A. tetraptera	2011	4.58 (3.97-5.26)	2.32 (1.88-2.82)	2.87 (2.38-3.42)	9.77 (8.89-10.7)
	2012	2.34 (1.90-2.84)	23.3 (22.0-24.6)	17.9 (16.8-19.1)	43.6 (42.0-45.1)
	Total	**6.92 (6.17-7.74)**	**25.6 (24.3-27.0)**	**20.8 (19.6-22.0)**	**53.3 (51.8-54.8)**
A. murissylvatici	2011	2.87 (2.38-3.42)	21.9 (20.7-23.0)	0.36 (0.20-0.59)	25.1 (23.8-26.5)
	2012	0.1 (0.03-0.24)	9.48 (8.61-10.4)	4.85 (4.22-5.54)	14.4 (13.4-15.5)
	Total	**2.96 (2.47-3.52)**	**31.4 (30.0-32.8)**	**5.2 (4.55-5.92)**	**39.6 (38.1-41.1)**
Mesocestoides spp.	2011	0 (0-0.09)	0.81 (0.56-1.13)	0.64 (0.43-0.94)	1.46 (1.12-1.87)
	2012	1.05 (0.76-1.41)	1.15 (0.85-1.52)	3.46 (2.93-4.06)	5.66 (4.98-6.40)
	Total	**1.05 (0.76-1.41)**	**1.96 (1.56-2.42)**	**4.11 (3.53-4.75)**	**7.12 (6.36-7.94)**

Overall nematodes increased by 66.9% in 2012 though this was driven by the increase in *A. tetraptera* in 2012 (353.7%) while total abundance *A. murissylvatici* recovered decreased by 42.6% in 2012. The total abundance of the cestode *Mesocestoides spp.* recovered increased by 288.5% in 2012.

Helminth species composition at all sites was the same overall between years. The only difference was the absence of *Mesocestoides spp.* in the sub-sampled site Coole (A) in 2011 (Table 4.5). The majority of helminths were recovered from Coole (69.9%) with the sub-sampled site Coole (B) having the highest sum total of helminths recovered

4.2.2.1 Component Community Structure of Helminths of Bank Voles

Overall *A. tetraptera* was the dominant helminth species recovered with a Berger-Parker Dominance Index of 0.53. However at Coole (B) *A. murissylvatici* was the dominant species in 2011. Site Coole (A) had the lowest Berger-Parker Index score in 2011 and the highest in 2012. *A. murissylvatici* was the dominant species in Coole (B) in 2011 but *A. tetraptera* dominated at all other sites and in Coole (B) in 2012 (Table 4.6). Simpson's Index showed diversity increased in 2012 except in Coole (A). Merlin in 2012 had the highest overall diversity score for all sites (Table 4.6).

Table 4.6 Helminth component community measures in bank voles by year of study and site.

	Year	Coole (A)	Coole (B)	Merlin
Total Species	2011	2	3	3
	2012	3	3	3
Berger-Parker	2011	0.62	0.88	0.74
	2012	0.67	0.68	0.68
Dominant Species	2011	*A. tetraptera*	*A. murissylvatici*	*A. tetraptera*
	2012	*A. tetraptera*	*A. tetraptera*	*A. tetraptera*
Simpson's Index of Diversity	2011	1.90	1.29	1.71
	2012	1.84	1.82	1.93

There was an increase in the number of voles with co-infections in 2012 (Fig 4.2). In 2011, 16.1% of bank voles carried 2 helminth species, the proportion increasing to 32.1% in 2012 ($\chi^2_1 = 2.17$, $p >$

0.05). There was also an increase in the number of voles carrying at least 1 helminth. In 2011, 32.3% of bank voles had no infections decreasing in 2012 to 6.41% ($\chi^2_1 = 19.7$, $p < 0.001$).

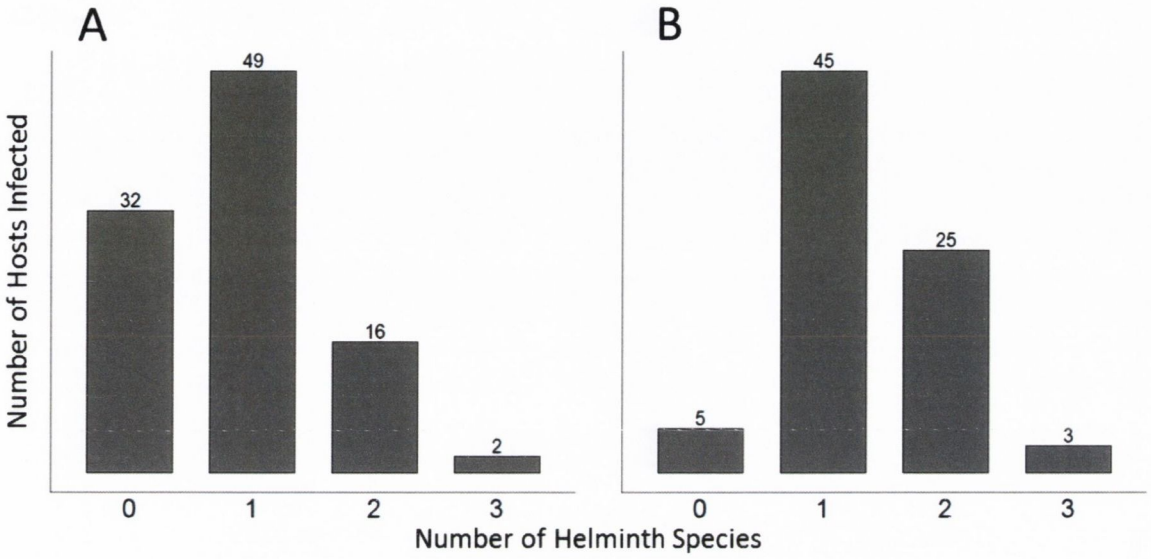


Figure 4.2 Frequency distribution of intestinal helminth species richness in bank voles in 2011 (A) and 2012 (B). Bank vole sample size is given above bars.

4.2.2.2 Infracommunity Structure of Helminths of Bank Voles

The maximum number of helminth species infecting bank voles was 3, which occurred at all sites in at least 1 year (Table 4.7). The mean number of helminths recovered from bank vole increased in 2012 by 122.2%. The increase occurred at all sites except Coole (A).

Table 4.7 Helminth infracommunity measures for bank voles by year and site.

Measure	Year	Coole(A)	Coole(B)	Merlin	Total Sample
Mean Species Richness (±S.E.M)	2011	0.64 ±0.098	1.04 ±0.11	0.77 ±0.11	0.88 ±0.07
	2012	1.17 ±0.15	1.36 ±0.11	1.13 ±0.10	1.33 ±0.07
	Total	**0.86 ±0.09**	**1.15 ±0.08**	**1.15 ±0.11**	**1.08 ±0.05**
Max Species	2011	1	3	2	2
	2012	3	2	3	2
Mean Helminths (±S.E.M)	2011	12.5 ±5.57	20.2 ±7.41	7.36 ±2.78	15.38 ±4.19
	2012	8.11 ±2.01	50.4 ±9.87	34.1 ±8.43	34.2 ±5.25
	Total	**10.7 ±3.31**	**30.9 ±6.11**	**23.3 ±5.40**	**23.6 ±3.36**
Mean Brillouin's (±S.E.M)	2011	0	0.04 ±0.02	0.06 ±0.04	0.03 ±0.01
	2012	0.04 0.03	0.20 ±0.05	0.09 ±0.03	0.12 ±0.02
	Total	**0.016 ±0.01**	**0.10 ±0.02**	**0.08 ±0.02**	**0.07 ±0.01**
Max Brillouin's	2011	0	0.53	0.54	0.54
	2012	0.35	0.67	0.66	0.67

Measures of dispersion (Appendix 1 Table 5A) showed *A. tetraptera* to be more aggregated than *A. murissylvatici*. For *A. tetraptera*, the Index of dispersion (I) was greater than 1 in all cases. In 2012, *A. murissylvatici* had an I of less than 1 at each site and for the combined data for the year.

Species Richness.

Over the two years of the present study, mean species richness in bank voles was 1.08 ±0.05 (Table 4.7). Species richness was greater in Merlin (1.15 ±0.11) than at the Coole with sub-sites combined (1.05 ±0.06), though the highest value was seen in Coole (B) in 2012. Mean species richness increased in 2012 and this increase was observed at all sites. Age class was the only significant factor in the minimum sufficient model for species richness, species richness increasing from juvenile to mature bank voles (GLM, family= Poisson, age class: $\chi^2_2 = 13.7$, P<0.001 Fig. 4.3).

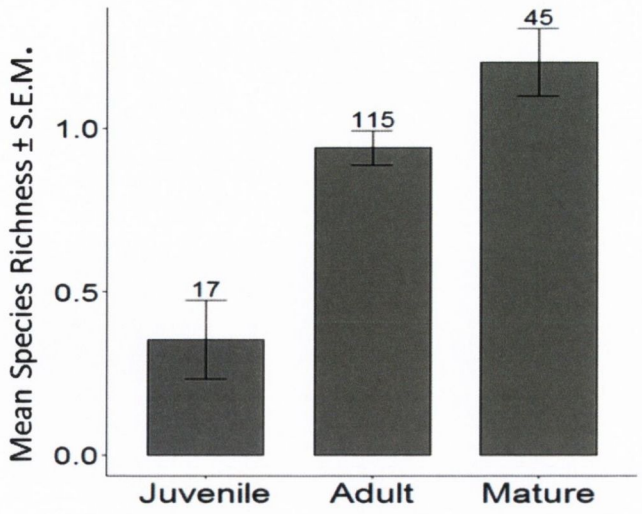


Figure 4.3 Mean helminth species richness (±S.E.M) for bank voles by age class.

The increase in mean species richness was rapid between juveniles and adult voles (217.1%), slowing between adult and mature voles (14.4%). Bank voles sampled from Coole (A) in 2011 showed no helminth co-infections while at the other sites, and at all sites in 2012, a proportion of voles carried more than one helminth species (Table 4.7).

Brillouin's Index of diversity.

Brillouin's Index increased significantly from juvenile to mature voles (GLM, family = quasi-poisson, age class: $F_{2, 174}$ =8.83, P<0.001, Fig. 4.4A), juvenile bank voles having an index of 0. Mean Brillouin's over the entire study was greater in Merlin (GLM, family = quasi-poisson, site: $F_{1, 174}$ =8.74, P<0.01, Fig. 4.4B) than at the combined Coole site, though the highest value was seen in the sub-sampled site Coole (B) in 2012 (Table 4.7). Maximum and mean Brillouin's Index increased overall in 2012 (GLM, family = quasi-poisson, year: $F_{1, 174}$ =7.36, P<0.01, Fig. 4.4C) and this increase occurred at all sites (Table 4.7).

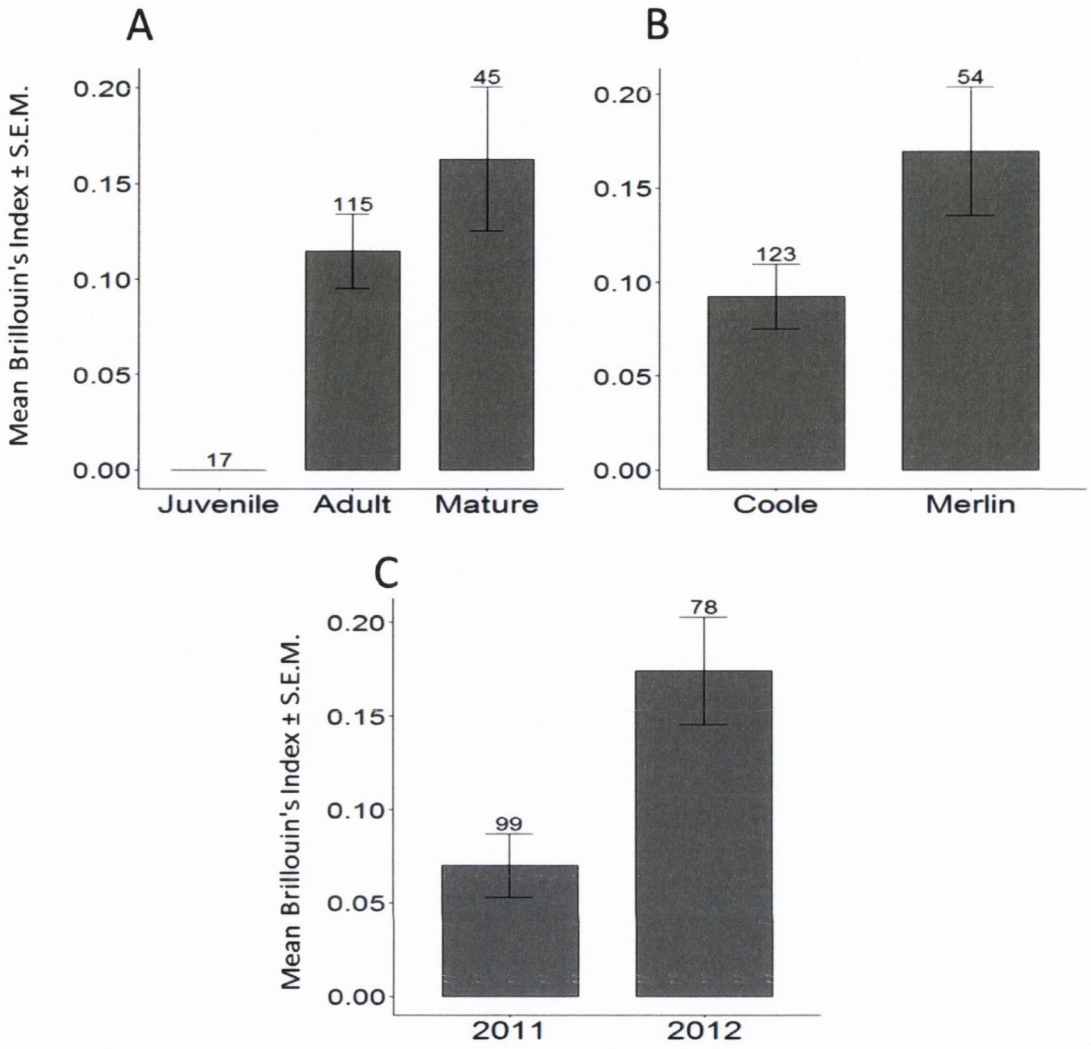


Figure 4.4 Brillouin's Index of Diversity (S.E.M) for bank voles by age class (A), site (B) and year (C)

Prevalence and Abundance of Individual Helminth Species

The prevalence and abundance of all helminth species recorded in bank voles in this study is summarised in Table 4.8.

Table 4.8 Prevalence (%) with 95% Clopper-Pearson confidence intervals and mean abundance (±S.E.M) for all helminths of bank vole by year and site.

Species	Year	Coole(A)	Coole(B)	Merlin	Total Sample
A. murissylvatici	2011	8 (1-26.0)[P] 4.80 ±3.92[A]	15.4 (6.88-28.1)[P] 17.7 ±7.47[A]	13.6 (2.9-34.9)[P] 0.68 ±0.37[A]	10.1 (4.95-17.8)[P] 10.7 ±4.10[A]
	2012	16.7(3.58-41.4)[P] 0.22 ±0.13[A]	39.3 (21.5-59.4)[P] 14.2 ±6.39[A]	31.3(16.1-50)[P] 6.34 ±2.44[A]	30.8 (20.8-42.2)[P] 7.74 ±2.55[A]
	Total	**11.6 (3.89-25.1)[P] 2.88 ±2.27[A]**	**23.8 (14.9-34.6)[P] 16.4 ±5.32[A]**	**18 (9.25-31.4)[P] 4.04 ±1.50[A]**	**19.2 (13.7-25.8)[P] 9.36 ±2.55[A]**
A. tetraptera	2011	56 (0.35-0.76) 7.68 ±4.33	48.1 (34.0-62.4) 1.87 ±0.44	54.5 (32.2-75.6) 5.45 ±2.60	51.5 (41.3-61.7) 4.13 ±1.26
	2012	83.3 (58.6-96.4) 5.44 ±1.56	92.9 (76.5-99.1) 34.9 ±7.73	81.3 (63.6-92.8) 23.4 ±7.00	85.9 (76.2-92.7) 23.4 ±4.15
	Total	**67.4 (51.5-81) 6.74 ±2.58**	**63.8 (52.3-74.2) 13.4 ±3.22**	**70.4 (56.4-82) 16.1 ±4.41**	**66.7 (59.2-76.6) 12.6 ±2.08**
Mesocestoides spp.	2011	0 (0-13.7) 0	15.4 (6.88-28.1) 0.65 ±0.33	9.09 (1.12-29.2) 1.23 ±0.85	10.1 (4.95-17.8) 0.61 ±0.26
	2012	16.7 (3.58-41.4) 2.44 ±1.56	3.57 (0.09-18.3) 1.71 ±1.71	28.1 (13.7-46.7) 4.53 ±1.61	16.7 (9.18-26.8) 3.04 ±0.97
	Total	**6.98 (1.46-19.1) 1.02 ±0.97**	**11.25 (5.28-20.3) 1.03 ±0.63**	**20.4 (10.6-33.5) 3.19 ±1.03**	**13.0 (8.42-18.9) 1.68 ±0.46**

[P] Prevalence (%) with 95% confidence intervals
[A] Abundance ± standard error of the mean

Aspiculuris tetraptera

A. tetraptera was the most prevalent helminth species occurring in 188 bank voles (66.7%, CI: 59.2-73.6; Table 4.8). Infection was more prevalent in 2012, increasing by 31.4% (GLM, family = binomial, year: χ^2_1=24.2, P<0.001, Fig. 4.5A). *A. tetraptera* prevalence increased through the age classes, increasing rapidly from juveniles to adults and slowing between adults and mature bank voles (GLM, family = binomial, age class: χ^2_2=10.7, P<0.01, Fig. 4.5B).

There was a significant increase in the mean abundance of *A. tetraptera* nematodes recovered in 2012 (Negative binomial GLM, year: LR_1=24.7, P<0.001, Fig. 4.6A). Mean abundance increased through the age classes overall but the effect varied significantly between sites and years. In Coole the juvenile age class carried the heaviest infections (Negative binomial GLM, site:age class: LR_2=9.21, P<0.05, Fig. 4.6B) occurring in 2012 (Negative binomial GLM, year:age class LR_2=7.07, P<0.05, Fig. 4.6C). However the juvenile age class only contained 6 to 11 individuals when bank voles were sub-divided in this way (Table 4.3).

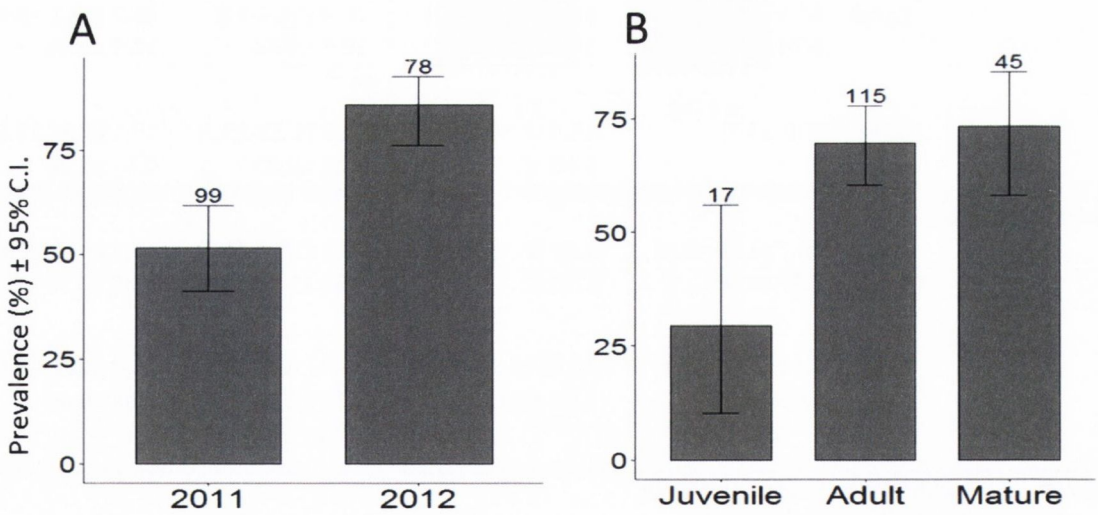


Figure 4.5 Prevalence (%) of *Aspiculuris tetraptera* in bank voles. Prevalence by year (A) and age class (B).

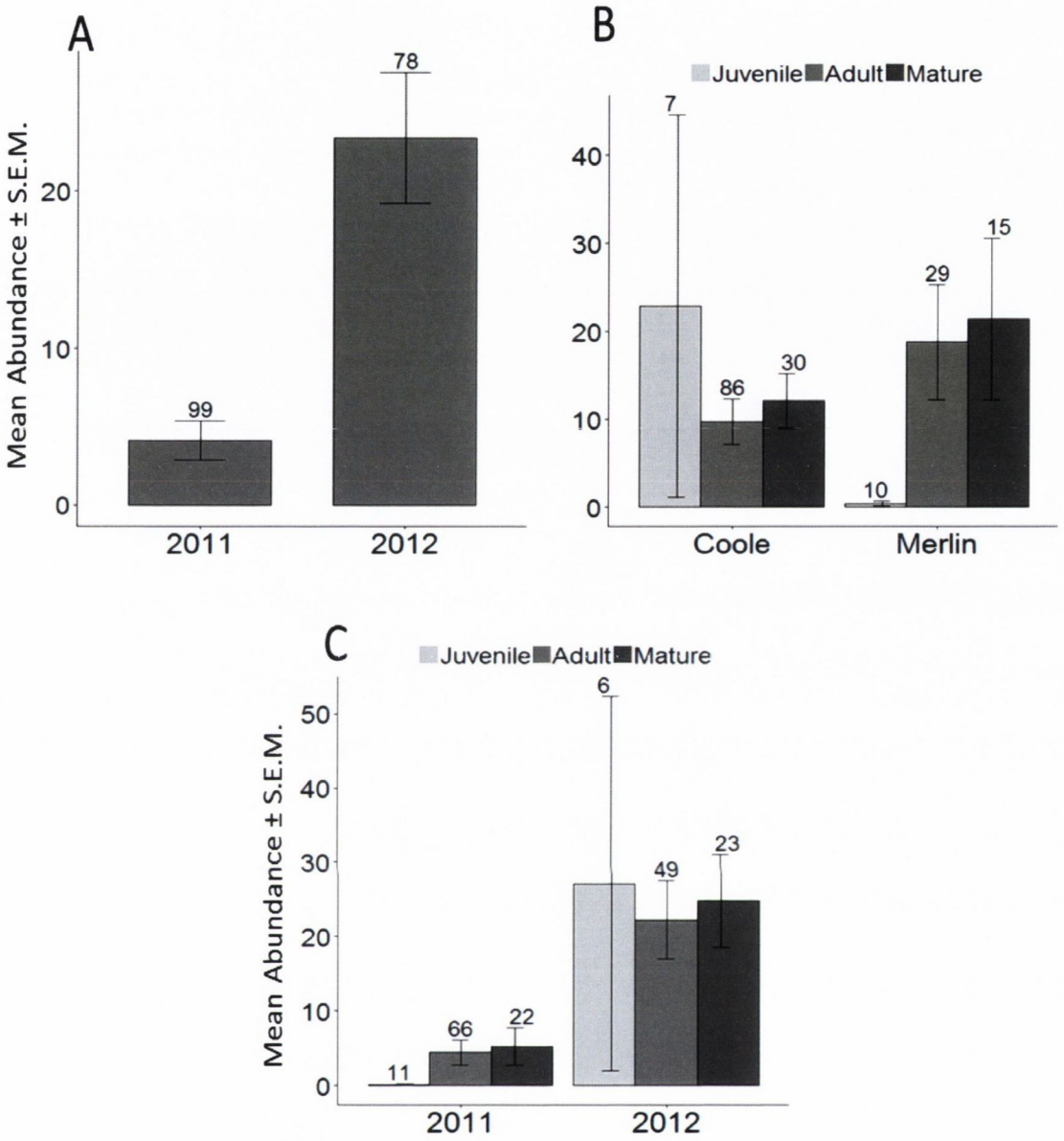


Figure 4.6 Mean abundance of *Aspiculuris tetraptera* in bank voles. Abundance by year (A), site and age class (B) and year and age class.

Aonchotheca murissylvatici

Fifty bank voles were infected with *A. murissylvatici* (28.2% CI: 21.7-35.5; Table 4.8). Only age class was significant in prevalence models, prevalence increasing through juveniles to mature bank voles (GLM, family = binomial, age class: χ^2_1 =14.8, P<0.001, Fig. 4.7). Mean abundance increased through the age classes, particularly in mature bank voles (Negative binomial GLM, age class: LR_2 =17.8, P<0.001, Fig. 4.8A). Overall there was a decrease in abundance from 2011 (10.6±4.09) to 2012 (7.74±2.55), driven by the decrease in Coole as there was an increase in mean abundance in Merlin (GLM, family = binomial, site:year: LR_1 =6.67 P<0.05, Fig. 4.8B). Abundance was higher in males (11.8±4.1) than in females (6.28±2.5) overall, but this varied between sites. Males in Coole carried heavier burdens while in Merlin females carried heavier burdens (Negative binomial GLM, site:sex: LR_1=4.02, P<0.05, Fig. 4.8C) which is probable due to the greater number of males collected from Coole.

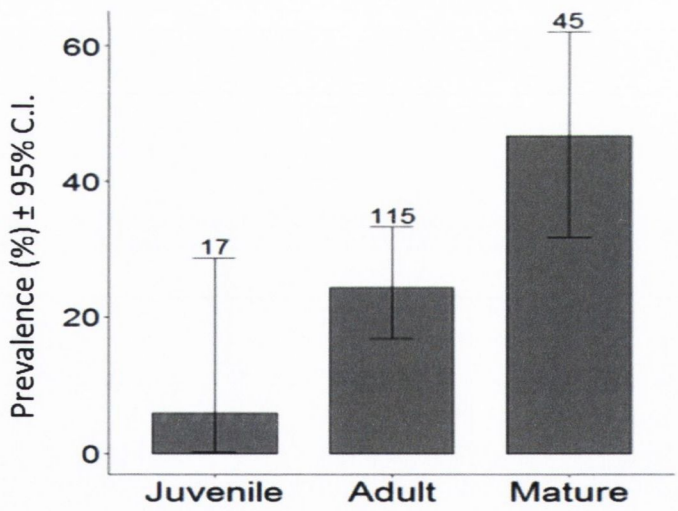


Figure 4.7 Prevalence (%) of *Aonchotheca murissylvatici* in bank voles by age class.

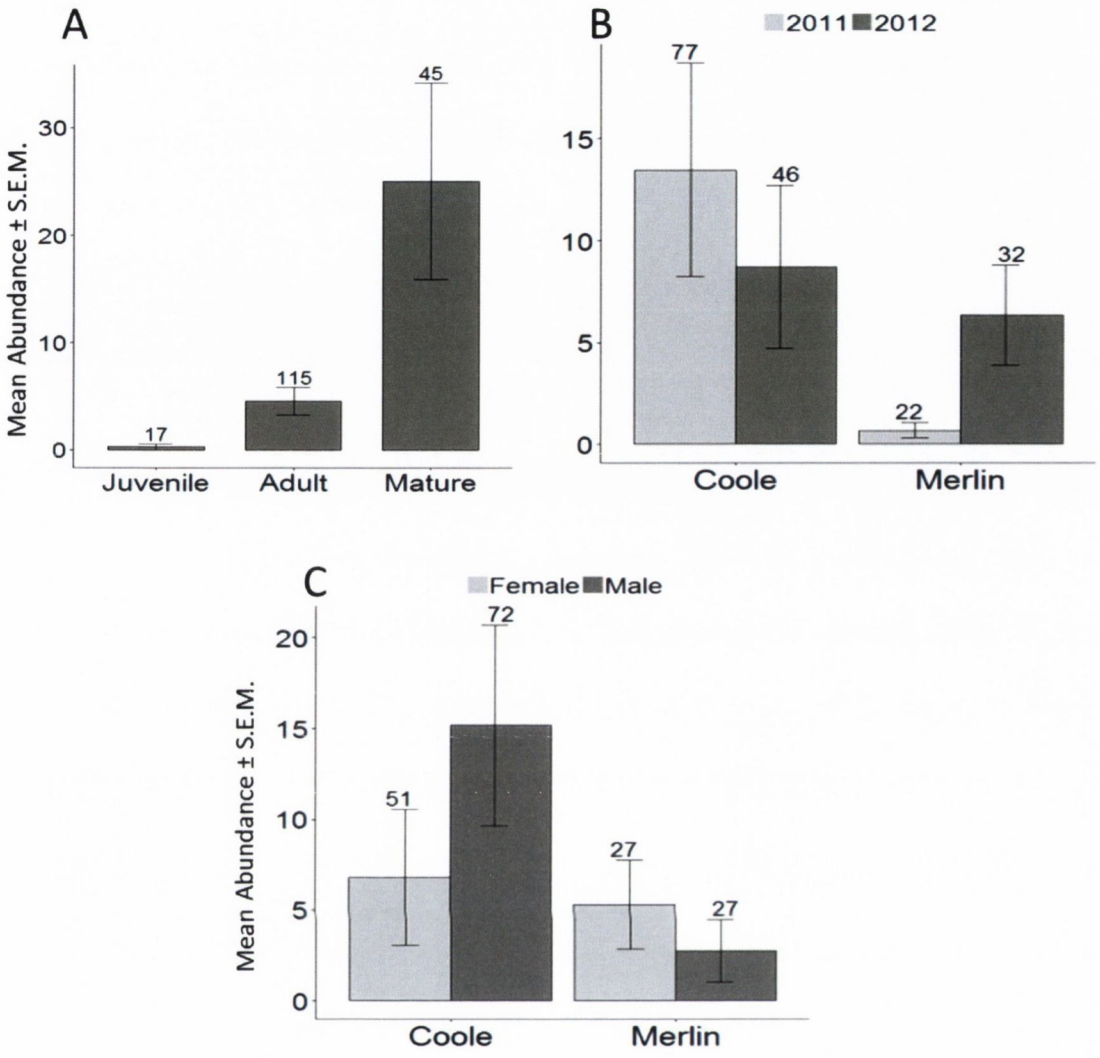


Figure 4.8 Mean abundance of *Aonchotheca murissylvatici* in bank voles by age class (A), site and sex (B) and site and year (C).

Mesocestoides spp.

A total of 23 voles carried *Mesocestoides spp.* (13% CI: 8.42-18.9; Table 4.8). No juvenile bank voles were infected. Age class significantly affected both prevalence (GLM, family = binomial, age class: χ^2_2 =10.0, P<0.01, Fig. 4.9A) and abundance (Negative binomial GLM, age class: LR_2=5.68, P<0.05, Fig. 4.10B). Prevalence was higher in Merlin (GLM, family = binomial, site χ^2_1 =4.8, P<0.05, Fig. 4.9B) and mean abundance increased in 2012 (Negative binomial GLM, year LR_1 =24.7 P<0.05, Fig. 4.10A).

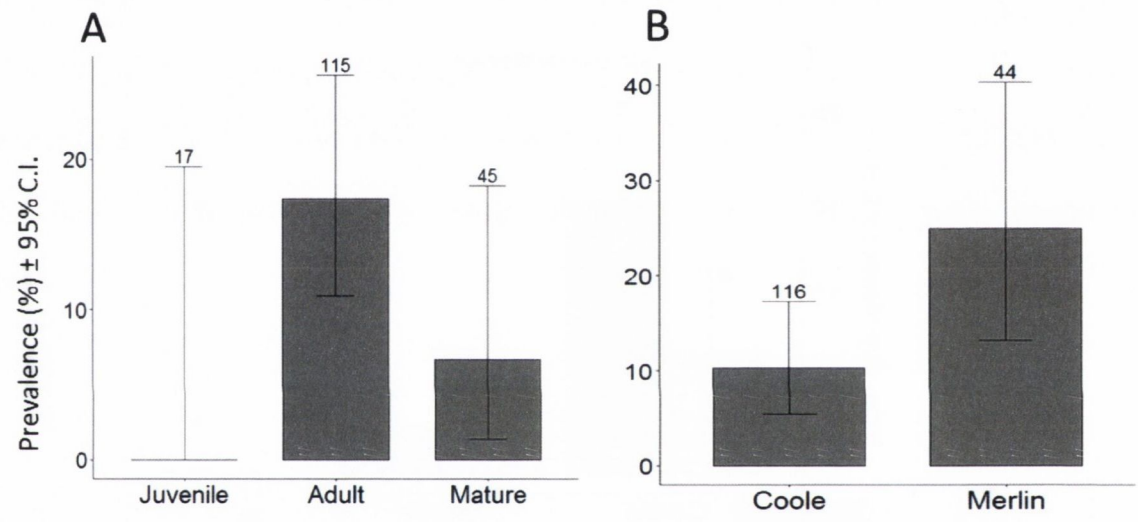


Figure 4.9 Prevalence (%) of *Mesocestoides spp.* in bank voles by age class (A) and site (B).

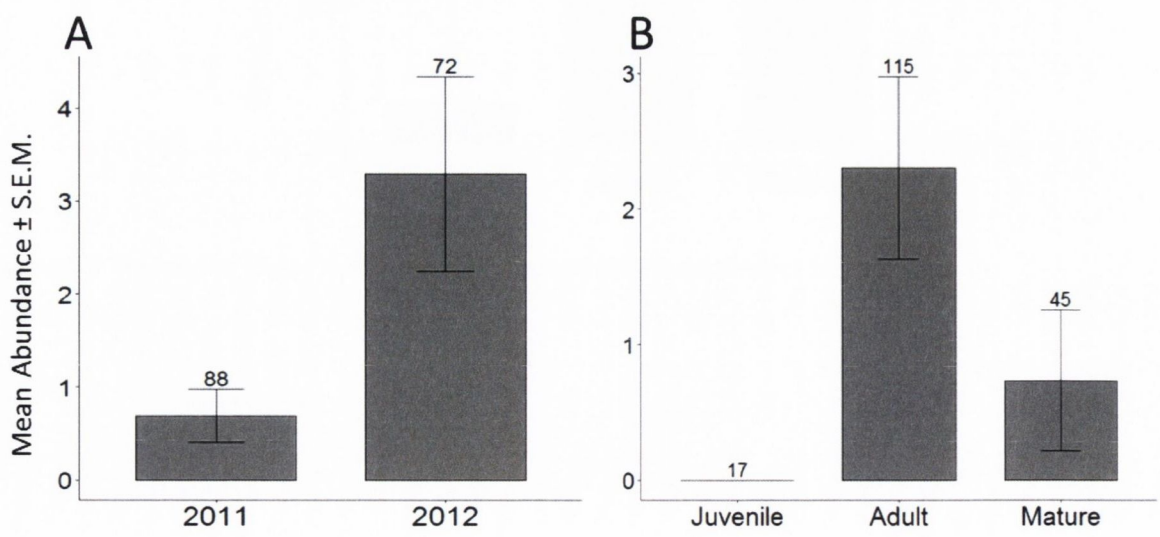


Figure 4.10 Mean abundance of *Mesocestoides spp.* in bank voles by year (A) and age class (B).

4.3 Discussion

Predictions of the characteristics of the helminth community likely to be found in invasive bank voles in Ireland were largely borne out in the present study. The intestinal helminth community was species poor, consisting of only 2 species; *Aspiculuris tetraptera* and *Aonchotheca murissylvatici*, both directly transmitted nematodes. A third species was recovered from the body cavity of bank voles, the tetrathyridia of a species of cestode from the *Mesocestoides* genus. All 3 species found in the bank voles appear well established, being found at both sites with prevalence above 10% in both years. A prevalence of less 10% is often used to classify a helminth species as rare (Lotz and Font 1994; Torre *et al.* 2013). Thus these parasites likely represent permanent host-parasite associations in bank voles in Ireland.

The low species diversity in Irish bank voles is not only due to the loss of their indigenous parasites during translocation and establishment, but also due to the low numbers of native helminths acquired in Ireland. Parasite richness within a particular host species is strongly correlated with the diversity of the free-living host species within a geographic location, especially the number of closely related species (Poulin 1995; Krasnov *et al.* 2004; Poulin *et al.* 2011c). Species richness in invading hosts will also depend on the number of generalist parasites hosted by native populations. For example, introduced trout acquire parasites from native salmonids, however if there were no related species in the area trout were still able to acquire a diverse assemblage of broad generalist parasites (Poulin and Mouillot 2003). Barton (1997) found that the rich parasite communities of invasive toads (*Bufo marinus*) in Australia were due in part to the large number of generalist species with low host-specificity hosted by native anurans. The introduced toads brought a number of specialist indigenous parasite species and then acquired many of the generalist native parasite species.

All three helminths found in bank voles in the present study infect more than one host species and so can be considered generalists. *A. murissylvatici* is a common nematode of both murid and

arvicolid rodents (Montgomery and Montgomery 1988; Justine and de Roguin 1990; Bjelić-Čabrilo *et al.* 2009; Milazzo *et al.* 2003); *A. tetraptera* is found in bank voles, house mice and can infect wood mice (Behnke 1974; Torre *et al.* 2013; Table 4.9) and *Mesocestoides* species are found in a range of intermediate hosts (Di Bella *et al.* 2003; Conn *et al.* 2011). However, beyond the parasites already recorded in Irish bank voles, opportunities for bank voles to encounter further new helminth species are limited. There are no other arvicoline host species in Ireland and only 3 other ground dwelling rodent species, meaning there are few opportunities for host switching from related host species.

In addition to *A. murissylvatici* O'Sullivan *et al.* (1982) found the trematode *Corrigia vitta* and nematode *Trichuris muris* in Irish bank voles, but at a prevalence of 1%. Therefore in total five helminth species have been recorded in bank voles in Ireland, two probably representing accidental infections rather than stable elements of the component community. In contrast, the Siberian chipmunk (*Eutamias sibiricus*) introduced to France in the 1970s, was found infected with 13 nematode species considered to be accidental infections (Pisanu *et al.* 2009). France has a much richer diversity of rodent species than Ireland (Montgomery *et al.* 2014) and the larger number of helminths species that chipmunks are exposed to increase the chances that some will form permanent host-parasite associations over time.

All three parasites recorded in the present study have also been recorded in bank voles in their indigenous ranges (Table 4.9). It is therefore possible that all three could have co-invaded along with the bank vole. Determining which parasites in an introduced population co-invaded and which were acquired after the invasion is difficult without long term data on native host-parasite associations. An alternative is to compare isolated native populations occurring simultaneously in the presence and absence of introduced species. If uninvaded native populations are host to the parasite in question, then a strong case can be made for the native status of the parasite. Smith and Carpenter (2006) compared Californian Channel Islands that had been invaded by the black rat (*Rattus rattus*) to islands within the chain that had not been invaded. Comparisons of invaded and uninvaded native

populations allowed the authors to propose that rats had introduced the whip worm *Trichuris muris* to the invaded islands, rather than acquiring the helminth from endemic deer mice (*Peromyscus maniculatus*).

In the present study both historical records (Appendix, Table 1A) and the comparison of isolated native host populations were used. The native Irish species most closely related and ecologically similar to the bank vole is the wood mouse (*A. sylvaticus*). As such, parasite species may be shared between these two hosts. The wood mouse is therefore the best candidate for investigating whether the helminths found in invasive bank voles are native or co-invaded. The wood mouse in Ireland occurs in populations outside the range of the vole (see Chapter 1, Fig 1.4) and several parasitological surveys of the ecologically similar native wood mice exist over a span of more than 30 years (Appendix, Table 1A).

In the present study *A. tetraptera* was recovered from bank voles only. The nematode has not been recorded in wood mice either in the present study, or in previous studies in Ireland (Appendix Table 1A; Chapter 2). A number of features favour a hypothesis of co-introduction for this nematode. *A. tetraptera* is directly transmitted, typically causes low pathology and can reach prevalence above 30% in populations where it is endemic (see references in Table 4.9). In the present study *A. tetraptera* was the most prevalent parasite of bank voles, reaching a prevalence of 85.9% in 2012. Parasites are often more infective and virulent to local host genotypes (Ebert 1994; Lively 1999), and the high prevalence of *A. tetraptera* in bank voles suggests *A. tetraptera* is well adapted to Irish bank voles.

Table 4.9 Studies of the bank vole in its indigenous ranges which include either *A. tetraptera*, *A. murissylvatici* or *Mesocestoides spp*. Prevalence and intensity (in brackets) is given where provided by the study.

Location	Sample size	*A. tetraptera*	*A. murissylvatici*	*Mesocestoides spp.*	All helminths[1]	Total species	Reference
Southern Norway	398	-	-	0.3% (60)	29.4% (3.2)	8	Tenora *et al.* (1979)
Serbia	588	0.17 (5)	16.4% (12.2l)	2.5% (1.67)	Nematodes- 60.2% (20.8) Cestodes -20.7% (3.67)	14	Bjelić-Čabrilo *et al.* (2011)
Poland 3 sites	40	2.5% (4)	-	2.5%	95% (114.7)	9	Behnke *et al.* (2001b)
	41	12.2% (64.8)	-	2.4%	68.3% (185.8)	6	
	58	58.6% (18.8)	-	1.7%	91.4% (17.6)	9	
						11 Total	
Poland	139	28.8%	-	2.2%	only infected animals analysed (77.2)	11	Barnard *et al.* (2002)
Poland	38 (only males analysed)	14.3% (0.8)	-	(+)[2]	nematodes 90.7% (21.7) cestodes 10.9% (0.1)	11	Barnard *et al.* (2003)
Poland	250	4.4%(6.8)	-	0.012	90% (167)	13	Bajer *et al.* (2005)
Germany	29	-	51.7 (41.6)	-	57.1% (25.9)	3	Klimpel *et al.* (2007b)
Poland 3 sites	112	16.1% (8.06)	-	0%	89.3% (23.25)	13	Behnke *et al.* (2008b)
	114	38.6% (12.7)	-	1.7%(58.7)	73.8% (243)	10	
	132	58.3% (12.3)	-	1.3%(13.2)	81.1% (10.56)	10	
						Total 13	
Serbia	138	1.14 (5)	25% (3)	-	63.8% (18.9)	7	Bjelić-Čabrilo *et al.* (2009)

Location	Sample size	*A. tetraptera*	*A. murissylvatici*	*Mesocestoides spp.*	All helminths[1]	Total species	Reference
France	12	-	66% (35)	-	83% (26)	4*	Pisanu *et al.* (2009)
	15	-	73% (159)	-	73% (126)	5*	
	15	-		-	-	4*	
						6 *Total	
Spain 2 sites	271	-	1.1% (1.5)	0.37% (4)	72.3%	14	Ribas *et al.* (2009)
	105		-	-	51.42%	10	
						Total 17	

[1]All helminths- only helminth associated with digestive tract, body cavity and surface of the liver are included

[2]No additional information other than presence provided

*Only digestive tract investigated

Most studies provide intensity rather than abundance, so intensity is recorded where provided.

In contrast, O'Sullivan *et al.* (1984) did not record *A. tetraptera* at all in bank voles from Ross Island Killarney, a surprising result considering the high prevalence recorded in the present study. The population examined by the authors may have been one on the leading edge of the bank vole's invasion front. Such populations can show reduced parasitism for reasons similar to those occurring in founder population. Phillips *et al.* (2010) showed with simple models, backed up by empirical data, that lung worm parasites in introduced toads (*Rhinella marina*) took three years to catch up to the host. Toads at the edge of invasion fronts were virtually parasite and pathogen free, leading to altered host population dynamics at the invasion front. At the dispersal rate of 1.79km/year estimated by Montgomery *et al.* (2012), bank voles would have been occupying Ross Island for less than five years and so could be considered as on the leading edge of the invasion front.

The bank vole may have still have acquired *A. tetraptera* locally from a host species other than the wood mouse. The normal host for *A. tetraptera* is the house mouse (Behnke 1974). While no house mice were ever found in traps during the course of this study, populations of house mice and bank voles probably co-occur at other sites and/or times of the year. Both bank voles and house mice make use of farmland hedgerows and intraspecific parasite transmission could occur in these habitats (Montgomery and Dowie 1993; Montgomery *et al.* 2012).

The composition of the parasite component community of an introduced host can be used to determine the geographic source location of the introduced host. Wilson *et al.* (1998) used parasite community composition to determine that wood mice on the Shetlands' Fair Isle likely originated from the British Isles, rather than Scandinavia as was originally thought. As the most prevalent parasite in Irish bank voles and a likely candidate for co-invasion, *A. tetraptera* should then occur in the original source population of the bank vole. Genetic analyses suggests that the bank vole originates from Germany (Stuart *et al.* 2007) and while *A. tetraptera* was not recorded in the German study cited (Klimpel *et al.* 2007b), the sample size was too small to make a definitive conclusion about infection prevalence of *A. tetraptera* in Germany. *A. tetraptera* is however often

recorded in bank voles from Poland which boarders Germany. Interestingly *A. tetraptera* but was not recorded in bank voles in studies from Spain, Italy or France (Table 4.9).

The cestode *Mesocestoides spp.* was found in wood mice in mice-vole sites but was absent from mice-only sites (Chapter 1). This cestode has also not been recorded in previous studies of wood mice in Ireland (Appendix, Table 1A). *Mesocestoides spp.* is however less likely to co-invade with the bank vole. *Mesocestoides spp*. may require up to three hosts to complete its life cycle. A first intermediate host appears necessary for the proglottids to be infective to the vertebrate intermediate hosts, though the identity of such hosts is unclear. Based on experimental results the first intermediate host is postulated to be an oribatid mite (Soldatowa 1944). Requiring three hosts increases the likely-hood that *Mesocestoides spp*. would be lost during establishment and spread of the bank vole. The prevalence of tetrathyridia in bank voles is low in its indigenous range, typically below 5% (Table 4.9), which also reduces the probability that it could occur in the small founder population.

If the bank vole did not introduce *Mesocestoides spp*. then a native species other than the wood mouse must be the source of infection. Tetrathyridia infect a wide range of secondary intermediate hosts, including species found in Ireland such as brown rats, shrews and house mice (Di Bella *et al.* 2003; Conn *et al.* 2011). The adult cestode could be supported by Irish species of definitive hosts such as badgers (*Meles meles*) and red foxes (*Vulpes vulpes*) (Thompson 1976; Jones *et al.* 1980; Kriska 1993). Both rats and shrews share forested habitats with the bank vole and shrews were on occasion found in traps during the study.

The introduction of a parasite with a complex life cycle is not completely without precedent. Some helminths with indirect life cycles can become established if they have a wide specificity to an intermediate host (Kennedy 1993) and a recent literature review of the topic showed a surprising number of parasites with indirect life cycles do co-invade, including trematodes, cestodes, nematodes and acanthocephalans (Lymbery *et al.* 2014).

The final helminth, *A. murissylvatici* was recorded in wood mice in both mice-vole and mice-only sites and is frequently recorded in wood mice in Ireland (Appendix, Table 1A). *A. murissylvatici* is a directly transmitted nematode and reaches prevalences above 30% in bank voles in Europe (Table 4.9). It is likely the nematode was acquired in Ireland, but the life history characteristics also make it a good candidate for co-invasion

Low parasite diversity in invasive species has been suggested as a mechanism for the success of invasive species. The Enemy Release Hypothesis (ERH) posits that a decrease in regulation by natural enemies (including parasites) results in an increase in distribution and abundance in invaded ranges (Keane and Crawley 2002; Torchin *et al.* 2002; 2003). Parasite diversity of invasive species can be compared in two ways. Biogeographical studies compare introduced populations to populations in their indigenous ranges. Community studies compare invasive species to similar native species occurring within the same biological community (Colautti *et al* 2004). Using a biogeographically approach to compare species richness in Irish bank voles to bank voles in Europe, it is clear that the invasive bank vole has a considerably reduced helminth community. However, comparing parasite diversity of a host across its entire range, rather than from its source population, can overestimate the number of parasites actually lost by the invader (Colautti *et al.* 2005). The bank vole is thought to have originated from Germany, however the only German study on bank voles used a small sample size from an urban region. The bank voles from Poland however have been well studied and make a suitable proxy for the Irish bank vole source population. Using this more conservative comparison of parasite species richness in bank voles from a single region, rather than across Europe, still suggests that the helminth species richness of indigenous voles (14 species, Table 4.9) is almost five times greater than invasive bank voles (3 species).

Enemy reduction can be quantified using the equation (N - I)/N, where N is the number of enemies in the indigenous range and I is the number of enemies in the introduced range (Torchin *et al.* 2003). The index ranges from 0 (no escape) to 1 (total escape). It was decided to use the Polish studies as a

proxy for Germany. Based on species richness, the proportion of parasite reduction in bank voles is (13-3)/13 = 0.77. The total prevalence of all helminth parasites in introduced bank voles (77.4%) was within the range of what is found in bank voles in Poland (68.3% - 95%, Table 4.9). Prevalence of parasitism in invasive species is often not as significantly different as species richness. In their meta-analysis of introduced species, Torchin *et al.* (2003) found that parasites introduced with their host had similar prevalence in indigenous and invasive ranges. Prevalence should therefore be taken into consideration when making a claim for enemy reduction. In some cases the prevalence and abundance of parasites is much higher in the invasive hosts than con-specific hosts from indigenous ranges. Invasive rabbit fish (*Siganus rivulatus*) showed lower parasite species diversity than rabbit fish from indigenous ranges, but the prevalence and abundance of a co-invading species of monogean was three time higher in invasive populations (Pasternak *et al.* 2007). On average parasite prevalence for marine invasive species has been found to be more than twice that of indigenous host populations (Torchin *et al.* 2002; Pasternak *et al.* 2007). The disruption of the pre-existing, co-evolved host-parasite relationships in invasive species may allow the parasites remaining to undergo competitive release, resulting in increased prevalence and abundance (Lello *et al.* 2004). This will reduce the benefits of lower species diversity.

Due to the low helminth diversity of Irish bank voles, there is the potential for the remaining species to undergo such competitive release. *A. tetraptera* has prevalence in Polish bank voles ranging between 2.5% to 58.6%, less than the highest prevalence of 85.9% recorded in the present study in 2012 but not dissimilar to the overall prevalence of 66.67%. The highest mean intensity recorded (64.8) in Poland was higher than any intensity recorded in the present study (highest mean intensity in Irish bank voles was 23). There does not appear to be a consistently higher prevalence or intensity of *A. tetraptera* in Irish voles and no suggestion of competitive release, despite Kloch *et al.* (2010) finding antagonistic interactions between *A. tetraptera* and other indigenous parasites in bank voles in Poland. Similarly, the mean prevalence and intensity of *A. murissylvatici* in Irish bank voles (28% and 60) is less that the highest prevalence and intensity recorded in bank vole in indigenous ranges

(73% and 159). *Mesocestoides spp.* however appears in Irish bank voles at a higher prevalence (13%) than in bank voles in Poland (1.3-2.5%).

Although studies have implied that invasive species are less parasitised, a number of confounding factors need to be taken into account in biogeographical comparisons of parasite richness. Differences in parasitism may simply be an artefact of sampling effort if a species is better studied in its indigenous range (Mitchell and Power 2003; Torchin *et al.* 2003). There is often a great deal of spatial variation in parasite component communities of the same host species (see chapter 3). Component communities across the rage of a species are likely to be made up of different combinations of parasite species forming the parasite fauna. If measures of parasite diversity and abundance are aggregated from a number of host populations, the number of parasites actually available for transport to a new region will be overestimated (Prenter *et al.* 2004). In the present study, using surveys from a single country reduces this error.

To demonstrate that that the loss of parasites is a mechanism underlying the success of an invasive species, both escape and release from parasites must be demonstrated. Release refers to a reduction in parasite diversity and prevalence, which must then be related to a measurable release from negative impacts of the parasites (Prenter *et al.* 2004). Introduced populations of marine invertebrates often reach larger body sizes than indigenous conspecifics, as do insular rodent populations on islands compared to mainland populations and enemy release is a speculated mechanism for this pattern (Michaux *et al.* 2002; Torchin *et al.* 2003). The average weight (20.0g ±0.28) and length (8.9 ±0.47) of bank voles sampled was similar to bank voles collected in Germany (19.5g and 8.4cm), suggesting that helminth reduction has not resulted in increased body sizes (Klimpel *et al.* 2007b). Reallocation of resources to other physiological processes, such as increased reproductive output or overwinter survival cannot be ruled out and warrants future exploration.

There are few invasion studies able to relate the recorded loss of parasites to demographic release and Prenter *et al.* (2004) argue that such studies demonstrate enemy reduction rather than release.

Therefore no definitive conclusions about the role of enemy release in the spread of bank vole in Ireland can be made from this study. However, the present study strongly suggests that bank voles have undergone a reduction in helminth parasite species. It appears that bank voles left behind or lost the majority of their helminth species during the invasion process. *A. tetraptera* may have co-invaded, but the remaining parasites are more likely to have been acquired in Ireland.

CHAPTER 5

Community Comparison of the Helminths of Irish Wood Mice and Bank Voles

5.1 Introduction

The ability of parasites to mediate interactions between host species has long been known thanks to the experiments of Park (1948). In these experiments the competitive outcome between two *Tribolium* beetle species was reversed by a shared sporozoan parasite *Adelina tribolii*. In mixed cultures of the beetles, *T. confusum* was driven extinct by the superior competitor *T. castaneum*. But when both beetles were infected, the parasite induced higher mortality in *T. castaneum,* causing the extinction of *T. castaneum* but allowing *T. confusum* to persist. These experiments showed that parasites, through having differential effects on hosts, could have keystone roles in structuring communities by mediating species co-existence or exclusion. Ecologists are now becoming increasingly aware that parasites could play similar roles in determining the success of biological invasions by mediating interactions between invasive and native host species (Prenter *et al.* 2004; Dunn *et al.* 2012).

Competition mediated by shared natural enemies is referred to as apparent competition (Holt 1977), however parasites do not have to be shared between species to influence competitive outcomes. Species interactions mediated by parasites, whether shared or not, has come to be termed parasite-mediated competition (Hatcher *et al.* 2006). There are three main ways in which parasite-mediated competition might modify the success of an introduced species. First, introduced species often escape a number of their own parasite species during the course of the invasion (Torchin *et al.* 2003; Torchin and Mitchell 2004). While invaders will accumulate native parasites, these will not always replace what was lost and invaders remain less parasitised than both conspecifics in their indigenous range and ecologically similar native species (Torchin *et al.* 2002; Lymbery *et al.* 2010; Roche *et al.* 2010). As parasites regulate host populations through effects on host mortality and fecundity rates

(Anderson and May 1978; Hudson *et al.* 1998), invasive species may have a competitive advantage over more heavily parasitised native species. For instance, introduced Asian tiger mosquitoes (*Aedes albopictus*) exist in populations that are infected with gregarine parasites and populations that are parasite free. Infected tiger mosquitoes have little impact on native mosquito (*Ochlerotatus triseriatus*), but uninfected tiger mosquitoes outcompete the native mosquito, reducing its survivorship and facilitating spread of the invader (Aliabadi and Juliano 2002).

Second, exotic parasites that co-invade with introduced species can transfer to phylogenetically or ecologically similar native hosts. The spillover of exotic diseases has had devastating and well documented impacts of wild-life. Examples include avian malaria in Hawaiian birds (Van Riper *et al.* 2002) and squirrel pox virus in British red squirrels (Tompkins *et al.* 2003). Typically the invader is unaffected by the disease compared to native species and acts as a reservoir for infection. Parasite mediated-competition, via spillover, is implicated in the decline of wild grey partridge *Perdix perdix* in the UK. Introduced pheasants *Phasianus colchicus* transmit the caecal nematode *Heterakis gallinarum* to the grey partridge, which suffers much greater pathology than the pheasant. Additionally, *H. gallinarum* cannot be maintained in pure partridge populations, and pheasants act as a disease reservoir, maintaining infections in mixed populations (Tompkins *et al.* 2000; 2001).

Thirdly, invasive hosts may acquire and actively transmit native parasites, increasing exposure of native hosts. While less attention has been devoted to the spillback of native parasites it is likely an important and underestimated negative impact of species invasions (Kelly *et al.* 2009b). Invasives can rapidly develop diverse parasite communities made up of acquired native parasites and so are more likely to transmit native parasites than to introduce exotic parasites (Torchin *et al.* 2003; Poulin and Mouillot 2003; Lettoof *et al.* 2013). Spillback can greatly impact on the competitive ability of native species if invaders suffer less pathology from native parasites. For example, experimental infection by the acanthocephalan *Pomphorhynchus laevis* causes behaviour alterations in the native amphipod *Gammarus pulex* but not in the invasive *Gammarus roeseli*. Infection in the native species

was also associated with decreases in resistance to bacterial infection and reduction in sugar reserves not seen in the invasive host (Cornet *et al.* 2009).

The very fact that invasive species are successful in invaded habitats may imply that any parasite mediated competition is asymmetrical and most negative impacts are experienced by native hosts. Introduced species, as naïve hosts, may be susceptible to native parasites, to the point that parasites will prevent successful establishment of introduced hosts. Most failed introductions go unnoticed and the causes of their failure go unrecorded. If, however an introduced species does become invasive, one can assume that native parasites do not severely supress the invasive species fitness. Similarly exotic parasites which co-invade are unlikely to be highly virulent in invading hosts as the stresses associated with translocation and establishment, added to pathology caused by parasites, will result in the death of infected individuals and selection for more resistant host genotypes (Colautti *et al.* 2004; Møller 2005; Strauss *et al.* 2012). Therefore successful co-invading parasites are unlikely to impact on the success of the invading species. But if co-invading parasites spillover to, and negatively impact native hosts, these can facilitate the invasion. The greater impact of co-invading diseases on native hosts is supported in the literature. In a review of 16 examples of co-introduced parasites that switched to native hosts, 14 (85%) were more virulent in native hosts than in the original invading host (Lymbery *et al.* 2014).

Parasite-mediated competition is likely to be strongest between invasive species that are both ecologically and phylogenetically similar to native species. Closely related species provide a more similar habitat for parasites in terms of immunological and physiological characteristics, and those that share similar ecologies will be exposed to the same parasites (Poulin and Mouillot 2004b; Klimpel *et al.* 2007a). Similar species will also compete for similar resources and parasite mediated competition may determine the outcome of that competition.

Ireland has a depauperate rodent community and so there are few species that can be considered similar to the invasive bank vole (*Myodes glareolus*). In particular there are no other vole (arvicoline)

species (Marnell *et al.* 2009). The bank vole is however unusual among the arvicoline rodents, showing ecological characteristics more similar to mice (muridae). Unlike other voles which are found in open habitats, bank voles are strongly associated with areas of heavy vegetation and show food preferences that are intermediate between insectivorous/granivorous murine and herbivorous arvicoline (Kikkawa 1964; Butet and Delettre 2011) Bank voles are therefore ecologically similar to the Irish native murid, the wood mouse (*Apodemus sylvaticus*) which is found alongside the bank vole in its invaded range in Ireland. Rodent species that share similar ecologies also have similar parasite communities (Begon *et al.* 1999). Bank voles and wood mice are often the dominant rodents in many parts of Europe and Britain. Studies of population dynamics where both species co-occur find little evidence of negative competitive interactions (Geuse and Bauchau 1985). In Ireland, however, Montgomery *et al.* (2012) found the presence of the bank vole negatively affects the abundance of the wood mice and this effect was greater in populations closer to the bank vole's point of introduction.

In order to analyse the helminth fauna of the invasive bank vole within a community context, quantitative comparisons of the helminth communities of the invasive bank vole and native wood mouse from shared sites in Ireland was carried out.

5.2 Results

5.2.1 Host Population Structure

5.2.1.1 Host sample size

A total of 329 rodents were collected from vole-mice sites comprising 152 wood mice (*Apodemus sylvaticus*) and 177 bank voles (*Myodes glareolus*) (Table 5.1). In 2011, wood mice made up the majority of the sample (52%) while in 2012 more bank voles were trapped (64%). Fewer wood mice and bank voles were caught in 2012 overall and the difference between years was greater for wood mice-: 28.9% of all wood mice and 44.1% of all bank voles were caught in 2012. The sex ratio was skewed towards male rodents overall (males 58.3%, females 41.6%). The sex ratio was closer to 1 in bank voles (1:2, males 55.9%, females, 44.1%) than in wood mice (1:6, males 61.2%, females, 38.8%, Table 5.1). This pattern was repeated in both years. In 2011 male wood mice accounted for 59.3% of all wood mice and male bank voles accounted for 53.5% of all bank voles. In 2012 male wood mice made up 65.9% and male bank voles 59% of their respective species.

Table 5.1 Numbers of wood mice and bank voles examined by site, year and sex.

Site	Year	Female		Male		Total	
		A. sylvaticus	*M. glareolus*	*A. sylvaticus*	*M. glareolus*	*A. sylvaticus*	*M. glareolus*
Coole (A)*	2011	16	16	27	9	43	25
Coole (B)*		14	21	20	31	34	52
Merlin		14	9	17	13	31	22
	Total	**44**	**46**	**64**	**53**	**108**	**99**
Coole (A)	2012	3	6	15	12	18	18
Coole (B)		8	8	7	20	15	28
Merlin		4	18	7	14	11	32
	Total	**15**	**32**	**29**	**46**	**44**	**78**
	Grand Total			**329**			

*See Chp.2 Materials and Methods for explanation of sub-sites A and B

Rodents classified as adult was the most common age group in both wood mice and bank voles, although there were proportionally more adult bank voles (65%) than adult wood mice (44.1%). Rodents classified as juveniles were trapped least but juvenile wood mice (23.0%) were trapped proportionately more often than juvenile bank voles (9.6%) (Table 5.2).

Table 5.2 Allocation of wood mice and bank voles to three age classes by year and site.

Site	Year	Juvenile		Adult		Mature	
		A. sylvaticus	*M. glareoulus*	*A. sylvaticus*	*M. glareoulus*	*A. sylvaticus*	*M. glareoulus*
Coole(A)	2011	11	2	12	18	20	5
Coole(B)		3	3	20	41	11	8
Merlin		15	6	13	7	3	9
	Total	**29**	**11**	**45**	**66**	**34**	**22**
Coole(A)	2012	0	0	6	12	12	6
Coole(B)		4	2	8	15	3	11
Merlin		2	4	8	22	1	6
	Total	**6**	**6**	**22**	**49**	**16**	**23**
Grand Total		**35**	**17**	**67**	**115**	**50**	**45**

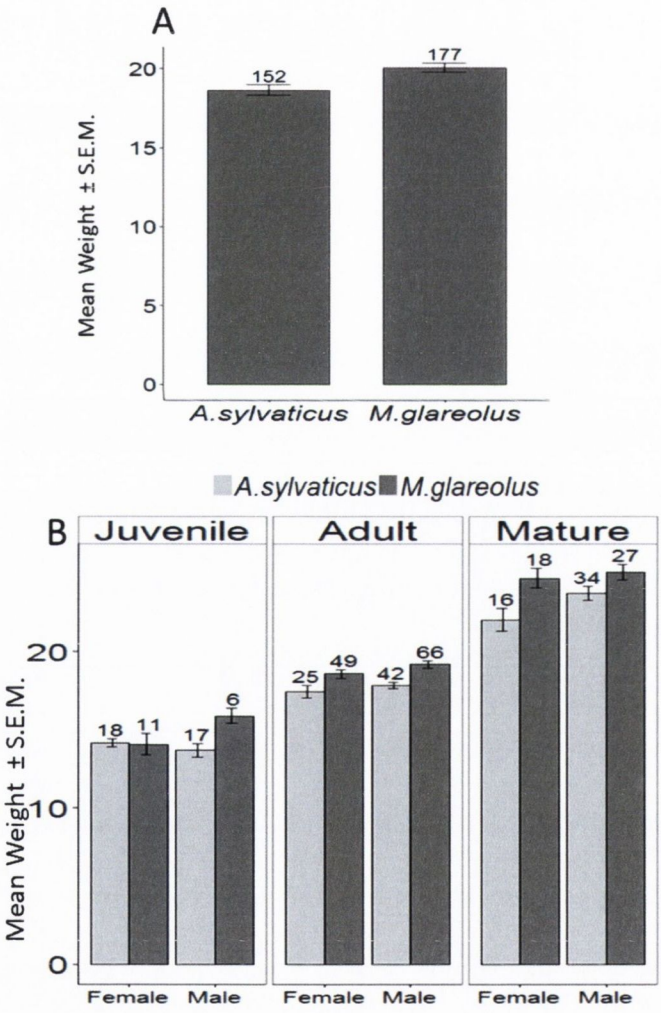
5.2.1.2 Morphometric measurements

For all GLM models, only significant results including the factor "species" (2 levels; *A. sylvaticus* and *M. glareolus*) are presented.

Weight

Bank voles (mean weight 20.1g ± 0.28g, range 8.19-31.0g) were heavier than wood mice (18.6g ±0.33g, range 8.53-28.1g) (GLM, family = Gamma, species: $F_{1,329} = 6.45$, $P<0.05$, Fig. 5.1A). Modelling revealed the difference was not uniform across host functional groups or year. On average the weight difference between female wood mice and bank voles (1.7g) was slightly greater than that between male wood mice and bank voles (1.4g). While juvenile female wood mice and bank voles had similar mean weights, compared to males, mature female bank voles were heavier than female wood mice (GLM, family = Gamma, sex:age class:species $F_{2, 329} = 4.47$, $P<0.05$, Fig. 5.1B).

In 2012 the weight difference between mature wood mice and bank voles was greater than it had been in 2011. This was the only year and age class where a relatively large difference in weight between mice and voles was recorded (GLM, family = Gamma, year:age class:species: $F_{2, 329} = 5.24$, $P<0.01$, Fig. 5.1C). There was also a significant site:age class:species interaction with mature bank voles in Merlin being significantly heavier that mature wood mice, likely due to the low sample size of mature wood mice at this site (GLM, family = Gamma, site:age class:species: $F_{2, 329} = 3.37$, $P<0.05$, Fig. 5.1D).



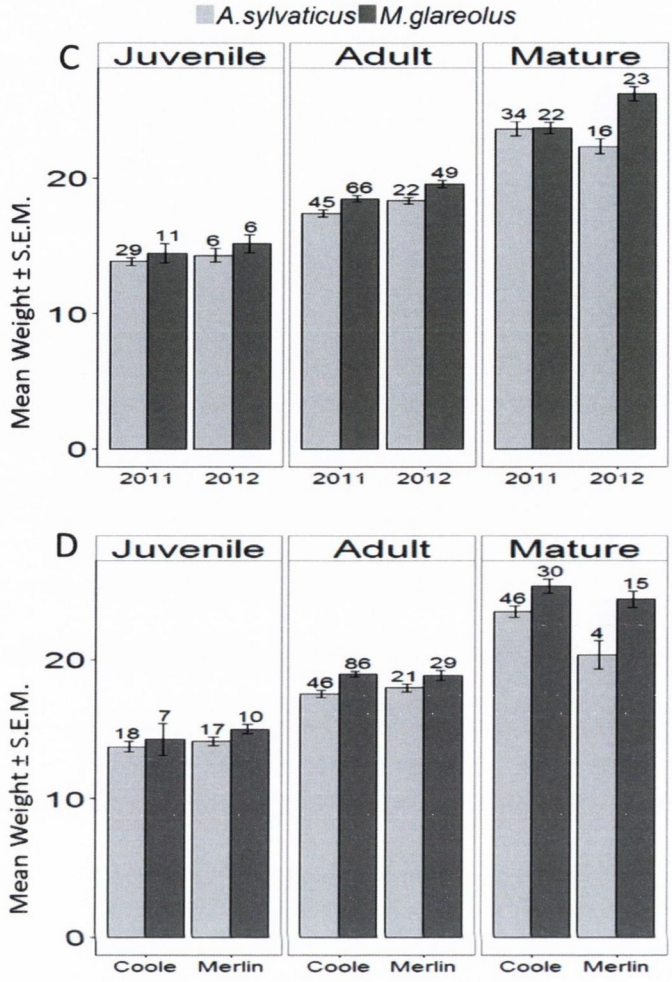


Figure 5.1 Mean body weight in wood mice and bank voles with standard error indicated by error bars. Sample size is given above error bars. Body weight by species (A), species, sex and age class (B), species, year and age class (C), species, site and age class (D).

Body length

Body length, measured as the distance from nose to anus, was significantly greater in bank voles (88.8cm ±0.47cm, range 66.7-104.7; wood mice 85.80cm ±0.88cm, range 18.3-107.7cm (GLM, family =Gamma, species $F_{1, 329} = 6.87$, $P<0.01$).

5.2.2 Helminth community structure.

The total number of helminths recovered from Galway sites was 15240, 74.5% of which were from wood mice and 25.5% from bank voles. There were 8 species of helminth recovered from wood mice and 3 recovered from bank voles (Table 5.3).

Table 5.3 Helminth species recovered from wood mice and bank voles by taxon.

	A. sylvaticus	*M. glareolus*
Taxon	**Helminth Species**	
Nematoda	*Syphacia stroma*	*Aspiculuris tetraptera*
	Aonchotheca murissylvatici	*Aonchotheca murissylvatici*
	Trichuris muris	
Cestoda	*Hymenolepis hibernia*	
	Skrjabinotaenia lobata	
	Mesocestoides spp.	*Mesocestoides spp.*
Trematoda	*Brachylaemus recurvum*	
	Corrigia vitta	

Wood mice and bank voles shared 2 species of helminth, the nematode *Aonchotheca murissylvatici* and cestode *Mesocestoides spp.* In both wood mice and bank voles most animals carried 1 helminth species (Fig 5.2). The percentage of rodents from which no parasites were recovered was higher in bank voles (22.6%) than wood mice (7.89%). A similar proportion of wood mice (28.3%) and bank voles (23.2) carried 2 helminth species while the proportion that carried 3 species (the maximum in bank voles, carried by 2.28% voles) was greater in wood mice (12.5%).

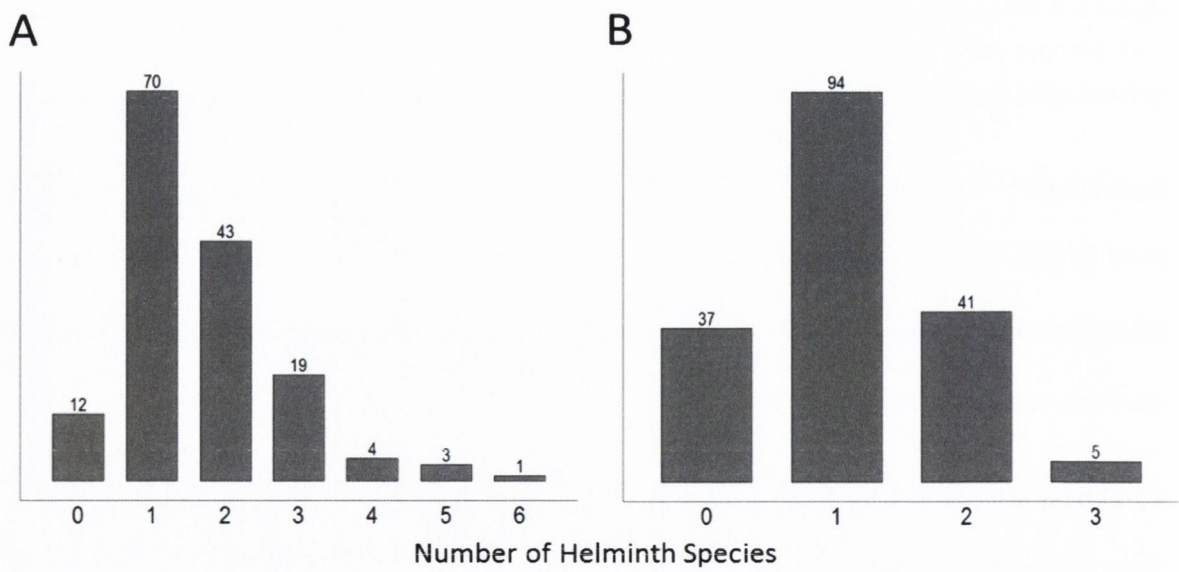


Figure 5.2 Frequency distribution of intestinal helminth species richness in wood mice (A) and bank voles (B). Sample size is indicated above the bars.

5.2.2.1 Component community structure of helminths of wood mice and bank voles

The Berger-Parker Dominance Index showed that in nearly all sites and both years a single species made up more than half of the individuals in the helminth community. The only exception to a measure below 0.5 was for wood mice in Merlin in 2012. *S. stroma* always dominated in wood mice and in bank voles, *A. tetraptera* dominated except in Coole (B) in 2011 when the dominant species was *A. murissylvatici*. Simpson's Index of diversity was generally lower in wood mice, reflecting the dominance of *S. stroma* in the wood mice samples (Table 5.4).

Table 5.4 Helminth component community measures in wood mice and bank voles by year and site.

	Year	Coole(A)		Coole(B)		Merlin	
		A. sylvaticus	*M. glareolus*	*A. sylvaticus*	*M. glareolus*	*A. sylvaticus*	*M. glareolus*
Total Species	2011	7	2	5	3	6	3
	2012	6	3	7	3	4	3
Berger-Parker	2011	0.88	0.62	0.91	0.88	0.91	0.74
	2012	0.97	0.67	0.91	0.68	0.40	0.68
Dominant Species	2011	*S. stroma*	*A. tetraptera*	*S. stroma*	*A. murissylvatici*	*S. stroma*	*A. tetraptera*
	2012	*S. stroma*	*A. tetraptera*	*S. stroma*	*A. tetraptera*	*S. stroma*	*A. tetraptera*
Simpson's Index	2011	1.27	1.90	1.20	1.29	1.20	1.71
	2012	1.07	1.84	1.20	1.82	1.12	1.93

5.2.2.2 Infracommunity structure of helminths of wood mice and bank voles

The maximum number of helminth species infecting wood mice was 6, occurring in Coole (A) in 2011. Bank vole infracommunities with all 3 helminths were only found in Merlin (Table 5.5). All shared helminths had a negative binomial distribution in wood mice and bank voles. Both helminths were more aggregated in bank voles (Table 5.6).

Table 5.5 Helminth infracommunity measures for wood mice and bank voles by year and site.

	Year	Coole(A)		Coole(B)		Merlin		Total Sample	
		A. sylvaticus	*M. glareolus*	*A. sylvaticus*	*M. glareolus*	*A. sylvaticus*	*M. glareolus*	*A. sylvaticus*	*M. glareolus*
Mean Species Richness	2011	1.40± 0.15	0.64 ±0.10	1.76± 0.15	0.88 0.09	1.00± 0.14	0.68 ±0.15	1.40 ±0.10	0.78 ±0.06
	2012	2.11± 0.20	1.00 ±0.11	2.73± 0.40	1.32 ±0.12	1.82± 0.26	1.13 ±0.10	2.25 ±0.18	1.17 ±0.06
	Total	**1.61± 0.13**	**0.79 ±0.08**	**2.06± 0.16**	**1.04 ±0.07**	**1.21± 0.13**	**0.94 ±0.09**	**1.64±0.09**	**0.95 ±0.05**
Max Species	2011	6	1	4	2	3	2	6	2
	2012	4	2	5	2	3	2	5	2
Mean number of helminths	2011	30.6±5.83	12.5±5.57	62 ± 27.15	20.2±7.41	28.6±7.50	7.36 ±2.78	40.2 ±9.1	15.38 ±4.19
	2012	266.1±130.6	8.11 ±2.01	140.7 ± 35.6	50.8±9.87	11.4 ± 2.99	34.1 ±8.43	159.3 ±56	34.2 ±5.25
	Total	**100.1±40.4**	**10.7 ±3.31**	**86.4 ±22.2**	**30.9 ±6.11**	**24.1± 5.67**	**23.3 ±5.40**	**74.7±17.9**	**23.6 ±3.36**
Mean Brillouin's Index	2011	0.13±0.04	0	0.21±0.05	0.04 ±0.02	0.06±0.02	0.06 ±0.04	0.13 ±0.02	0.03 ±0.01
	2012	0.26±0.06	0.04 ±0.03	0.28±0.06	0.20 ±0.05	0.29±0.09	0.09 ±0.03	0.27 ±0.04	0.12 ±0.02
	Total	**0.16±0.03**	**0.02±0.01**	**0.23±0.04**	**0.10 ±0.02**	**0.12±0.03**	**0.08 ±0.02**	**0.17±0.02**	**0.07 ±0.01**
Max Brillouin's Index	2011	1.19	0	0.81	0.53	0.54	0.54	1.19	0.54
	2012	0.79	0.35	0.79	0.67	0.8	0.66	0.8	0.67

Table 5.6 Measures of dispersion for helminth species shared by wood mice and bank voles by year and site. Index of dispersion (I, variance to mean ratio) and negative binomial (k).

	Year	Coole(A)				Coole(B)				Merlin				Total Sample			
		k		*I*		*k*		*I*		*k*		*I*		*k*		*I*	
		WM	BV	WM	BV	WM	BV	WM	BV	WM	BV	WM	BV	WM	BV	WM	BV
A. murissylvatici	2011	0.03	0.01	19.6	80	0.07	0.1	108.5	164.2	0.03	0.06	2	4.52	0.03	0.06	93.6	156.1
	2012	-	0.54	1.85	1.35	-	0.11	11.3	80.7	nd	0.09	nd	30.1	0.10	0.08	11.3	65.5
	Total	**0.06**	**0.03**	**16.1**	**78.1**	**0.09**	**0.11**	**84.6**	**138.1**	**0.02**	**0.07**	**2**	**29.9**	**0.05**	**0.07**	**74.6**	**122.7**
Mesocestoides spp.	2011	-	0.02	3.00	14.3	-	0.15	-	8.53	-	0.03	-	13.0	0.01	0.08	3.00	10.3
	2012	-	0.05	-	18.0	-	0.01	7.43	48.0	-	0.09	-	18.4	0.01	0.04	7.81	24.2
	Total	**-**	**0.03**	**3.00**	**16.9**	**-**	**0.07**	**7.83**	**23.7**	**-**	**0.06**	**-**	**18.1**	**0.01**	**0.06**	**7.13**	**19.9**

k – negative binomial, I – variance to mean ratio.
WM – wood mouse, BV – bank vole.
nd – not possible to calculate parameters due to small sample size

Species Richness of Intestinal Helminths

Mean helminth species richness was significantly higher in wood mice (GLM, family= Poisson, species: $\chi^2_1 = 19.1$, P<0.001, Fig. 5.3A, Table 5.5).

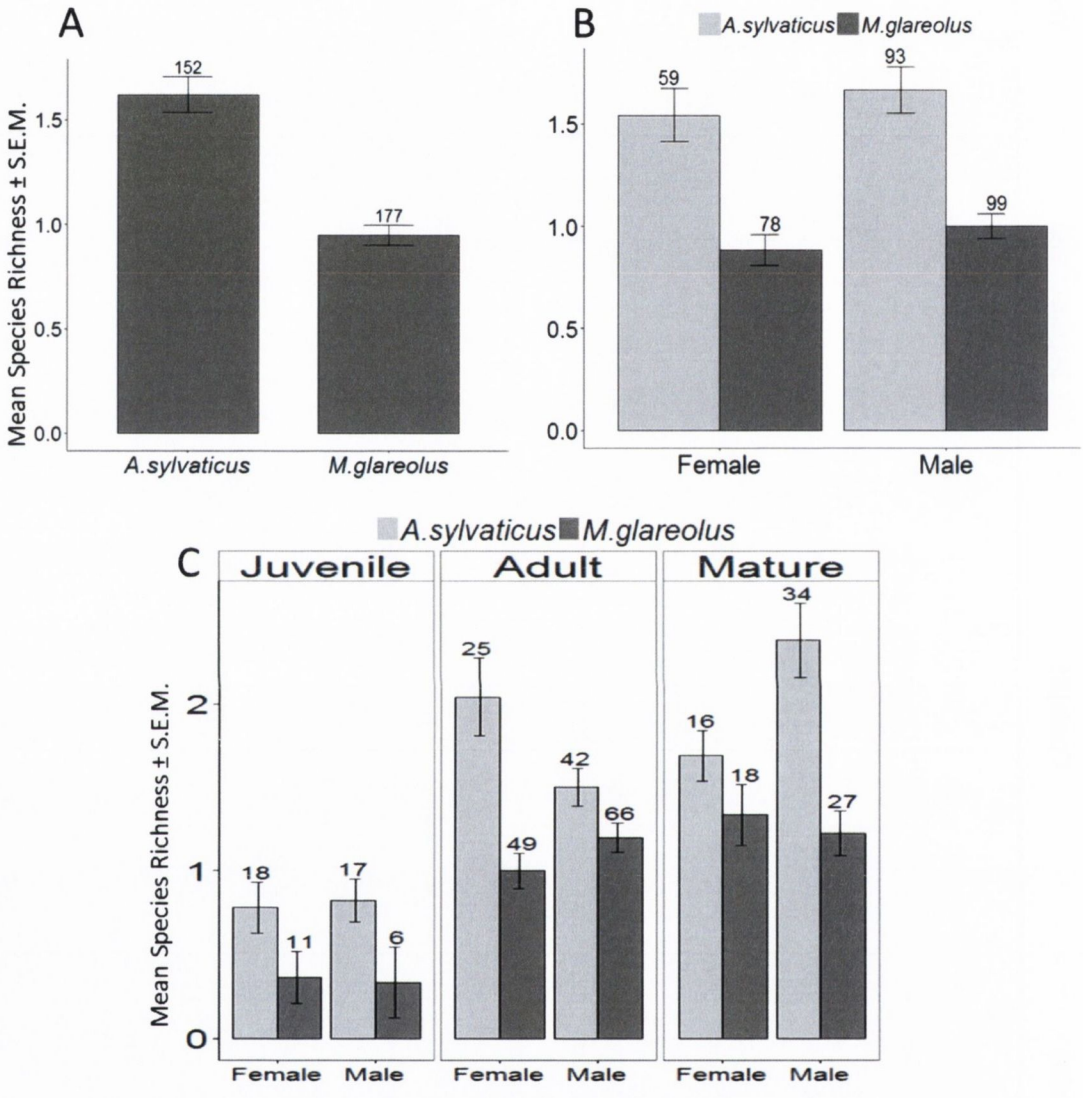


Figure 5.3 Mean helminth species richness in wood mice and bank voles. Helminth species richness by species (A), sex and species (B) and sex, age class and species (C).

There were significant interactions when species richness was analysed among the various host functional groups. The difference in species richness was greater between female wood mice and bank voles (1.42) than between male rodents (0.55) (GLM, family= Poisson, sex:species: $\chi^2_1 = 4.94$, P<0.01, Fig. 5.3B). The difference in species richness between female juvenile wood mice and bank

voles was similar to that between male juvenile wood mice and bank voles. More variation was however revealed in the adult and mature age classes. The difference in species richness between rodents was greatest between female wood mice and bank voles in the adult age class, but in the mature age class the greatest difference was seen between male rodents (GLM, family=Poisson, sex:age class:species $\chi^2_2 = 6.95$, P<0.01, Fig. 5.3C).

Brillouin's Index of Diversity

Over all wood mice had a significantly higher Brillouin's index than bank voles (GLM, family = quassi-poisson, species: $F_{1, 172} = 40.5$, P<0.001, Fig. 5.4, Table 5.5).

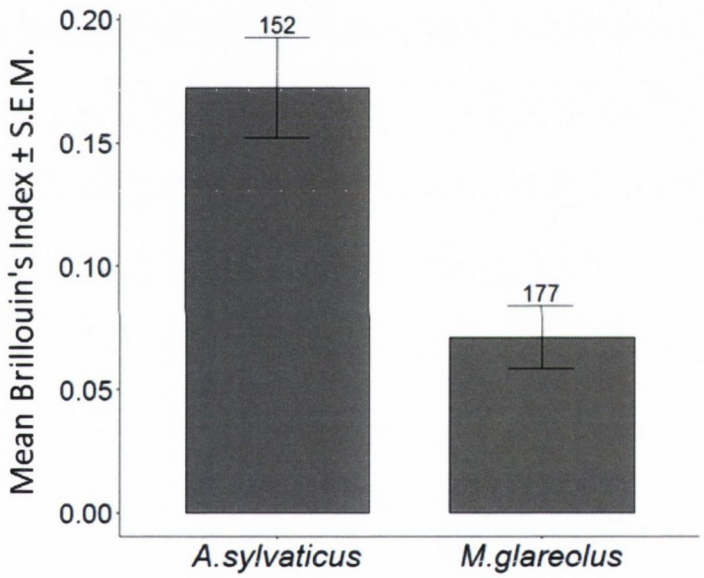


Figure 5.4 Brillouin's Index of Diversity (S.E.M) for wood mice and bank voles.

Prevalence and Abundance of Shared Helminths in Wood Mice and Bank Voles

For the total sample, significantly more wood mice (92.1%) were infected with at least 1 helminth, (bank voles: 77.4%) (GLM, family= binomial, species: $\chi^2_1 = 32.4$, P<0.001, Fig 5.5A). For both wood mice and bank voles, prevalence of helminth infection increased in 2012 (Table 5.7).

Table 5.7 Prevalence (%) with 95% Clopper-Pearson confidence intervals and mean abundance ± standard error for all helminths of wood mice and bank vole by year and site.

Species	Year	Coole(A)		Coole(B)		Merlin		Total Sample	
		A. sylvaticus	*M. glareolus*	*A. sylvaticus*	*M. glareolus*	*A. sylvaticus*	*M. glareolus*	*A. sylvaticus*	*M. glareolus*
All helminths	2011	93 (80.9-98.5)[P] 30.6 ±5.83[A]	64 (42.5-82.0)[P] 12.5 ±5.57[A]	100 (89.7-100)[P] 62.9 ±27.1[A]	73.1 (59.0-84.4)[P] 20.2 ±7.41[A]	74.2 (55.4-88.1)[P] 28.6 ±7.47[A]	54.4 (32.2-75.6)[P] 7.36 ±2.78[A]	89.8 (82.5-94.8)[P] 40.2 ±9.14[A]	66.7 (56.5-75.8)[P] 15.4 ±4.19[A]
	2012	100 (81.5-100) 266.1 ±130.6	88.9 (65.3-98.6) 8.11 ±2.01	93.3 (68.1-99.8) 140.7 ±35.6	92.9 (76.5-99.1) 50.8 ±9.87	100 (71.5-100) 11.4 ±3.0	90.6 (75.0-98.0) 34.3 ±8.42	97.7 (88-99.9) 159.3 ±56.0	91 (82.4-96.3) 34.2 ±5.24
	Total	**95.1 (86.3-99) 100.1 ±40.4**	**74.4 (58.8-86.5) 10.7 ±3.33**	**98 (89.1-99.9) 86.4 ±22.2**	**80 (69.6-88.1) 30.9 ±6.11**	**81 (65.9-91.4) 24.1 ±5.67**	**75.9 (62.4-86.5) 23.3 ±5.40**	**92.1 (86.6-95.9) 74.7 ±17.9**	**77.4 (70.5-83.3) 23.7 ±3.35**
A.murissylvaticis	2011	9.3 (2.6-22.1) 0.70 ±0.56	8 (1-26.0) 4.80 ±3.92	26.5 (12.9-44.4) 4.62 ±3.84	40.4 (27.0- 54.9) 17.7 ±7.47	3.2 (1.0-16.7) 0.06 ±0.06	13.6 (2.9-34.9) 0.68 ±0.37	12.9 (7.27- 20.8) 1.75 1.23	26.3 (17.9-36.1) 10.7 ±4.10
	2012	22.2 (6.4-47.6) 0.39 ±0.20	16.7 (3.58-41.4) 0.22 ±0.13	40.0 (16.3-67.7) 3.27 ±1.57	39.3 (21.5-59.4) 14.2 ±6.39	0 (0-28.5) 0	31.3 (16.1-50.0) 6.34 ±2.44	22.7 (11.5-37.8) 1.27 0.57	30.8 (20.8-42.2) 7.74 ±2.55
	Total	**13.1 (5.84 24.2) 0.61 ±0.40**	**11.6 (3.89-25.1) 2.88 ±2.27**	**30.6 (18.3-45.4) 4.20 ±2.69**	**23.8 (14.9-34.6) 16.4 ±5.32**	**2.38 (0.06 -12.6) 0.05 ±0.048**	**18. (9.25-31.4) 4.04 ±1.50**	**15.8 (10.4- 22.6) 1.61 ±0.89**	**28.2 (21.7- 35.5) 9.36 ±2.55**
Mesocestoides spp.	2011	2.33 (0.06-12.29) 0.07 ±0.07	8 (0.98-26.0) 0.72 ±0.64	0 (0-10.3) 0	28.8 (17.1-43.1) 1.40 ±0.48	0 (0-11.2) 0	9.10 (1.12-29.2) 1.23 ±0.85	0.93 (0.02-5.05) 0.03 ±0.03	19.2 (12.0-28.3) 1.19 ±0.35
	2012	0 (0-18.5) 0	16.7 (3.58-41.4) 2.44 ±1.56	13.3 (1.66-40.5) 1.10 ±0.73	3.57 (0.09-18.3) 1.40 ±0.48	0 (0-28.5) 0	28.1 (13.7-46.7) 4.53 ±1.61	9.09 (2.53-21.7) 0.36 ±0.25	16.7 (9.18-26.8) 3.04 ±0.97
	Total	**1.63 (0.04-8.80) 0.05 ±0.05**	**11.63 (3.89-25.1) 1.44± 0.75**	**4.08 (0.50-13.98) 0.33 ±0.24**	**20.0 (11.9-30.4) 1.51 ±0.67**	**0 (0-8.41) 0**	**20.4 (10.6-33.5) 3.19 ±1.03**	**1.97 (0.4-5.66) 0.13 ±0.08**	**18.1 (12.7-24.6) 2.00 ±0.47**

Prevalence was also affected by a significant sex:species interaction There was a greater difference in the prevalence of infection between female wood mice (89.8% CI: 79.2-96.2) and female bank voles (71.8% CI: 60.5-81.4) compared to male wood mice (93.5% CI86.5-97.6) and male bank voles (81.8% CI: 72.8-88.9) (GLM, family= binomial, sex:species χ^2_1 = 31.3, P<0.05, Fig. 5.5B). There was also a difference in prevalence between rodent species within the various age classes (GLM, family= binomial, age class:species χ_2^2 = 31.9, P<0.001 Fig. 5.5C). The difference in the prevalence of infection between adult rodents (wood mice: 97.1% CI: 89.6-99.6; bank voles: 80.9% CI: 72.5-87.6) was similar to that between mature rodents (wood mice: 100% CI: 92.9-100; bank vole: 84.4% CI: 70.5-93.5) while a greater difference was seen between juvenile rodents (wood mice: 71.4% CI: 53.7-85.4; bank vole 35.3% CI: 14.2-61.7).

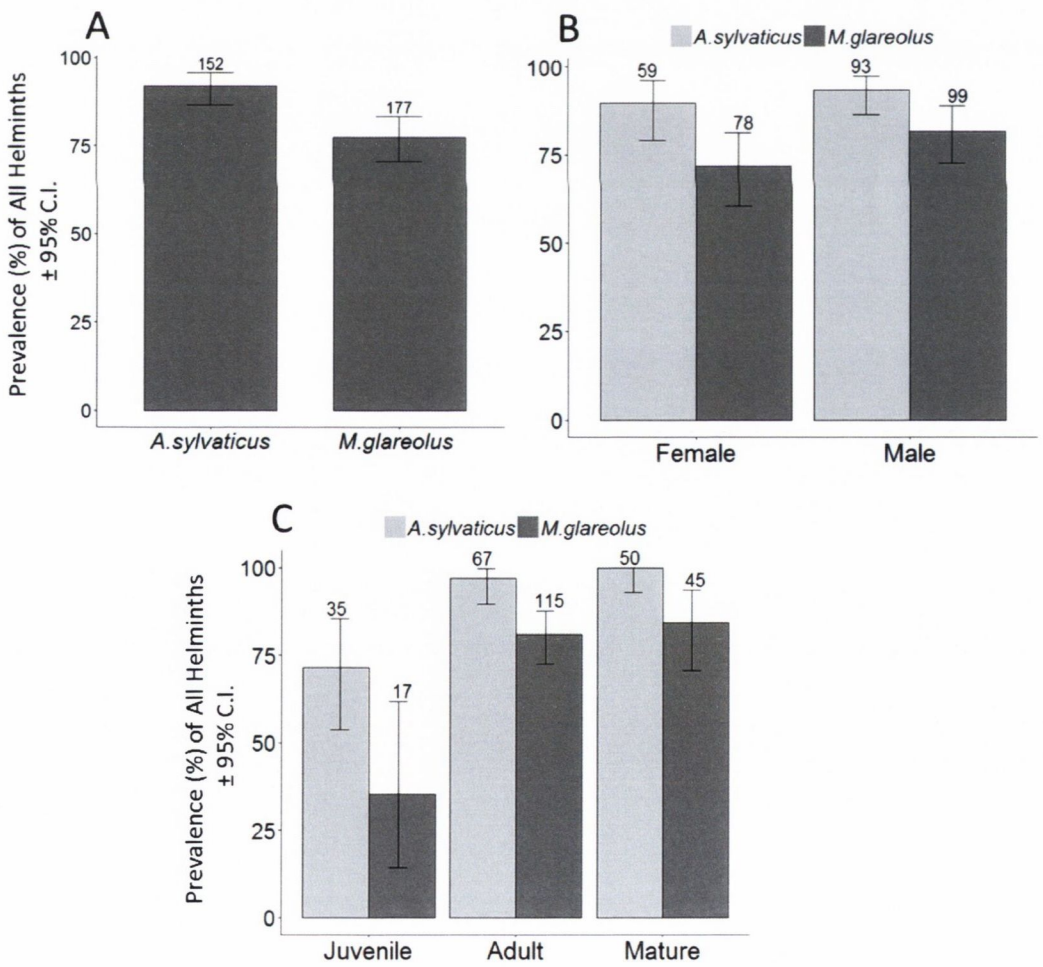


Figure 5.5 Prevalence (%) of all helminths in wood mice and bank voles. Prevalence by species (A) sex and species (B) and age class and species.

Full factorial abundance models could not be fitted for abundance of all helminths, nor could simpler models without interaction terms, therefore non-parametric tests were used. Wood mice had significantly higher mean helminth burden (74.7 ±17.9) than bank voles (22.0 ±3.2), (Mann-Whitney U test, species: z= 5.53, P<0.001 Fig 5.6). Mean helminth abundance increased for both species in 2012 (Table 5.7).

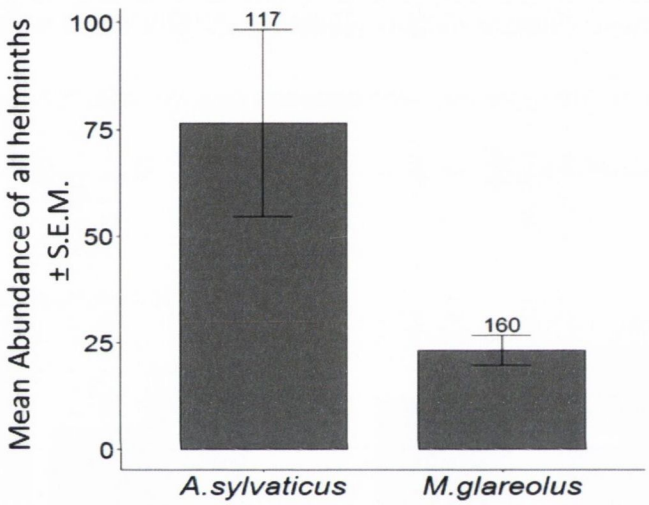


Figure 5.6 Mean abundance of all helminths in wood mice and bank voles.

Prevalence and Abundance of shared helminth species

Aonchotheca murissylvatici

A total of 24 wood mice (15.8%, CI: 10.4-22.6) were infected with *A. murissylvatici* compared to 50 bank voles (28.2%, CI: 21.7- 35.5, Table 5.7) (GLM, family= binomial, species: χ_1^2 = 6.93, *P*= 0.01, Fig. 5.7A). Mean abundance of *A. murissylvatici* was also greater in bank voles (9.36 ±2.55; wood mice (1.61 ±0.89) (GLM, family= Negative binomial, Species: LR_1 = 23.3, P<0.001, Fig 5.7B).

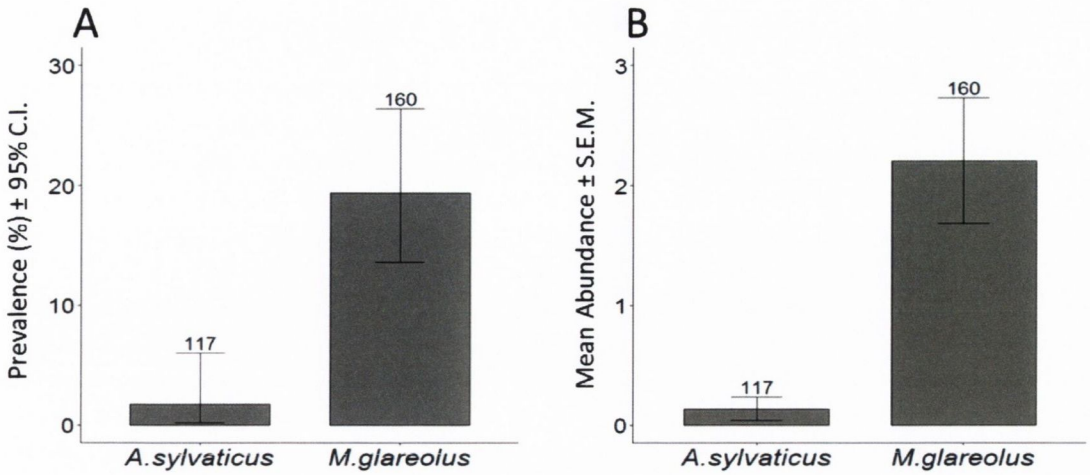


Figure 5.7 Prevalence (%) (A) and mean abundance (S.E.M.) (B) of *Aonchotheca murissylvatici* in wood mice and bank voles.

Mesocestoides spp.

Only 3 wood mice (1.97% CL:0.4-5.66) carried *Mesocestoides spp.* tetrathyridia while 32 bank voles (18.1% CL:12.7-24.6, Table 5.7) were infected (GLM, family = binomial, species: χ^2_1 = 22.4, P<0.001, Fig. 5.8A). Overall abundance of *Mesocestoides spp.* was significantly higher in bank voles (2.00 ±0.47; wood mice 0.13 ±0.08) (GLM, family= Negative binomial, species: LR_1 = 21.6, P<0.001, Fig. 5.8B). The increase in *Mesocestoides spp.* cysts followed the general trend of other helminths in this system, increasing from 2011 to 2012 in both wood mice and bank voles (Table 5.7).

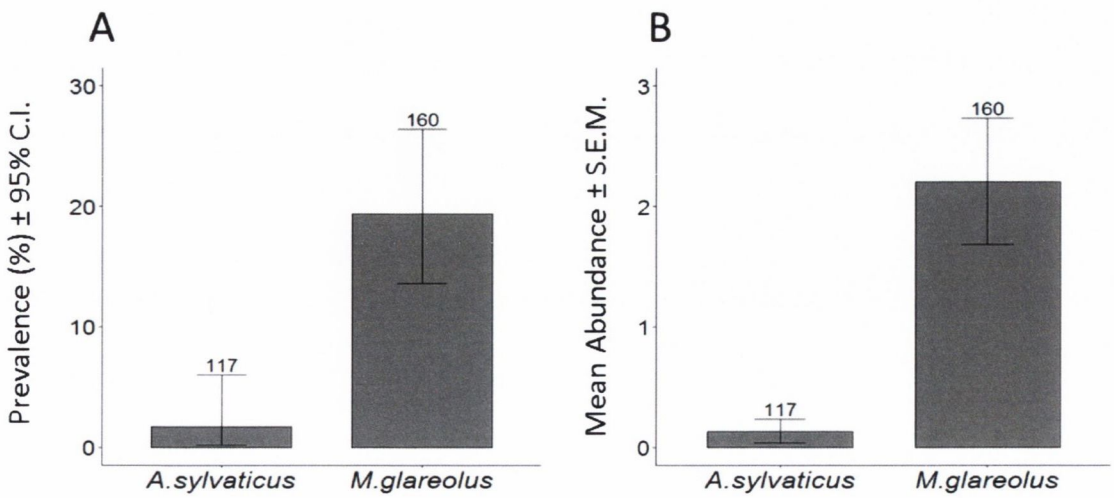


Figure 5.8 Prevalence (%) (A) and mean abundance (S.E.M.) (B) of *Mesocestoides spp.* in wood mice and bank voles.

5.3 Discussion

This chapter provides a parasitological examination of an invasive species in a community context. By comparing the helminth parasites of the invasive voles to the native wood mice where they co-occurred, it was clearly demonstrated that the invasive species is less parasitised, whether measuring species richness, prevalence of infection or mean abundance of helminths. Wood mice and bank vole helminth communities were dominated by directly transmitted Oxyurid nematodes. Cestodes were found in both host species but trematodes were missing entirely from bank voles while two species were collected from wood mice. This reflects the differences in diet between the two species, confirming the more omnivorous nature of the wood mouse (Butet and Delettre 2011).

Despite their ecological similarity, bank voles and wood mice only shared two parasites, *Mesocestoides spp*. and *A. murissylvatici*. The probability that two host species will share parasites is not only a function of their phylogenetic relatedness, but also their ecological similarity (Poulin and Mouillot 2003; Cooper *et al.* 2012). Perlman and Jaenike (2003) make the distinction between the potential host range and the actual host range realised by a particular parasite species. A parasite's potential host range is determined by intrinsic properties of the host such as physiological, biochemical, and behavioural characteristics. Intrinsic properties have a genetic basis and so closely related host species provide similar habitats for the parasite. A parasite's actual host range is a subset of its potential host range, modified by extrinsic ecological factors that act to reduce or prevent exposure between host and parasite. The transmission biology of the parasite will play a role in determining exposure rates (Woolhouse *et al.* 2005).

The nematode genus *Syphacia* provides a useful exploration of these concepts. In its indigenous range the bank vole is infected with the Oxyurid nematode *Syphacia petrusewiczi* (Meszaros 1978; Behnke *et al.* 2001b). As closely related parasites will be able to tolerate similar host intrinsic conditions, the wood mouse parasite *S. stroma* is a candidate native parasite for vole acquisition. However because of the transmission biology of *S. stroma*, encounter rates between bank voles and

parasite propagules will be low. The eggs of *S. stroma* are infective very soon after being laid and transmission relies on infected hosts encountering each other regularly as well autoinfection through grooming. As bank voles and wood mice tend to avoid each other spatially and temporally, opportunities for interspecific transmission are reduced. Differences in host ecology would explain why *S. stroma*, despite being closely related to parasites found in bank voles, was not recovered from bank voles during the course of this study. Similarly, Jex *et al.* (2006) found that host-specificity of Oxyurid in arthropods was driven mainly by differences in host ecology rather than parasite specificity to the hosts examined.

A second parasite that might be expected to be found in both rodents is *A. tetraptera*. *A. tetraptera* has been found in other parasitological surveys of wood mice in Europe (Tenora *et al.* 1977; Pisanu *et al.* 2009; Torre *et al.* 2013) and has also been shown to be able to infect wood mice under laboratory conditions, though it does not establish as successfully in wood mice as in the house mouse (*Mus musculus*), considered to be the normal host (Behnke 1974). However, of the three helminths found in voles, *A. tetraptera* was the only one that was not also found in wood mice. So while the wood mouse is a compatible host, there appears to be no spillover of *A. tetraptera* from bank voles in the two wood mice populations investigated, even though prevalence in bank voles was particularly high in 2012.

If, as it appears from other studies, wood mice are compatible host for *A. tetraptera*, a possible explanation of their parasite-free status may again be due to low encounter rates between wood mice and *A. tetraptera* eggs. *A. tetraptera* has a direct lifecycle but unlike *Syphacia*, eggs are released with the faeces and take about a week to reach maximum infectivity (Anya 1966). Environmental contamination is the most likely source of infection and close contact between wood mice and bank voles is not necessary for interspecific transfer. The spatial and dietary niche segregation between wood mice and bank voles (Fairley and Jones 1976; Butet and Delettre 2011)

did not prevent the vole acquiring two other shared directly-transmitted nematodes which suggests that this is not enough to prevent the transfer of *A. tetraptera* between the two hosts.

It is possible that *A. tetraptera* does not establish in wood mice due to cross immunity from, or competitive interactions with, other helminths. The most likely candidate is *S. stroma* as prevalence of this nematode is high and wood mice are exposed as juveniles in the nest (see Chp. 3). Stahl (1966) found negative correlations in the abundance of *S. obvelata* and *A. tetraptera* infections in inbred mice. The early infection of wood mice with *S. stroma* may be particularly important as the sequence of infection appears to determine the antagonistic interaction between these two nematodes. Mice infected with *S. obvelata* and later challenged with *A. tetraptera* had 50% fewer *A. tetraptera* compared to control mice with no *S. obvelata* infection. In the reverse case no significant reduction in *A. tetraptera* burden was detected.

A murissylvatici is a common nematode of both murid and arvicolid rodents, having a wide host range in these groups (Montgomery and Montgomery 1988; Justine and de Roguin 1990; Milazzo *et al.* 2003; Bjelić-Čabrilo *et al.* 2009) as well as in more distantly related rodents (Pisanu *et al.* 2009). Parasitological surveys in Europe and Ireland record *A. murissylvatici* having a lower prevalence and intensity in wood mice than bank voles, suggesting bank voles are the more competent host (O'Sullivan *et al.* 1984; Pisanu *et al.* 2009). The present study found similar results; both prevalence and abundance of *A. murissylvatici* was significantly higher in bank voles. For a native parasite with density-dependent transmission, introduced species with higher than zero competence are likely to increase transmission rates and prevalence (Telfer and Brown 2012). It was argued in chapter 4 that *A. murissylvatici* is a native parasite acquired by the bank vole. Therefore the greater prevalence and abundance of this nematode in the invasive species could cause spillback to the native wood mouse.

Prevalence and abundance of *A. murissylvatici* in wood mice was greater overall in mice-vole sites, though it was not found in the vole-mice site Merlin in 2012. The very low relative population size of mice at this site may account for the disappearance. Montgomery and Montgomery (1990) found *A.*

murissylvatici at a higher prevalence and abundance in wood mice in Ireland in sites not occupied by bank voles, though the peak values came from spring and summer samples. The higher spring/summer infection rate may be related to larger proportion of green food in the wood mouse diet prior to the availability of seeds later in the summer. Langley and Fairley (1982) suggested the eggs of *A. murissylvatici* stuck to vegetation and caused spring and early summer peaks. Despite these differences some weight is added to the hypothesis that bank voles are causing a spillback of *A. murissylvatici* to wood mice by analysing the replicated sites in Coole separately. In site B, the relative population size of bank voles was higher than in site A, likely due to the greater degree of ground cover found here. Site B was also the site in which wood mice had the greater prevalence and abundance of *A. murissylvatici*. Overall the combined mice-vole relative population of site B was less than the wood mice population in mice-only sites, so the argument can be made that species composition of hosts rather than over all host density is driving the higher prevalence *A. murissylvatici* in wood mice in mice-vole sites.

A second case for parasite spillback might be made for the other shared parasite. *Mesocestoides spp.* was not recorded in the mice-only sites, so a comparison of the prevalence in wood mice in the absence of bank voles cannot be made. *Mesocestoides spp.* also has an indirect life-cycle, so infection in wood mice cannot be linked to an increase in prevalence in bank voles as simply as directly transmitted parasites. For instance, if the definitive host of *Mesocestoides spp.* preys to a much greater degree on wood mice, the greater prevalence of infection in voles may not make much difference in the overall rate of transmission. However it is of interest that *Mesocestoides spp.* has not been recorded in wood mice in Ireland and the majority of those studies were in mice-only populations (Appendix, Table 1A). O'Sullivan *et al.* (1984) surveying a mixed population did not find the cestode in either rodent.

While prevalence of both *Mesocestoides spp. and A. murissylvatici* was low in the wood mouse even with the presence of the bank vole, without the bank vole these parasites may disappear more

frequently from wood mice populations. In modelling a two host community, Holt *et al.* (2003) showed how the threshold density needed for the pathogen establishment is dependent on the varying rates of intra- and interspecific transmission. If one species is not a competent host and does not contribute to transmission at all, the focal host will have to be at the threshold density before pathogen establishment will occur. However, when both species are competent hosts, then pathogen establishment may occur more readily in the two host community than when the host species occur alone. Applying this to the two parasites found in this system, bank voles could maintain infection of these parasites in wood mice even when the threshold densities of wood mice are below that required for parasite transmission. What may be expected in areas invaded by bank voles is greater parasite persistence in wood mouse component communities.

The results presented here allows for the intriguing possibility that the success of the bank vole at the expense of the wood mouse may be due in part to differences in parasitism. The detrimental effects of helminth parasite not only increase with parasite burden, but with diversity of parasites species too. Increasing helminth species richness has been associated with lower levels of abdominal fat and host body mass (Lello *et al.* 2005), increased immune investment (Bordes and Morand 2009) and more severe disease outcomes than expected from single infections (Ezeamama *et al.* 2008). In multiple infections, synergistic interactions between helminths, and helminths and microparasites, can facilitate further infections (Behnke *et al.* 2009; Ezenwa *et al.* 2010). Therefore the paucity of parasite species carried by the bank vole may result in significantly less pathological impact than occurs in the wood mouse.

The two helminths that have likely been acquired by the bank vole in Ireland are not novel host-parasite associations. Each have been recorded in bank voles in their indigenous range (see table 4.9 Chapter 4). However, while these infections are not novel host-parasite associations they will be novel genetic variants. Parasites impose selective pressures on their hosts, as do hosts on parasites, resulting in local adaption. Parasites are therefore more infective and virulent to local host

genotypes (Ebert 1994; Lively 1999). This would further reduce the impact that shared native parasites have on the invasive species. On the other hand, invasive species may be more susceptible to native parasites if, due to small founder populations or population bottlenecks, they experience reduced genetic diversity and increased disease susceptibility. For instance, low allelic diversity in antigen presenting proteins of the major histocompatibility complex results in increased parasitic infection in stickleback fish (*Gasterosteus aculeatus*) (Kurtz *et al.* 2004). Studies on the mtDNA of bank voles in Ireland have found low levels of variation suggesting the bank vole founder population was small, or that the population went through a bottleneck during range expansion (Ryan *et al.* 1996; Stuart *et al.* 2007). Low allelic diversity in the bank voles may be a reason why the shared native parasites infect bank voles more successfully.

Of course bank voles and wood mice are infected by a range of other parasites and escape from one guild cannot be extrapolated to all other parasite guilds. While chipmunks introduced to France had much poorer helminth communities compared to native rodents, Ixodid ticks were more common in introduced chipmunks than native rodents (Pisanu *et al.* 2010). There have been fewer investigations of non-helminth parasites of bank voles and wood mice in Ireland. Telfer *et al.* (2005) investigating the blood borne bacteria *Bartonella* found the Irish bank voles do not carry the two species of *Bartonella* that infect wood mice. In contrast, Irish bank voles have accumulated almost as diverse an ectoparasite assemblage as wood mice (Fairley 1963; 1970). O'Sullivan *et al.* (1982), sampling both bank voles and wood mice from Ross Island, Killarney, found bank voles were hosts to all three species of ectoparasite found on wood mice, including a fourth species only found on bank voles, though this was a single individual. For two of the flea species, bank voles were infected at a significantly higher prevalence than wood mice. The single species of tick recorded was equally prevalent on wood mice and bank voles. Telfer *et al.* (2005) also found higher prevalence of fleas on bank voles than wood mice. The bodies of wood mice and bank voles may present a more similar habitat to ectoparasites than their intestinal tracts do to helminths as arvicoline and murine rodents have differing intestinal morphology based on their diet. Bank voles have a long digestive tract and

large ceacum suited to large quantities of low quality food. The wood mice digestive tract is shorter and caecum smaller as their diet consists of a greater proportion of concentrated food such as arthropods (Butet and Delettre 2011).

The findings of Montgomery *et al.* (2012) suggest the gradual replacement of the wood mouse by the bank vole. The study was confined to farmland hedgerows, however the present study also found the relative population sizes of wood mice were lower in woodland habitats where the bank vole was present (Appendix, Table 2A). As discussed, there are three ways parasites might mediate competition between introduced and native host species; spillover of co-invading parasites, spillback of acquired native parasites and lower parasitism in invaders compared to natives. This study has shown that in terms of helminth infections, the bank vole is less parasitised than the wood mice. There does not appear to be any spillover of introduced helminth from bank vole to wood mouse but there is evidence of spillback of two shared native helminths.

CHAPTER 6

General Discussion

Species invasions provide natural perturbation experiments across spatial and temporal scales that can be useful for exploring a wide range of questions in ecology and evolution, as well as exploring the role of parasites in natural communities. The aim of this thesis was to take advantage of such a natural experiment and investigate the host-parasite relationship in the context of a biological invasion. This included investigating not only an invasive host, but also the impact of invasions on the parasite community of an ecologically similar native species. The model system comprised the helminth communities of the introduced bank vole (*Myodes glareolus*) and the native wood mouse (*Apodemus sylvaticus*) in Ireland.

Montgomery and Montgomery (1990) suggested that the species composition of helminths in Irish wood mice may be stable over a wider geographical scale. The authors however did not examine wood mice populations where they co-occurred with bank voles. Species invasion and introduced parasites are one way in which component communities are altered (Poulin 2007b) and so a comparison of wood mice populations co-occurring with bank voles and those existing outside the invaded range was undertaken (Chapter 3). The results suggested that spillover of introduced helminths from the bank vole to the wood mouse was not occurring. Other than the cestode *Mesocestoides spp.* there were no unique helminth species occurring in mice-vole sites. The possibility that *Mesocestoides spp.* was spilling over from bank voles was considered unlikely as this parasite is probably native to Ireland, but cannot be dismissed entirely without further investigations. Therefore, despite the presence of the bank vole, the regional species composition of the intestinal helminth fauna of wood mice in Ireland shows some stability. Studies in Ireland ranging from 1980 (Appendix, Table 1A) to the present study reveal a relatively stable suite of helminths, subject to local fluctuations in occurrence, prevalence and abundance.

Bank voles however may have had an effect on the transmission dynamics in mice-vole sites. In the presence of bank voles, wood mice had a significantly lower abundance of the nematode *S. stroma*. The smaller relative population size of wood mice in mice-vole sites was proposed as a mechanism. If bank voles are the cause of reductions in wood mice, then this represents an example of the dilution effect due to susceptible host regulation (Keesing *et al.* 2006). As a cross-sectional study, the mechanisms underlying the patterns observed in the present study can only be hypothesised. Combining observational and experimental manipulations such as bank vole removal and exclusion, though arduous, would provide more definitive evidence that dilution is occurring in wood mice due to the presence of bank voles.

A central goal of host-parasite community ecology is to identify the causes of parasite aggregation and variation in parasite intensities within and between host populations (Barnard *et al.* 2003). Data from chapter 3 was also used to investigation the intrinsic and extrinsic factors shaping helminth communities in a small rodent. Site was the most important factor explaining differences helminth prevalence and abundance between wood mice populations, in agreement with similar studies examining the factors shaping helminth communities in wood mice (Montgomery and Montgomery 1990; Abu-Madi *et al.* 2000; Behnke *et al.* 2001b). It is clear the factors shaping the helminth communities of wood mice are largely context-dependent, which must be taken into consideration when searching for generalisations in parasite community ecology. There was also significant differences in the helminth community structure between the two years surveyed, which highlights the need for parasitological surveys that examine a number of sites over more than one year.

Data from the present study updates and adds to the records on helminth communities in wood mice, the most recent published study being from 1996 (Ryan and Holland 1996). Maintaining a good parasitological record of native species is of vital importance in the context of species invasions. Such records allow researchers to better identify and track changes in parasite dynamics caused by invasive species. As species poor communities may be at a greater risk of invasions,

particularly from areas with similar environmental conditions (Hooper *et al.* 2005), Ireland's depauperate mammal community is especially vulnerable. Certainly the temperate climate of Ireland would not present a barrier to many small mammals found in Britain or in much of Europe. Accidental introductions in Ireland are likely to be common - recent invasive species alerts in Ireland have included the Siberian Chipmunk (*Tamias sibiricus*), raccoon (*Procyon lotor*) and hazel dormouse (*Muscardinus avellanarius*) (Invasive Species Ireland 2010; 2011; National Biodiversity Centre 2012).

The gastro-intestinal helminth community of invasive bank voles in Ireland was extremely impoverished compared to bank voles in indigenous ranges (Chapter 4). In order to determine if this pattern occurs across all parasite taxa a more complete census of the parasite fauna including microparasites and ectoparasites, is needed. Reduced parasitism in invasive species is one requisite of the enemy release hypothesis (ERH), the idea that the success of many invasive species is due to escape from natural enemies occurring in their indigenous range (Torchin *et al.* 2002; 2003). ERH is a popular explanation for the success of invasive species but experimental testing of the hypothesis is scarce and the proposed link between reduced parasitism and increased fitness is assumed rather than definitively proven in invasion literature (Colautti *et al.* 2004; Gendron *et al.* 2012). Conclusive tests of enemy release requires experimental manipulations by either parasite removal from hosts in their indigenous range, or the addition of parasites in invaded ranges, followed by measures of fitness or demographic changes (Perkins *et al.* 2008).

A hypothesis complementary to ERH, the evolution of increased competitive ability (EICA) hypothesis, focuses on the consequences of the loss of natural enemies upon immune investment. The hypothesis suggests that the reduction in natural enemies allows introduced species to reallocate resources from defence mechanisms to growth and reproduction (Blossey and Nötzold 1995). Testing the EICA hypothesis is probably more practical than ERH, particularly in a mammalian system where experimental manipulation raises logistical and ethical concerns. Evidence that successful invaders have altered immune responses is accumulating. Lee *et al.* (2005) found that

invasive house sparrows had a reduced inflammatory response to an antigen challenge compared to the tree sparrow, a less successful invader. This in turn reduced the cost and potential danger of mounting an inflammatory response to a novel parasite in the invaded environment.

A reduction in immune investment can of course leave host populations susceptible to parasite infection. Along with reduced immunity, the low genetic diversity of invaders, due to founder effects, could make invasive species vulnerable to disease outbreaks and epidemics (Perkins *et al.* 2008). Bank vole populations in Ireland show low genetic diversity (Ryan *et al.* 1996; White *et al.* 2013) and determining if bank voles have also reduced immune investment is not only of ecological and evolutionary interest, but also of public health concern. Bank voles are hosts for parasites with zoonotic potential such as *Puumala* virus, a Hantavirus which causes haemorrhagic fever and renal failure syndrome in humans (Clement *et al.* 2009). The finding of *Mesocestoides spp.* in this study, another potentially zoonotic parasite (Fuentes *et al.* 2003), further highlights the need for continued parasitological observation of bank voles.

Wood mice and bank voles shared two species of helminth. Infection was asymmetrical with prevalence and abundance of both shared parasites being higher in bank vole. One of the shared species, *Aonchotheca murissylvatici,* was found at all sites and comparison of prevalence and abundance in wood mice in mice-vole sites and mice-only sites could be made (Chapter 5). The higher prevalence and abundance of *A. murissylvatici* in wood mice in mice-vole sites strongly suggested bank voles were amplifying infection in wood mice through the process of spillback of a native parasite (Kelly *et al.* 2009a; 2009b). Shared parasites have the potential to mediate competition between host species (Tompkins *et al.* 2000), particularly if the parasites disproportionally impact upon one species. Prevalence and abundance of *A. murissylvatici* in wood mice, even in the presence of the bank voles, was low and the impact of this parasite is probably not significant at the level of the population.

However, bank voles and wood mice likely share parasites from other taxa that could have a more significant impact. For example the shared pathogen cowpox virus is known to affect survival and reproduction in bank voles and wood mice (Turner *et al.* 2014). Determining if a particular parasite species is having a larger detrimental effect on wood mice, or if the loss of parasites in bank voles gives them a competitive advantage may help to explain the apparent negative effect of bank voles on population numbers of wood mice (Montgomery *et al.* 2012). Bank voles were also less parasitised than wood mice overall, which may also confer a competitive advantage to the bank vole. Whether lower parasitism found in the bank vole extends to microparasites and ectoparasite needs to be investigated as community studies (comparing co-occurring native and invasive species) often show that invasive species are not less parasitised than native species overall (Colautti *et al.* 2005).

From the above discussion, there are numerous questions that could be addressed and explored using the Irish bank vole-wood mouse system. Indeed, this system has a number of features that make it an ideal model system. Small mammal communities in Irish woodlands are very simple. During this project, house mice (*Mus musculus*) were never found in traps, the only other small mammal trapped accidentally was the pygmy shrew (*Sorus minutus*) and on two occasions young brown rats (*Rattus norvegicus*). The fact that wood mice and bank voles are trapped together suggests they regularly interact and share many of the same resources.

The ecology and parasitology of wood mice and bank voles has been well studied, they are straightforward to trap with no regulatory restrictions placed on their collection. The bank vole is widespread throughout Europe and occurs alongside wood mice in many habitats which could serve as controls to Irish populations. Bank voles are continuing to spread in Ireland (White *et al.* 2013) and hosts at the edge of range expansions have been found to be less parasitised than core populations (Phillips *et al.* 2010). Comparisons of these populations may give useful insights into immune investment in invading species.

There is a lack of empirical studies on the role of immunity in invasion biology (White and Perkins 2012). The development of immune assays and molecular techniques, particularly for use in small wild rodents (Jackson *et al.* 2011; Turner *et al.* 2011) make the invasive bank vole system in Ireland particularly conducive to such investigations. The reduced helminth diversity of invasive voles, particularly if this extends to other parasite taxa, could provide an ideal model system for immune functioning in a wild system. Such a system would also be useful to the field of ecological immunology (ecoimmunology) which seeks to explain natural variation in immune function, specifically how the immunity varies in the real world, outside the controlled conditions of the laboratory (Sheldon and Verhulst 1996).

The present study is the first to comprehensively evaluate the gastro-intestinal helminths of the bank vole in Ireland. Rigorous statistical methods, within a community ecology framework, were used to compare helminth parasitism in the bank vole to the native wood mice in an invasive species context. The role of parasites in biological invasions, and in ecological processes in general, is increasingly recognised as important. However in order to generate useful generalisations, numerous studies across a wide range of biological invasions is vital. The data collected during this study is an important contribution to this goal, particularly as mammal studies are underrepresented in the parasitological-invasion literature. The study also updated the parasite fauna of small rodents in Ireland, with two new helminth records.

The major finding of this thesis is that significant differences in helminth richness, prevalence and abundance exist between bank voles in Ireland and bank voles in indigenous ranges, as well as between introduced bank voles and Irish wood mice. The results highlight the need to take parasites into account when dealing with biological invasions. For instance a reduction in parasitism may well be a characteristic of another invasive mammal, the white-toothed shrew (*Crocidura russula*), presently expanding its range in Ireland (McDevitt *et al.* 2011). Reduced parasitism may be important in helping conservation managers understand the success of these invasive mammals in

Ireland. Results presented in the thesis also showed the potential for an invasive species to alter disease dynamics in a native species, even when the species belong to different genera. This suggests that ecological similarity is an important consideration when determining the parasitological impact of invasives on native species.

Future work should build on the findings presented in this thesis using the Irish bank vole-wood mouse system as a model system to explore the host-parasite relationship in an invasive species context. In particular robust empirical studies are needed to explore the dilution effect and consequences of host diversity on disease transmission, the role of ecoimmunology in invasions and the extent of parasite-mediated competition in natural communities.

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APPENDIX

Appendix A

Table 1A Studies of helminth species associated with the alimentary canal, body cavity and liver found in *A. sylvaticus* in Ireland.

		Cestode				Trematode				Nematode			
Reference	**Location**	*C. lobata*	*T. taeniaeformis*	*H. straminea*	*H. diminuta*	*B. recurvum*	*C. vita*	*P. muris*	*G. spumosa*	*C. murissylvatici*	*S. stroma*	*H. polygyrus*	*T. muris*
Langley, Fairley (1982).	Merlin Woods Galway (V-)	x	x			x	x	x	x	x	x		
O'Sullivan *et al*. (1984).	Ross Island Killarney (V+)	x	x	x		x	x	x			x	x	x
Montgomery, (1988; 1989; 1990).	County Down (V-)	x	x		x	x	x			x	x	x	x

(V+)- sites where the wood mice were sympatric with bank voles; (V-) - sites were the vole was not present at the time of the study.

Table 2A Relative population size of wood mice and bank voles in all study sites, including sub-sites, by year.

		2011		2012	
Mice Sites		**Mice**	**Vole**	**Mice**	**Vole**
	Knocksink (A)	0.37	-	0.44	-
	Knocksink (B)	0.40	-	0.46	-
	Total Knocksink	0.38	-	0.45	
	Santry	0.38	-	0.31	-
Mice-vole Sites	Coole (A)	0.10	0.11	0.13	0.13
	Coole (B)	0.13	0.23	0.13	0.20
	Total Coole	0.11	0.17	0.13	0.16
	Merlin	0.21	0.15	0.07	0.15

Table 3A Climatic Data for mice-vole sites and mice-only sites in 2011 and 2011

Rainfall: total mm

	Mice-Vole Sites[1]				Mice onlySites[2]			
	Winter	**Spring**	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**
2010	138.7	120.2	135.4	282.3	50.3	43.4	55.3	78.5
2011	195.5	202	142.5	381.4	54.3	28.3	48.8	94.4
2012	340.6	114.5	206.3	225.2	45.1	58.6	103.7	75.5

Temperature: mean max

	Mice-Vole Sites[1]				Mice-only Sites[2]			
	Winter	**Spring**	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**
2010	7.5	13.6	18.8	14.6	5.8	12.5	19.1	13.1
2011	8.3	14	16.9	14.6	6.8	13.7	17.8	15.1
2012	10.4	13.7	17.8	13.3	8.8	12.4	17.8	12.5

[1]Mice-vole sites – Weather station Culliagh Beg is situated in the Maam valley, N 53° 34' 36" Longitude W 09° 39' 53"
[2]Mice sites – Weather station is situated at Dublin Airport, N 53° 25' 17" W 06° 17' 52"
Winter (December, January, February); Spring (March, April, May); Summer (June, July, August); Autumn (September, October, November)

Table 4A Measures of aggregation for individual species of helminths by year and site in *A. sylvaticus*. Index of dispersion (*I*) variance to mean ratio) and negative binomial (*k*)

	Year	KnockA		KnockB		Santry		Coole(A)		Coole(B)		Merlin		Combined	
		k	*I*	*k*	*I*	*k*	*I*	*k*	*I*	*k*	*I*	*k*	*I*	*k*	*I*
S. stroma	2011	0.84	324.2	0.66	671.2	0.53	559.1	0.4	56.3	0.34	439.3	0.14	70	0.34	592.9
	2012	0.46	1021	0.74	861.5	0.72	967.5	0.31	1203.1	0.69	123	0.2	18.9	0.4	1020
	Total	**0.66**	**542.9**	**0.65**	**809.2**	**0.59**	**838.7**	**0.27**	**1052.5**	**0.38**	**291.1**	**0.14**	**70.8**	**0.35**	**845.3**
H. polygyrus	2011	0.85	42.7	1.46	8.6	-	-	-	-	-	-	-	-	0.99	38.8
	2012	0.61	38.7	2.09	13	-	-	-	-	-	-	-	-	0.98	40.1
	Total	**0.74**	**40.9**	**1.4**	**12.4**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**0.94**	**39.6**
T. muris	2011	0	0	0	0.94	<0.001	0.98	0.15	2.44	0.44	1.95	0	0	0.12	2.07
	2012	0.05	3.33	0.13	1.61	0.34	2.82	0.19	1.59	0.37	1.84	0	0	0.16	2.73
	Total	**0.02**	**3.38**	**0.4**	**1.21**	**0.17**	**3**	**0.15**	**2.24**	**0.42**	**1.87**	**0**	**0**	**0.12**	**2.53**
A.muris-sylvatici	2011	0	nd	0	0	nd	0	0.03	19.56	0.07	108.49	0.03	2	0.03	94.1
	2012	0	>0.001	0.04	15.16	nd	4.48	0	108.5	0	11.26	0	0	0.01	10.2
	Total	**0**	**>0.001**	**0.01**	**15.26**	**nd**	**4.75**	**0.06**	**16.12**	**0.09**	**84.57**	**0.02**	**2**	**0.05**	**64.4**
H. hibernia	2011	0.28	1.8	0.42	2.44	0.07	6.39	0.001	1.02	0	0	0.02	2	0.12	3.22
	2012	0.11	18.5	0.23	96.7	0.15	6.8	0	0	0.03	53.9	0	0	0.08	73.1
	Total	**0.09**	**17.5**	**0.15**	**90.9**	**0.1**	**6.68**	**0.001**	**54**	**0.01**	**2**	**0.02**	**2**	**0.06**	**66**
C. lobata	2011	0.05	7.07	0.01	11	<0.01	4	0.06	7.81	0.23	2.43	0.16	2.97	0.06	5.97
	2012	0.21	3.54	0	0	0.06	22.9	0.67	9	1.23	2.3	0.92	2.8	0.15	13.9
	Total	**0.09**	**5.23**	**0.004**	**11**	**0.03**	**23.1**	**0.12**	**13.09**	**0.35**	**2.84**	**0.21**	**3.72**	**0.08**	**13.23**
C. vitta	2011	0.9	8.7	0.35	11.8	0.21	20	0.03	25.9	0	0	0.08	14.7	0.18	14.82
	2012	0.72	8.48	0.63	15.5	0.5	31.1	0.05	2	0.06	2	0.47	8.17	0.28	25.7
	Total	**0.8**	**9**	**0.35**	**17.5**	**0.28**	**33**	**0.03**	**25.69**	**0.02**	**2**	**0.14**	**12.01**	**0.2**	**23.2**

	Year	KnockA		KnockB		Santry		Coole(A)		Coole(B)		Merlin		Combined	
		k	*I*	*k*	*I*	*k*	*I*	*k*	*I*	*k*	*I*	*k*	*I*	*k*	*I*
B. recurvum	2011	nd	0	0.25	1.33	0	0	0.04	4.45	0.08	2.91	0.1	1.62	0.04	3.01
	2012	0.11	22.6	0.21	1.94	0.22	5.94	0.1	2.41	0.03	31.09	0.09	2	0.09	18.51
	Total	**0.03**	**24.2**	**0.18**	**1.7**	**0.09**	**6.47**	**0.05**	**3.77**	**0.03**	**27.2**	**0.09**	**1.72**	**0.05**	**17.4**

I Index of Dispersion – variance to mean ration. Larger than one indicates negative binomial distribution.
k Negative binomial exponent Smaller values of k indicate greater levels of aggregation
nd – not possible to calculate parameters.

Table 5A. Measures of aggregation for individual species of helminths by year and site in *M. glareolus*. Index of dispersion (*I*) variance to mean ratio) and negative binomial (*k*)

Species	Year	Coole(A)		Coole(B)		Merlin		Total Sample	
		k	*I*	*k*	*I*	*k*	*I*	*k*	*I*
A. murissylvatici	2011	0.01	80	0.1	164.2	0.06	4.52	0.06	156.1
	2012	0.54	1.35	0.11	80.7	0.09	30.1	0.08	65.5
	Total	0.03	78.1	0.11	138.1	0.07	29.9	0.07	122.7
A. tetraptera	2011	0.2	61.1	0.37	5.38	0.24	27.3	0.23	38.3
	2012	0.91	8.02	0.77	48	0.39	66.5	0.47	57.6
	Total	0.34	42.6	0.24	61.8	0.29	65.1	0.27	61
Mesocestoides spp.	2011	0.02	14.3	0.15	8.53	0.03	13	0.08	10.3
	2012	0.05	18	0.01	48	0.09	18.4	0.04	24.2
	Total	0.03	16.9	0.07	23.7	0.06	18.1	0.06	19.9

I Index of Dispersion – variance to mean ration. Larger than one indicates negative binomial distribution.
k Negative binomial exponent calculated using maximum likelihood method in MASS package R. Smaller values of k indicate greater levels of aggregation
nd – not possible to calculate parameters.