Ecological Replacement of *Peromyscus maniculatus gracilis* by *Peromyscus leucopus* in northern Michigan

by

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ABSTRACT

Climate-induced ecological replacement of *P. m. gracilis* by *P. leucopus* has been documented with long-term studies in the Great Lakes Region. Gradually warming winters over the last 30-40 years in this area have facilitated northward range expansion of *P. leucopus*, and communities in which *P. leucopus* and *P. m. gracilis* co-occur have become characterized by strong numerical dominance of *P. leucopus*. I conducted a three year field study of syntopic *P. leucopus* and *P. m. gracilis* in northern Michigan to identify niche differences and investigate the mechanisms by which these differences facilitate ecological replacement.

P. leucopus consistently experienced a longer breeding season than *P. m. gracilis*. *P. leucopus* and *P. m. gracilis* also differed in the survivorship of overwintered mice. This results in differences in the relative contributions of overwintered and young-of-year females to annual reproductive output, and may be a previously unreported niche difference between species. Ecological replacement of *P. m. gracilis* by *P. leucopus* results from the interaction between environmental conditions, niche differences, and species interactions.

Abundance differed strongly in two out of three years, with *P. leucopus* outnumbering *P. m. gracilis* in 2011 and 2012. Increases in abundance of *P. leucopus* are well explained by enhanced survival conferred by increasingly warming conditions. Reproductive output in *P. leucopus* is highly dependent upon reproduction by overwintered females. Mild winters allow for increased abundance of breeding females in the spring and more favorable breeding conditions which facilitate successful early reproduction and lower mortality.

The role of interspecific competition in ecological replacement in this species pair has not been previously investigated, and the role of competition in regulation of population growth remains unclear. Nevertheless, there was evidence that interspecific competition may influence

replacement. Declining abundance of *P. m. gracilis* was caused by reduced reproduction by young-of-year females rather than by changes in survival, and these phenomena may be better explained by interspecific social interactions than by environmental conditions alone. Increasingly warm winters may shift the competitive balance in this community to favor *P. leucopus* by allowing this species to establish territories earlier than *P. m. gracilis*.

CHAPTER 1.

WHY ARE SOUTHERN *PEROMYSCUS* REPLACING THEIR NORTHERN COUNTERPARTS?

1.1   CLIMATE-INDUCED RANGE SHIFTS

Predicting the effect of environmental fluctuations on the abundance and distribution of species has long been a major challenge for ecologists (Ives 1995), and its importance has become even more pressing in light of global climate change (Gilman *et al.* 2010). Environmental conditions are undergoing rapid and directional change; average land temperatures, for example, are predicted to increase 1.2-4°C by the year 2100 (IPCC 2007). Significant ecological consequences are expected. Climate-induced range shifts are already taxonomically widespread (Parmesan and Yohe 2003; Araujo *et al.* 2006; Parmesan 2006; Kelly and Goulden 2008; Moritz *et al.* 2008) and appear to have accelerated in recent years (Chen *et al.* 2011). Range shifts are often accompanied by more subtle changes in population abundance, community structure and composition, and organismal physiology (Sala *et al.* 2000; Parmesan and Yohe 2003; Williams and Jackson 2007).

Environmental change can differentially affect species in a community because each has its own physiological optimum (Huey *et al.* 2009) and may experience abiotic conditions differently (Helmuth *et al.* 2005). Changes in temperature can alter an organism's energetic requirements, which affect survival, reproductive rates, individual growth, and activity patterns (Gilchrist

1995). Changes to the abiotic environment can cause simultaneous and differing responses of species within a community and lead to faunal turnover (Blois and Hadly 2009).

1.2   ECOLOGICAL REPLACEMENT IN MICHIGAN *PEROMYSCUS*

In Michigan, range shifts and subsequent ecological replacement of 'northern' species by their 'southern' counterparts has been observed in several species of small mammals (Myers *et al.* 2009). One of these species pairs is the 'southern' white-footed mouse, *Peromyscus leucopus,* and the 'northern' woodland deer mouse, *P. maniculatus gracilis*, which occur together in northern Michigan forests. Much of the range of *P. m. gracilis* lies to the north of Michigan, in Ontario and Quebec. *Peromyscus leucopus*, in contrast, is at the northern limits of its range in this region.

Expansion of the northern limit of the range of *P. leucopus* has been observed at least since the early 20th century.   Reports from New York and Massachusetts from the early 1900s indicate that while the ranges of *P. leucopus* and *P. m. gracilis* did not yet overlap, the northern limit of the range of *P. leucopus* was quickly approaching the southern limit of the range of *P. m. gracilis* (Miller Jr. and Rehn 1901). In the more recent past, ecological replacement of *P. m. gracilis* by northward-expanding populations of *P. leucopus* has been observed in Minnesota (Long 1996).

In Michigan, Hooper (1942) noted the dispersion of *P. leucopus* northward up the entire Lower Peninsula and restriction of *P. m. gracilis* to northern counties in the Lower Peninsula and the Upper Peninsula. Over the last 30 years, abundance of *P. leucopus* has increased in the northern Lower Peninsula, and the northern boundary of the range of this species has expanded to include much of the Upper Peninsula. These changes have coincided with an overall decline in abundance of *P. m. gracilis*, including local extirpation from many areas that it formerly inhabited (Myers *et al.* 2005). In the northern Lower Peninsula, communities in which *P. leucopus* and *P. m. gracilis* co-occur have become characterized by strong numerical dominance of *P. leucopus* (Myers *et al.* 2009).

Early range shifts in *P. leucopus* and *P. m. gracilis* have been hypothesized to be due to human modification and land use (Klein 1960); the ability to colonize disturbed sites quickly may be a

general attribute of the genus (Zwolak and Foresman 2007). More recently, however, long-term studies indicate that both range shifts and ecological replacement are likely due to warming climates (Myers *et al.* 2005). Abundance of *P. leucopus*, in particular, appears to be extremely sensitive to winter conditions such that mild winters are associated with high spring abundance and increased population growth rate of this species (Myers *et al.* 2005).

1.3   DIFFERENTIAL ADAPTATIONS IN A DIRECTIONALLY CHANGING ENVIRONMENT

The earliest ecological models seeking to predict the consequences of climate change utilized the 'climate envelope' approach, which correlates species' occurrences with climatic and environmental variables (Zarnetske *et al.* 2012). The limits of the geographic distributions of many species are set primarily by environmental parameters (Brown *et al.* 1996). Species ranges are generally predicted to track the shifting boundaries of suitable environmental conditions (Graham *et al.* 1996; Williams and Jackson 2007; Zarnetske *et al.* 2012). Niche differences can facilitate coexistence when regular environmental fluctuations favor different species at different times (Adler *et al.* 2007; Caceres 1997) but can lead to rapid changes in abundance when environmental fluctuations are directional (Ernest *et al.* 2008). Independently shifting ranges of species tracking their environmental optima can thus result in ecological replacement at range edges.

Studies investigating faunal turnover often reference established differences between species such as differing thermal optima (Davis *et al.* 1998a, 1998b; Huey *et al.* 2009), habitat specialization (Badgley *et al.* 2008; Blois and Hadly 2010), diet breadth (Attum *et al.* 2006), resource requirements (Tilman and Lehman 2001; Zavaleta *et al.* 2003), specialist predators or pathogens (Rand and Tscharntke 2007), and dispersal abilities (Angert *et al.* 2011). *P. leucopus* and *P. maniculatus* exhibit extreme morphological and ecological similarity (Horner 1954; Wolff and Hurlbutt 1982; Feldhamer *et al.* 1983; Wolff 1985; Long and Long 1993). Both species have been generally described as habitat generalists within deciduous forests (Barry and Francq 1980), have wide diet breadths (Wolff *et al.* 1985; Lackey *et al.* 1985), and are able to quickly colonize disturbed habitats (Zwolak and Foresman 2007). Both species serve as a prey base for a variety of generalist mammalian predators (King 1968), and are infested by the same range of

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parasites (Levine *et al.* 1985; Rand *et al.* 1993; King 1968). Because *P. leucopus* and *P. m. gracilis* are so similar, differences between species where they co-occur, if they exist, are subtle.

There is evidence that *P. leucopus* and *P. maniculatus* are adapted to differing environmental conditions and may thus have differing environmental optima. *P. maniculatus* more regularly uses torpor, builds more insulated nests, stores more food, and consumes less food during the winter (Wolff and Durr 1986; Tannenbaum and Pivorun 1988; Pierce and Vogt 1993) than *P. leucopus*, suggesting that *P. maniculatus* is better adapted to harsh winters. *P. leucopus*, on the other hand, is vulnerable to cold winters (Howard 1951), particularly to low temperatures and deep frosts (Madison *et al.* 1984; Long 1973). Abundance of *P. leucopus* where it occurs without *P. m. gracilis* in northern Michigan is higher and increases faster in years following mild winters than years following harsh winters, suggesting enhanced overwinter survival and more successful reproduction when winters are short (Myers *et al.* 2005).

Over the last several decades, winters have become shorter and milder in the Great Lakes Region (Myers *et al.* 2005). It has been suggested that fluctuations in abundance of these species are more likely due to differing environmental optima than to interspecific interactions (Wolff 1996). Increasingly warm conditions to which *P. leucopus* is well adapted are occurring more often, resulting in increases in abundance. Conditions to which *P. m. gracilis* is well adapted, however, are occurring less frequently. This can result in slowed population growth and lower abundance, or, if conditions are outside the tolerable range of *P. m. gracilis*, local extinction. In the latter case, ecological replacement could result without species interactions playing a role.

1.4 THE ROLE OF BIOTIC INTERACTIONS IN CLIMATE-INDUCED FAUNAL TURNOVER

In the last several years, studies have increasingly emphasized the importance of biotic interactions in shaping species responses to directional environmental change (Tylianakis *et al.* 2008; Gilman et al 2010; Urban *et al.* 2012; Zarnetske *et al.* 2012). Interactions between species can play a dominant role in structuring abundance and distribution (Connell 1983; Schoener 1983). Long-term studies indicate that interactions are complex and can affect the structure of communities and the dynamics of ecosystems (Brown *et al.* 2001; Ernest *et al.* 2008).

Interspecific interactions thus have the potential to affect how species and communities respond to environmental change (Ives 1995; Fox and Morin 2001; Poloczanska *et al.* 2008). Predictive models utilizing the climate envelope approach have largely excluded the effect of species interactions and have yielded results of inconsistent accuracy, but often improve when interactions are incorporated (Guisan and Thuiller 2005; Araujo and Luoto 2007; Heikkinen *et al.* 2007).

Climate change frequently alters the strength and direction of interspecific interactions, including strengthening competitive effects that influence abundance of multiple species in a community (Zarnetske *et al.* 2012). Recent empirical studies suggest that competition can facilitate climate-induced extinctions (Sinervo *et al.* 2010; Jankowski *et al.* 2010) by lowering fitness and population abundances (Urban *et al.* 2012). Competition at range boundaries may explain observations that species adapted to warmer climates generally colonize warming areas faster than resident species disappear (Kelly and Goulden 2008).

Within communities undergoing turnover, variation in the responses of species to climate change may shift competitive balances to favor some species over others (reviewed in Tylianakis *et al.* 2008). Differences between co-occurring species in a community can become novel sources of competitive advantages (Brown *et al.* 2001; Tilman and Lehman 2001; Zavaleta *et al.* 2003). Changes in climate can either ameliorate or magnify differences in competitive ability (Gilman *et al.* 2010) but can also alter the nature of the interactions, for example by changing competitive dominance to dependence (Pennings *et al.* 2003; Suttle *et al.* 2007).

Empirical studies evaluating the role of biotic interactions in the responses of species to climate change typically focus on communities in which niche differences between species have been well-established and interspecific interactions have been shown to regulate population growth through manipulative experiments and other approaches (Davis *et al.* 1998a, 1998b; Tilman and Lehman 2001; Zavaleta *et al.* 2003). Climate-induced shifts in competitive balances within these communities can then be inferred by correlating changes in relative abundance to changes in environmental conditions (Attum *et al.* 2005). Other studies assess the performance and/or fitness of single species under a range of varied environmental conditions to predict performance

under more extreme conditions, then compare relative performance between species to predict outcomes of interspecific interactions (Huey *et al.* 2009).

However, in many systems, the role of biotic interactions in population regulation or the structuring of current species distributions is unknown and difficult to establish, and alternative approaches are needed. Jankowski *et al.* (2010) demonstrated that interspecific aggression was more intense at range boundaries than centers for birds distributed along an elevational gradient, and indirectly implicated interspecific competition as a mechanism for maintaining range boundaries. If interspecific interactions structure current range limits, then it is likely that these interactions will influence how ranges will shift in response to climate change. Additional studies of social behaviors and population demographics at range boundaries or in regions where species' ranges overlap may be fruitful in systems where manipulative experiments to establish the presence of interspecific interactions are difficult.

1.5   INTERSPECIFIC COMPETITION IN CO-OCCURRING *P. LEUCOPUS* AND *P. M. GRACILIS*

Regular variations in climate may promote stability within communities by ameliorating effects by superior competitors (Post 2012). In the absence of competition, many cold-adapted species can persist in environments even after their optimal habitat disappears because their absolute rates of population growth remain positive; with competition, these species become extinct once better adapted competitors arrive (Urban *et al.* 2012). Coexistence of *P. leucopus* and *P. m. gracilis* close to the northern range boundary of *P. leucopus* may have been maintained by differential winter adaptations and the frequency of mild versus harsh winters (Wolff 1996). This balance, however, has been upset by recent climatic warming in the northern Great Lakes region (Myers *et al.* 2005). It is possible that *P. m. gracilis* is able to persist in areas that are becoming increasingly warm if *P. leucopus* were not also increasing in abundance; the combination of sub-optimal environmental conditions and increased density of *P. leucopus* may lead to ecological replacement.

The role of interspecific interactions in the replacement of *P. m. gracilis* by *P. leucopus* has not previously been investigated, perhaps due to uncertainty regarding the importance of such

interactions to population dynamics in communities where these species co-occur. Though there is some evidence of interspecific territoriality (Dooley Jr. and Dueser 1996) and microhabitat partitioning (Wilson 1968; Geluso 1971; Master 1977; Holbrook 1978), it has also been hypothesized that co-occurring *P. leucopus* and *P. maniculatus* interact ecologically as a single species with neutral population dynamics (Wolff 1996).

Do co-occurring *P. leucopus* and *P. m. gracilis* compete in northern Michigan? The exclusion of one species from the niche of another is difficult to demonstrate (Connell 1983; Schoener 1983). Direct field tests for competition typically involve removal experiments, in which enclosures are built around study plots and species densities within are manipulated and monitored (e.g. Brown and Munger 1985; reviewed in Connell 1983). For *P. leucopus* and *P. m. gracilis*, enclosures are impractical because of their required size and because *Peromyscus* are adept at climbing (M'Closkey 1975). This approach is thus seldom used to detect competition in co-occurring *Peromyscus*.

Peromyscus populations are characterized by relatively low density and relatively small annual fluctuations in numbers (Terman 1968), suggesting that population growth is controlled (Harland *et al.* 1979). Density-dependent regulation of population growth is often reported in single species populations. Reproductive output has been found to be inversely proportional to population density in *P. leucopus* (Burt 1940; Manville 1949), and high densities can cause *P. maniculatus* to cease breeding earlier than normal (Canham 1969; Sadleir 1974). Reproductive inhibition of young-of-year (YOY) *P. maniculatus* has been experimentally demonstrated in natural populations and may be mediated by density of breeding adults (Lusk and Millar 1989; Terman 1993). Mortality within a season may also be density dependent, with peaks in density associated with reduced survival (Beer and MacLeod 1966; Goundie and Vessey 1986; Schug *et al.* 1991).

Regulation of annual population growth in *P. leucopus* and *P. maniculatus* is hypothesized to be mediated by behavior (Harland *et al.* 1979). Adult males may display aggressive behavior towards juveniles and impact their survival (Sadleir 1965). Available territories in which to breed may be a sex- and season-specific limiting resource (Bujalska 1973; Harland *et al.* 1979), and resident females actively exclude other females from their home ranges during the breeding

season (Nicholson 1941; Metzgar 1971, Harland *et al.* 1979). Social interactions, particularly among breeding females, may thus play a role in population regulation and contribute to fluctuations in abundance. The victor in aggressive contests tends to depend on residency status (resident or intruder) rather than species identity (Wolff *et al.* 1983), suggesting equality in competitive ability. These observations suggest that population growth in communities where *P. leucopus* and *P. maniculatus* co-occur could depend on both intra- and inter-specific social interactions.

It may be possible to indirectly test for the existence of interspecific competition in this system by investigating the spacing of individuals across the study grid. This approach has so far only been used to gain evidence of intraspecific competition within *Peromyscus* populations. Investigations of the spatial distribution of individuals in *Peromyscus* populations have largely focused on females, probably because of their role in reproduction (Burt 1940; Lackey *et al.* 1985). It has been hypothesized that in polygynous mating systems, in which males invest more energy in competition for resources than in paternal care (Wolff 1989), females may be more strongly influenced than males by seasonal changes in population dynamics and environmental conditions (Trivers 1972). Studies indicate that spacing between adult female mice is approximately regular during the breeding season (Metzgar 1971; Fairbairn 1977; Harland *et al.* 1979), but aggregated during the rest of the year (Metzgar 1979; Mihok 1979). The maintenance of spatial relationships necessitates social interaction such as mutual avoidance (reported in *Clethrionomys*; Viitala and Hoffmeyer 1985) or overt aggression (Dooley Jr. and Dueser 1996).

The presence of these aggressive contests suggests a potential mechanism involving interspecific interactions governing range boundary dynamics and species replacement among *Peromyscus*. Even if *P. leucopus* and *P. m. gracilis* interact with neutral dynamics where they co-occur (Wolff 1996) and neither species is more likely than the other to win aggressive contests (Wolff *et al.* 1983), differences in overwinter survival or timing of the start of the breeding season in these two species could translate into competitive dominance of one species over another due to differences in residency status. Replacement of *P. maniculatus* by *P. leucopus* could for example occur if shifting climate regimes allow *P. leucopus* to establish territories before *P. maniculatus* each year.

1.6   DISSERTATION GOALS AND DESCRIPTION

Understanding the mechanisms by which directionally changing climate regimes alter community structure is critical to accurately predict how global climate change will continue to impact natural communities. What are the biological mechanisms that drive the replacement of *P. m. gracilis* by *P. leucopus* in northern Michigan? Though there is evidence that faunal turnover in this species pair is driven by long-term changes in climate, the mechanisms by which increasingly warm conditions result in increased abundance of *P. leucopus* and decreased abundance of *P. m. gracilis* are not well understood.

In this dissertation, I present results from a three year field study of syntopic *P. leucopus* and *P. m. gracilis* that seeks to fill existing gaps in knowledge regarding the mechanisms of faunal turnover by providing a detailed examination of population dynamics in a community of co-occurring 'northern' and 'southern' species. Investigation of short-term population dynamics in communities undergoing replacement can be useful in informing predictions on long-term changes in community structure in *P. leucopus* and *P. m. gracilis* and in other assemblages that might be governed by similar mechanisms.

This study was located in the Pigeon River State Forest, one of the few remaining areas in Michigan's Lower Peninsula where *P. m. gracilis* is regularly found and where it occurs syntopically with *P. leucopus*. The site is close to the northern range boundary of *P. leucopus*. This provides a unique opportunity to examine the differing responses of *P. leucopus* and *P. m. gracilis* to the same changes in abiotic environmental conditions. This research combines a unique location (a community in which climate-induced replacement is occurring in close proximity to range boundaries) with a detailed examination of the mechanisms by which differences between species lead to differences in reproductive success in a directionally shifting environment; such a study has not been done before.

In Chapter 2, I describe changes in abundance of *P. leucopus* and *P. m. gracilis* over the course of the study, broadly compare patterns of population growth, and discuss annual variation in the winter conditions experienced by mice. Community structure shifted from roughly equal

abundance in 2010 to strong numerical dominance of *P. leucopus* in 2011 and 2012. This change coincided with differences in the length and severity of winter; the winter preceding 2012 was the shortest and mildest observed, while winters preceding 2010 and 2011 were associated with lower average temperatures which extended longer into the spring.

In Chapters 3 and 4, I identify and describe broad species differences in traits including survivorship, reproductive patterns, and breeding season length. Shifts in relative abundance and community structure are ultimately caused by differences in reproductive success. Changes in reproductive success result from changes in the survival and reproductive rates of individuals (Millar *et al.* 1992), yet the specific patterns of changes in survivorship at juvenile and adult stages, and of reproductive rates of different age classes occurring in these populations as one species replaces the other is unknown. Here I describe the population demography occurring in this site over a set of years which involved trends both in warming and species' relative abundances. I consider how differences between species facilitate replacement by investigating the relative contributions of survivorship and reproductive patterns to differences in reproductive success.

I specifically consider the importance of interspecific interactions to replacement in this system using several different methods. In Chapter 5, I assess temporal variation in the spatial distribution of *P. leucopus* and *P. m. gracilis* to determine if this spacing is related to the abundance of these two species and hence the likelihood of competitive or other interspecific encounters. In addition, I use several analyses to indirectly assess the influence of species interactions in replacement. In Chapter 4, I present and test a hypothesis by which successful early breeding by *P. leucopus* could result in a competitive advantage mediated by interspecific social aggressive encounters, which might explain how gradually warming winters shift the competitive balance within this community.

Finally, in Chapter 6, I provide a summary and synthesis of results from the entire study. The connections between species differences, fluctuations in reproductive success, changes in environmental conditions, and interspecific social interactions are discussed. I ask whether changes in the abundance of *P. leucopus* and *P. m. gracilis* be explained solely by differences in the responses of each species to warming climates. I describe how some patterns of abundance

can be directly explained by warming climatic conditions. I then identify patterns that are not well explained by warming alone, and discuss plausible species interaction mechanisms that could cause them.

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TEMPORAL FLUCTUATIONS IN RELATIVE ABUNDANCE OF SYNTOPIC *PEROMYSCUS LEUCOPUS* AND *PEROMYSCUS MANICULATUS GRACILIS*

2.1 SUMMARY

Climate-induced ecological replacement of the 'northern' *P. maniculatus gracilis* by the 'southern' *P. leucopus* has been documented with long-term studies in the Great Lakes Region (Long 1996; Myers *et al.* 2005). Gradually warming winters over the last 30-40 years in this area have facilitated northward range expansion of *P. leucopus*, and communities in which *P. leucopus* and *P. m. gracilis* co-occur have become characterized by strong numerical dominance of *P. leucopus* (Myers *et al.* 2009). I conducted a three year study of co-occurring *P. leucopus* and *P. m. gracilis* to investigate changes in mouse abundance, compare rates of reproduction and survival, and assess the mechanisms by which niche differences facilitate ecological replacement.

In this chapter, I compare patterns of population growth of *P. leucopus* and *P. m. gracilis* over the three years of the study by investigating seasonal variation in trap success (the proportion of traps set that captured mice) and mouse abundance. Mouse abundance data were analyzed using a Poisson regression model with distinct mean structures for each species and year and basis-splines to account for time dynamics. Trap success and estimates of abundance were compared between species to identify differing trends in population growth. I also describe annual trends

in temperature and precipitation to identify fluctuations in environmental conditions experienced by mice during this study.

Trap success and estimated abundance for *P. leucopus* were significantly greater than for *P. m. gracilis* in two out of three years in this study. *P. leucopus* and *P. m. gracilis* occurred at similar frequencies in 2010 and early 2011; however, after July 2011 community composition shifted to favor *P. leucopus*, and relative abundance of *P. leucopus* remained high for the remainder of the study. This shift in relative abundance is consistent with the pattern of faunal turnover that has been observed in the Great Lakes Region (Long 1996; Myers *et al.* 2005). Disparities in abundance between species appear to result from both increases in the *P. leucopus* population and decreases in the *P. m. gracilis* population, and the relative contributions of these two factors differ in 2011 and 2012.

Abundance of *P. leucopus* was significantly greater in 2011 and 2012 than in 2010, and this pattern may have been affected by the severity and length of the preceding winters. For *P. leucopus,* the highest trap success, overall abundance, and spring abundance all occurred in 2012, which was preceded by the mildest and shortest winter during this study. Abundance and trap success of *P. m. gracilis,* on the other hand, was not associated with winter conditions in the same manner. Overall numbers of of *P. m. gracilis* were lowest in 2012 despite high spring abundance, and this was due to noticeably reduced numbers between June and September.

2.2   INTRODUCTION

Environmental conditions are undergoing rapid and directional change; average land temperatures, for example, are predicted to increase 1.2-4°C by the year 2100 (IPCC 2007). Climate-induced range shifts are already taxonomically widespread (Parmesan and Yohe 2003; Araujo *et al.* 2006; Parmesan 2006; Kelly and Goulden 2008; Moritz *et al.* 2008) and appear to have accelerated in recent years (Chen *et al.* 2011). Range shifts are often accompanied by changes in population abundance, community structure and composition, and organismal physiology (Sala *et al.* 2000; Parmesan and Yohe 2003; Williams and Jackson 2007). At range

boundaries, species with distributions that lie primarily in lower latitudes are apparently replacing their higher latitude counterparts (Myers *et al.* 2009).

In Michigan, range shifts and subsequent ecological replacement of 'northern' species by their 'southern' counterparts has been observed in several species of small mammals (Myers *et al.* 2009). One of these species pairs is the 'southern' white-footed mouse, *Peromyscus leucopus,* and the 'northern' woodland deer mouse, *P. maniculatus gracilis*, which occur together in northern Michigan forests. *Peromyscus leucopus* is broadly distributed in the eastern and central United States, from southernmost Canada to the Yucatan peninsula and from the Atlantic coast to the western Great Plains. *P. m. gracilis* is the Michigan forest-dwelling subspecies of *P. maniculatus*; much of the range of *P. m. gracilis* lies to the north of Michigan, in Ontario and Quebec. *P. leucopus* and *P. maniculatus* are sympatric throughout much of their geographic ranges, and they are regarded as sister species (Bradley *et al.* 2007).

Expansion of the northern limit of the range of *P. leucopus* has been observed at least since the early 20th century. Reports from New York and Massachusetts from the early 1900s indicate that while the ranges of *P. leucopus* and *P. m. gracilis* did not yet overlap, the northern limit of the range of *P. leucopus* was quickly approaching the southern limit of the range of *P. m. gracilis* (Miller Jr. and Rehn 1901). In the more recent past, ecological replacement of *P. m. gracilis* by northward-expanding populations of *P. leucopus* has been observed in Minnesota (Long 1996).
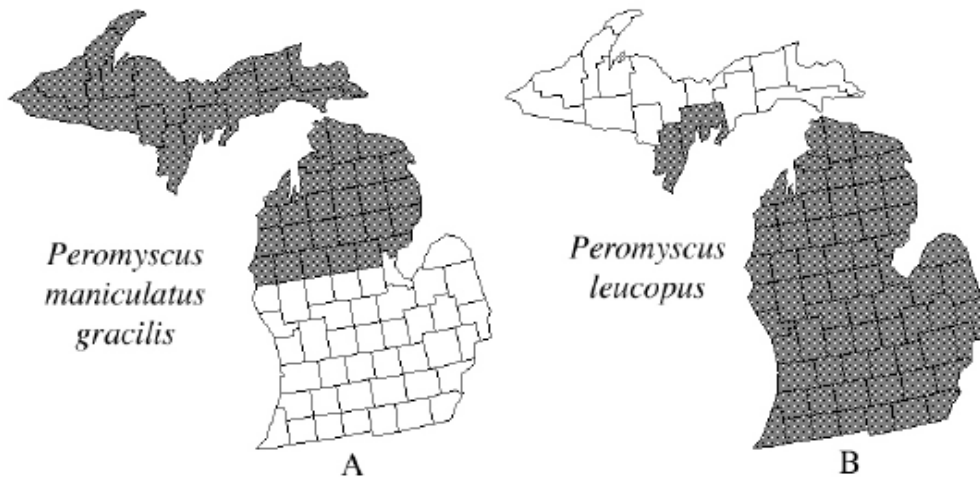
Figure 2-1: Pre-1990 distribution maps of (A) *P. maniculatus gracilis* and (B) *P. leucopus.* Figure reproduced from Myers *et al.* (2005).

Peromyscus leucopus is at the northern limits of its range in northern Michigan. Hooper (1942) noted the dispersion of *P. leucopus* northward up the entire Lower Peninsula and restriction of *P. m. gracilis* to northern counties in the Lower Peninsula and the Upper Peninsula (Figure 2-1). Over the last 30 years, abundance of *P. leucopus* has increased in the northern Lower Peninsula, and the northern boundary of the range of this species has expanded to include much of the Upper Peninsula (Figure 2-2). These changes have coincided with an overall decline in abundance of *P. m. gracilis*, including local extirpation from many areas that it formerly inhabited (Myers *et al.* 2005). In the northern Lower Peninsula, communities in which *P. leucopus* and *P. m. gracilis* co-occur have become characterized by strong numerical dominance of *P. leucopus* (Myers *et al.* 2009).
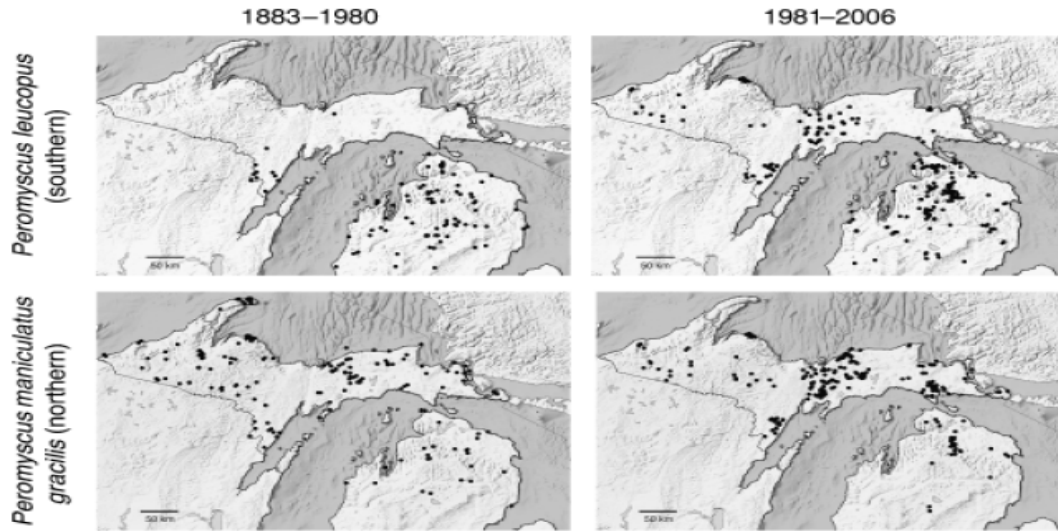
Figure 2-2: Trapping records of *P. leucopus* (top) and *P. m. gracilis* (bottom) in northern Michigan. Records from 1883-1980 (left) and 1981-2006 (right) document expansion of *P. leucopus* into Michigan's Upper Peninsula and concurrent decline of *P. m. gracilis*. Figure modified from Myers *et al.* (2009).

Early range shifts in *P. leucopus* and *P. m. gracilis* were hypothesized to be due to human modification and land use (Klein 1960); the ability to colonize disturbed sites quickly may be a general attribute of the genus (Zwolak and Foresman 2007). More recently, however, long-term studies indicate that both range shifts and ecological replacement are likely due to warming climates (Myers *et al.* 2005).

In this chapter, I use trapping records from a three year field study of syntopic *Peromyscus leucopus* and *P. m. gracilis* in northern Michigan to investigate fluctuations in abundance in an area where ecological replacement is occurring. While a general pattern of faunal replacement of 'northern' species by their 'southern' counterparts has been established for several species of rodents in Michigan (Myers *et al.* 2009), this study provides a more detailed look at population dynamics in a community of co-occurring 'northern' and 'southern' species. I conclude that a combination of increases in *P. leucopus* abundance and decreases in *P. m. gracilis* abundance leads to long-term regional trends of replacement. A targeted and specific assessment of population trends such as this will lead to a better understanding of the factors driving species turnover in a directionally changing environment.

2.3   METHODS

2.3.1   PIGEON RIVER TRAPPING PROTOCOL

I monitored a community of syntopic populations of *P. leucopus* (PL) and *P. m. gracilis* (PMG) in the Pigeon River State Forest (Figure 2-3) for three consecutive years from April to October. This area is unique because it is located in one of the few remaining areas in Michigan's Lower Peninsula where PMG is regularly found and where it occurs syntopically with PL. The trapping grid is located in a large plot of continuous forest. The size of the large trees and the condition of the forest floor suggest that it has not been logged for >50 years, and it is protected from future logging. The habitat consists of mature northern hardwoods with an open understory; the dominant tree species on the grid include sugar and red maple (*Acer saccharum* and *A. rubrum*), red oak (*Quercus rubra*), American beech (*Fagus grandifolia*) and white ash (*Fraxinus americana*).

Figure 2-3: Map depicting the location of the trapping grid, in the Pigeon River State Forest near Vanderbilt, MI.

The trapping grid is a square aligned with cardinal directions. Sides are of length 400 meters, with 400 total trap stations distributed evenly across the area and permanently marked with unique identifiers (a letter and number combination). The distance between trap stations in any cardinal direction is 20 meters. The grid was trapped for 1-2 sessions per month, during which

trapping occurred on 3-5 consecutive days. There was an interval of 2-5 weeks between sessions, except in May 2011 and 2012 when trapping was more frequent in order to document the first emergence of young-of-year.

Due to the large number of trap stations and the high capture rate at some times of year, the grid was never trapped in its entirety on any one night. Between 40 and 280 traps, or 2-12 rows, were set each day. From May through August in 2011 and 2012, alternating north-south rows (denoted by letters) were trapped on consecutive nights so that all trap stations were open at least once during each session. In April, September, and October of all years, summer 2010, and 2013, only every other row was trapped. This results in uneven sampling intensity across the rows of the grid (Table 2-1).

TABLE 2-1: SAMPLING INTENSITY ACROSS NORTH-SOUTH ROWS OF THE GRID

MONTH	DD	CC	BB	AA	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
APRIL	0	0	1	1	1	0	2	0	2	0	2	0	2	0	1	0	0	0	0	0
MAY	3	1	3	1	3	1	3	1	2	1	2	1	2	1	2	1	1	1	1	1
JUNE	0	9	0	9	6	8	0	8	6	5	0	5	5	8	0	8	6	8	0	8
JULY	0	8	0	8	2	8	0	8	0	8	0	8	0	8	0	8	2	8	0	8
AUGUST	0	6	0	6	1	5	1	5	1	5	1	5	1	5	1	5	1	5	1	5
OCTOBER	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1
2010 TOTAL	3	25	4	26	13	23	6	23	11	20	5	20	10	23	4	23	10	23	2	23
MAY	3	6	3	6	3	6	3	7	2	3	2	3	3	3	4	6	3	5	3	2
JUNE	4	4	4	4	4	4	4	4	4	3	4	3	3	3	3	4	3	4	3	3
JULY	3	4	3	4	3	4	3	4	3	4	3	4	3	4	3	4	3	4	3	4
AUGUST	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1
OCTOBER	0	2	0	2	0	2	0	2	0	2	0	2	0	2	0	2	0	2	0	2
2011 TOTAL	12	17	12	17	12	17	12	18	11	13	11	13	11	13	12	17	11	16	11	12
APRIL	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	1	2	1	2	1
MAY	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
JUNE	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
JULY	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
AUGUST	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3
SEPTEMBER	0	3	0	3	0	3	0	3	0	3	0	3	0	3	0	3	0	3	0	3
OCTOBER	0	2	0	2	0	2	0	2	0	2	0	2	0	2	0	2	0	2	0	2
2012 TOTAL	15	21	15	21	15	21	15	21	15	21	15	21	15	20	15	20	15	20	15	20
JUNE 2013	0	2	0	2	0	2	0	2	0	2	0	2	0	2	0	2	0	2	0	2
GRAND TOTAL	30	65	31	66	40	63	33	64	37	56	31	56	36	58	31	62	36	61	28	57

Table 2-1: Sampling intensity across north-south rows of the grid. The number of times traps were set out along each row is reported; each time a row was trapped, traps were set at all 20 trap sites along the row.

2.3.2 PIGEON RIVER CENSUS - MOUSE HANDLING

I led a team of between one and four undergraduate students to conduct live-trapping during each sampling session. Roughly equal numbers of large (3 x 3.5 x 9") and small (2 x 2.5 x 6.5") folding aluminum Sherman live-traps were baited with rolled oats and opened each afternoon. Adjacent traps were of different sizes to diffuse any effect of trap size on mouse captures. Traps were set in the afternoon and checked the following morning, and mice were returned to the locations where they were trapped after processing.

Individual mice were tagged with stainless steel ear tags (National Band and Tag Co., Newport, KY) stamped with unique identification numbers for re-identification. PL and PMG are similar in appearance and difficult to distinguish (Smith and Speller 1970; Feldhamer *et al.* 1983; Bruseo *et al.* 1999). Identification to species was determined in the field using ear length and appraisal of pelage and later verified by protein electrophoresis of salivary amylase (Aquadro and Patton 1980).

For each capture, the location of the trap station, and the sex, weight, age, and reproductive condition of the mouse were recorded. Mice were weighed to the nearest 0.5 gram using a Pesola spring scale. Mice were categorized into 3 age classes, which are associated with distinct pelage characteristics (Collins 1923). Juveniles leave the nest shortly after weaning, at approximately 21 days after birth (King *et al.* 1963); their pelage is uniformly gray. At around 40-45 days of age (Nicholson 1941), mice enter into the post-juvenal molt, during which gray pelage is replaced with brown fur typical of adults (King 1968). The duration of the molt from the first appearance of new pelage averages about 25 days (Storer *et al.* 1944; Gottschang 1956); during this time individuals are classified as sub-adults and are recognized by the presence of two distinct fur types. Molting is complete roughly 65 to 70 days after birth (Gottschang 1956; Nicholson 1941; Baker 1983), after which individuals are considered adults.

Females were categorized in the field as either non-reproductive (NT, nipples not visible) or reproductive (NE, nipples visible). Additionally, female mice were recorded as either visibly pregnant (swollen abdomen and abnormally high weight) or not pregnant. Reproductive condition of male mice was assessed by visibility of the testes and recorded as 'testes abdominal' (scrotal sac not enlarged, non-reproductive) or 'testes scrotal' (scrotal sac well developed,

reproductive). Because reproductive condition of males was often difficult to classify decisively and can change on a relatively short time scale (i.e., hours), only information from female mice was used to draw conclusions regarding reproductive traits.

2.3.3 DATA ANALYSIS

Abundance of PL and PMG was documented by trap success, the number of mice caught per trap set (#mice/#traps), rather than the number of mice captured due to variation in trapping effort. To assess variation in mouse population size within years, trap success was calculated for the first half (before July 15) and second half (after July 15) of each year. For each time period, records were combined to calculate an overall trap success. Trap success was compared between species and time periods using chi-squared analysis.

Records of mean temperature, precipitation, and snowfall were obtained for the months of December-February from the NOAA weather station in Gaylord, MI, located approximately 25 miles SSW of the Pigeon River grid. In addition to these weather data, I obtained the dates when ice melts over Douglas Lake, located approximately 35 miles NNW of the grid, from the University of Michigan Biological Station. The date of ice break up on lakes in the spring has been used as an integrative indicator of the length of the preceding winter, with later ice-out dates associated with longer winters (Myers *et al.* 2005). Mean winter temperature and snowfall were compared between years using two-sample t-tests or ANOVA (analysis of variance) to assess the relative harshness of winter conditions experienced by mice. To account for inherent monthly variation, differences between years were assessed by comparing deviations of recorded means from historical averages rather than the means themselves.

2.3.4 A FUNCTIONAL POISSON REGRESSION MODEL OF PL AND PMG ABUNDANCE

To model the expected abundance of mice (measured as the number of mice per trap) over time, I used a Functional Poisson Regression model with a distinct mean structure for each species by year combination, combined with basis-splines to parameterize the effect of time. Further, I

offset the daily count by the number of traps set to account for inconsistencies in trapping effort. The model chose a linear combination of several piecewise polynomial functions (basis functions, or splines) that provided the best fit to the observed data. Using maximum likelihood, the regression selected the best values for the coefficients of that linear combination, and then predicted how many mice should be caught on a given day. The model smooths the raw data, interpolates from existing data points to predict abundance between trapping sessions, and allows for assessment of annual and seasonal changes in abundance.

A functional regression is a technique for analyzing data whose mean varies non-linearly with respect to quantitative factors. In this case, the response variable (the mean) was the expected number of mice caught per trap on each day. This number was related non-linearly to time (both annually and seasonally) and species. The data were modeled with a Poisson distribution, which are commonly used when the data are counts. Poisson regression may provide a poor fit to count data that are overdispersed; however, overdispersion was not observed in this case because trap success was consistently low overall (less than 40% at maximum).

In this model, the seasonal effect of time was parameterized by basis-splines, which are commonly used when the goal is to estimate a quantity that varies smoothly with respect to time. The use of basis-splines increased the power of the model (by pooling data from multiple days to predict a single value), allowed for bridging of gaps when no data were available, and allowed the pattern of mouse abundance over time to be informed by the data.

The model utilized distinct mean structures for each species and year, so that each predicted seasonal pattern of abundance was independent from the others. No fixed relationships were assumed, so that peaks in abundance were not constrained to occur at the same time, and the rates of increase and decrease in abundance depended only on the raw data.

2.4 RESULTS

2.4.1 CENSUS RESULTS

108 nights of trapping were conducted in 2010, 2011, 2012, and 2013 (Table 2-2). The grid was trapped the most regularly and intensely during the middle of the breeding season, from May through August of each year. Because only one sampling trip was conducted in 2013, all analyses only include records from 2010-2012 unless otherwise noted.

TABLE 2-2: NUMBER OF TRAPPING DAYS										
YEAR	FIRST	LAST	DAYS	APRIL	MAY	JUNE	JULY	AUG.	SEPT.	OCT.
2010	4 Apr.	2 Oct.	30	2	4	9	8	6	0	1
2011	3 May	10 Oct.	32	0	8	8	7	3	0	4
2012	7 Apr.	21 Oct.	42	6	12	4	6	5	5	4
2013	1 Jun.	4 Jun.	4	0	0	4	0	0	0	0
TOTAL			108	8	20	25	21	14	5	9

Table 2-2: Number of days on which trapping was conducted. Dates of the first, last, and number of days (total and per month) trapped per month are reported for each year of the study.

The census resulted in a total of 19,820 trap-nights (the total number of traps set) and 2510 captures of identified PL and PMG (Table 2-3). Sampling intensity was similar in 2010 and 2011, during which 5940 and 5840 traps were set over 30 and 32 days, respectively. Sampling intensity was greater in 2012, in particular because of increased trapping in April and May. 7640 traps were set over 42 days in 2012.

TABLE 2-3: NUMBER OF CAPTURES OF PL AND PMG

YEAR	DAYS SAMPLED	TRAP-NIGHTS	PL	PMG	TOTAL CAPTURES
2010	30	5940	168	208	376
2011	32	5840	564	241	805
2012	42	7640	1207	106	1313
TOTAL (2010-2012)	104	19420	1939	555	2494
2013	4	400	11	5	16
GRAND TOTAL	108	19820	1950	560	2510

Table 2-3: Number of captures of PL and PMG. The number of days sampled, the number of trap-nights (traps set multiplied by number of days), and the number of captures (PL, PMG, and total captures) are reported for each year of the study.

A total of 753 individual mice, 591 PL and 162 PMG, were tagged and successfully identified to species using salivary amalyse (Table 2-4). The average number of captures per tagged individual ranged from 2.5 in 2011 to 3.9 in 2010 to 4 in 2012. Of the 753 tagged mice, 151 of them were known to have survived a winter, either because they were trapped both in the fall prior to and spring following a winter (23 mice), or because they were first trapped as adults early in the spring before annual breeding began (128 mice).

TABLE 2-4: NUMBER OF TAGGED MICE

| | DISAPPEARED DURING WINTER | | | | | | | OVERWINTERED | | | | | | |
| | PL | | | PMG | | | TOT. | PL | | | PMG | | | TOT. |
	F	M	TOT.	F	M	TOT.		F	M	TOT.	F	M	TOT.	
2010	12	20	32	21	26	47	79	3	6	9	1	7	8	17
2011	92	121	213	27	21	48	261	11	25	36	13	9	22	58
2012	116	119	235	14	12	26	261	27	30	57	4	3	7	64
2013	1		1				1	2	6	8	1	3	4	12
TOT.	221	260	481	62	59	121	602	43	67	110	19	22	41	151

Table 2-4: The number of mice that were individually tagged and identified to species. Mice are categorized as either overwintered (known to survive a winter) or disappeared (were trapped in the fall prior to but not the spring after a winter). Numbers of PL, PMG, males (M), and females (F) are also reported.

The general seasonal population growth pattern is similar for both species. Mouse numbers start out low, increase to a maximum, and then decline (Figure 2-4). There are, however, clear differences in abundance between years and species as well as in the shapes of seasonal trends.
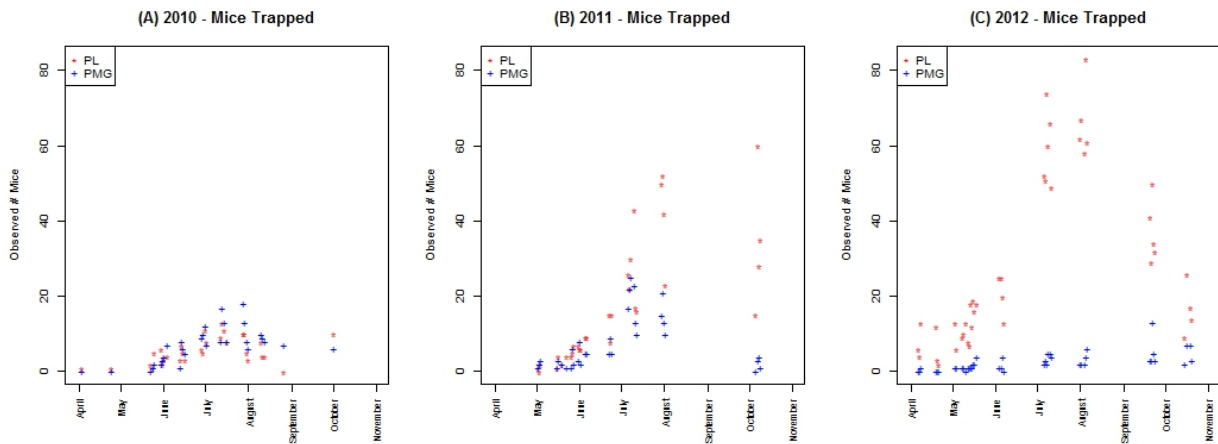
Figure 2-4: Raw trapping data from 2010, 2011, and 2012. For each day on which trapping occurred, the number of PL (red) and PMG (blue) are plotted.

2.4.2 TEMPORAL VARIATION IN TRAP SUCCESS

The raw data were used to calculate and compare trap success (#mice/#traps) between species and time periods. Overall trap success was the lowest in 2010 and the highest in 2012 (χ^2=358.5, P<.0001), ranging from 6.3% to 17.2% per year. These patterns appear to be due to a marked increase in PL numbers in 2011 and 2012 (Figure 2-4).

Trap success was generally higher in the latter half of each year (overall, Early: 9.2%; Late: 22.7%; χ^2=622.2, P<0.0001); however the species differ (Figure 2-5). Trap success of PL is significantly greater in the second half of the year in 2011 (χ^2=521.9, P<0.0001) and 2012 (χ^2=361.7, P<0.0001), and there was a non-significant trend for the same in 2010 (P=0.1). Trap success of PMG is significantly greater in the second half of the year in 2010 (χ^2=17.3, P<0.0001), 2011 (χ^2=13.8, P=0.0002), and 2012 (χ^2=56.4, P<0.0001).
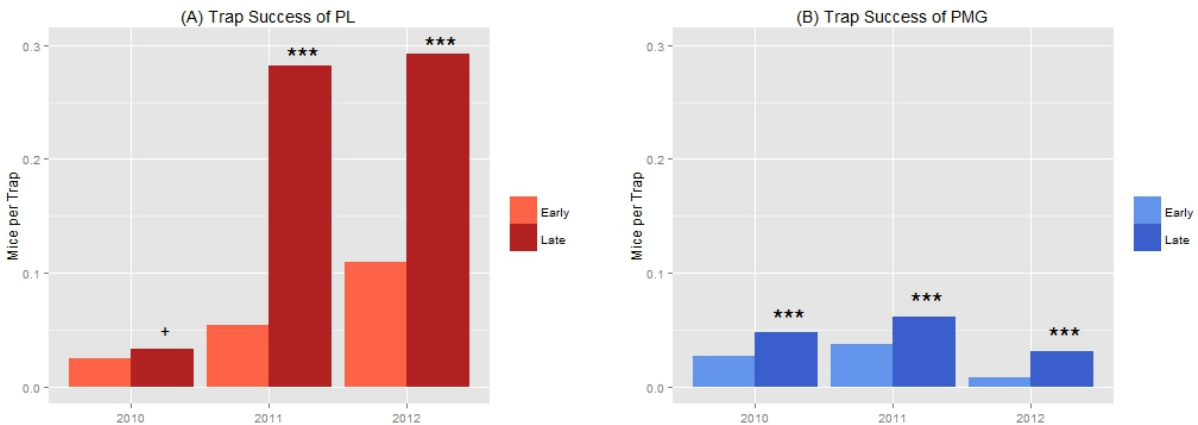
Figure 2-5: Trap success of (A) PL and (B) PMG. Trap success is measured as the number of mice per trap, in 2010, 2011, and 2012. Trap success in the first half (Early, all records before July 15) and second half (Late, all records after July 15) are reported separately. Chi-squared analysis was used to compare trap success within species between Early and Late time periods. Significance of differences in trap success between time periods is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

In 2010, PMG were more likely to be caught than PL (Table 2-5), but this difference came about only after July 15. Trap success of PL was always higher than that of PMG in 2011; however, this difference was not as pronounced before July 15 as it was after July 15. In 2012, trap success of PL was higher than that of PMG throughout the year.

Trap success of PL was greatest in 2012 and lowest in 2010 (χ^2=626.5, P=<0.0001). Trap success of PMG did not differ between 2010 and 2011 (χ^2=3.0, P=0.085). In 2012, however, trap success of PMG was lower than in 2010 (χ^2=65.2, P<0.0001) or 2011 (χ^2=97.9, P<0.0001).

TABLE 2-5: COMPARISON OF TRAP SUCCESS OF PL AND PMG

	TRAPS SET	#PL	%PL	#PMG	%PMG	x^2	P
EARLY	3740	95	0.025	102	0.027	0.19	0.664
LATE	2200	73	0.033	106	0.048	5.96	0.015*
2010 TOTAL	5940	168	0.028	208	0.035	4.18	0.041*
EARLY	4760	259	0.054	174	0.037	17.07	3.6E-05**
LATE	1080	305	0.282	67	0.062	182.41	1.5E-41***
2011 TOTAL	5840	564	0.097	241	0.041	138.33	6.2E-32***
EARLY	5640	624	0.111	44	0.008	533.45	5.0E-118***
LATE	2000	583	0.292	62	0.031	499.82	1.0E-110***
2012 TOTAL	7640	1207	0.158	106	0.014	1008.19	3.0E-221***

Table 2-5: Comparison of trap success of PL and PMG in 2010, 2011, and 2012 using Chi-squared analysis. Trap success is calculated as #mice caught/#traps set, and is calculated for the first half (Early, all records before July 15 combined) and the second half (Late, all records after July 15 combined) of each year. Significance of differences between species in trap success is marked (*: P<0.05; **: P<0.01; ***: P<0.001).

2.4.3   POISSON REGRESSION – GOODNESS OF FIT

The Poisson regression model interpolated from irregularly spaced observed data to produce a curve estimating the expected number of mice per trap between the first and last trapping days of the year. The accuracy of model predictions was reduced when there were long gaps between trapping sessions because no data were present to inform abundance trajectories. Typical times between trapping sessions were roughly two weeks, but there were two longer gaps. No trapping was conducted between August 28 and October 1 in 2010; however, mouse abundance had reached maxima prior to August 28, so the gap did not greatly affect model predictions. No trapping was conducted between August 5 and October 7 in 2011, and maximum abundance for

both species had not yet been reached. The model yielded unrealistic predictions for mouse abundance during that time. For this reason, model predictions during the gap in 2011 are not reported.

Goodness of fit of the model to the data was assessed using three graphical procedures. Figure 2-6 compares model results (the predicted number of mice per trap for PL and PMG with 95% confidence intervals) with observed trap success. Due to low capture rates, 95% confidence intervals are widest at the beginning and end of the season, particularly in 2010 when very few mice were caught through mid-June.
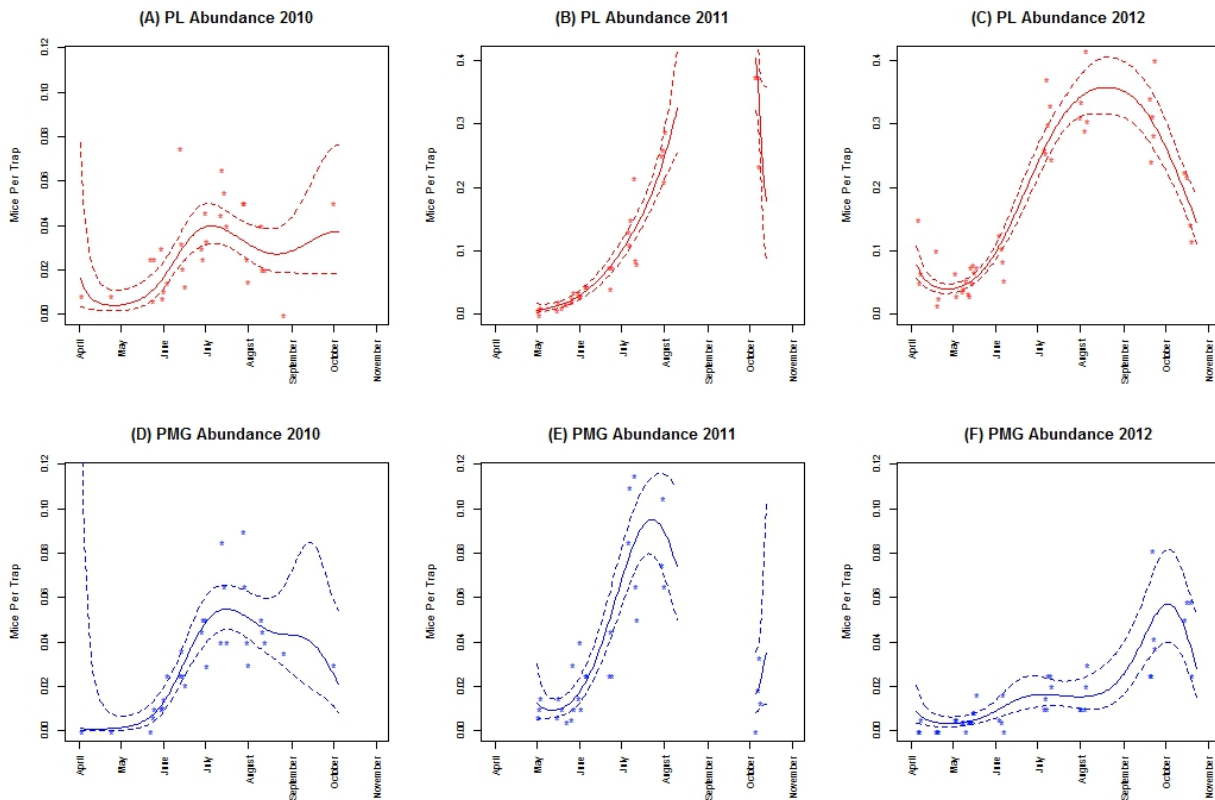
Figure 2-6: Comparison of the observed number of mice per trap to model predictions of abundance of PL (A-C) and PMG (D-F) in 2010, 2011, and 2012. The Poisson regression model interpolated from irregularly spaced observed data to produce a curve estimating the expected number of mice per trap between the first and last trapping days of the year. Mean predicted abundance (solid lines), 95% confidence intervals (dashed lines), and trap success (points) are plotted.

A second diagnostic test (Figure 2-7) plots the observed number of mice per trap versus expected values, utilizing a square root transformation which is variance stabilizing for the Poisson distribution. The points follow a roughly 1:1 ratio; high observed values lead to correspondingly high predicted values. Exceptions occur when observed values are 0, and at very high observed values. When no mice are caught, the model will sometimes predict that a small number of mice are present. Similarly, when many mice are caught, the model will predict that fewer are present. This is because predictions are shifted up or down based on the value of surrounding points. When values are fluctuating over consecutive days, more points are likely to be shifted.
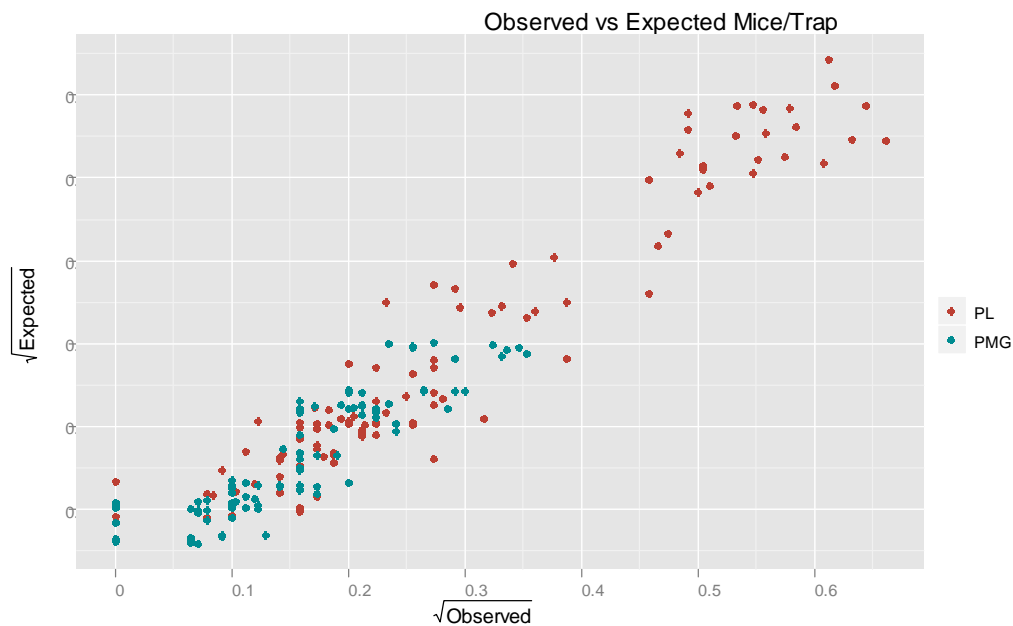
Figure 2-7: First diagnostic test of goodness of fit of the poisson model to observed data. Observed number of mice per trap (x-axis) are plotted against model expectations (y-axis), utilizing a square root transformation. A 1:1 ratio, such as observed here, indicates that abundances of PL (red) and PMG (blue) predicted by the model are a good fit to the data.

Lastly, I plotted the standardized residuals of each estimate against the fitted values. The standardized residuals are a measure of how much the fitted value differ from the observed value at each point (day of trapping). If the Poisson model is a good fit, the standardized residuals should be homogeneous. This appears to be the case for both species (Figure 2-8).
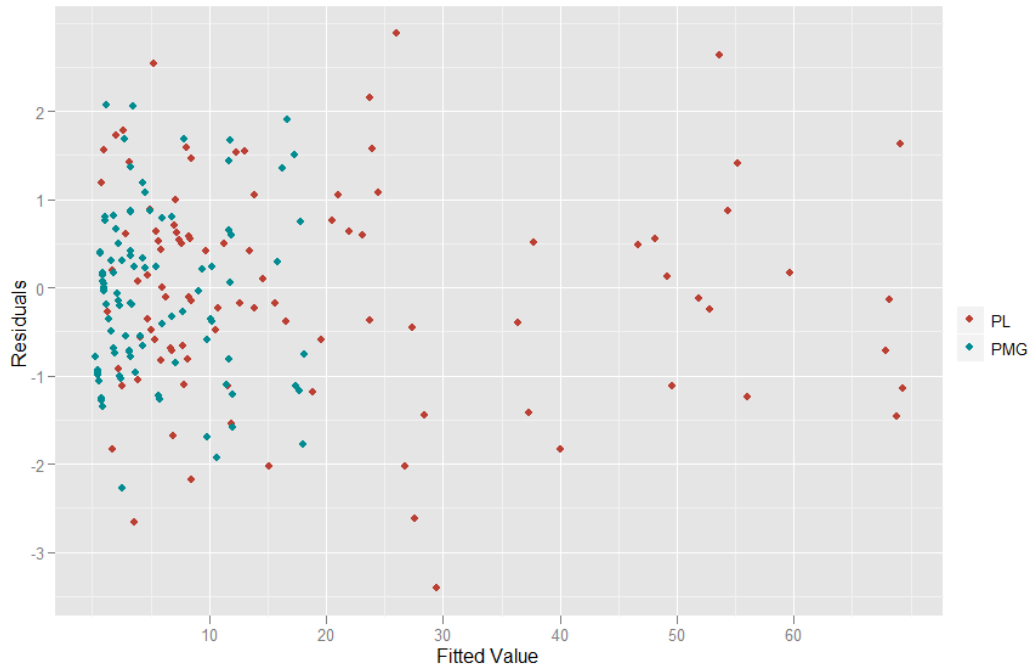
Figure 2-8: A second diagnostic test of the goodness of fit of the poisson model to observed data. Fitted values (x-axis) are plotted against the standardized residuals of each estimate (y-axis). A homogenous distribution of points above and below a y-value of 0 is indicative of a satisfactory fit.

2.4.4   POISSON REGRESSION - CHANGES IN MOUSE ABUNDANCE OVER TIME

Estimates of PL and PMG abundance obtained from the Poisson regression model were used to visualize changes in mouse abundance over time and are consistent with analyses performed on the observed data. No statistical analyses were conducted using abundances predicted by the model. Rather, model results are reported as figures that illustrate changes in species abundance; statistical tests are based on raw data.

In 2010, abundances of PL and PMG were the most similar of any year (Figure 2-9). Abundance of PMG was greater than abundance of PL in the second half of the year, and over a small period of time from mid-July to August the 95% confidence intervals did not overlap (Figure 2-9A), suggesting that PMG abundance was significantly greater than PL abundance in the latter half of the year.

In the first half of 2011 (Figure 2-9B), PL abundance was greater than PMG abundance, but confidence intervals overlapped until approximately the beginning of July. This is consistent with analysis of the raw data, which indicated that the difference between PL and PMG in trap success was greater in late 2011 than it was in early 2011. Abundance of PL and PMG diverged after July 2011, and PL abundance remained significantly higher than PMG abundance for the rest of the study (Figure 2-9C).
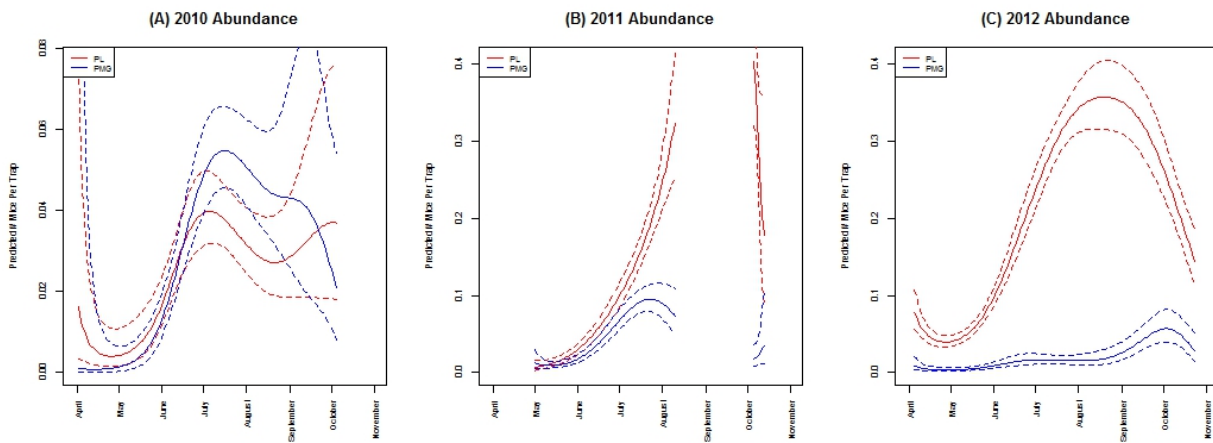
Figure 2-9: Predicted abundance of PL and PMG in (A) 2010, (B) 2011, and (C) 2012. The expected number of mice per trap (solid line) and 95% confidence intervals (dotted lines) are shown. Due to low overall abundance, a different scale is used in 2010 (A). Model predictions of mouse abundance between August 5 and October 7, 2011 (B) are not reported due to a long gap in trapping.

PL abundance increased in each year, and PL abundance in 2011 and 2012 was much greater than in 2010 (Figure 2-10A). Abundance of PL in spring 2010 and 2011 was similar; however, in 2011 PL abundance increased through late August, whereas in 2010 it reached a maximum in July. In 2012, spring numbers of PL were the highest of any spring, and overall PL numbers were the highest out of all years.

Abundances of PMG in 2010 and 2011 were not significantly different, even though maximum abundance in 2011 was greater than that in 2010 (Figure 2-10B). Overall abundance of PMG in

2012 was lower than in 2010 and 2011, even though maximum abundance was comparable. This difference was due to reduced abundance from June through September.
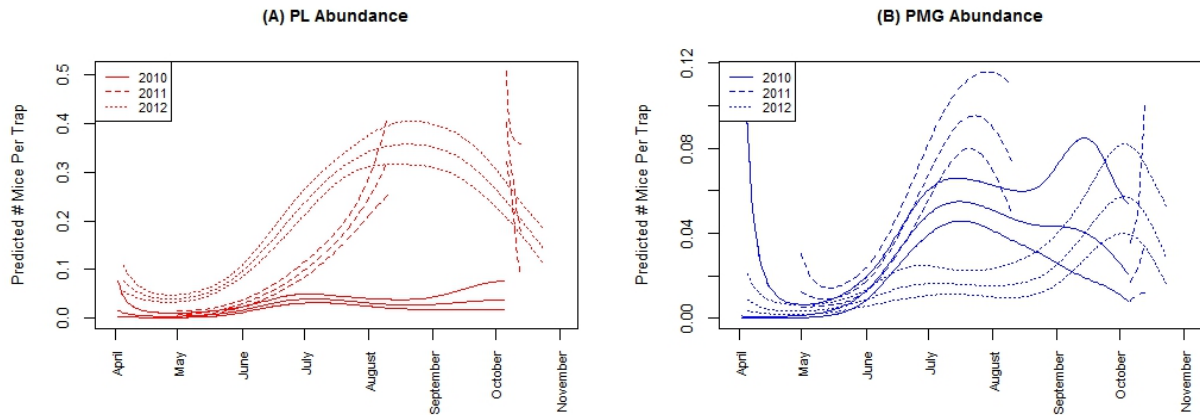
Figure 2-10: Abundance of (A) PL and (B) PMG, compared between years. Estimates of abundance (middle lines) and 95% confidence intervals (outer lines) are shown.

Relative abundance of PL was calculated as #PL/(#PL+#PMG) from model estimates of mouse abundance and is plotted in Figure 2-11. Patterns of relative abundance may be especially sensitive to overall abundance. In spring 2010, overall trap success was low (less than 5 mice were captured per day) and no PMG were trapped at all until the beginning of May, resulting in an apparent high relative abundance of PL even though actual numbers were very low. For most of 2011 and during 2012, however, mouse numbers were always higher than they were in 2010, so high values of PL relative abundance reflect real differences in the abundance of PL and PMG. PL and PMG occurred at roughly equal frequencies in 2010 and the first half of 2011 (Figure 2-11). After mid-July 2011, abundance of PL increased while that of PMG did not, resulting in a community that consisted mainly of PL. While both PL and PMG were present on the grid and trapped in spring 2012, PL abundance was much higher than PMG abundance. This trend continued throughout the summer and into the fall.
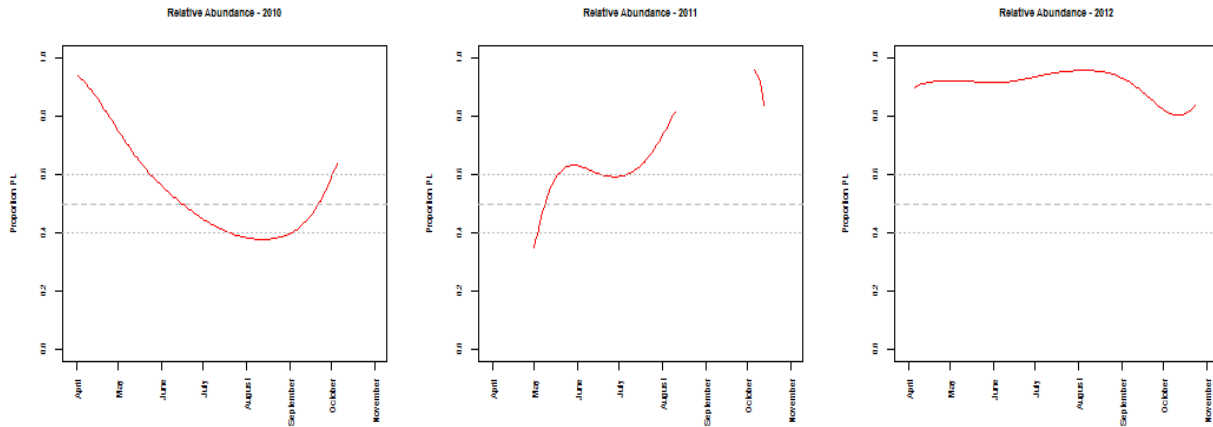
Figure 2-11: Relative abundance of PL in 2010, 2011, and 2012, measured as (#PL)/(#PL + #PMG). Values were calculated from model estimates of the expected number of mice per trap. A relative abundance of 0.5 is marked on the plots with a coarse dashed gray line, while relative abundance values of 0.4 and 0.6 are marked with fine dashed gray lines. High relative abundance of PL in the beginning of 2010 is probably an artifact of low total abundance.

2.4.5 SEVERITY OF WINTER CONDITIONS

All three winters relevant to this study were characterized by less than normal snowfall (Table 2-6). Snowfall was highest in the winter of 2010-2011 and the least in 2011-2012; however, no significant differences were found between winters in the mean deviation from historical averages in snowfall (F=0.029, P=0.87).

TABLE 2-6: WINTER CONDITIONS ON THE PIGEON RIVER GRID

WINTER YEAR	TEMPERATURE (°F)		SNOWFALL (IN)		ICE BREAK UP
	MEAN	DEVIATION	MEAN	DEVIATION	
2009-2010	19.93	0	24.07	-7.43	March 30
2010-2011	17.93	-2.06	28.03	-4.57	April 11
2011-2012	24.5	4.97**	22.83	-9.13	March 20
HISTORICAL AVERAGE	19.82		32.02		April 15

Table 2-6: Climatic data from the winters preceding each year of the study, obtained from a weather station in Gaylord, MI, 25 miles SSW of the Pigeon River Grid. Long-term historical averages of winter (December-February) temperature and snowfall are compared to yearly means for each winter prior to census sampling. Dates of ice break-up over Douglas Lake, 35 miles NNW of the grid, are also reported as an estimate of the length of winter. Significance of differences between winters in the deviation from historical averages is marked with asterisks (*: $P<0.05$; **: $P<0.01$).

The winter of 2011-2012 was the mildest and shortest experienced by mice during this study. Mean winter temperature was the highest in 2011-2012, when it averaged approximately 5 degrees warmer than normal. Mean winter temperature was significantly higher in 2011-2012 than in either 2009-2010 ($t=-7.9$, $df=3$, $P=0.004$) or 2010-2011 ($t=-5$, $df=2$, $P=0.032$). Ice break-up also occurred the earliest in the winter of 2011-2012.

Mean winter temperature was the lowest in 2010-2011 and was 2 degrees colder than the historical average; however, mean temperature in the winters of 2009-2010 and 2010-2011 were not significantly different ($t=1.4$, $df=2.6$, $P=0.27$). Ice persisted on Douglas Lake the longest in the winter of 2010-2011, when ice break up did not occur until April 11. The date of ice break-up was 12 days later in the winter of 2010-2011 than 2009-2010. This suggests that the winters of 2009-2010 and 2010-2011 were of comparable severity, but the winter of 2010-2011 may have been longer.

2.5   DISCUSSION

I conducted a three year study documenting abundance of PL and PMG at a site where both occur syntopically in northern Michigan. Abundance differed strongly in two out of three years, with PL outnumbering PMG in 2011 and 2012 (Figure 2-12). Changes in the pattern of relative abundance (excluding early 2010) suggest that community structure shifts from an equal composition of PL and PMG in late 2010 and early 2011 to a community composed of mainly PL (Figure 2-11). What caused the disparities in abundance of each species observed in 2011 and 2012? The winter conditions experienced by mice may provide a partial explanation.
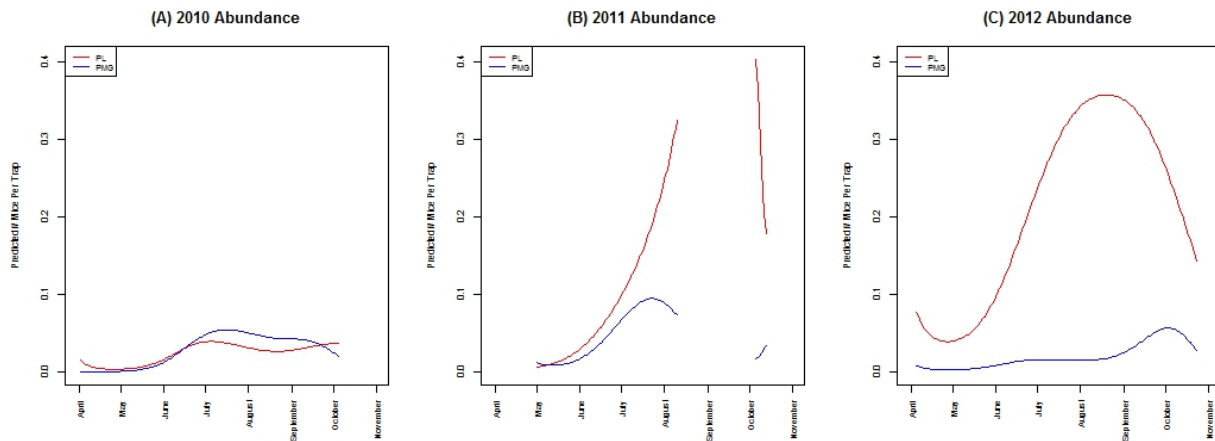
Figure 2-12: Predicted abundance of PL and PMG in (A) 2010, (B) 2011, and (C) 2012. Mean predictions (number of mice per trap) are plotted without 95% confidence intervals for ease of between-species comparison.

In a long term study in northern Michigan, Myers *et al.* (2005) found that PL abundance is higher in springs following short and mild winters, and that high spring abundance of that species is often correlated with higher rates of seasonal population growth and thus with high fall abundance. They found that a good predictor of spring PL abundance was the date of ice break-up on nearby lakes, an estimate of the length of winter.

In this study, abundance of PL increased significantly from each year to the next and was highest in 2012 (Figure 2-13). The preceding winter (2011-2012) was the mildest and shortest

experienced by mice during this study, consisting of higher than normal winter temperatures, lower than average snowfall, and an unusually early date of ice break up on Douglas Lake (Table 2-6). Spring abundance of PL was higher in 2012 than in any other year, and PL abundance both increased quickly during the breeding season and remained high through the fall. This is consistent with the expectation of higher abundance in years following short winters.

Winter conditions in 2009-2010 and 2010-2011, while harsher than those in 2011-2012, did not differ significantly from each other in either temperature or snowfall (Table 2-6). PL abundance in spring 2010 and 2011 was lower than in 2012, and abundance in fall 2010 was the lowest of any year. These observations are consistent with expectations of lower spring abundance (and consequently lower fall abundance) following long and harsh winters. In 2011, however, the PL population grew at a faster rate and to a greater maximum than in 2010 despite similarly low spring numbers and comparable severity of the preceding winter. This suggests that some factor unrelated to winter weather allowed more successful reproduction of PL in 2011.
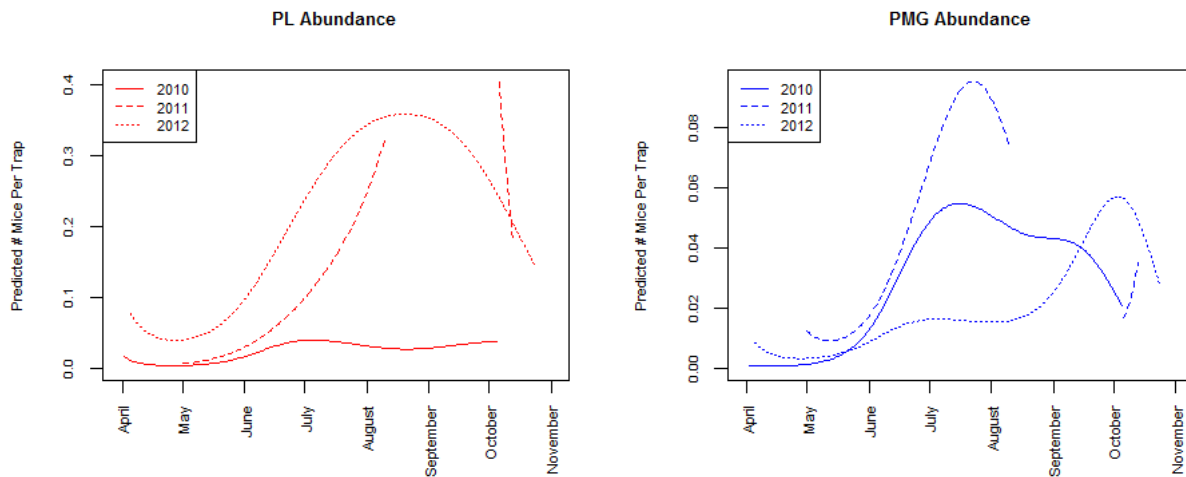
Figure 2-13: Abundance of PL (left) and PMG (right) in 2010, 2011, and 2012.

In contrast to PL abundance, PMG abundance was less variable and did not increase significantly during the study, nor was it related to winter conditions in the same way that PL abundance was. One possible explanation for the decline of PMG is that this species, because its distribution lies

mainly to the north of Michigan, is not adapted to the increasingly warmer conditions. Laboratory experiments suggest that there is an optimal temperature range between which reproduction is maximized, and that the optimal range may differ for 'northern' and 'southern' populations (Bronson and Pryor 1983). If PMG is declining due to physiological limitations, then abundance of PMG is expected to be higher in years following harsh winters but lower in years following mild winters. Patterns in this study seem to support this hypothesis - PMG abundance is higher in 2010 and 2011, but much reduced in 2012.

Nonetheless, there is some evidence that reduced PMG abundance in 2012 was not caused by warming winters. Neither spring abundance nor maximum abundance of PMG were reduced in 2012 relative to the other years; rather, the rate of increase was slow for much of the year, and unusually low numbers were observed between June and September (Figure 2-13). 2010 and 2011 were preceded by relatively harsh winters, but spring abundance of PMG was low in 2010 but not 2011. Further, PMG abundance increased at a faster rate and to a greater maximum in 2011 than in 2010. These patterns in spring abundance and rate of population increase suggest that population growth was influenced by other factors in addition to winter conditions.

Is abundance of PL and PMG influenced by interspecific competition? While it is unknown whether PL and PMG are competitors where they co-occur in northern Michigan, their ecological similarity suggests that this is a possibility. Chapters 4-6 discuss the possible role of competition in replacement in more detail. Nonetheless, some patterns of PMG abundance described in this chapter suggest that competition may be occurring. In 2011, when PL populations were increasing rapidly, PMG abundance declined more quickly from its maximum, while abundance in 2010 (when PL numbers were low) exhibited a slower decline and remained fairly high for several months after maximum abundance was reached. It is possible that PMG suffered reductions in population growth after mid-July when PL abundance began to increase significantly. In 2012, when PL populations were very high, PMG abundance was reduced between June and September. PMG abundance in 2012 did not change until it began to increase in September, coinciding with a decrease in PL abundance.

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CHAPTER 3.

DIFFERENCES IN SURVIVAL AND REPRODUCTION INFLUENCE REPLACEMENT IN MICHIGAN *PEROMYSCUS*

3.1   SUMMARY

I documented abundance of syntopic *P. leucopus* and *P. m. gracilis* in northern Michigan during a three year study. Abundance differed strongly in two out of three years, with *P. leucopus* outnumbering *P. m. gracilis* in 2011 and 2012 (Chapter 2). In this chapter, I compared survival and reproduction of co-occurring *P. leucopus* and *P. m. gracilis* in order to investigate the biological mechanisms that result in increased relative abundance of *P. leucopus*. Available evidence suggests that these species share similar life histories and reproductive rates; however, little information is available regarding populations where the two species occur in sympatry in the northern Great Lakes region. I estimated and assessed the per-capita number of litters produced by breeding females, the frequency with which litters are born, and the proportion of young-of-year (YOY) that breed in their natal year. I compared survival (estimated as persistence on the trapping grid) of overwintered (OW) and YOY mice.

Overwintered (OW) *P. leucopus* females consistently persisted longer and had more litters than OW *P. m. gracilis* females, and OW *P. leucopus* females contributed more to overall reproduction than OW *P. m. gracilis* females. No other consistent differences between species were found; however, survival, rate of reproduction, and the proportion of breeding YOY all varied substantially. Unique combinations of small differences between species in these traits may explain the patterns of abundance observed in this study. Variation in reproductive output of *P. leucopus* was found to be well explained by survival of OW and YOY females. Decreases

in *P. m. gracilis* abundance were caused by reduced reproduction by YOY females, which were observed in each successive year.

3.2   INTRODUCTION

Species differences can facilitate coexistence when regular environmental fluctuations favor different species at different times (Adler *et al.* 2007; Caceres 1997) but can lead to rapid changes in abundance when environmental fluctuations are directional (Ernest *et al.* 2008). Wolff (1996) suggested that the coexistence of *P. leucopus* and *P. maniculatus* may depend on differences in their winter adaptations, which cause one species to predominate when winters are short and mild and the other when winters are long and harsh.

There is some evidence that *P. leucopus* has an advantage in mild winter weather conditions while *P. m. gracilis* has an advantage in harsh conditions. In a long term study in northern Michigan, Myers *et al.* (2005) suggested that the decline in *P. m. gracilis* populations and concurrent rise in *P. leucopus* was attributable to long term climatic trends, particularly the overall decrease in the length of winter in this area. Abundance of *P. leucopus* is higher and increases faster in years following short winters than those following long ones, suggesting both enhanced survival and more successful reproduction when winters are short.

While both species experience high winter mortality (Myers *et al.* 2005), *P. m. gracilis* may be less negatively affected by severe and long winters, perhaps because it stores a greater quantity of food and builds more insulated nests (Wolff and Durr 1986; Pierce and Vogt 1993; Long 1996). On the other hand, *P. leucopus* may be especially vulnerable to cold winters (Howard 1951). At the northern edge of its range, *P. leucopus* suffers significant declines in abundance in severe winter conditions, such as cold temperatures and deep frost (Long 1973). Coexistence of these two species may have been maintained by differential winter adaptations and the frequency of mild versus harsh winters (Wolff 1996); however, this balance has been upset by recent climatic warming in the northern Great Lakes region.

I documented abundance of syntopic *P. leucopus* and *P. m. gracilis* in northern Michigan during a three year study. The changes in relative abundance observed in this community lend support to observations that *P. leucopus* is replacing *P. m. gracilis* in this region (Chapter 2). Abundance of these two species differed strongly in two out of three years, with *P. leucopus* outnumbering *P. m. gracilis* in 2011 and 2012. In 2012, following the mildest winter of the study, disparities in abundance between *P. leucopus* and *P. m. gracilis* were the largest observed. *P. leucopus* abundance was higher in the spring and increased to a greater maximum than in any other year, consistent with the findings of Myers *et al.* (2005). Overall abundance of *P. m. gracilis* was lowest in 2012 due to noticeably reduced numbers between June and September.

The biological mechanisms that result in increased relative abundance of *P. leucopus* in 2011 and 2012 are unclear and are the subject of this investigation. Ultimately, in order for *P. leucopus* to gain a numerical advantage in years following short and mild winters, it must have a greater annual reproductive output (i.e., produce more offspring that survive and reproduce) than *P. m. gracilis*. Annual reproductive output of a population depends on the reproductive success of its constituent individuals, and individual reproductive success is highly variable (Harland *et al.* 1979; Millar *et al.* 1992). Individual variation in survival and reproduction could thus result in significant differences between these species in overall population growth.

In this chapter, I compare survival and reproduction of co-occurring *P. leucopus* and *P. m. gracilis*. Is there any evidence that life-history traits of *P. leucopus* make it better adapted to mild winters, while *P. m. gracilis* is better suited for long winters? Temporal variation of survival and reproductive rates are investigated as possible sources of disparities in relative abundance.

3.2.1   BREEDING BIOLOGY OF *P. LEUCOPUS* AND *P. MANICULATUS GRACILIS*

The life cycle and breeding biology are similar for many species of *Peromyscus*, including *P. leucopus* and *P. m. gracilis* (King 1968; Gyug and Millar 1981; Baker 1983; Lackey *et al.* 1985). The normal gestation period of *Peromyscus* ranges from 21 to 27 days, with an overall average of 23 days (King 1968). *P. leucopus* and *P. m. gracilis* experience post-partum estrus and can

become pregnant shortly after giving birth (King 1968). They exhibit prolonged gestation periods as a result of delayed implantation when nursing a previous litter; the extent to which the gestation period is extended for lactating females averages 2 to 7 days (Svihla 1932; Baker 1983).

Changes in body weight of pregnant females have been well documented, primarily in laboratory mice (Millar 1982; Millar and Innes 1985; Millar 1985); weights observed during this study were consistent with these reports. Typical weight of non-breeding adult *P. leucopus* and *P. m. gracilis* is approximately 19-21 grams (Svihla 1932; King 1968; Millar 1985). Body weight remains relatively low for much of pregnancy, then increases dramatically a few days before parturition; a pregnant female 1-2 days prepartum may be approximately 79% heavier than non-breeding females (Millar 1975). Visual signs of pregnancy have been reported to be detectable as early as 5 days into gestation, and pregnancy becomes increasingly obvious as parturition approaches (Millar *et al.* 1979). Body weight is reduced immediately after parturition, but remains approximately 20% greater than non-breeding weight throughout lactation (Millar 1975).

Weight of newborn young averages approximately 9% of adult weight (King 1968), or about 1.8 grams, for both *P. leucopus* and *P. maniculatus* (Svihla 1932). Postnatal growth in *Peromyscus* has been studied extensively (King 1968). Body weight is tightly associated with age in juveniles (King 1958, 1968; King and Eleftheriou 1959). At three weeks old, approximately the age at which weaning is complete and mice leave the nest on their own, body weight is about 11 grams and roughly 50% of mature weight (Dice and Bradley 1942; King 1958, 1968). At four weeks after birth, mice weigh about 60% of mature weight, or about 13 grams (King 1968). Growth rates of young from weaning to 40 days of age are not significantly different between *P. leucopus* and *P. maniculatus* (Gyug and Millar 1981).

Age classes are associated with distinctive pelage characteristics, and developmental molts occur with known chronology during the developmental process (Collins 1923). Weaning of young is usually complete by the time young are 21 days old (King *et al.* 1963), after which they are able to leave the nest and enter into the trappable population. Mice reach sexual maturity and are ready to mate approximately 44 to 48 days after birth (Clark 1938; King 1968), and as early as 34-35 days (Clark 1938; Millar 1985). This overlaps with the onset of the post-juvenal molt, which begins at 40 to 45 days of age (Nicholson 1941), during which the gray pelage

characteristic of juveniles is replaced with brown fur typical of adults (King 1968). The duration of the molt from the first appearance of new pelage averages about 25 days (Storer *et al.* 1944; Gottschang 1956), and is complete roughly 65 to 70 days after birth (Gottschang 1956; Nicholson 1941; Baker 1983).

3.2.2 TRAITS INFLUENCING REPRODUCTIVE OUTPUT

Reproductive output is influenced by both survival and reproduction. Factors such as litter size, the number and frequency of litters, age at first reproduction, longevity, and survival all contribute to an individual's reproductive success. Though broad differences between species in vital rates have not been reported (Millar *et al.* 1979), variability among individuals in reproductive success (Millar *et al.* 1992) suggests the opportunity for small differences in survival and reproduction to result in significant differences in annual reproductive output.

Mean litter size for *P. leucopus* and *P. maniculatus* is 3-6 neonates (Svihla 1932; King 1968; Baker 1983; Millar 1985); however there is much variation. Variation in litter size in *Peromyscus* has been studied intensely and has been correlated with both environmental and intrinsic factors (Myers *et al.* 1985; Millar 1984). Litter size is influenced by environmental factors such as latitude (Millar *et al.* 1979) and season (Millar 1978; Morris 1996), and by maternal variables such as mass (Myers and Master 1983; Goundie and Vessey 1986), parity (Lackey 1978; Millar 1982; Myers and Master 1983), and age (Havelka and Millar 2004). The age at which mice reach sexual maturity does not differ between *P. leucopus* and *P. maniculatus* (King 1968; Millar *et al.* 1979). Nonetheless, there is individual variation in the timing of first reproduction (Lusk and Millar 1989), which could contribute to differences in reproductive output because mice that start breeding while young may have more opportunities reproduce.

Similarly, longevity can have a large impact on reproductive success because longer-lived individuals have more lifetime opportunities to breed (reviewed in Clutton-Brock 1988); however, long life does not necessarily correlate to higher fitness. The frequency with which breeding females have litters is also an important contributor to differences in reproductive output. Individuals that reproduce quickly during a short life may be equally as successful as

those that live a long time and reproduce at a slower rate, depending on the survival and reproduction of offspring (Stearns 1976). It is usually assumed that there is a tradeoff between reproductive effort and lifespan, with high reproductive effort correlated with short lifespan (Stearns 1976).

Reports based on laboratory animals suggest that *P. maniculatus* have a maximum life span of five to eight years, with a mean of just over three years (Dice 1933; Davis 1990). Laboratory reared *P. leucopus* have been reported to live from 4 (Sacher and Hart 1978) to 6 years (Burger and Gochfeld 1992). In the wild, mice rarely reach their potential maximum lifespans (Phelan and Austad 1989). Studies of survivorship demonstrate that few individuals in natural populations survive to maturity and produce surviving offspring (Clutton-Brock 1988, Schug *et al.* 1991), and even fewer live long enough to die of old age (Banfield 1974). Studies in Michigan (Burt 1940) and Pennsylvania (Pearson 1953) report that less than 4% of all *P. leucopus* live more than 1 year. Howard (1949) found less than 1% survival of *P. maniculatus* after 17 months. For Michigan *P. leucopus*, 90% mortality at 174 days with a median of 62 days has been reported (Snyder 1956); however, Adler and Wilson (1987) note that a small number of *P. leucopus* were known to be alive on their trapping grid in southeastern Massachusetts for up to 2 years.

Seasonal population increases are also often less than the potential for the population (Harland *et al.* 1979). Females are capable of producing litters at a rate of one per month (King 1968, Harland *et al.* 1979). In the wild, however, breeding females average 1-3 litters per year (Harland *et al.* 1979; Lackey *et al.* 1985; Schug *et al.* 1991; Kurta 1995), and overwintered females produce more litters on average than young-of-year females in the season of their birth (Harland *et al.* 1979). Reproductive success among individuals in natural populations is highly variable (Millar *et al.* 1992), and much of this variation is attributable to survival (Schug *et al.* 1991). Females that survive longer have proportionally more litters than short-lived females (Millar *et al.* 1992).

The correlation of parity and maternal age with litter size (Lackey 1978; Millar 1982 ; Myers and Master 1983; Havelka and Millar 2004) indicates that the relationship between persistence and reproductive output may not be strictly linear. This suggests that overwintered females

contribute more to overall reproduction than do young-of-year females, if they survive for a similar amount of time. In Michigan, overwintered females could produce up to 4 litters during the breeding season (Baker 1983; Kurta 1995); however, field studies from this area indicate that few overwintered individuals survive the entire length of the summer (this study; Myers, personal communication). Instead, late-summer litters are typically produced by mice that were born earlier in the summer (Millar *et al.* 1979; Havelka and Millar 2004). Differences between species in the survival of overwintered females could thus be a key contributor to differences in population growth.

Winter survival is another factor that contributes to reproductive success. Higher abundance in the spring means more opportunities for reproduction, and increased numbers of overwintered females could result in more rapid population growth. Even though both species experience high winter mortality, *P. m. gracilis* may be less negatively affected by severe and long winters (Long 1996; Myers *et al.* 2005), possibly due to increased investment in winter survival. A biological basis for these expectations is provided by the observations that *P. m. gracilis* from New York store a greater quantity of food and build relatively more insulated nests than *P. leucopus* from North Carolina (Pierce and Vogt 1993), and *P. m. nubiterrare* (a montane subspecies of *P. maniculatus* that is morphologically similar to *P. m. gracilis*) from North Carolina undergo torpor to survive difficult conditions more regularly than *P. leucopus* from South (Tannenbaum and Pivorun 1988).

Lastly, reproductive success may also be influenced by social interactions. The social organization of *P. maniculatus* and *P. leucopus* is such that home ranges of males and females overlap, but females tend to have exclusive territories and exclude immigrating females from those territories (Nicholson 1941; Metzgar 1971; Millar *et al.* 1992). Several studies have reported a negative correlation between population density and reproductive activity and output in *P. leucopus* (Burt 1940; Manville 1949). Socially induced reproductive inhibition of young-of-year females by overwintered females has been demonstrated in natural populations of *P. maniculatus* (Lusk and Millar 1989), and may cease altogether in highly dense populations (Canham 1969). Survival may be density dependent, in that the number of young weaned is inversely proportional to the number of adults in the population (Rintamaa *et al.* 1976). It is thus possible that social interactions may in part determine how beneficial it is to breed early and

rapidly, and that this trade-off between survival and reproduction could be reflected in variation in the frequency of litters and the age at first reproduction.

3.3   METHODS

3.3.1   CATEGORIZATION OF MICE

I monitored sympatric populations of *P. leucopus* (PL) and *P. m. gracilis* (PMG) in the Pigeon River State Forest from April to October for three consecutive years. Please refer to Chapter 2 for trapping protocol and reports on trapping frequency and intensity. Individual mice were tagged with unique identification numbers and categorized according to their sex, age, reproductive status, and cohort for further analysis. These categorizations are summarized in Table 3-1. They fall into 4 main groupings based on the frequency of determination:

1. Age, reproductive status, and weight were recorded during each capture. Three age classes were recognized based on pelage characteristics – juvenile (J, uniformly gray pelage), sub-adult (SA, presence of molt lines), and adult (A, brown dorsal pelage and white ventral fur).

2. Reproductive condition of females was assessed as either non-reproductive (NT, nipples not visible) or reproductive (NE, nipples visible). Mice were weighed to the nearest 0.5 grams.

3. Residency status, overwintered status, and age at first appearance (AF) were determined once for each individual. An individual was considered to be a resident if it was known to have remained on the trapping grid for more than 14 days (Harland *et al.* 1979), and thus present for at least 2 trapping sessions. Categorization of mice as residents (R) or non-residents (NR) was necessary so that transient individuals could be excluded from comparisons of persistence.

4. Each mouse either did not overwinter (NOW) or did overwinter (OW). Mice were known to overwinter if they were caught both in the year preceding a winter and in the year after (OW-R, overwinter-recaptured), but also if they were first caught as adults in the early spring before breeding had begun (OW-NR, overwinter-not recaptured). OW-NR mice are known to have been alive the previous fall, but because they were not trapped at that time, the age at first appearance (AF) is unknown. AF for all other mice was recorded as their age (A, SA, J) at first capture.

5. Individuals were classified as either OW (overwintered) or YOY (young-of-year) in each year that they were trapped on the grid. This classification is referred to as "annual age." Mice that were captured in two consecutive years were considered to be OW in the second year. Annual age of mice in their first year (for many, the first year was also the only year) on the grid was determined by the age at first appearance (AF). All mice first caught as juveniles and sub-adults were YOY during that year. Mice first trapped in the spring or early summer as adults were considered OW if they were trapped before breeding began. The age of adult mice that first appeared on the grid after the beginning of June could not be determined. Only mice of known annual age were used to assess differences between OW and YOY mice.

TABLE 3-1: CATEGORIZATIONS OF MICE

VARIABLE	DEFINITION	DESCRIPTION
FEMALE REPRODUCTIVE STATUS		**AT EACH CAPTURE**
NE	NIPPLES EXPOSED	• Visible nipples indicate that a female mouse is in reproductive condition
NT	NIPPLES TINY	• Nipples that are not visible indicate that a female is not in reproductive condition
AGE – EACH CAPTURE		**AT EACH CAPTURE**
A	ADULT	• Adult mice have brown dorsal fur and white ventral fur
SA	SUB-ADULT	• Sub-Adult mice are identified by visible molt lines on the sides of the body
J	JUVENILE	• Juvenile mice are uniformly gray
AGE - AT FIRST CAPTURE (AF)		**ONCE PER INDIVIDUAL**
A	ADULT	• Unknown for OW-NR mice.
SA	SUB-ADULT	• For all others, AF is the age of the individual at its first capture.
J	JUVENILE	
AGE - ANNUAL		**ONCE PER MOUSE PER YEAR**
YOY	YOUNG-OF-YEAR	• Mice that were born in a given year.
		• All mice SA or J at first capture are YOY.
OW	OVERWINTERED	• Mice that were known to survive a winter
OVERWINTERED STATUS		**ONE STATUS PER INDIVIDUAL**
NOW	DID NOT OVERWINTER	• Mice that were not known to survive a winter
OW-R	OVERWINTERED - RECAPTURED	• Captured in the fall prior to and spring after the winter
OW-NR	OVERWINTERED – NOT RECAPTURED	• Captured only in the spring after the winter
		• FD, AF are unknown
RESIDENCY STATUS		**ONE STATUS PER INDIVIDUAL**
R	RESIDENT	• Mice that remain on the grid for more than 14 days
NR	NON-RESIDENT	• Mice that remain on the grid for less than 14 days

Table 3-1: List of categorizations of mice that are referenced in this chapter. Frequency of categorization and methods of determination are listed.

3.3.2 ESTIMATING PERSISTENCE AND REPRODUCTIVE RATES

Longitudinal trapping records of females were used to estimate seasonal per-capita reproductive output and the frequency of litters (or time between litters). Trapping records of all mice were also used to calculate total (TTG) and annual persistence (ATG). Table 3-2 describes the traits and their method of estimation.

TABLE 3-2: ESTIMATES OF PERSISTENCE AND REPRODUCTIVE RATES

VARIABLE	DEFINITION	DESCRIPTION
FIRST AND LAST APPEARANCE		
FD	AN ESTIMATE OF DATE OF FIRST APPEARANCE	• OW-NR mice: last trapping day of the fall prior to the date of first capture (used to calculate TTG) • All others: actual date of first capture
LD	DATE OF LAST CAPTURE	• The date of disappearance from the grid.
PERSISTENCE		
TTG	TOTAL TIME SPENT ON THE GRID	• Estimate of overall persistence. • Number of days between FD and LD.
ATG	TIME SPENT ON THE GRID IN A SINGLE YEAR	• Number of days present in each year • Used to estimate annual persistence.
REPRODUCTIVE TRAITS		
#LIT	PER-CAPITA REPRODUCTION	• Number of known pregnancies per female • Estimated using changes in weight and reproductive status
FREQ	FREQUENCY OF LITTERS	• Average time between litters • Estimated as #Lit/ATG

Table 3-2: Methods of estimation of reproductive rates and survival of PL and PMG.

For each individual, the first (FD) and last (LD) date of capture were obtained from trapping records. For most mice, the date of first capture is an estimate of the date of their first appearance on the grid (i.e., when they first immigrated to the area or emerged from natal nest sites). This is not the case for OW-NR mice, which appeared on the grid at some unknown time before their date of first capture, so both the timing of their first appearance on the grid and their age at the time is unknown. For this reason, OW-NR mice have been removed from many of the analyses that follow.

An individual is known to be alive for the duration between its first and last capture, and individuals are assumed to have remained in the area for this duration. The total amount of time an individual spent on the grid (TTG) was calculated as the number of days between its first and last captures. To calculate TTG for OW-NR mice, FD was estimated as the last trapping day in the fall prior to the date of their first capture. For all mice that survived a winter, annual persistence (ATG) was calculated for each year they were found on the grid.

Pregnancies were detected in the field using visual cues (swollen abdomen) and supplemented with longitudinal data documenting fluctuations in body weight. Changes in body weight of pregnant females have been well documented, primarily in laboratory mice (Millar 1982; Millar and Innes 1985; Millar 1985); weights observed during this study were consistent with these reports.

Pregnancies could also be detected by changes in female reproductive status. A female's nipples enlarge in preparation for lactation shortly before she gives birth to her first litter. In this study, the exact date of parturition is known for 3 females that gave birth while inside a Sherman trap. The nipples of these 3 females become exposed about 3-4 days before parturition, around the 19th day of pregnancy assuming 23 days for gestation. Due to continual breeding (Sharpe and Millar 1991), nipples remain visible throughout the breeding season.

Because there is no winter breeding in Michigan *Peromyscus* (Myers *et al.* 2005), over-wintered females captured in the spring have small nipples. Thus, when overwintered females were found with enlarged nipples early in the year, they were likely to be pregnant. Similarly, if a female was found with enlarged nipples at first capture, it was inferred that this individual was or had been pregnant at least once during the season. For each female for which data were available, the number of known pregnancies was recorded. Each known pregnancy was assumed to result in a successful litter.

3.3.3   ESTIMATES OF REPRODUCTION AND SURVIVAL

I investigated three reproductive characteristics and three measures of survival of PL and PMG to assess differences between species that might contribute to total population growth. Shifts in

community structure are ultimately caused by differences in reproductive success of the species that make up the community. Total annual reproductive output of a species consists of reproduction of OW and YOY females. Reproductive output is influenced by reproductive traits such as the rate at which breeding individuals have litters and the age of an individual at first reproduction. Reproductive success also depends on winter survival and the length of time that an individual persists during the breeding season (Figure 3-1).
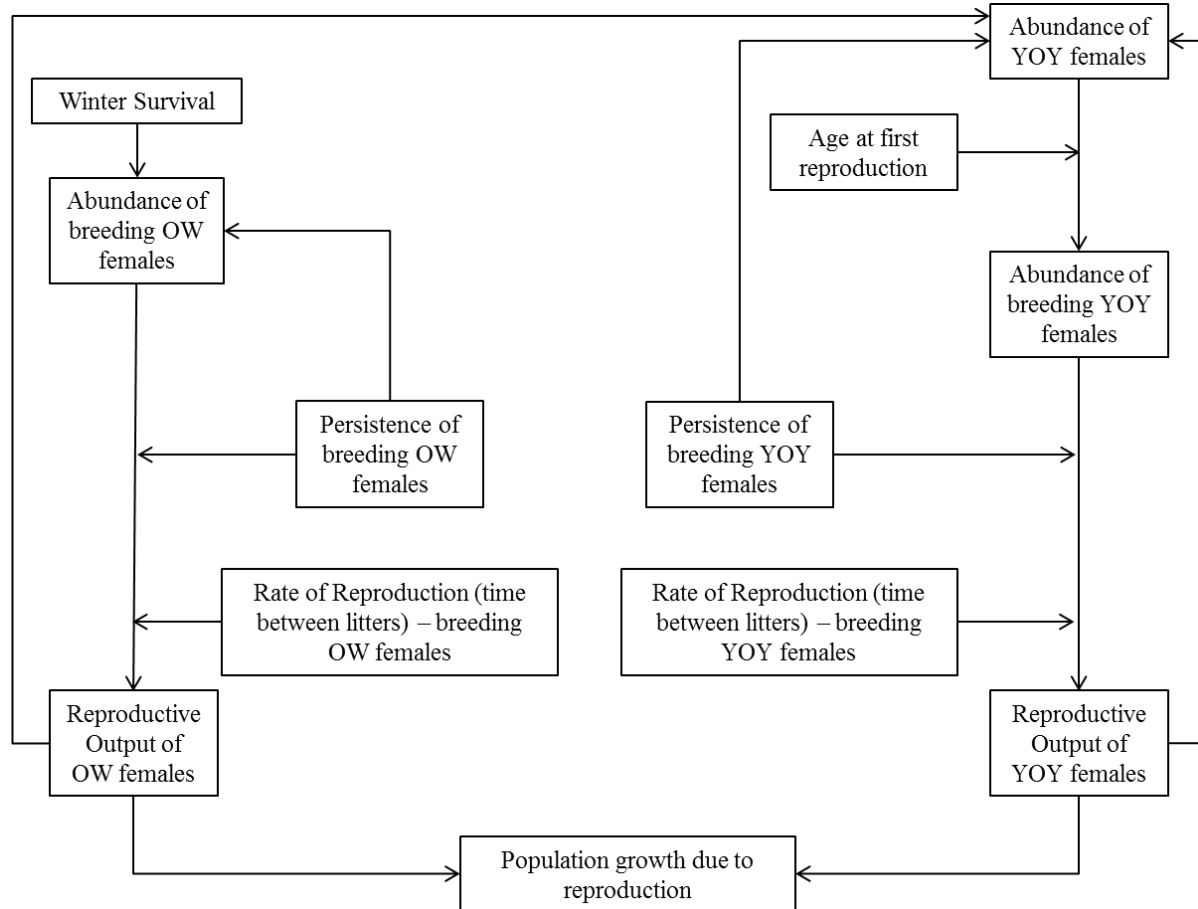
Figure 3-1: Conceptual model of species traits investigated in this study that influence population growth due to reproduction. Traits influencing reproduction are represented in boxes, and the effect of each factor (either directly on another factor or indirectly on another effect) is indicated with directional arrows.

Reproductive output of OW and YOY females was estimated as the per-capita number of known pregnancies and compared between species and cohorts using two-sample t-tests. The frequency

with which breeding females have litters is an important contributor to overall population growth because individuals that reproduce quickly during a short life may be equally successful as those that live longer and reproduce at a slower rate (Stearns 1976). The frequency of litters for each breeding female was estimated as the number of known pregnancies divided by annual persistence (ATG) on the grid. I compared the frequency of litters between species and between OW and YOY females to determine whether there was variation in the length of time between litters.

The age at which reproduction begins significantly impacts population growth via reproduction, effectively shortening generation time (Cole 1954). The age at which female mice reach sexual maturity is not reported to differ between PL and PMG (King 1968; Millar *et al.* 1979); however, there may be individual variation in the timing of first reproduction (Lusk and Millar 1989). While I was not able to determine the exact age of individuals in this study, I investigated the proportion of YOY mice that were known to breed in the year of their birth to make broad comparisons between PL and PMG.

Enhanced winter survival increases the abundance of breeding OW females in the spring and thus has direct influence on reproduction by this cohort. Winter survival was estimated as the proportion of mice that were trapped in both the fall prior to and the spring after a winter. Fisher's Exact test was used in lieu of Chi-squared analysis due to small sample sizes.

Much of the difference between potential and observed reproductive output in some *Peromyscus* populations is attributable to survival (Schug *et al.* 1991), so that females that survive longer have proportionally more litters than short-lived females (Millar *et al.* 1992). No direct measures of longevity were possible; however I used the total time that an individual was known to spend on the grid (TTG) as a rough estimate. Average TTG was compared between groups (species, gender, age at first appearance, reproductive status) and years using two-sample t-tests.

Persistence within a single season was assessed using three methods – the proportions of mice that became residents on the grid, annual persistence (ATG), and the probability of loss of an individual between one trapping session and the next. Differences in the proportion of mice that established residency on the grid was investigated using either Chi-squared analysis or Fisher's Exact test when sample sizes were low. Annual persistence (ATG, the length of time an

individual was known to be present during a single year) was compared between species and cohorts using two-sampled t-tests.

The probability of loss of an individual from the marked population was calculated for each two week period during the study. Because mortality and emigration may depend on factors such as predation pressure and population density, it is likely that the proportion of the population lost changes within a season. A time interval of two weeks was chosen to coincide with the average length of gaps between trapping sessions. Individuals were assumed to have been present on the grid for the entire duration between their first and last capture, and an individual was considered lost only when it disappeared permanently from the marked population. To detect more general seasonal differences in the probability of loss, time periods were grouped into two categories: early season, or before July 15; and late season, or after July 15. The proportion of mice lost from the population was compared between species, genders, years, and seasonal categories using chi-squared analysis.

I additionally investigated two factors that could influence survival. The average weight of mice in the fall was compared between overwintered and non-overwintered mice with two-sample t-tests. Average dates of first appearance on the grid (FD) were compared among residents and between residents and non-residents to investigate possible density dependent effects that could affect persistence and disappearance.

Table 3-3 provides a summary of the traits investigated, how characteristics were estimated, the statistical tests used, and restrictions on the datasets used in analyses. Datasets were often restricted to certain subgroups for analysis; the most common was exclusion of OW-NR mice. Because OW-NR mice were known to have been alive in the fall prior to their first capture, the timing of their first appearance on the grid (FD) and their age at the time (AF) were unknown. It is likely that there were other mice present in the fall that escaped detection altogether, so the inclusion of OW-NR mice may bias analyses in which proportions of mice are compared (i.e., out of all known incoming immigrants or new births, how many became residents or overwintered). Comparisons of reproductive characteristics were restricted to residents because longitudinal records were required. Some analyses of survivorship were also restricted to resident mice in order to better distinguish the effects of mortality from emigration.

TABLE 3-3: COMPARISONS OF SURVIVAL AND REPRODUCTION OF PL AND PMG

TRAIT	ESTIMATE	STATISTICAL TEST	RESTRICTIONS
NUMBER OF LITTERS	Number of known pregnancies	Welch's 2-sample t-test	Resident females
FREQUENCY OF LITTERS	Time between pregnancies	Welch's 2-sample t-test	Resident breeding females
AGE AT FIRST REPRODUCTION	Proportion of breeding YOY	Fisher's Exact Test	Resident YOY
LONGEVITY	Overall persistence (TTG)	Welch's 2-sample t-test	All mice
WINTER SURVIVAL	Proportion of mice that overwinter	Fisher's Exact Test	Exclude OW-NR
ANNUAL SURVIVAL	Probability of loss	Chi-squared Test	All mice
	Proportion that became residents	Chi-squared or Fisher's Exact Test	Exclude OW-NR
	Annual persistence (ATG) – YOY in natal year	Welch's 2-sample t-test	Resident YOY; All known OW (include OW-NR)
FACTORS AFFECTING SURVIVAL	Effect of weight on overwintering	Welch's 2-sample t-test	OW-R
	Effect of FD on residency	Welch's 2-sample t-test	Exclude OW-NR

Table 3-3: Description of analyses comparing survival and reproduction between PL and PMG.
Three reproductive traits (number of litters, frequency of litters, and age at first reproduction) and three measures of survival (winter survival, overall survival, and annual survival) were investigated. Trait, method of estimation, the statistical test used to compare between groups, and restrictions on the datasets used for analyses are listed.

3.4   RESULTS – REPRODUCTION

3.4.1   NUMBER OF LITTERS (KNOWN PREGNANCIES)

The number of pregnancies was estimated for each resident female; each pregnancy was assumed to result in a successful litter. The per-capita number of litters (total litters/number of resident females) was calculated for OW and YOY PL and PMG.

Differences between species: Overall, breeding female PL produced more litters per-capita than breeding female PMG (t=3.9, df=103, P=0.0002). This was particularly noticeable in 2011 and 2012 (Figure 3-2). YOY PMG females produced more litters than YOY PL females in 2010 (t=-2.8, df=6, P=0.03), however YOY PL females produced more litters than YOY PMG females in both 2011 (t=2.4, df=11, P=0.039) and 2012 (t=6.4, df=31, P<0.0001; Figure 3-3A). OW PL females produced significantly more litters than OW PMG females (t=3.6, df=49, P=0.0007) in all years (Figure 3-3B).
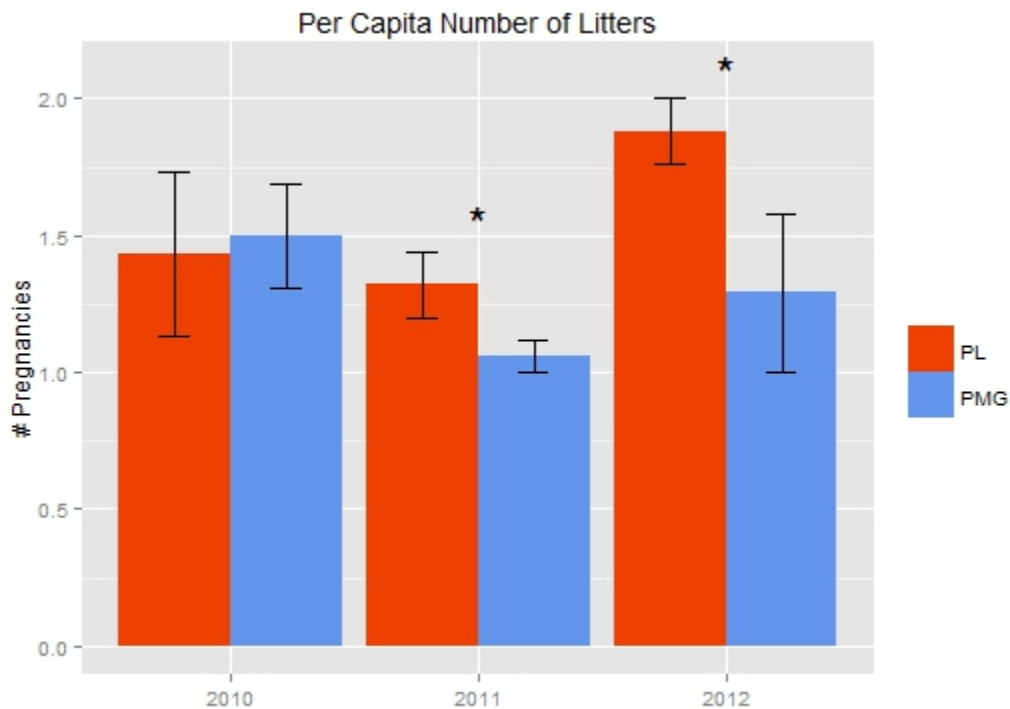
Figure 3-2: Per-capita number of litters produced by female PL and PMG in 2010, 2011, and 2012. Mean number of litters per female and standard errors of the means are reported. Significance of differences between species in the number of litters is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

Within-species variation: PL YOY females produced the most litters in 2012 and the least in 2010 (t=-2.1, df=29, P=0.049). This pattern is reversed for PMG YOY females (df=8, P=0.002). The number of litters produced by known OW females did not differ between years for either PL (P=0.62) or PMG (P=0.5). PL OW females averaged more litters than PL YOY females in all

years (t=-2.3, df=53, P=0.025), but OW and YOY PMG females did not differ in this respect (P=0.66).
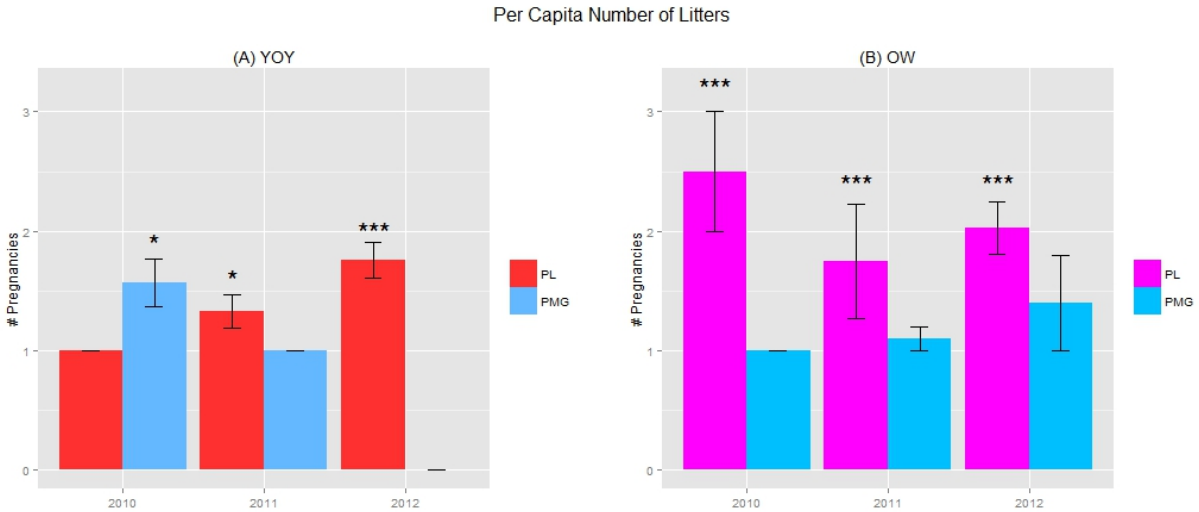
Figure 3-3: Per-capita number of litters produced by female (A) YOY and (B) OW mice in 2010, 2011, and 2012. Mean number of litters per female and standard errors of the means are reported. Significance of differences between species in the number of litters is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

3.4.2   FREQUENCY OF LITTERS

For each resident female that was known to have at least one litter, the frequency of litters was calculated as annual persistence (ATG) divided by the number of known pregnancies. I compared the frequency of litters between species and mice of different age classes to determine whether length of time between litters differed among groups.

TABLE 3-4: AVERAGE TIME BETWEEN LITTERS (DAYS)

	PL					PMG				
	N	#LIT	ATG	FREQ	SE	N	#LIT	ATG	FREQ	SE
2010	7	1.43	55.14	38.12	6.00	8	1.50	46.75	36.50	12.03
2011	22	1.32	59.86	50.27	6.86	18	1.06	45.83	43.89	7.20
2012	59	1.88	79.17	44.01	3.24	7	1.29	67.86	56.33	9.55
ALL	88	1.70	72.43	45.11	2.81	33	1.21	50.73	44.74	5.27
YOY	38	1.53	59.84	41.58	3.96	15	1.27	44.00	38.53	7.36
OW	35	2.03	93.09	49.11	4.66	16	1.19	52.31	45.08	7.37

Table 3-4: Comparison of the average time between litters, calculated for each female as annual persistence (ATG) divided by the number of known pregnancies. Means and standard errors are reported for the number of litters (#LIT), ATG, and frequency of litters (FREQ). Significance of differences between species in the frequency of litters is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

Differences between species: No differences were found between species in the frequency of litters (Table 3-4).

Within-species variation: No differences in the frequency of litters were found between years for OW females of either species or for PL YOY (Figure 3-4), though variation was high. For PMG YOY, the average time between litters was shorter in 2010 than in 2011 (t=-1.98, P=0.05).
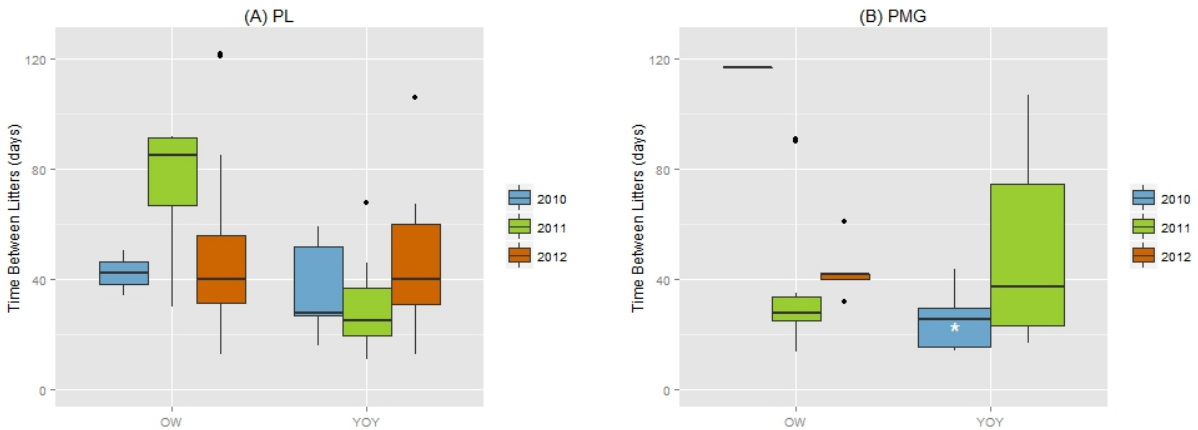
Figure 3-4: Boxplots of the frequency of litters, measured as the average time between litters (#Lit/ATG), for known OW and YOY (A) PL and (B) PMG. Medians and inter-quartile ranges are reported. Significance of differences between years is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

3.4.3   AGE AT FIRST REPRODUCTION (PROPORTION OF BREEDING YOUNG-OF-YEAR)

The age at which reproduction begins significantly impacts population growth via reproduction, effectively shortening generation time (Cole 1954). I was not able to assess age directly in this study; I thus calculated the proportions of YOY PL and PMG that bred in their natal year to make broad comparisons between species.

Differences between species: There was no difference between species in the proportion of known YOY females that bred in the year of their birth in 2010 or 2011 (Table 3-5). In 2012, however, a greater proportion of PL YOY bred than PMG (P=0.023)

Within-species variation: There was a significant reduction in the proportion of breeding PMG YOY in 2012 compared to the other years (P=0.021). There was no difference in the proportion of breeding PL YOY among years (P=0.55).

TABLE 3-5: BREEDING STATUS OF YOY IN THEIR YEAR OF BIRTH

	PL			PMG			P-VALUE
	YES	NO	%BREED	YES	NO	%BREED	
2010	5	2	0.71	7	2	0.81	1
2011	12	4	0.75	8	4	0.67	0.691
2012	21	11	0.66	0	4	0	0.023*

Table 3-5: Proportion of YOY PL and PMG that bred in the summer of their birth. The number of YOY that were known to breed (Yes) and were not known to breed (No) are also reported. Fisher's Exact Test was used to test for equality between species in the proportion of breeding YOY, and the P-values for between-species comparisons are reported. Significance of differences between species are marked (*: P<0.05).

3.5   RESULTS – LONGEVITY AND SURVIVAL

Much variation in individual reproductive success is attributable to longevity and survival (Schug *et al.* 1991; Millar *et al.* 1992). Females that survive longer have proportionally more litters than short-lived females (Millar *et al.* 1992). In this section, I assess individual variation in longevity (estimated as TTG), overwinter survival, and survivorship during a season (estimated as ATG).

3.5.1   LONGEVITY - OVERALL PERSISTENCE (TTG)

I compared total persistence (TTG, the number of days between an individual's FD and LD) between species, between males and females, and among years, as a proxy for longevity. Out of 740 tagged mice trapped from 2010-2012, only 12 (1.62%) were known to have persisted on the grid for one year or more. 10 of these were PL (8 male, 2 female), and 2 were PMG (1 male, 1 female). For both species, there was a period of rapid loss of individuals before TTG reaches 100 days, followed by a plateau leading into another period of more rapid loss (Figure 3-5).
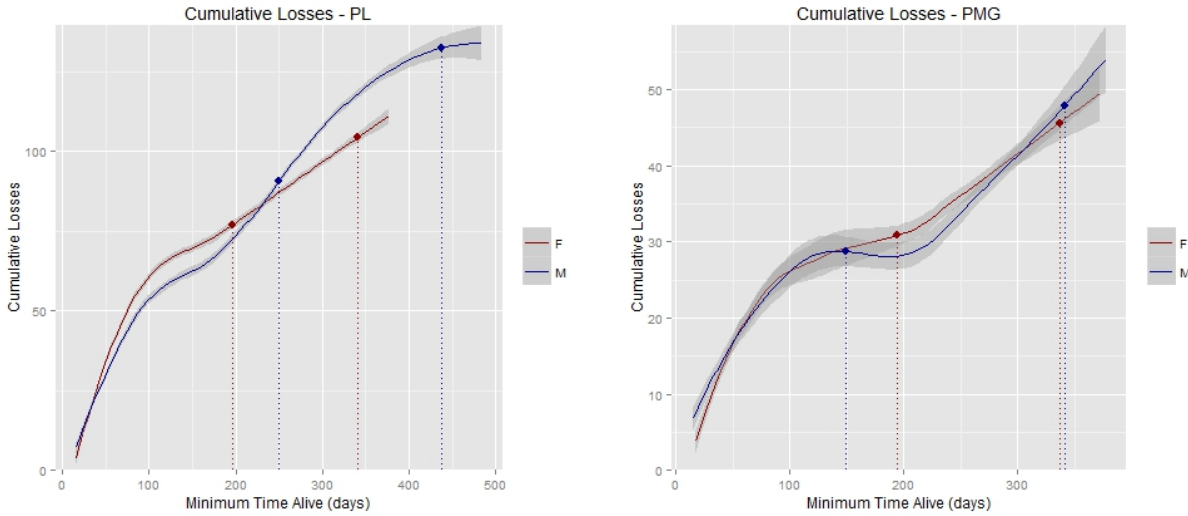
Figure 3-5: Cumulative losses of PL and PMG with respect to total persistence time (TTG). Dates on which 50% and 90% of individuals are lost are marked on the curves with points, and dotted lines indicate associated TTG values.

Differences between species: No significant differences in TTG were found between species, though there was a non-significant trend for PL males to remain on the grid longer than PMG males (t=1.1, df=83, P=0.29, Table 3-6).

Within-species variation: There was a non-significant trend for males of both species to persist longer than females (t=-1.8, df=321, P=0.079). The oldest known PL male and female remained on the trapping grid for 484 and 377 days, respectively. The oldest known PMG male and female remained for 377 and 372 days.

	TABLE 3-6: TOTAL PERSISTENCE OF PL AND PMG								
	FEMALES			MALES			ALL		
	N	TTG	SE	N	TTG	SE	N	TTG	SE
2010	9	122.78	42.89	13	169.31	39.29	22	150.27	28.86
2011	30	145.17	24.10	43	190.58	20.49	73	171.92	15.72
2012	70	134.77	12.33	68	147.02	12.91	138	130.80	8.90
PL TOTAL	109	136.64	10.81	124	164.46	10.89	233	151.45	7.73
2010	10	61.80	27.05	20	116.45	26.30	30	98.23	20.02
2011	24	167.21	23.88	16	175.44	33.41	40	170.50	19.34
2012	11	122.09	26.99	9	138.56	38.88	20	129.50	22.38
PMG TOTAL	45	132.76	16.53	45	141.84	18.40	90	137.30	12.31

Table 3-6: Average total persistence (TTG), the number of days between the date of first capture (FD) and the date of last capture (LD), of resident mice.

3.5.2   WINTER SURVIVAL

The proportion of mice that overwintered (excluding OW-NR mice) was compared between species, genders, and age at first capture for the winters of 2010 and 2011. Winter survival was not assessed for the winter of 2012-2013 because no mice that were trapped in fall 2012 were trapped again in spring 2013. Fisher's Exact Test was used rather than Chi-squared analysis due to low numbers in some groups.

TABLE 3-7: WINTER SURVIVAL							
	PL			PMG			
	NOW	OW-R	%OW-R	NOW	OW-R	%OW-R	P
2010	32	2	0.063	47	0	0	0.173
2011	193	19	0.098	48	2	0.042	0.385
TOTAL	225	21	0.093	95	2	0.021	0.031*

Table 3-7: Winter survival – the number of mice that were trapped in the fall that either were not trapped again (NOW) or were trapped again the following spring (OW-R). The proportion of mice known to overwinter (%OW-R) was compared between species using Fisher's Exact Test; P-values are reported.

Of mice trapped in the falls of 2010 and 2011, less than 10% were trapped again the following spring. When data from both winters were combined, a greater proportion of PL overwintered than PMG (Table 3-7). When both species were combined, a greater proportion of mice tended to overwinter in 2011, but this result is not significant (P=0.12). Low numbers of overwintering mice of both species in 2010 and PMG overall may preclude accurate assessment of differences in the probability of overwintering.

3.5.3 ANNUAL SURVIVAL

3.5.3.1 PROBABILITY OF LOSS

The probability of loss of an individual from the marked population over two week time periods (approximately from one trapping period to the next) was averaged for the first half (before July 15) and second half (after July 15) of each year (Table 3-8).

Differences between species – Females: A greater proportion of PMG females, both reproductive (χ^2=3.78, P=0.049) and non-reproductive (χ^2=4.23, P=0.039), were lost from the population early in the season than were PL females.

Differences between species – Males: During the second half of 2012, a greater proportion of PL were lost than PMG (χ^2=9.41, P=0.002). This difference was significant for males (χ^2=9.28, P=0.002), but not females (χ^2=0.3, P=0.238).

TABLE 3-8: PROBABILITY OF LOSS OVER 2-WEEK PERIODS											
	MALES (M)				FEMALES (F)				REPRODUCTIVE FEMALES (NE)		
	PL		PMG		PL		PMG		PL		PMG	
	L	%L	L	%L	L	%L	L	%L	L	%L	L	%L
EARLY	7	0.22	7	0.28	5	0.24	6	0.20	1	0.09	2	0.13
LATE	14	0.45	21	0.57	5	0.63	15	0.83	5	0.83	9	0.90
2010	21	0.33	28	0.45	10	0.34	21	044	6	0.35	11	0.43
EARLY	36	0.44	14	0.30	15	0.30**	21	0.54**	11	0.32**	14	0.61**
LATE	44	0.49	15	0.71	23	0.43	12	0.41	13	0.43	7	0.51
2011	80	0.47	29	0.43	38	0.37	33	0.49	24	0.38	21	0.57
EARLY	61	0.31	5	0.45	53	0.30	7	0.32	30	0.28*	5	0.56*
LATE	72	0.61**	2	0.14**	83	0.70	8	0.53	46	0.88	3	1.00
2012	133	0.42	7	0.28	136	0.46	15	0.41	76	0.48	8	0.67

Table 3-8: Probability of loss of an individual over 2-week periods (approximately from one trapping session to the next). The ratio of losses to all losses plus retentions was summed for the first half (before July 15) and second half (after July 15) of each year. Significance of differences between species is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

3.5.3.2 PROBABILITY OF ESTABLISHING RESIDENCY

Residents were mice that were captured multiple times and were known to persist on the grid for at least 14 days. They were likely to have established territories on the grid. Non-residents, on the other hand, were more likely to be transient or dispersing individuals. Because both PL and PMG establish core home ranges and the victor in aggressive contests is typically the resident rather than intruder (Dooley Jr. and Dueser 1996), the proportion of mice that become residents may reflect the difficulty of establishing territories. Out of 740 mice tagged from 2010-2012,

207 (152 PL and 55 PMG) were known to be alive on the grid for more than 14 days and were therefore categorized as residents (Table 3-9).

TABLE 3-9: NUMBER OF MICE ESTABLISHING RESIDENCY

	NON-RESIDENTS (NR)								RESIDENTS (R)							
	FEMALES				MALES				FEMALES				MALES			
	A	SA	J	T	A	SA	J	T	A	SA	J	T	A	SA	J	T
2010	2	1	3	6	0	3	10	19	0	2	5	7	2	4	2	8
2011	42	18	13	73	63	18	22	176	11	6	10	27	17	7	5	29
2012	21	19	33	73	36	10	35	154	11	13	19	43	21	6	11	38
PL	65	38	49	152	99	31	67	349	22	21	34	77	40	17	18	75
2010	3	2	7	12	2	7	4	25	0	2	7	9	1	4	8	13
2011	2	5	9	16	6	2	6	30	1	2	10	13	0	4	3	7
2011	5	1	1	7	3	0	3	13	3	0	4	7	4	0	2	6
PMG	10	8	17	35	11	9	13	68	4	4	21	29	5	8	13	26

Table 3-9: The number of mice that either became residents (R) or did not become residents (NR). Mice are categorized by gender and age at first capture. OW-NR mice are excluded because AF is unknown.

Differences between species: Overall, a greater proportion of PMG became residents in their first year of capture than PL (χ^2=8.57, P=0.003), but this varied by gender, age at first capture, and year. PMG were more likely to become residents than PL when establishing residency in 2011 (χ^2=4.48, P=0.034), but not in 2010 (P=0.99) or 2012 (P=0.13; Figure 3-6A). PMG juveniles were more likely to become residents than PL juveniles (χ^2=8.84, P=0.003). A greater proportion of PMG males became residents than PL males (χ^2=5.47, P=0.019), especially those first caught as juveniles (χ^2=6.85, P=0.009). The proportion of PMG females that became residents was greater than that of PL females (χ^2=2.47, P=0.12); however, this result was not significant.
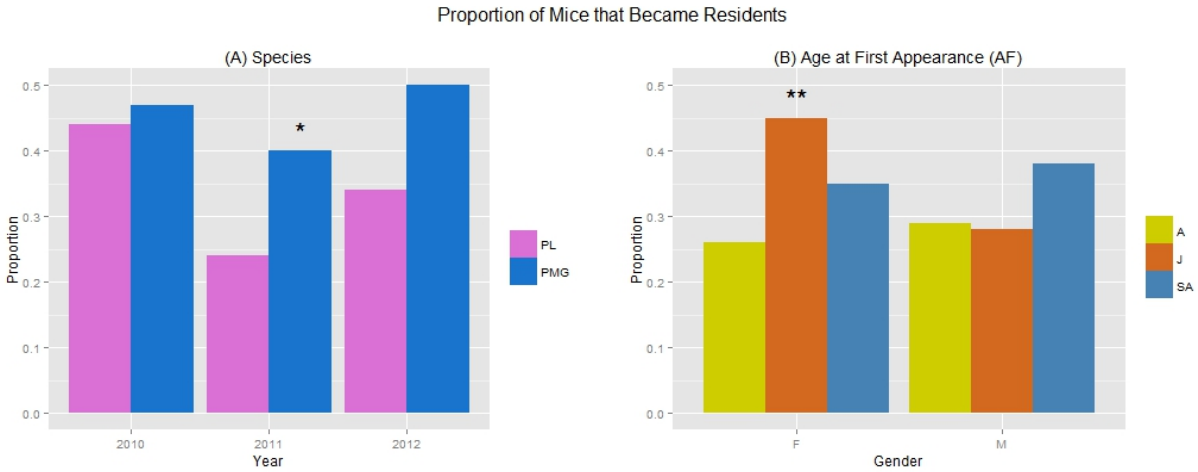
Figure 3-6: The proportion of mice that became residents, compared between (A) PL and PMG, and (B) mice of different ages at first appearance. Significance of differences in the proportion of residents are marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

Within-species variation: The proportion of PMG that became residents did not differ among years (χ^2=0.19, P=0.73; Figure 3-6A). PL, however, were less likely to become residents in 2011 than in either 2010 (χ^2=5.07, P=0.024) or 2012 (χ^2=5.52, P=0.019). Of mice first captured as juveniles, more females became residents in their first year of capture than males for PL (χ^2=6.8, P=0.009), but not for PMG (P=0.87). Taken together, results suggest that juvenile PL males were the least likely of all groups to become residents.

Female mice were more likely to become residents if they appeared on the grid as juveniles rather than adults (χ^2=8.4, P=0.004; Figure 3-6B), and this pattern is seen for both PL (χ^2=4, P=0.044) and PMG (χ^2=3.5, P=0.046). The proportion of males that became residents did not differ between ages at first capture (P=0.46).

3.5.3.3   PERSISTENCE OF YOY RESIDENTS IN THEIR NATAL YEAR

This analysis compared the average annual persistence (ATG) of YOY residents in the year of their birth. Enhanced persistence of female YOY has the potential to lead to increased per-capita reproductive output if it leads to additional opportunities to breed. Only residents that were known to be YOY (i.e., first captured as juveniles or sub-adults) were included in these analyses.

Differences between species: Overall, PL YOY residents tended to persist longer on the grid in the year of their birth than YOY PMG residents (t=1.8, df=108, P=0.08), but this result was not significant. YOY female PL and PMG residents did not differ in ATG in any year (Figure 3-7). YOY male PL and PMG residents did not differ in ATG except in 2011, when there was a non-significant trend for YOY PL males to persist longer than YOY PMG males (t=1.7, df=16, P=0.1).

Figure 3-7: Annual persistence (ATG) of resident mice in the year that residency is established for (A) females and (B) males. Significance of differences in ATG between species is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

Within-species variation: Within species, there was no difference in persistence between male and female YOY, except in 2011 when YOY PMG females persisted longer than YOY PMG

males (t=2.3, df=16, P=0.037). Female YOY PL and male YOY PMG persisted longer in 2012 than in any other year (Figure 3-8). Male YOY PL did not differ in ATG in any year. Female YOY PMG persisted longest in 2011 (t=-1.8, df=15, P=0.09), though this result was not significant.
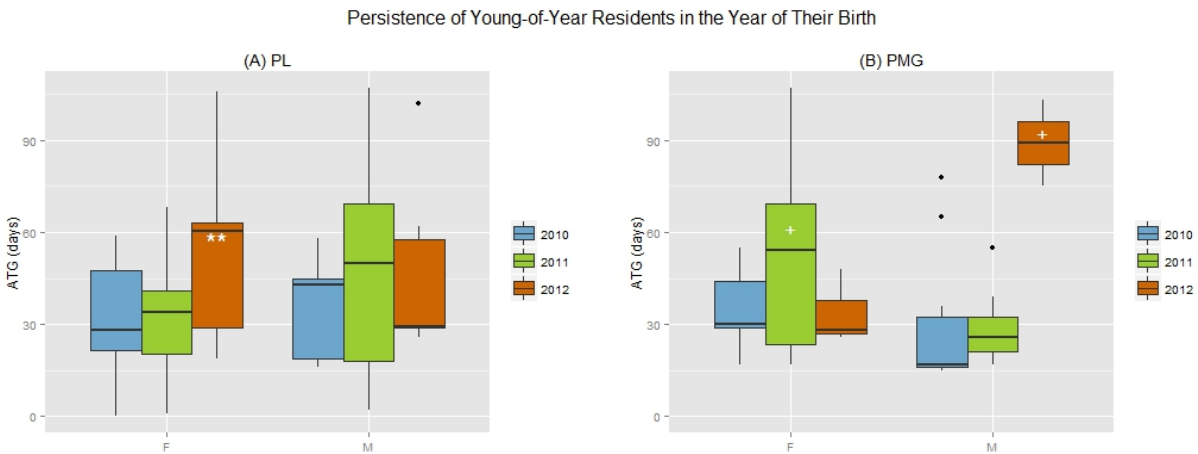
Figure 3-8: Annual persistence (ATG) of YOY resident mice in the year of their birth for (A) PL and (B) PMG. Significance of differences between years in ATG is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

3.5.3.4 PERSISTENCE OF OVERWINTERED RESIDENTS

Reproductive output by overwintered females is often a large contributor to overall reproduction (Lusk and Millar 1989), probably because of increased litter sizes relative to younger mice (Havelka and Millar 2004). Enhanced persistence of OW females could thus lead to greater overall reproduction. I compared annual persistence (ATG) among OW mice in their second year on the grid (i.e., in the year after overwintering).

Differences between species: OW PL females persisted longer in their second year of residency than OW PMG females (t=2.5, df=53, P=0.015). OW PL and PMG males, on the other hand, did not differ in ATG in the second year of residency (P=0.77). ATG of OW PMG was less variable

than for PL, so that more OW PMG were lost in a shorter amount of time, while losses of OW

PL occurred at a more steady rate (Figure 3-9).
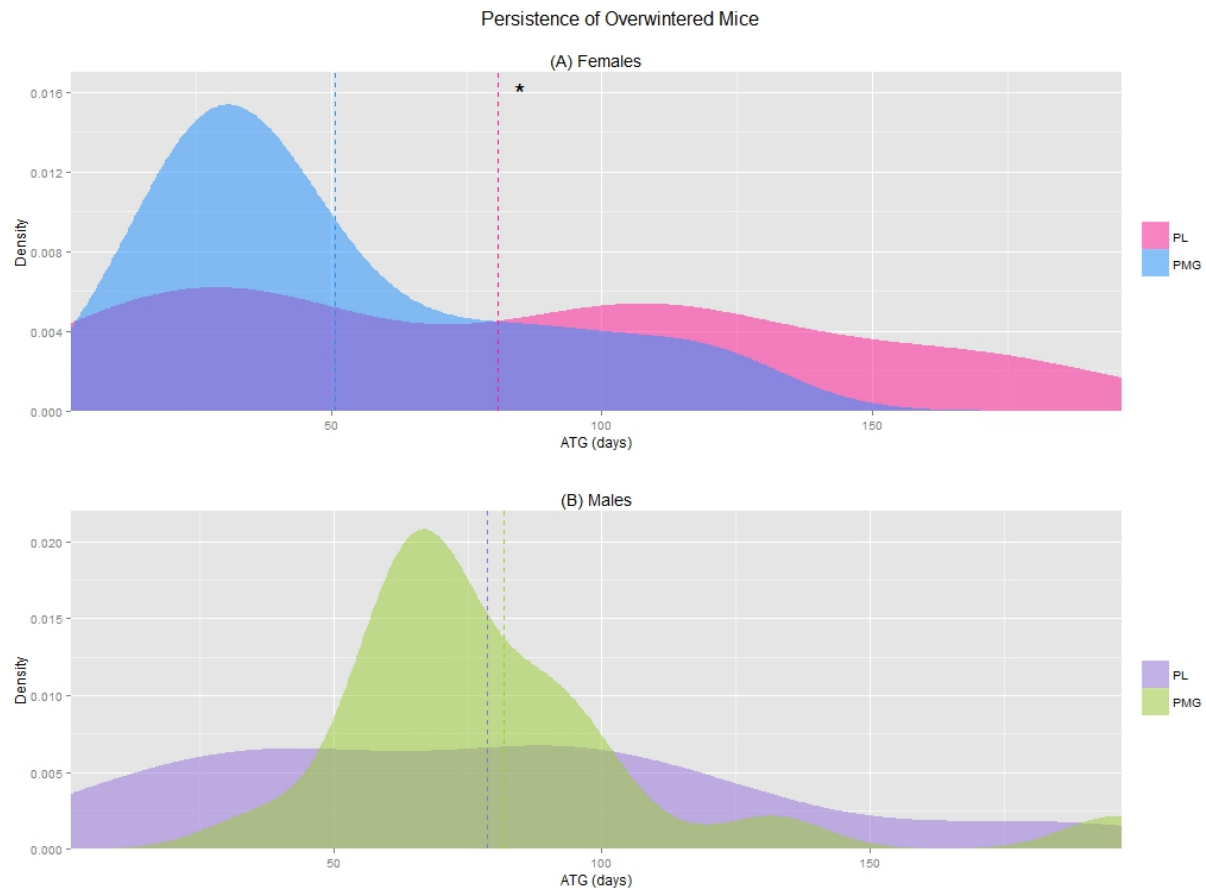
Figure 3-9: Probability density function of the distribution of annual persistence (ATG), shown for OW (A) females and (B) males in the second year of residency. Mean ATG is marked with vertical dashed lines. Significance of differences between species in ATG is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

Within-species variation: OW PL males and females did not differ in annual persistence in the

second year of their residency (P=0.84; Table 3-10). For PMG, in contrast, OW males persisted

longer than OW females (t=-2.8, df=35, P=0.008).

TABLE 3-10: ANNUAL PERSISTENCE (ATG) OF OW MICE

	N	MIN	25%	MEDIAN	MEAN	75%	MAX	SD
PL F	41	2.00	35.00	91.00	80.85	121.00	196.00	57.84
PL M	61	1.00	39.00	72.00	78.62	117.00	197.00	52.58
PMG F	18	14.00	27.00	38.00	50.72**	67.75	121.00	33.29
PMG M	19	36.00	63.50	70.00	81.68**	90.00	196.00	34.58

Table 3-10: Annual persistence (ATG) of overwintered (OW) mice in the second year of residency. Minimum, maximum, median, and mean ATG are reported, as well as 25% and 75% percentiles and standard deviation. Significance of differences between OW male and female residents is marked (+: $0.05 < P < 0.1$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$).

3.5.3.5 COMPARISON OF PERSISTENCE OF OVERWINTERED AND NEW RESIDENTS

To assess whether either survival of new residents (either immigrants or individuals born on the grid) was affected by the presence of OW mice, I compared annual persistence (ATG) of all known OW mice present on the grid in the spring to that of YOY mice that first appeared on the grid in the spring and early summer.

Within-species variation – PL: In 2012, there was no difference in ATG of OW and new residents for either female (P=0.37) or male (P=0.6) PL. OW PL females persisted longer than new PL female residents in 2010 (t=9, df=4, P=0.0007) and 2011 (t=3.6, df=5, P=0.018), but not 2012 (P=0.37). OW PL males persisted longer than new PL male residents in 2010 (t=2.4, df=7, P=0.044), but in 2011 there was a non-significant trend for new PL male residents to persist longer than OW PL males (t=-1.5, df=15, P=0.1).

Figure 3-10: Comparison of annual persistence (ATG) of OW mice in the second year of residency and residents that appeared on the grid in spring/early summer for (A) PL females and (B) PL males. Significance of differences between annual age (OW or new) is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

Within-species variation – PMG: OW and new resident PMG females did not significantly differ in persistence time in 2011 (P=0.44) or 2012 (P=0.64). The one OW PMG female in 2010 persisted longer than new resident females; however, a statistical comparison was not possible. OW PMG males persisted longer than new PMG male residents in 2010 (t=2.5, df=11, P=0.032) and 2011 (t=7.5, df=12, P=8.69E-06), but not in 2012 (P=0.92).
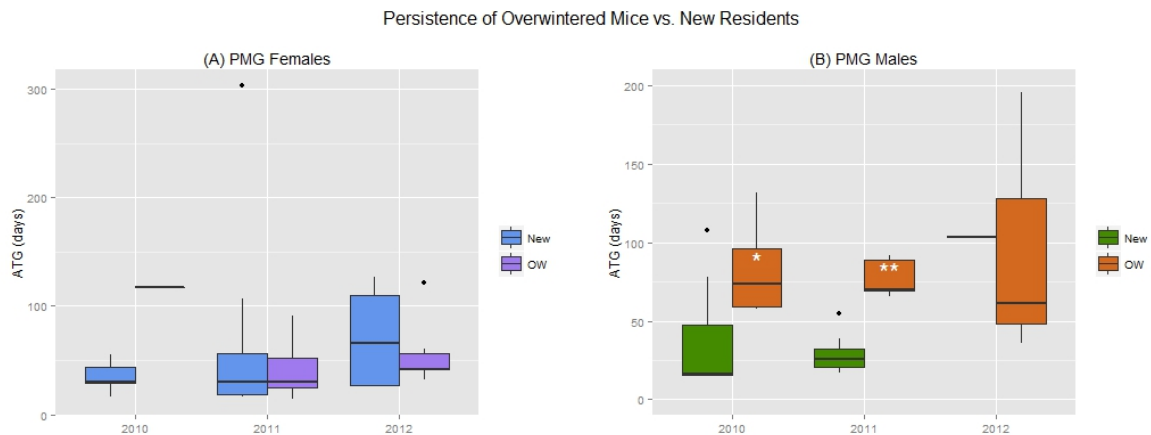
Figure 3-11: Comparison of annual persistence (ATG) of OW mice in the second year of residency and new incoming residents for (A) PMG females and (B) PMG males. Significance of differences between annual age (OW or new) is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

3.6 FACTORS THAT AFFECT SURVIVAL

3.6.1 IMPACT OF FALL WEIGHT ON WINTER SURVIVAL

Size may affect an individual's likelihood of winter survival, if larger mice have a greater amount of energy stored in fat. I compared the average weight of mice that overwintered (OW) and mice that were captured in the fall but did not overwinter (NOW) to assess whether heavier mice were more likely to overwinter than lighter ones. These analyses included only mice whose last recorded weight was measured after the end of August. For PL that overwintered, fall weight was available for 4 mice, 2 female PL and 2 male PL (Table 3-11). These mice were significantly heavier than PL that did not overwinter (t=3.7, df=24, P=0.001).

TABLE 3-11: FALL WEIGHT OF OW AND NOW MICE – PL 2011

	FEMALES			MALES			TOTAL		
	N	WT. (G)	SE	N	WT. (G)	SE	N	WT. (G)	SE
OW	2	22.5	2	2	21.75	0.25	4	22.13***	0.85
NOW	57	15.48	0.38	55	17.92	2.37	112	16.68***	1.18

Table 3-11: Mean fall weight in grams of OW and NOW mice for PL in 2011. The number of mice (N), mean fall weight, and the standard errors of the means are reported for females, males, and all PL. Significance of differences in weight between OW and NOW mice is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

3.6.2 IMPACT OF DATE OF FIRST APPEARANCE (FD) ON ANNUAL PERSISTENCE

3.6.2.1 FD OF RESIDENTS AND NON-RESIDENTS

Do mice that appear on the grid early tend to become residents, while ones that appear later tend to disappear? The date when mice first appear on the grid (FD) may influence social interactions because mice with established territories have an advantage in interference contests over new arrivals (Dooley Jr. and Dueser 1996). In order to assess whether the timing of an individual's

arrival on the grid could influence the probability of establishing residency, I compared the dates of first appearance (FD) of residents and non-residents. OW-NR mice were excluded from these analyses because their FD and AF are unknown. Mice that became residents appeared on the grid significantly earlier than those that did not (PL: t=-8.1, df=322, P<0.0001; PMG: t=-2.9, df=121, P=0.005; Figure 3-12).
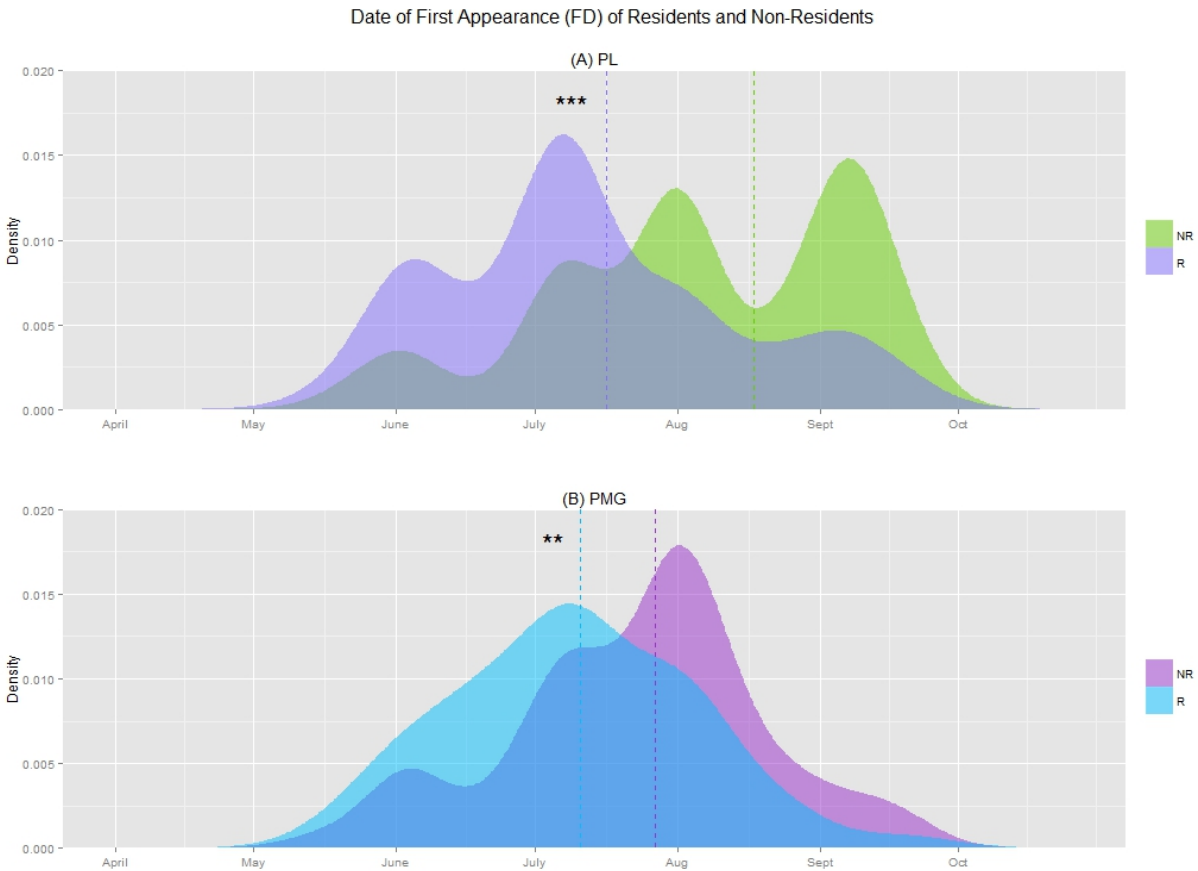
Figure 3-12: Probability density function of the distribution of dates of first appearance (FD) of residents (R) and non-residents (NR) for (A) PL and (B) PMG. Means are marked with dashed lines. Significance of differences between mean FD are marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

3.6.2.2   COMPARISON OF FD AMONG RESIDENT MICE

FD was compared among resident PL and PMG to determine if there were differences between species in the timing of arrival of mice that were able to establish territories.

Differences between species: PMG residents appeared on the grid earlier than PL residents in 2011 (t=3.3, df=68, P=0.002; Figure 3-13), but PL residents tended to appear on the grid earlier than PMG residents in 2012 (t=-1.7, df=16, P=0.1). In 2010, female PL residents tended to appear on the grid later than female PMG residents (t=1.8, df=7, P=0.1), but male PL residents appeared on the grid earlier than male PMG residents (t=-2.1, df=12, P=0.05), resulting in no overall difference between species in FD (P=0.99).
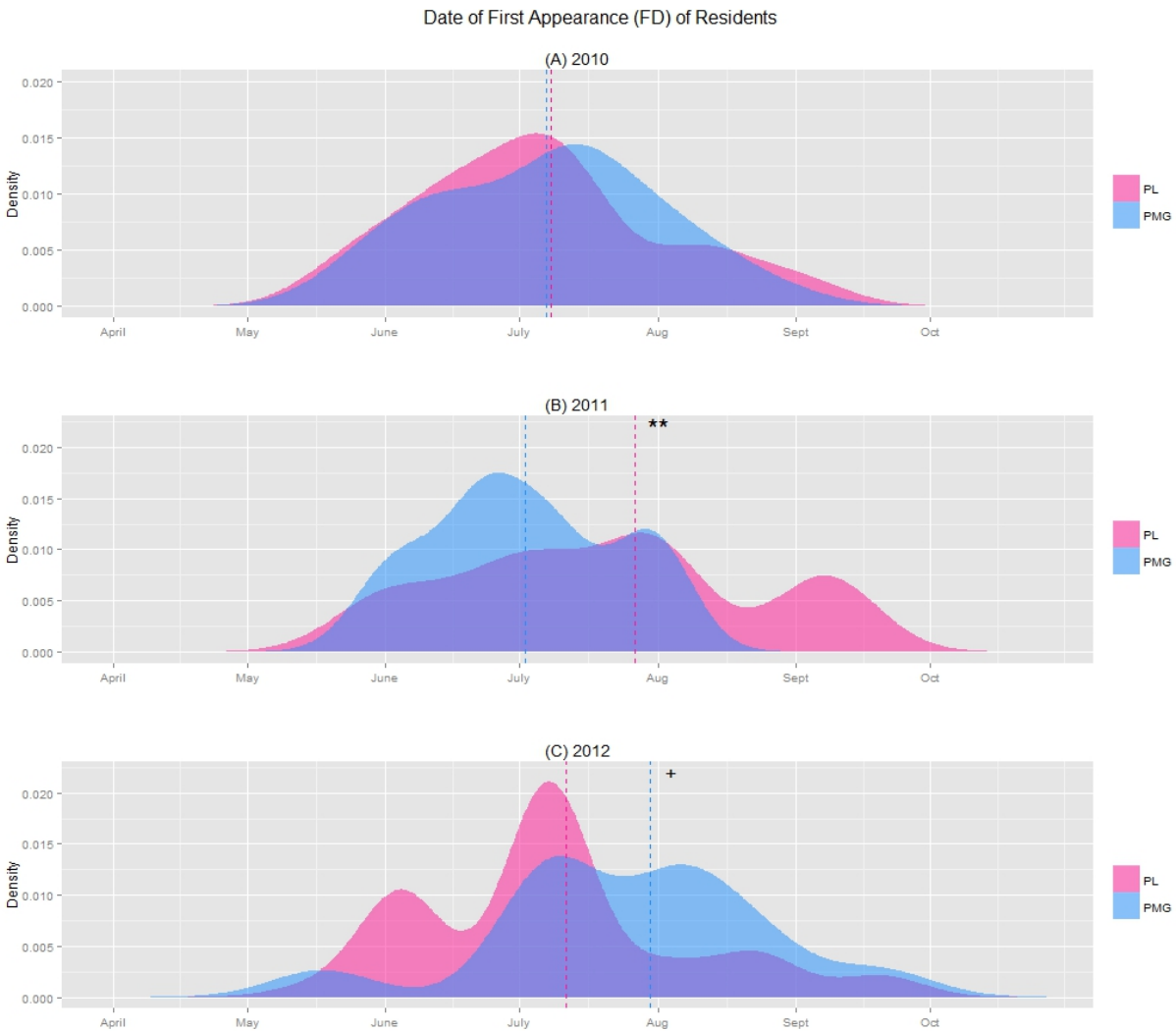
Figure 3-13: Probability density function of the distribution of dates of first appearance (FD) of PL and PMG residents in (A) 2010, (B) 2011, and (C) 2012. Mean FD is marked with dashed vertical lines. Significance of differences between species in FD is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

Within-species variation - PL: PL females that became residents appeared on the grid earlier than PL males that became residents, but this result is marginally insignificant (t=-1.83; df=150; P=0.069; Table 3-12). PL female residents appeared on the grid the latest in 2011, and significantly later in 2011 than in 2012 (t=2.4, df=42, P=0.023). PL male residents appeared earlier in 2010 than in either 2011 (t=-2.4, df=19, P=0.03) or 2012 (t=-2.1, df=14, P=0.05).

PL residents that were first caught as juveniles appeared the earliest of any age class, those first caught as adults appeared the latest, and those first caught as sub-adults had FD intermediate between juveniles and adults (t=3.4, df=79, P=0.027; Figure 3-14A).

TABLE 3-12: AVERAGE DATES OF FIRST APPEARANCE OF RESIDENT MICE - GENDER

	FEMALES				MALES			
	N	FD	MEAN	SE	N	FD	MEAN	SE
2010	7	Jul. 15	105.71	15.56	8	Jul. 1	91.88	8.63
2011	27	Jul. 26	116.48	8.97	29	Jul. 28	118.83	7.64
2012	43	Jul. 1**	92.28	4.93	38	Jul. 23**	113.84	5.75
PL	77	Jul. 11$^+$	101.99	4.53	75	Jul. 22$^+$	113.43	4.30
2010	9	Jun. 16***	76.56	5.23	13	Jul. 22***	113.23	5.04
2011	13	Jul. 9$^+$	99.46	5.51	7	Jun. 21$^+$	81.86	6.82
2012	7	Jul. 20	111.00	14.60	6	Aug. 11	133.17	13.93
PMG	29	Jul. 4$^+$	95.14	5.06	26	Jul. 18$^+$	109.38	5.63

Table 3-12: Average dates of first appearance (FD) of PL and PMG male and female residents in 2010, 2011, and 2012. The number of mice (N), mean FD, and the standard error of the mean (SE) are reported. Mean FD is reported as the number of days from April 1 of each year and the corresponding date. Significance of differences between male and female residents in FD is marked (+: 0.05<P<0.1; *:P<0.05; **:P<0.01; ***:P<0.001).

Within-species variation – PMG: PMG females that became residents appeared on the grid earlier than PMG males that became residents, but this result is marginally insignificant (t=-1.88, df=52, P=0.065). Male and female PMG residents appeared on the grid the latest in 2012 (t=-2.5, df=17, P=0.024). PMG female residents appeared earlier in 2010 than in 2011 (t=-3, df=20, P=0.007), however PMG male residents appeared earlier in 2011 than in 2010 (t=3.7, df=12, P=0.003).

PMG residents that were first caught as adults appeared on the grid significantly later than those first caught as sub-adults (t=2.4, df=15, P=0.032) or juveniles (t=3.4, df=10, P=0.007; Figure 3-14B).
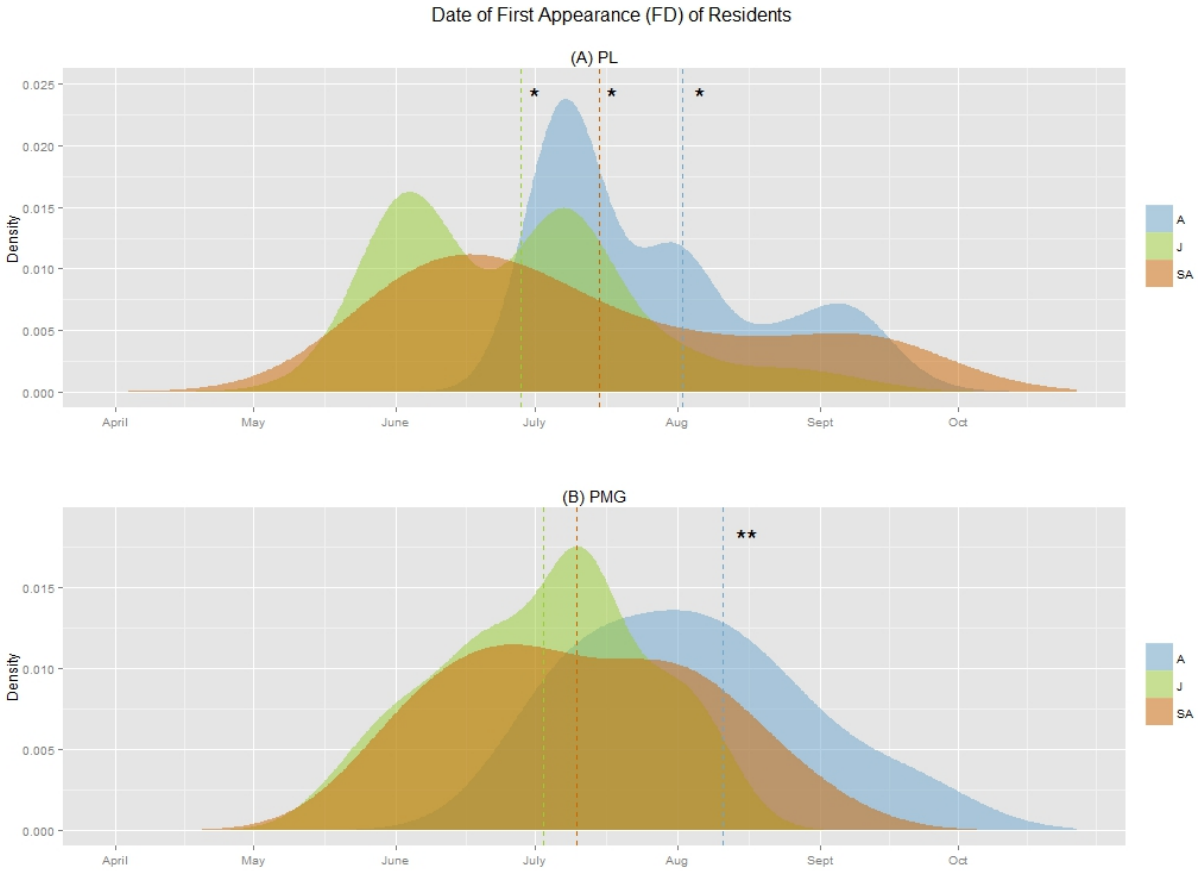
Figure 3-14: Probability density function of the distribution of the dates of first appearance (FD) of resident (A) PL and (B) PMG, compared between residents of different ages at first appearance (AF). Mean FD is marked with dashed vertical lines. Significance of differences between mice of different AF is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

3.7   DISCUSSION

3.7.1   VARIATION IN SURVIVAL AND REPRODUCTION

Shifts in community structure are ultimately caused by differences in reproductive success of the species that make up the community, which is determined by the survival and reproduction of individuals. Extreme morphological and ecological similarities between these two species have been noted by many authors (Horner 1954; Wolff and Hurlbutt 1982; Feldhamer *et al.* 1983; Wolff 1985; Long and Long 1993); however, few studies have provided a detailed examination of population dynamics from communities in which climate-induced replacement is occurring. How do PL and PMG differ in traits relating to survival and reproduction, and how does variation in these traits result in differences in reproductive success?

3.7.1.1   REPRODUCTIVE OUTPUT

The per-capita number of litters is, along with litter size, a direct determinant of the total reproductive output of an individual. I found a maximum of 5 known pregnancies for a single resident female in this study, with an average of 1.7 and 1.2 pregnancies for PL and PMG, respectively. These numbers fall within ranges reported in the literature (Harland *et al.* 1979; Baker 1983; Millar *et al.* 1992). Disparities in PL and PMG abundance were reflected in the per-capita number of litters. PL females had significantly more litters than PMG females on average, and significantly more in 2011 and 2012 (Figure 3-2).

3.7.1.2   LONGEVITY

Studies of laboratory animals suggest that PMG may have a greater maximum lifespan than PL (Dice 1933; Sacher and Hart 1978; Davis 1990; Burger and Gochfeld 1992), which if true, might compensate for differences in long-term reproductive output and slow the rate of faunal turnover. In this study, however, no significant differences between species were found in overall persistence (Table 3-6; TTG, used as a proxy for longevity). TTG values observed in this study fall within the range reported for *Peromyscus* in natural populations (Howard 1949; Snyder

1956; King 1968; Adler and Wilson 1987). In the wild, mortality may be related largely to extrinsic factors and may be independent of age in older mice (Clutton-Brock 1988). Because so few mice approach the physiological limits of longevity (King 1968; Schug *et al.* 1991), differences between species in maximum lifespan may not be relevant to reproductive success.

3.7.1.3 WINTER SURVIVAL

Differences have been noted between PL and PMG, particularly in traits dealing with winter survival. PL is be more vulnerable than PMG to cold winters (Howard 1951); populations of this species have been reported to be nearly extirpated by deep frosts during harsh winters (Long 1973). PMG may be superior to PL in winter adaptations including the use of torpor, nest building, food storage, and lower food consumption (Wolff and Durr 1986; Tannenbaum and Pivorun 1988; Pierce and Vogt 1993), and thus may have an advantage over PL in some years (Long 1996).

There was a non-significant trend for a greater proportion of both species to overwinter in 2011 than in the harsher winter of 2010, which could be explained by differences in winter conditions (Chapter 2). A greater proportion of PL may have overwintered than PMG (Table 3-7). It is possible that current winter conditions in the Great Lakes Region are no longer harsh enough for PMG to have enhanced overwinter survival compared to PL, and that conditions now consistently favor PL. Due to low numbers of overwintering mice of both species in 2010 and overwintering PMG overall, it was difficult to accurately assess differences between species in winter survival using data from this study.

3.7.1.4 CONTRIBUTION OF OW FEMALES TO REPRODUCTION

It has been suggested that much of the variation in individual reproductive success is attributable to longevity and survival (Schug *et al.* 1991; Millar *et al.* 1992). Females that survive longer have more litters than short-lived females (Millar *et al.* 1992). Further, maternal age and parity are correlated with litter size (Havelka and Millar 2004), so that the relationship between

survival and reproductive output may not be linear. Reproductive output by overwintered females is often an important contributor to overall reproduction (Lusk and Millar 1989), in part because of increased litter sizes relative to younger mice (Havelka and Millar 2004). The contribution of OW females to population growth may be constrained by their survivorship in the spring and summer (Millar *et al.* 1979). Though capable of producing up to 4 litters during a single season (Baker 1983), few overwintered individuals survive the entire length of summer and realize their full reproductive potential (Havelka and Millar 2004). Enhanced persistence of OW females could thus lead to greater overall reproduction.

In this study, persistence of OW PL females was consistently longer than that of OW PMG females, and reproductive PMG females were more likely to disappear from the grid than reproductive PL females during the first half of the breeding season (Table 3-8). Loss of OW PMG, both males and females, was concentrated over a period of approximately 60 days in the spring, while losses of OW PL were more evenly distributed throughout the spring and summer (Figure 3-9). Differences in the pattern of persistence of OW females were responsible for differences between species in the per-capita number of litters by this cohort. OW PL females persisted in the population for 23 days longer and produced one more litter on average than OW PMG females.

Differences between PL and PMG in the persistence of OW females also resulted in significant differences between species in the relative contribution of OW and YOY females to total reproduction. Studies suggest that OW females produce more litters on average than YOY females (Harland *et al.* 1979). This relationship was observed for PL in all years of this study, but PMG OW and YOY females did not differ in the per-capita number of litters produced, except in 2012 when no PMG YOY bred (Table 3-5).

3.7.1.5 REPRODUCTIVE RATE (TIME BETWEEN SUCCESSIVE LITTERS)

Longer-lived individuals have more lifetime opportunities to breed (reviewed in Clutton-Brock 1988); however, long life does not necessarily correlate with greater reproductive success. Individuals that reproduce quickly during a short life may be equally as successful as those that

live a long time and reproduce at a slower rate, depending on the survival and reproduction of offspring (Stearns 1976). In this study, I found no differences between species in the frequency with which breeding females produce litters (Table 3-4), which is consistent with reports from other studies suggesting that there may be less variation in the frequency of litters than in other reproductive traits (Millar *et al.* 1979; Schug *et al.* 1991).

Nonetheless, some variation in the average time between litters was observed for PMG YOY females. Breeding YOY PMG had litters most often 2010 (approximately once per month) when total adult density was low, but produced litters less frequently in 2011 (once every 44 days) when total density of adults was high. High population density may cause the rate of reproduction to slow; several studies have reported a negative correlation between population density and reproductive activity and output in *P. leucopus* (Burt 1940; Manville 1949).

At high densities, waiting longer between successive pregnancies may be beneficial to the survival of young. The number of young weaned may be inversely proportional to the number of adults in the population (Rintamaa *et al.* 1976). Increased duration of maternal care enhances the survival and growth of neonates (Harland and Millar 1980), and growing to a larger size may allow newly-emerging young to establish territories with greater ease (Garten 1976; Bowers and Smith 1979). In species that experience post-partum estrus, nursing of a litter may be terminated abruptly by parturition; young from the older litter are often forced out of the nest when a new litter is born (Svihla 1932). Thus, if the time between two successive litters is too short, young may be forced to leave the nest even though they would still benefit by continued maternal care.

3.7.1.6   AGE AT FIRST REPRODUCTION

The age at first reproduction may influence population growth more than either longevity or the number of litters produced (Cole 1954), and small changes in this trait have the potential to greatly impact population abundance. Females of both species reach sexual maturity at approximately 44 days after birth (King 1968), but not all YOY begin breeding at this age. PL and PMG in northern Michigan typically breed in the summer of their birth (Myers *et al.* 2005); however, young that are born close to the end of the breeding season often delay the onset of reproduction until the following spring (Howard 1949). One explanation for this is that delaying reproduction increases

survivorship of young. In this study, late-appearing mice were significantly less likely than early appearing ones to remain on the grid (Figure 3-12), suggesting either increased mortality or emigration. Late-born young may have a disadvantage finding and establishing territories necessary for breeding; they may also be smaller than early-born young at the onset of winter, decreasing their chances of surviving until the spring (Table 3-11).

Further, though maternal age is correlated with litter size in both PL and PMG (Millar *et al.* 1992; Havelka and Millar 2004), prior reproductive experience may not be necessary. Litter size increases from the first to subsequent litters among females breeding in their natal year, but not among females that first bred as overwintered adults (Havelka and Millar 2004). For those YOY that delay reproduction, some of the costs incurred by not breeding in their year of birth may be compensated by higher litter sizes when they do begin to breed.

In this study, approximately 70% of YOY resident females bred in their natal year (Table 3-5). YOY residents of both species tended to first appear on the grid in early July (Figure 3-14), and the proportion of YOY residents that appeared after mid-August was not significantly different between species (PL: 11/90; PMG: 1/46; P=0.12). Thus, comparisons of the proportion of breeding YOY between species should not be affected by differences in the number of late-arriving YOY residents. There was no difference between species in the proportion of known YOY females that bred in the year of their birth in 2010 or 2011, and this proportion did not vary between years. There was, however, one notable exception.

In 2012, there was a significant reduction in the proportion of breeding PMG YOY. While 15 out of 21 YOY PMG resident females bred in their natal year in 2010 and 2011, none (out of 4) bred in 2012 (Table 3-5). Trap records for these individuals were regularly spaced, and three were trapped on the grid as non-breeding adults. This suggests that the observed reduction in the proportion of breeding YOY PMG reflects a real difference in the population.

One possible explanation for delayed onset of first reproduction in YOY PMG is the increased density of breeding adult PL, which caused increased total density of breeding adults even though PMG numbers were low. Socially induced reproductive inhibition of YOY females by OW females has been demonstrated in natural populations of *P. maniculatus* where YOY do not typically breed in their natal year (Haigh 1983), such that the removal of OW females results in

sexual maturation and breeding of YOY (Lusk and Millar 1989). The number of YOY that breed appears to be influenced by the density of mature females present (Lusk and Millar 1989). Little is known regarding reproductive inhibition in Michigan PL and PMG, possibly because YOY usually breed in their natal year.

3.7.1.7 EASE OF ESTABLISHING TERRITORIES

It has been suggested that PL and PMG are territorial and the victor in aggressive contests is usually the resident rather than the intruder (Dooley Jr. and Dueser 1996). Thus, the high rates of loss of newly-appearing mice (those that did not become residents), while not a direct indicator of reproductive success per se, may reflect the difficulty with which mice establish territories. Rates of loss of new mice (either those that immigrated or YOY born on the grid) were similar for female PL and PMG, and newly appearing females of both species were more likely to become residents if they first appeared on the grid as juveniles (Figure 3-6). On the other hand, juvenile male PMG were more likely than juvenile male PL to become residents (Table 3-9). The proportion of PMG that became residents did not change annually; however, PL were less likely to become residents in 2011 than in 2010 or 2012 (Table 3-9). These results suggest that newly-appearing PL experienced either higher mortality or were more likely to emigrate in 2011, but that PMG were not affected in the same way. I suggest in Chapter 4 that this may have been caused by a later onset of breeding of PL relative to PMG in 2011.

Juvenile males were the least likely of all demographic categories to establish residency in this study, which is consistent with results from other studies (Harland *et al.* 1979). It may be beneficial for younger females to quickly establish territories and find suitable nesting sites in preparation for reproduction. Males, on the other hand, tend to have larger home ranges and explore more new areas (King 1968, Harland *et al.* 1979), and may experience higher mortality rates as juveniles than females (Harland *et al.* 1979). Adult males may also be aggressive towards younger males and may negatively impact survival (Sadleir 1965; Petticrew and Sadleir 1974).

3.7.1.8 SOCIAL INTERACTIONS AND SURVIVAL

Social interactions, including the effect of OW females on YOY females, may also be reflected in survivorship. Females maintain exclusive home ranges during the breeding season (Metzgar 1971; Harland *et al.* 1979) and may be limited by the availability of nest sites rather than food resources (Lusk and Millar 1989). When density is high, reduced availability of territories may result in increased aggressive social interactions, with negative impacts on survivorship and reproduction. Further, OW females are more likely to win aggressive contests over YOY, both because of their potentially larger size and because they have already established residency (Dooley Jr. and Dueser 1996). If this is true, then mice that appear on the grid early should be less likely to disappear from the grid than those that appear later, and persistence of immigrating YOY should be negatively correlated with persistence of OW residents.

Results from this study are consistent with these predictions. A mouse that appeared on the earlier grid was more likely to establish residency than one that arrived later (Figure 3-12). For both species, persistence of new YOY females was negatively correlated with persistence of OW females (Figure 3-10A; Figure 3-11A). Though the cause of this relationship is unknown, this result suggests that social interactions can have an effect on survival and reproduction.

3.7.2 EXPLAINING PATTERNS OF PL AND PMG ABUNDANCE

Changes in the pattern of relative abundance of PL during this study indicate that community structure shifts from an equal composition of PL and PMG in late 2010 and early 2011 to a community composed of mainly PL (Chapter 2). What caused the disparities in relative abundance observed in 2011 and 2012, and why did the same not occur in 2010?

PL and PMG were found in approximately equal abundance in 2010 (Chapter 2). YOY PMG averaged more litters in 2010 than in any other year, and significantly more litters than YOY PL (Figure 3-3). OW PMG females, however, averaged fewer litters than OW PL females due to reduced spring/summer persistence. This suggests that in 2010, increased reproduction by YOY females compensated for reduced reproduction by OW females, resulting in approximately equal population growth due to reproduction (Figure 3-15).
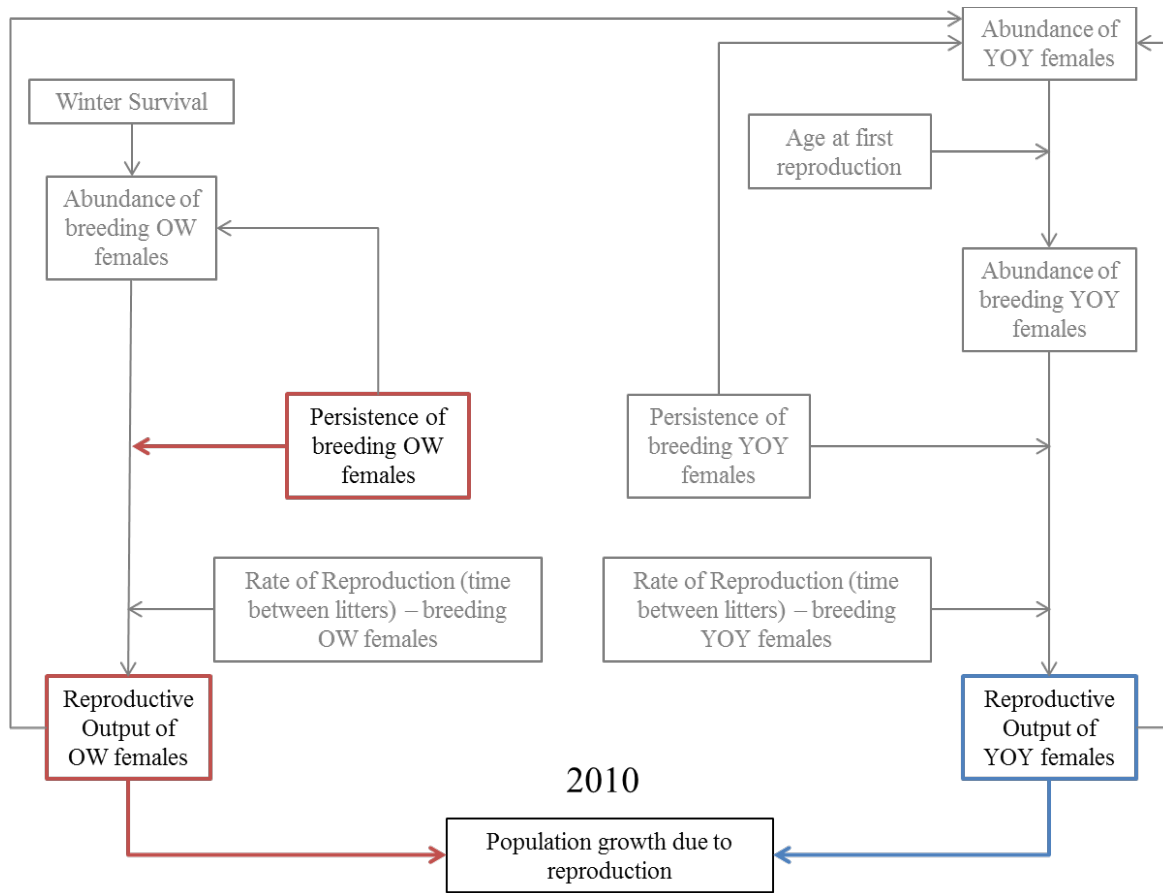
Figure 3-15: Comparison of survival and reproduction of PL and PMG in 2010. Gray boxes and arrows indicate traits in which PL and PMG did not differ. Colored boxes and arrows indicate observed differences between species. Color of boxes represents advantages of PL (red) and PMG (blue).

In 2011, abundance of PL and PMG was similar until mid-July, but PL outnumbered PMG thereafter (Chapter 2). Enhanced persistence of OW PL females may explain increased PL abundance. On average, OW PL females persisted about 23 days longer than OW PMG females, but this difference was roughly double that in 2011. OW PL females also survived longer in 2011 than in any other year. Based on comparisons of PMG abundance in 2010 and 2011, I suggested in Chapter 2 that PMG may have suffered reductions in population growth after mid-July 2011. There is some evidence to support that claim. PMG YOY produced fewer litters but persisted longer on the grid in 2011 than in 2010. A combination of enhanced persistence of PL OW females and reduced reproductive rates in PMG YOY resulted in numerical dominance of PL in 2011 (Figure 3-16).
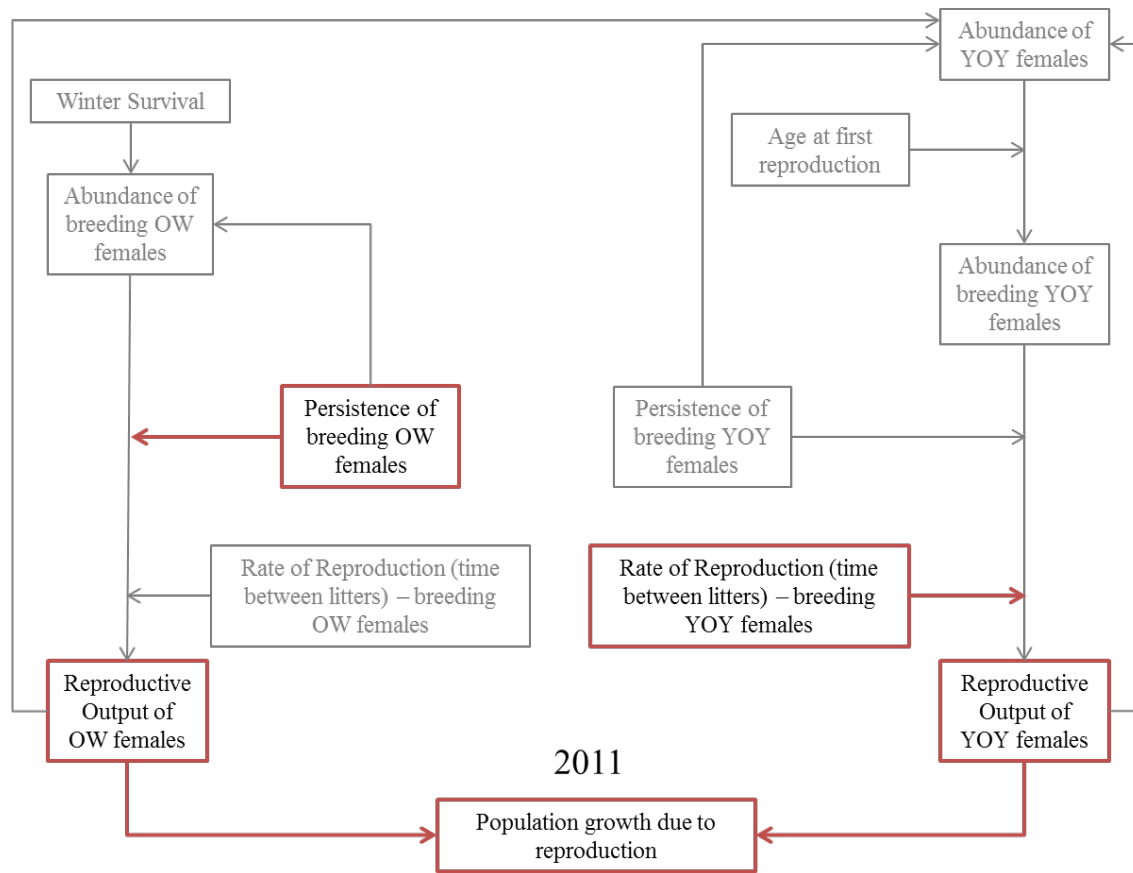
Figure 3-16: Comparison of survival and reproduction of PL and PMG in 2011. Gray boxes and arrows indicate traits in which PL and PMG did not differ. Colored boxes and arrows indicate observed differences between species. Color of boxes represents advantages of PL (red) and PMG (blue).

In 2012, spring abundance of both PL and PMG were higher than in previous years, probably due to the relatively mild and short preceding winter. Abundance of PL grew at a higher rate and to a greater maximum than PMG, and relative abundance of PL remained above 80% for much of the year. Abundance of PMG was significantly lower in 2012 than the previous years due to reduced abundance between July and September (Chapter 2). YOY PL females both produced more litters and persisted longer in 2012 than in any other year, suggesting that enhanced survival allowed for proportionally more reproduction. In contrast, no YOY PMG bred in 2012, significantly reducing population growth in this species. These factors led to numerical dominance of PL throughout the year (Figure 3-17).
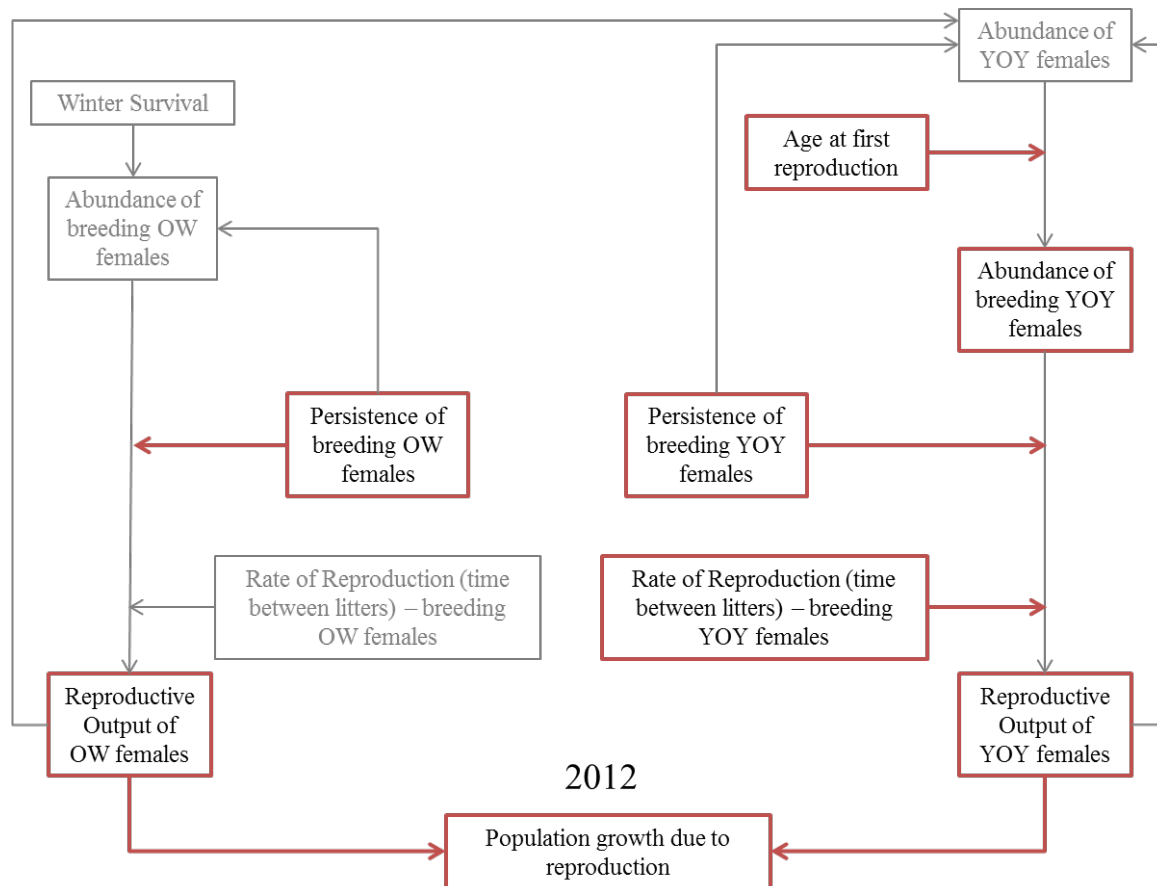
Figure 3-17: Comparison of survival and reproduction of PL and PMG in 2012. Gray boxes and arrows indicate traits in which PL and PMG did not differ. Colored boxes and arrows indicate observed differences between species. Color of boxes represents advantages of PL (red) and PMG (blue).

Survival and reproductive rates measured in this study exhibited high individual variation, which is consistent with the literature (Millar *et al.* 1992). Nonetheless, PL and PMG may inherently differ in the pattern of spring/summer persistence of OW females, resulting in significant differences between species in the relative contribution of OW and YOY females to total reproduction. No other consistent differences in survival and reproduction were found; however, in each year PL and PMG differed in other aspects of survival and reproduction, and unique combinations of these differences led to the observed patterns of abundance (summarized in Table 3-13).

TABLE 3-13: DIFFERENCES IN SURVIVAL AND REPRODUCTION

	PATTERN	PL	PMG
2010	Equal Abundance	Enhanced survival of OW	Reduced survival of OW Increased reproduction by YOY
2011	More PL, especially after July	Enhanced survival of OW*	Reduced survival of OW Reduced reproduction by YOY
2012	More PL	Enhanced survival of OW Enhanced survival of YOY	Reduced survival of OW No reproduction by YOY

Table 3-13: Summary of differences between PL and PMG in survival and reproduction that contribute to patterns of abundance observed during this study.

Results suggest that increases in abundance of PL are well explained by survival (persistence of OW and YOY females leads to more reproduction). Decreases in abundance of PMG, on the other hand, are associated with reduced reproductive rates (in 2011) and delayed onset of first reproduction (in 2012) of YOY females. In each successive year, reproduction by PMG YOY was reduced, and this coincided with increasingly large disparities in PL and PMG abundance.

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CHAPTER 4.

BREEDING SEASON LENGTH OF SYNTOPIC *PEROMYSCUS LEUCOPUS* AND *PEROMYSCUS MANICULATUS GRACILIS* IN NORTHERN MICHIGAN

4.1   SUMMARY

Climate-induced ecological replacement of the 'northern' *P. m. gracilis* by the 'southern' *P. leucopus* has been documented with long-term studies in the Great Lakes Region (Long 1996; Myers *et al.* 2005). Gradually warming winters over the last 30-40 years in this area have facilitated northward range expansion of *P. leucopus*, and communities in which *P. leucopus* and *P. m. gracilis* co-occur have become characterized by strong numerical dominance of *P. leucopus* (Myers *et al.* 2009). I monitored syntopic populations of *P. leucopus* and *P. m. gracilis* at a site in northern Michigan from 2010-2012. Abundance of *P. leucopus* was significantly greater than that of *P. m. gracilis* in two out of three years, and disparities in abundance resulted from both increases of *P. leucopus* and decreases of *P. m. gracilis* (Chapter 2). In Chapter 3, I found that differences between species in survival of overwintered (OW) and young-of-year (YOY) females led to increased reproductive output of *P. leucopus*. Slowed population growth rate of *P. m. gracilis* were due to slowed reproductive rate of YOY females (in 2011) and delayed onset of first reproduction (in 2012).

In this chapter, I investigated the seasonal breeding patterns of syntopic *P. leucopus* and *P. m. gracilis* and assessed the dates of onset and cessation of breeding and the length of the breeding season. I found that *P. leucopus* experiences a breeding season that is 24 days longer than *P. m. gracilis*. Patterns observed during this study were consistent with the hypothesis that early breeding is advantageous in years following mild winters and disadvantageous when winters are

more harsh. I propose that an earlier onset and later cessation of breeding in mild conditions confers both a numerical and competitive advantage to *P. leucopus*. Patterns in reproductive rates, particularly in the decrease in the proportion of breeding young-of-year *P. m. gracilis*, suggest that the disadvantages of a later onset of breeding may manifest in a density-dependent manner.

I also investigated rates of botfly infestation and the effect of infestation on reproductive patterns and the distribution of births across the year. I found that bot fly infestation was highest in 2012, consistent with reports that rates of infestation are highest following years of high mouse abundance (Burns *et al.* 2005). The seasonal distribution of *P. leucopus* births in 2012 also suggests that the reproductive output of this species was less than its potential in July and August, and bot fly infestation is a potential cause. Differential prevalence of bot fly infestation may thus have the potential to slow the rate of faunal turnover.

4.2   INTRODUCTION

As winters in the northern Great Lakes region have become shorter and milder over the last 30 years, the range of the 'southern' white-footed mouse, *Peromyscus leucopus*, has expanded by several hundred kilometers, coinciding with a decline in abundance of residents in sympatrically-occurring populations of the 'northern' woodland deer mouse, *P. maniculatus gracilis* (Myers *et al.* 2005). Myers *et al.* (2005) suggested that the decline in *P. m. gracilis* populations and concurrent rise in *P. leucopus* were attributable to long term climatic trends, particularly the overall decrease in the length of winter in this area.

I documented abundance of *P. leucopus* and *P. m. gracilis* in northern Michigan for 3 years, and I found that changes in relative abundance were consistent with faunal turnover, and at least some of this pattern may be influenced by winter conditions (Chapter 2). For example, in 2012, following the mildest and shortest winter encompassed by this study, *P. leucopus* had a greater reproductive output than *P. m. gracilis*. While increase in abundance of *P. leucopus* has been

well documented in this area, both the biological mechanisms that allow increased reproduction and the nature of the advantage conferred to this species under mild conditions are unclear.

In Chapter 3, I investigated differences between species in survival and reproduction, and I found that differences in survival, especially of overwintered (OW) females, led to increased reproductive output of *P. leucopus*. While no other consistent differences were found, small differences in the rate of reproduction and the proportion of young-of-year (YOY) that bred in their natal year were observed. Unique combinations of small differences between species in survival and reproduction may explain the observed changes in annual reproductive output.

In addition to the survival and rate of reproduction (i.e., the time between successive litters) of individuals within a population, breeding season length can greatly influence total annual reproductive output. It has been suggested that *Peromyscus* with short breeding seasons have a lower annual reproductive output than *Peromyscus* with longer breeding seasons (Millar *et al.* 1979). The length of the breeding season varies geographically among *Peromyscus* populations, from 2-3 months in Wyoming (Brown 1966) and Canada (Fuller 1969) to 10-12 months in the central United States (Brown 1964). Not surprisingly, the general trend is that individuals in colder, northern, or alpine environments have the shortest breeding seasons (Millar *et al.* 1979; Millar and Innes 1985).

Variation between years in the onset and cessation of breeding at a locality has long been suggested to be related to environmental factors for many small mammals (Jewell 1966; Sadleir 1970), including *P. leucopus* and *P. maniculatus* (Jameson 1953; Sheppe 1963; Brown 1964; Sadleir 1974). The seasonal cycle of changes in day length (photoperiod) is one cue that many temperate-zone mammals use to regulate reproductive timing (Heideman *et al.* 1999), and it has been suggested that photoperiod may be a primary cue for the initiation of spring breeding by *P. maniculatus* (Price 1966; Millar and Herdman 2004) and *P. leucopus* (Whitaker 1940; Heideman *et al.* 1999). Spring breeding is stimulated by increasing photoperiod and is mediated by temperature such that breeding begins following sudden rises in temperature that coincide with increasing day length (Sadleir 1974).

An influence of temperature on both the onset and cessation of breeding is expected given the known effects of temperature on metabolic processes (Hayward 1965a; Sadleir *et al.* 1973).

Newborn mice suffer decreased growth rates at low temperatures and require greater maternal care in the nest (King 1968; Harland and Millar 1980). Breeding females must balance this need with longer bouts of foraging outside the nest to meet the energetic requirements of lactation (Millar and Innes 1985; Millar *et al.* 1990). Reproduction in harsh conditions can thus result in both reduced maternal survival and reproductive success.

The cessation of breeding in higher latitude populations is thought to be closely tied to declining temperature. Winter breeding in these populations is reported to be rare (Linduska 1942; Jameson 1953; Brown 1945; Millar *et al.* 1979), probably because low winter temperatures increase maintenance costs (Sadleir *et al.* 1973) and energy requirements of lactation (Harland and Millar 1980) cannot be met. It is thus advantageous for mice to cease breeding from mid-summer onwards when temperatures decline so that subsequent lactations will not occur (Sadleir 1974).

Individuals in syntopic populations of *P. leucopus* and *P. m. gracilis* experience the same climatic conditions; thus, if they differ in breeding season length, the explanation must lie in species-specific responses to environmental cues such as temperature or photoperiod. Because *P. m. gracilis* prefers cooler, more boreal microclimates (Long 1996), and because there is often a positive correlation between temperature and initiation of breeding (Hayward 1965b; Millar and Gyug 1981), *P. m. gracilis* may begin reproducing later than *P. leucopus* due to its microhabitat associations.

Bot fly (*Cuterebra* sp.) parasitism of *P. leucopus* and *P. maniculatus* is widespread in natural populations (Wecker 1962; King 1968; Burns *et al.* 2005), and infestation has the potential to alter both individual reproductive output and population-wide breeding patterns. Mounting evidence indicates that bot fly infestation enhances survival (Wecker 1962; Goertz 1966; Hunter *et al.* 1972; Munger and Karasov 1991; Clark and Kaufman 1990; Burns *et al.* 2005), but negatively impacts reproduction. Infested females have fewer litters and fewer total offspring than uninfested females (Burns *et al.* 2005), and parasitized males have considerably compromised gonadal development (Wecker 1962; Timm and Cook 1979), suggesting a diversion of resources from reproduction to body maintenance (Burns *et al.* 2005). Population growth rates may also be negatively correlated with infestation prevalence (Burns *et al.* 2005).

In this chapter, I investigate the seasonal breeding patterns of syntopic *P. leucopus* and *P. m. gracilis*. I assess the dates of onset and cessation of breeding, the length of the breeding season and the distribution of births across the year. I also investigate rates of botfly infestation and the effect of infestation on reproductive patterns. The advantage conferred by a longer breeding season could lead to the differences in survival and reproduction observed in Chapter 3.

4.3   METHODS

I monitored syntopic populations of *P. leucopus* and *P. m. gracilis* in the Pigeon River State Forest in northern Michigan from April to October for three consecutive years. Individual mice were tagged with unique identification numbers. Age, reproductive status, and mass were recorded during each capture. Three age classes were recognized based on pelage characteristics – juvenile (J, uniformly gray pelage), sub-adult (SA, presence of molt lines), and adult (A, brown dorsal pelage and white ventral fur). Reproductive condition of females was assessed as either non-reproductive (NT, nipples not visible) or reproductive (NE, nipples visible). Mice were weighed to the nearest 0.5 grams. Please refer to Chapter 2 for a complete trapping protocol.

The first trapping sessions in all years were timed to occur at least two weeks before the first emergence of young-of-year mice. In 2010 and 2012, trapping sessions began in early April to document numbers and survival of overwintered adults; juveniles were not present in trapping records until mid- to late May. No trapping was done during April 2011; trapping in May began 2 weeks before either reproductive females or juveniles appeared. Differences found in in the timing of the onset of breeding in 2011 thus reflect actual differences in breeding patterns rather than an artifact of sampling.

4.3.1   DETECTING PREGNANCIES

Pregnancies were detected in the field using visual cues and supplemented with longitudinal data documenting fluctuations in body weight. Changes in body weight of pregnant females have

been well documented, primarily in laboratory mice (Millar 1982; Millar and Innes 1985; Millar 1985); weights observed during this study were consistent with these reports. Typical weight of non-breeding adult *P. leucopus* and *P. m. gracilis* is approximately 19-21 grams (King 1968; Millar 1982; Millar and Innes 1985; Millar 1985). Body weight remains relatively low for much of pregnancy, then increases dramatically a few days before parturition; a pregnant female 1-2 days prepartum may be approximately 79% heavier than non-breeding females (Millar 1975). Visual signs of pregnancy have been reported to be detectable as early as 5 days into gestation, and pregnancy becomes increasingly obvious as parturition approaches (Millar *et al.* 1979). Body weight is reduced immediately after parturition, but remains approximately 20% greater than non-breeding weight throughout lactation (Millar 1975).

A female's nipples enlarge in preparation for lactation shortly before she gives birth to her first litter. In this study, the exact date of parturition is known for 3 females that gave birth while inside a Sherman trap. The nipples of these 3 females become exposed about 3-4 days before parturition, around the 19th day of pregnancy assuming 23 days for gestation. Due to continual breeding (Sharpe and Millar 1991), nipples remain visible throughout the breeding season. They recede after a female weans her last litter of the season. Based on longitudinal records for 10 mice from 2012, the minimum length of time it takes for nipples to recede after the birth of a litter is about 54 days. Because there is no winter breeding in Michigan *Peromyscus* (Myers *et al.* 2005), overwintered females captured in the spring have small nipples. Thus, when overwintered females are found with enlarged nipples, they are likely to be pregnant. In some cases, records of changes in reproductive status in the spring could be used to estimate a date of parturition when records were not frequent enough to document changes in weight. For each female for which data were available, the number of known pregnancies and estimated dates of parturition were recorded.

4.3.2   ESTIMATES OF THE NUMBER OF MICE BORN

4.3.2.1   ESTIMATING DATES OF BIRTH FROM PREGNANCIES

To estimate the number of mice born from known pregnancies, each pregnancy was assigned a litter size that was randomly drawn from possible values of between 3 and 6, based on reports of mean litter size of *P. leucopus* and *P. maniculatus* (Svihla 1932; King 1968; Baker 1983; Millar 1985). Each known pregnancy was assumed to result in a successful litter, and no losses were assumed to occur prior to weaning.

Because of gaps in longitudinal trapping records, it is likely that some pregnancies that occurred on the grid escaped detection. Nonetheless, analyses that compare *P. leucopus* and *P. m. gracilis* should not be biased unless there are differences between species in nestling mortality or trappability. Longitudinal records were used to assess trappability (i.e., the likelihood that a mouse is captured after it encounters a trap). I compared the number of times an individual was caught to the number of times that it could have potentially been caught, then compared the proportion of captures between species using either Chi-squared analysis or Fisher's Exact test. Data from this study were insufficient to investigate nestling mortality. Nestling mortality is variable (estimates of 12-50% mortality have been reported) but does not appear to differ significantly between *P. leucopus* and *P. maniculatus* (Howard 1949; Fairbairn 1977; Sullivan 1977; Harland *et al.* 1979).

4.3.2.2   ESTIMATING DATES OF BIRTH BASED ON PELAGE AND JUVENILE WEIGHT

I estimated a date of birth for all individual mice based on the age at which they first entered the population, which is an estimate of the latest possible date of birth. The life cycle is similar for many species of *Peromyscus*, including *P. leucopus* and *P. m. gracilis* (King 1968; Baker 1983; Lackey *et al.* 1985). Age classes are associated with distinct pelage characteristics, and developmental molts occur with known chronology during the developmental process (Collins 1923). Weaning of young is usually complete by the time young are 21 days old (King *et al.* 1963), after which they are able to leave the nest and enter into the trappable population. The post-juvenal molt, during which gray pelage characteristic of juveniles is replaced with brown

fur typical of adults (King 1968), begins at 40 to 45 days of age (Nicholson 1941). The duration of the molt from the first appearance of new pelage averages about 25 days (Storer *et al.* 1944; Gottschang 1956), and is complete roughly 65 to 70 days after birth (Gottschang 1956; Nicholson 1941; Baker 1983).

Body weight is tightly associated with age in juveniles (King 1958, 1968; King and Eleftheriou 1959). At three weeks old, approximately the age at which weaning is complete and mice leave the nest on their own, body weight is about 11 grams and roughly 50% of mature weight (Dice and Bradley 1942; King 1958, 1968). At four weeks after birth, mice weigh about 60% of mature weight, or about 13 grams (King 1968). Due to the close association between age and postnatal growth, I estimated date of birth for 'small' (under 11 grams) and 'large' (11 or more grams) juveniles as 21 or 28 days before the date of first capture. Trends in body weight in older mice tend to be less regular than in juveniles (Dice and Bradley 1942; King 1968), and I made no attempt to more precisely determine age for older mice. Date of birth for mice that entered the grid as sub-adults or adults was estimated as 45 or 70 days prior to the date of first capture, respectively.

4.3.3   LENGTH OF BREEDING SEASON

All estimated dates of birth were combined into a single dataset, from which dates of onset and cessation of breeding, as well as the length of the breeding season, were calculated for *P. leucopus* (PL) and *P. m. gracilis* (PMG) for each year of the study. Because the total number of births was estimated by combining estimates from these two methods, some mice were counted twice – once when it first appeared on the grid, and once because the individual's mother was trapped while pregnant.

The breeding season is considered to be the period of time during which reproduction is occurring in a population, and is sometimes calculated as the time between the first and last recorded births of the season (Millar *et al.* 1979; Tkadlec 2000). Evidence suggests that the onset of breeding among overwintered females is synchronized (Sadleir 1974); however, variation in the responsiveness of mice to cues regulating the onset of breeding (Heideman *et al.*

1999) could result in abnormally early or late breeders that are not representative of the population as a whole.

I thus estimated the length of the breeding season as the interval between 10th and 90th percentiles of all estimated births within each year. This estimate was chosen because it is routinely used to assess breeding season length in birds (Evans *et al.* 2005; Moller *et al.* 2010; Gullett *et al.* 2013). The beginning/onset and end/cessation of breeding were defined as the date on which 10% and 90% of all births had occurred, respectively. Mean breeding season length, dates of onset and cessation, and dates of first and last birth were compared between PL and PMG using analysis of variance (ANOVA). The dates of the first and last known births were compared to estimates of population-wide dates of onset and cessation in order to assess individual variation. All statistical analyses were conducted in R, version 3.02 (R Development Core Team 2013).

4.3.4   SPRING GROUND TEMPERATURE

To investigate the possible effect of microhabitat associations on the initiation of breeding, I measured below-ground temperature of randomly selected and evenly spaced trap locations. Temperature was measured at 51 total trap sites (33 in 2011 and 18 in 2012) with Thermochron iButton temperature data loggers from Maxim Integrated Products (San Jose, CA, U.S.). iButtons were buried 5 inches deep at each site and logged temperature 6 times a day from November through May.

Mean spring temperature was calculated for each trap site as the average of all temperatures logged between March 1 and April 30. Because there appeared to be a clear transition from the colder and less variable temperatures of winter to warmer spring conditions, I calculated an additional summary measure for each site. This measure, the 'date of warming', was determined for each site as the date when logged temperatures exceeded the average spring temperature for that site.

Because only a small fraction of sites were sampled with iButtons, I recorded the number of PL and PMG captures in a 40m radius around each site. Trap records prior to June 22 were used in

order to restrict analysis to spring captures. I assessed trends in the number of female PL and PMG captures using analysis of variance (ANOVA) with mean spring temperature and date of warming of capture sites as predictors. I then assessed differences between species in the effect of mean spring temperature and date of warming on the number of captures using analysis of covariance (ANCOVA).

4.3.5 PREVALENCE OF BOT FLY INFESTATION

Infestation prevalence was calculated as the percentage of mice observed to have at least one bot fly infestation, out of all mice captured. Mice were considered to be infested if a botfly larvae or scar was visible. Infestation prevalence was compared between species, males and females, breeding condition of females, and age at infestation. Because incidence of bot flies was sometimes low, Fisher's Exact test was used to test for equal proportions of infested and uninfested mice.

4.4   RESULTS

4.4.1   TOTAL NUMBER OF BIRTHS

A date of birth was estimated for a total 583 PL and 154 PMG (Table 4-1). 191 PL pregnancies and 47 PMG pregnancies were detected, leading to an estimated 966 PL births and 239 PMG births. The estimated number of births for PL and PMG was similar in 2010; however, PL births outnumbered PMG births in both 2011 and 2012. This result reflects the observed differences in PL and PMG abundance observed in those years (Chapter 2).

TABLE 4-1: NUMBER OF ESTIMATED BIRTHS

	PL				PMG			
	AGE	PREG.	BIRTHS - PREG	TOTAL BIRTHS	AGE	PREG.	BIRTHS - PREG	TOTAL BIRTHS
2010	51	10	53	104	67	12	56	123
2011	289	54	274	563	57	25	136	193
2012	243	127	639	882	30	10	47	77
TOTAL	583	191	966	1549	154	47	239	393

Table 4-1: Total numbers of estimated births occurring on the Pigeon River Grid in 2010, 2011, and 2012. The number of births estimated from age at first capture (Age) and from pregnant females (Female Births) sum to the total number of births. The number of pregnancies detected (Preg) is also listed.

PL produced the fewest births in 2010, and the most in 2012 (Figure 4-1A). While the maximum number of births produced in 2012 is about the same as in 2011, over 300 more PL were born in 2012 due to increased reproductive output between April and July in 2012. PMG produced the fewest births in 2012, and the most in 2010 (Figure 4-1B).
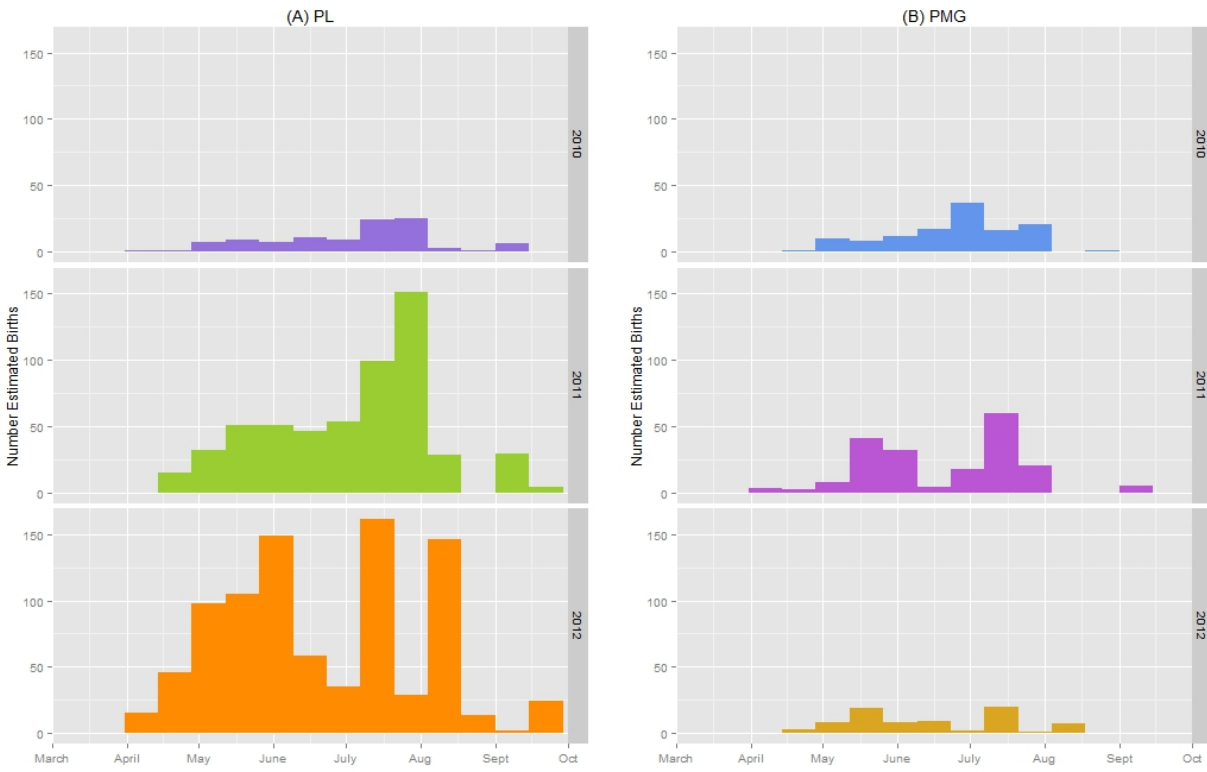
Figure 4-1: Histograms of the number of estimated births occurring on the grid for (A) PL and (B) PMG in 2010, 2011, and 2012. Bars represent the number of births estimated to occur in each 14 day interval from March through October.

4.4.2   THE SEASONAL DISTRIBUTION OF BIRTHS
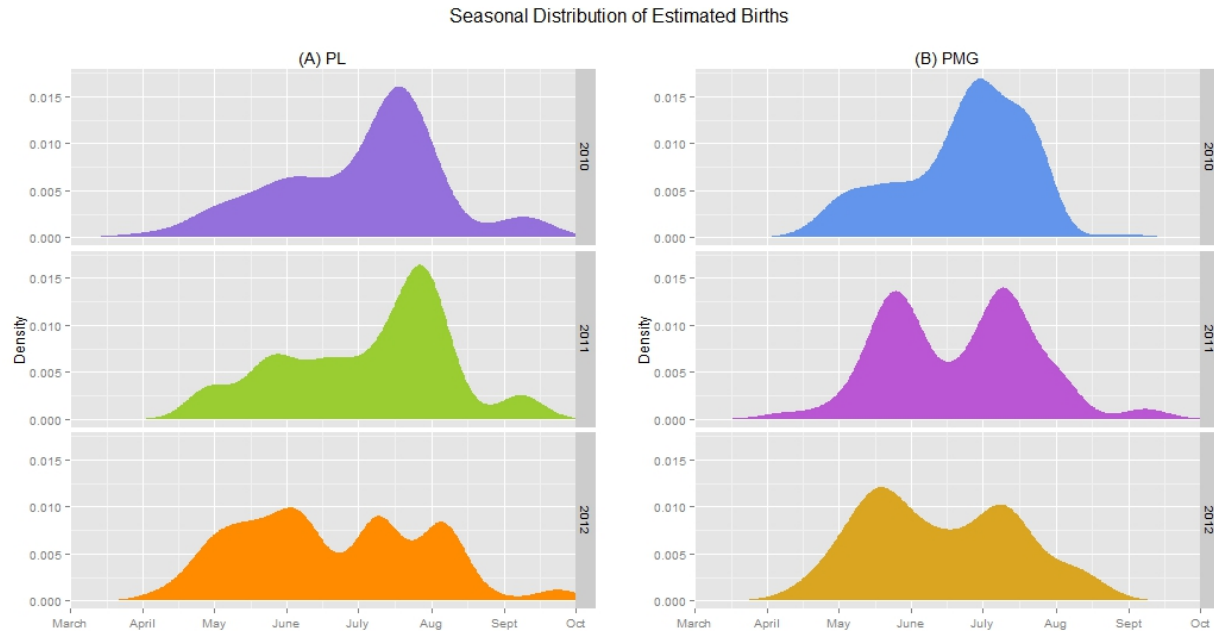
Figure 4-2: Probability density function of the seasonal distribution of the number of estimated births for (A) PL and (B) PMG.

Patterns in the seasonal distribution of births (Figure 4-2) suggest that there were two general patterns of population growth during this study. For PL in 2010 and 2011 and PMG in 2010, the number of births remained roughly constant until about July, when there was a peak in reproductive output (Figure 4-2). A different pattern was observed for PL in 2012 and PMG in 2011 and 2012; the number of births is bimodal, with one bout of reproduction occurring soon after the onset of breeding and another occurring later in the season. These patterns are reflected in the estimated abundance of juveniles modeled using Poisson regression (Figure 4-3; refer to Chapter 2 for methods).
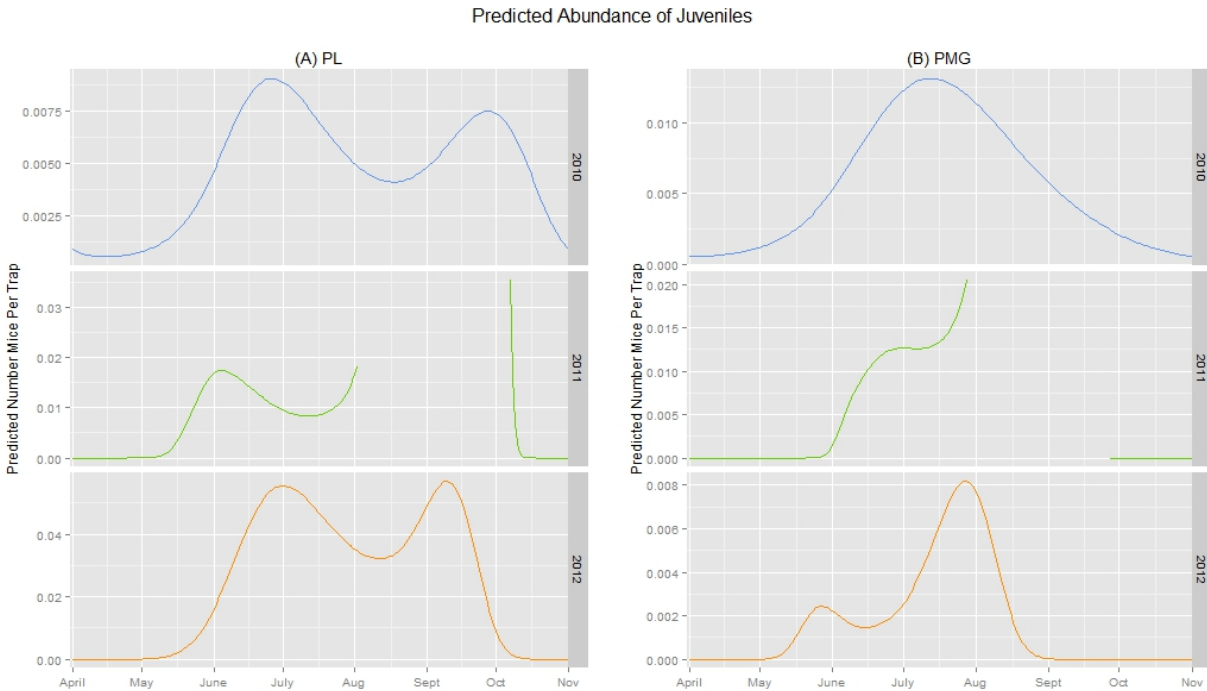
Figure 4-3: Abundance of juvenile (A) PL and (B) PMG over time in 2010, 2011, and 2012. Predicted abundances were modeled from trap success of juvenile mice using Poisson regression. Missing data in 2011 are due to a gap between trapping sessions of approximately 1.5 months, leading to inaccurate model predictions.

4.4.3 LENGTH OF THE BREEDING SEASON

Table 4-2 lists the estimated dates of the onset and cessation of breeding, as well as an estimate of the length of the breeding season for PL and PMG in 2010, 2011, and 2012. On average, PL experienced a breeding season that was 135 days (4.5 months) in length, while for PMG the breeding season averaged 111 days (3.6 months). This difference is statistically significant (F=6.8, P=0.05).

TABLE 4-2: LENGTH OF THE BREEDING SEASON

	FIRST BIRTH (FB)	LAST BIRTH (LB)	DAYS BETWEEN FB AND LB	ONSET (10%)	CESSATION (90%)	LBS
PL						
2010	Mar. 28	Sep. 12	167	Apr. 18	Aug. 28	132
2011	Apr. 22	Oct. 9	170	May 9	Sept. 16	130
2012	Mar. 23	Sept. 27	187	Apr. 17	Sept. 9	145
PMG						
2010	Apr. 19	Aug. 31	134	May 2	Aug. 21	111
2011	Apr. 6	Sept. 9	156	Apr. 21	Aug. 24	125
2012	Apr. 9	Aug. 12	125	Apr. 26	Jul. 31	96

Table 4-2: Dates of the onset and cessation of breeding and the length of the breeding season (LBS) for PL and PMG in 2010, 2011, and 2012. Breeding season length (LBS) was calculated as the number of days between the 10th and 90th percentiles of estimated births. The number of days between the first and last recorded births (Days Between) is also reported.

In all years, the first recorded birth occurred around the end of March or early April, and population-wide breeding began in late April or early May. Overall, there was no significant difference between species in either the date of onset of breeding (P=0.84) or the date of the first birth (P=0.51); however, species-level differences may be masked by annual variation. PL began breeding in mid-April in both 2010 and 2012, but not until early May in 2011 (Figure 4-4A). A similar pattern was found for PMG, which began breeding in early May in 2010, but late April in the other years (Figure 4-4B).
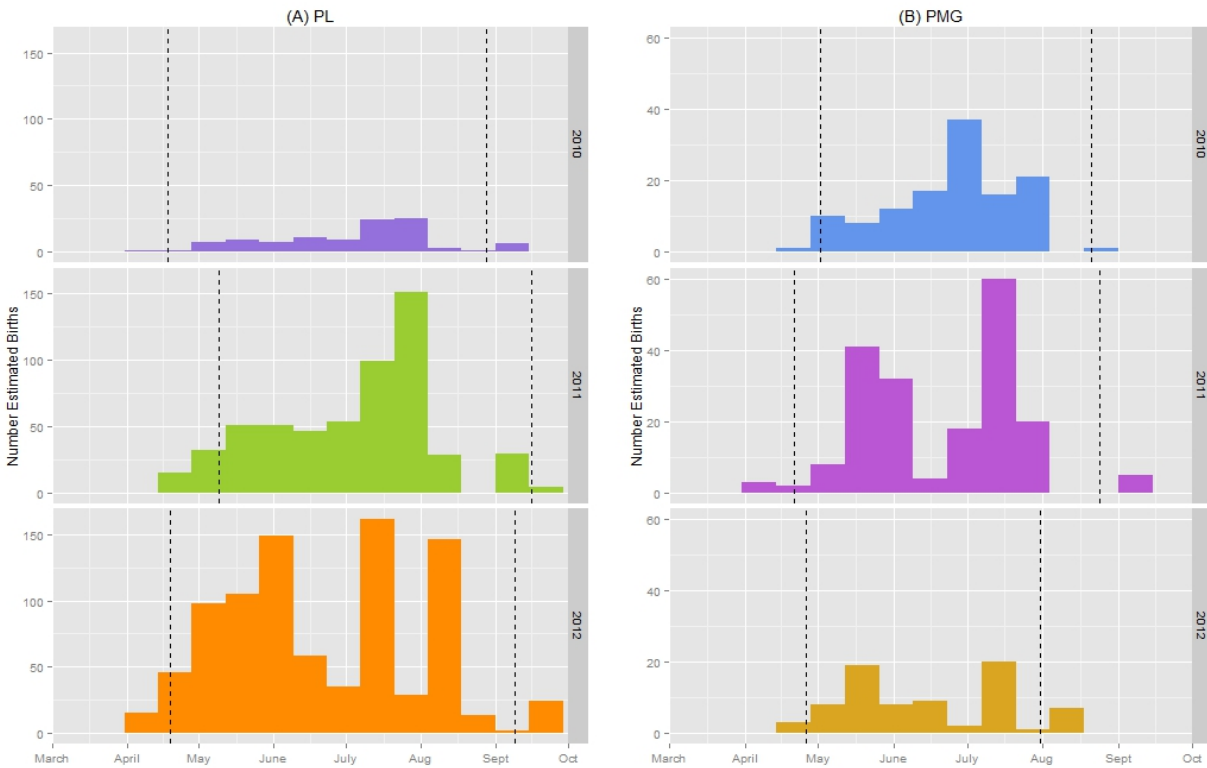
Figure 4-4: Seasonal distribution of the number of estimated births of (A) PL and (B) PMG. The dates of onset and cessation of breeding are marked with vertical dashed lines.

On average, cessation of breeding occurred in early September for PL and late August for PMG, a difference of 23 days which was not statistically significant (P=0.067). The date of the last PL birth tended to be later than the date of the last PMG birth, but this difference was also not statistically significant (P=0.061). There was again annual variation in the cessation of breeding within each species. PL stopped breeding in early September in 2010 and 2012, but continued to breed until mid-September in 2011. PMG stopped breeding in late August in 2010 and 2011, but breeding ceased nearly a month earlier in 2012.

PL experienced its longest breeding season in 2012, when it bred for about 10 days longer than the other years. While breeding season length was similar in 2010 and 2011, both onset and cessation of breeding occurred later in 2011. PMG, on the other hand, experienced a shortened breeding season in 2012 due to an earlier cessation. In 2011, PMG began breeding 5 days earlier

than in 2012 and 11 days earlier than in 2010, leading to a longer breeding season in 2011 than in any other year.

I assessed the variation in the timing of onset and cessation of breeding by comparing the number of days between the first (or last) known birth and the date on which 10% (or 90%) of births had occurred. Early- and late- breeding PMG had litters approximately 2 weeks before (or after) the norm for the population. For early- and late- breeding PL, this number is almost 3 weeks (Table 4-3).

TABLE 4-3: INDIVIDUAL VARIATION IN ONSET AND CESSATION OF BREEDING

	PL			PMG		
	FB - ONSET	LB - CESSATION	DIFFERENCE IN LBS	FB - ONSET	LB - CESSATION	DIFFERENCE IN LBS
2010	20	15	35	13	10	23
2011	17	23	40	15	16	31
2012	24	18	42	15	12	29
MEAN	20.33*	18.67[+]	39.00*	14.33*	12.67[+]	27.67*
SE	2.03	2.33	2.08	0.67	1.76	2.40

Table 4-3: Individual variation in the dates of onset and cessation of breeding for PL and PMG. In each year, the number of days between the first known birth and the date of onset (the date when 10% of all births had occurred), the number of days between the date of cessation of breeding (the date when 90% of all births had occurred) and the last known birth, and the sum of these intervals is reported. Mean differences and standard errors are also reported. Significance of differences between species is marked (+: 0.05<P<0.1; *: P<0.05).

Overall, there was less variation in the duration of the breeding season for PMG than for PL (F=12.7, P=0.024); that is, there were not as many PMG as PL that either bred very early or very late. The number of days between the first birth and the onset of breeding was, on average, significantly greater for PL than PMG (F=7.9, P=0.048). The number of days between the cessation of breeding and the last birth also tended to be greater for PL than PMG (F=4.2, P=0.1), but this result was not significant. This suggests that there were fewer PMG than PL that bred very early or very late.

4.4.4   TRAPPABILITY

Trappability was estimated as the number of actual captures divided by the number of opportunities for capture. Differences between species in trappability of females have the potential to bias the number of births estimated from trapping records because pregnancies of mice trapped less often would be overlooked more often. There was no significant difference between PL and PMG females in trappability in any year during this study (Table 4-4). PMG males, however, were trapped with greater efficiency than PL males in all years.

TABLE 4-4: TRAPPABILITY OF PL AND PMG							
PL			PMG			STATISTICS	
POSSIBLE	TRAPPED	%TRAP	POSSIBLE	TRAPPED	%TRAP	x^2	P
2010							
FEMALES 117	69	0.59	108	75	0.69	2.24	0.135
MALES 187	85	0.45	90	153	0.68	14.59	0.0001***
2011							
FEMALES 458	225	0.49	207	113	0.55	1.49	0.222
MALES 241	599	0.40	95	179	0.53	8.74	0.003**
2012							
FEMALES 764	404	0.53	35	78	0.45	1.41	0.219
MALES 348	800	0.44	32	102	0.31	4.97	0.026*

Table 4-4: Trappability of PL and PMG. Trappability was calculated as #actual captures/#possible captures. Significance of differences between species is marked (+: 0.1<P<0.05; *: P<0.05; **: P<0.01; ***: P<0.001).

4.4.5   GROUND TEMPERATURE

Below-ground temperature at 33 trap stations in 2011 and 18 trap stations in 2012 was logged between March 1 and April 30. At all sites, ground temperature was low (around 0°C) and displayed little fluctuation at the beginning of March. This pattern was typical of temperatures during the winter, which in both years remained within 1° of freezing (data not shown). In both years, when conditions began to warm, temperature began to fluctuate and in many cases

displayed a regular cycle due to differences between daytime and nighttime temperatures. This pattern of warming began earlier in 2012 than it did in 2011 (Figure 4-5), suggesting that the winter preceding 2012 was shorter than the one preceding 2011. This result is consistent with climatic data suggesting that the winter preceding 2012 was shorter and milder than the winter preceding 2011 (Chapter 2).
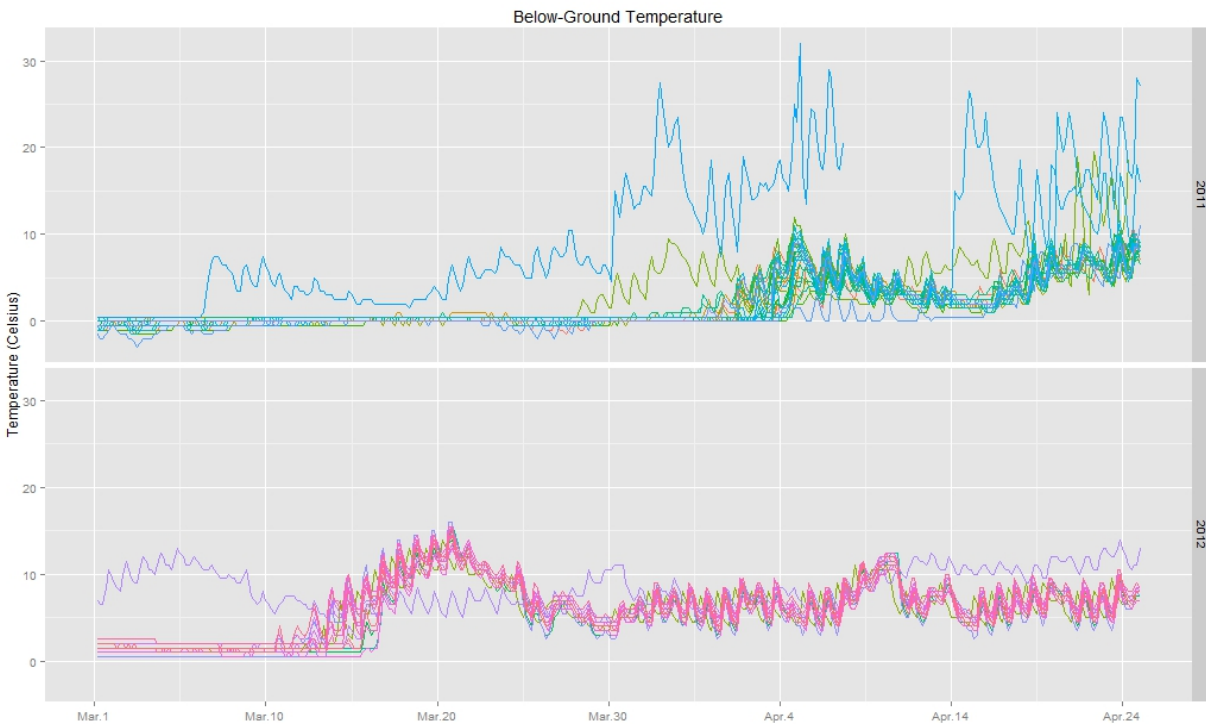
Figure 4-5: Below-ground temperature logged by iButtons at 51 trap stations in 2011 and 2012 from March 1 through April 30 of each year.

It is unclear whether the clear outlier in 2011 (the first blue line that deviates from the rest; Figure 4-5) was due to actual temperature differences. The high maximum temperature (over 30°C) and that the iButton at this location ceased to log temperature around April 7 suggests that these readings may have been due to a hardware malfunction. Nevertheless, variation in temperature did exist, especially towards the end of April in 2011.

Mean spring temperature of a site was strongly correlated with the date of warming at that site (F=548.3, P<0.0001). There was little variability in both mean ground temperature and dates of

warming among sampled sites (Table 4-5). Ground temperature at most sites was within 0.1 °C of the mean of all sites in 2011 and 0.25 °C in 2012. Similarly, the date of warming for most sites was within 1 day of the average date of warming in both years.

	2011 (33 SITES)			2012 (18 SITES)		
	MEAN TEMP (°C)	WARM	DATE	MEAN TEMP (°C)	WARM	DATE
MIN	0.73	30.33	Mar. 30	4.99	0.83	Mar. 1
MAX	3.69	41.00	Apr. 9	8.60	16.83	Mar. 17
MEAN	1.81	38.54	Apr. 7	6.11	13.89	Mar. 14
SE	0.10	0.38		0.19	0.84	

TABLE 4-5: IBUTTON TEMPERATURE MEASUREMENTS

Table 4-5: Spring temperature logged by ibuttons in 2011 and 2012.   For each ibutton (site), mean temperature (average of all temperatures logged between March 1 and April 30) and date of warming (date when logged temperature first rises above the average spring temperature for that site) were calculated. Summary statistics (minimum, maximum, mean, and standard error of the mean) for all sites in 2011 and 2012 are reported. Dates of warming are reported both as the number of days from March 1 and as a corresponding date.

4.4.6   MOUSE CAPTURES AND GROUND TEMPERATURE

If PL and PMG are associated with different microhabitats, and if these microhabitats are associated with differences in microclimate, then differences in the onset of breeding may be a result of differences in microclimate experienced by females of each species. For each site at which temperature was logged, the number of captures of female PL and PMG from April through mid-June in a 40m radius was counted. Trends in the number of captures were assessed using mean spring (March and April) temperature and date of warming of capture sites as predictors.
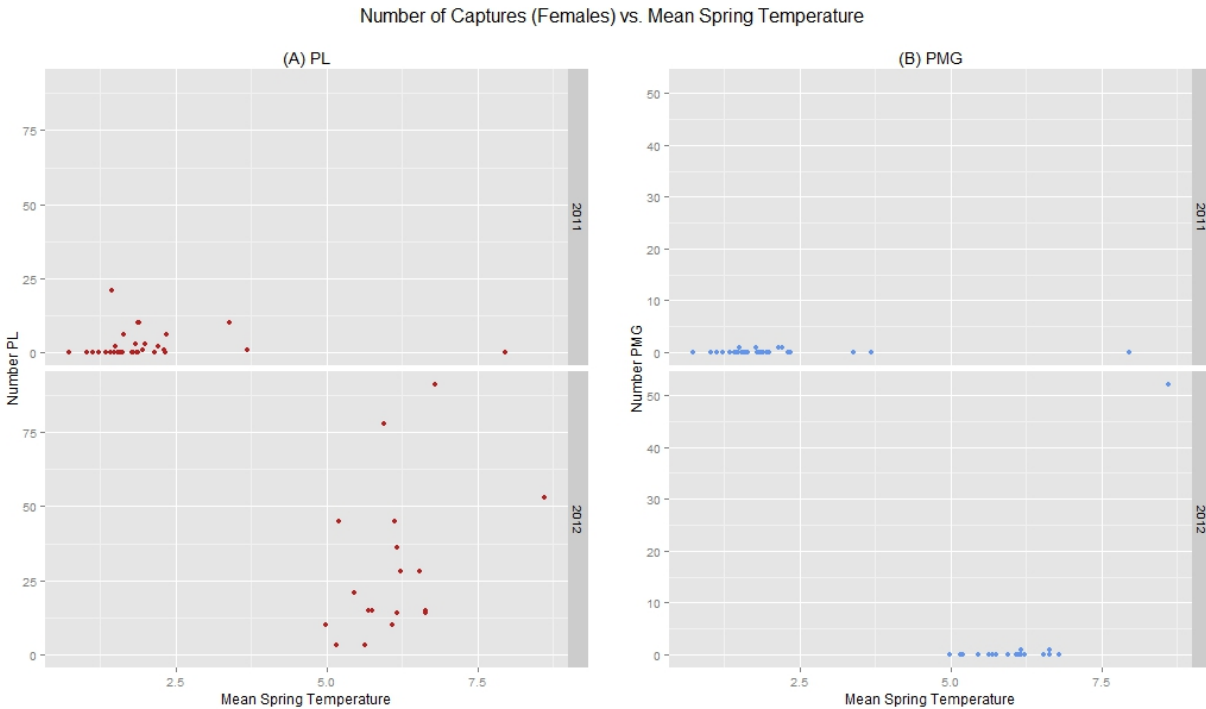
Figure 4-6: The number of captures of female (A) PL and (B) PMG in relation to mean spring temperature at sites which captures were made.   Each point represents one site; spring captures of all female mice within a 40m radius were counted (y-axis), and plotted against the mean of all temperatures logged at that site between March 1 and April 30 (x-axis).

In 2012, PL females tended to be captured at sites with warmer spring temperature (F=3, P=0.1; Figure 4-6A), but this result was not significant. Female PL captures were not correlated with the date of warming of capture sites in 2012 (F=1.3, P=0.27). The number of female PMG captures, on the other hand, was highly correlated with both spring site temperature (F=22.91, P=0.0002) and the date of site warming (F=125.4, P=6E-09). This trend is due to the large number of captures (52) near one site in 2012 (Figure 4-6B), which was associated with both high mean temperature and early date of warming.

These data suggest that there may be differences in the effect of microclimate on the number of PL and PMG captures, especially in 2012. Because spring PMG captures were low in the vicinity of all sites with one exception, it is unclear whether this result is an artifact of low sample size, or whether PL captures were not associated with temperature in the same manner. I thus investigated the differences between trends in PL and PMG captures using analysis of

covariance (ANCOVA). No significant effect of species was detected in the relationship between spring site temperature and captures in either 2011 (F=0.04, P=0.83) or 2012 (F=0.7, P=0.41). Similarly, the relationship between the date of warming at capture sites and the number of captures was not different for PL and PMG in either 2011 (F=1.38, P=0.25) or 2012 (F=0.03, P=0.87).

4.4.7   PREVALENCE OF BOT FLY INFESTATION

Bot fly prevalence was calculated as the proportion of mice out of all tagged mice that hosted at least one bot fly larva. Overall, prevalence of bot fly infestation was the highest in 2012 (P<0.0001). A greater proportion of PL were infested with bot flies in 2012 than in either 2010 (P<0.0001) or 2011 (P<0.0001), but infestation prevalence did not differ between 2010 and 2011 (P=0.24). Overall infestation prevalence of PMG was low, and no infested PMG were caught in 2011. The most infested PMG were caught in 2012, and this was significantly greater than infestation prevalence in 2011 (P=0.011).

TABLE 4-6: PREVALENCE OF BOT FLY INFESTATION OF PL AND PMG

	PL			PMG			STATISTICS
	UNINFESTED	INFESTED	% INFESTED	UNINFESTED	INFESTED	% INFESTED	P (FET)
MALES	39	1	0.025	40	2	0.048	1
FEMALES	17	1	0.056	33	0	0	0.353
2010	56	2	0.034	73	2	0.027	1
MALES	175	2	0.011	33	0	0	1
FEMALES	129	2	0.015	44	0	0	1
2011	304	4	0.013	77	0	0	0.588
MALES	111	55	0.331	17	1	0.056	0.014*
FEMALES	97	56	0.366	18	3	0.143	0.049*
2012	208	111	0.348	35	4	0.103	0.002**

Table 4-6: Prevalence of bot fly infestation of PL and PMG in 2010, 2011, and 2012. Infestation prevalence of bot flies was calculated as the number of mice that had at least one bot fly divided by the total number of mice. Significance of differences between species are marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

The genders did not differ in infestation rate in either PL (P=0.15) or PMG (P=1). Reproductive condition of females also did not affect the incidence of bot flies for PL (P=0.88) or PMG (0.28). Adult and younger PMG were infested at approximately equal rates (P=0.43; Figure 4-7). PL adults, however, were more likely to be infested than younger PL; this was found for both males (P=0.002) and females (P=0.033).

PL had a higher incidence of botfly infection than PMG in 2012, and this was true of both males and females (Table 4-6). Prevalence of bot flies in adult PL was significantly greater than in PMG adults (P<0.0001), but this difference was not significant for sub-adult and juvenile mice (P=0.13).
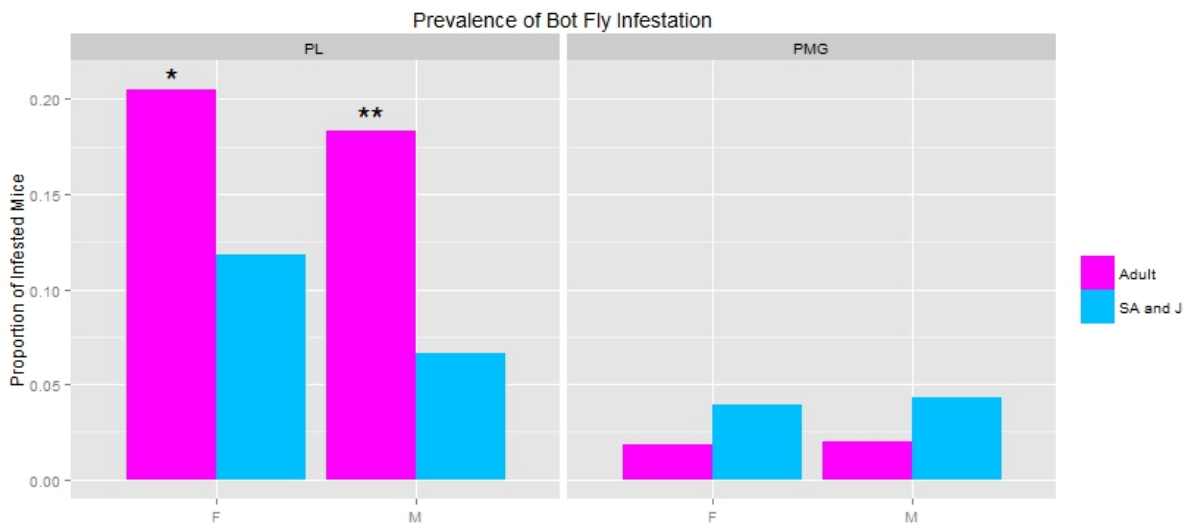
Figure 4-7: Prevalence of bot fly infestation of male and female PL and PMG. Significance of differences between adults and younger mice is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

4.5 DISCUSSION

4.5.1 THE LENGTH OF THE BREEDING SEASON

Abundance of PL was significantly greater than that of PMG in two out of three years in this study (Chapter 2), and these differences are reflected in the number of estimated births. A bimodal distribution of births was often observed during this study (Figure 3-2); this lends support to the hypothesis that there is a mid-summer lull in breeding in these species (Wolff 1996), which may be caused in part by the loss of overwintered females from the population. Though it is likely that some pregnancies were overlooked due to inconsistencies in longitudinal trapping records, there was no difference between species in trappability (Table 4-4); thus, the number of pregnancies should be underestimated for PL and PMG in the same way. Can differences in the length of their breeding seasons explain the changes in abundance of each species observed during this study?

Photoperiod is a primary cue for the initiation of spring breeding for *P. maniculatus* (Price 1966; Millar and Herdman 2004) and *P. leucopus* (Whitaker 1940; Heideman *et al.* 1999). Spring breeding is stimulated by increasing photoperiod and is mediated by temperature such that breeding begins following sudden rises in temperature that coincide with increasing day length (Sadleir 1974). Similarly, the cessation of breeding in higher latitude populations is thought to be closely tied to declining temperature, perhaps due to the increased cost of maintenance at lower temperatures (Sadleir *et al.* 1973) and energy requirements of lactation (Harland and Millar 1980).

Individuals in syntopic populations of PL and PMG experience the same climatic conditions; thus, if they differ in breeding season length, the explanation must lie in species-specific responses to environmental cues such as temperature or photoperiod. There is some evidence that responsiveness to photoperiod is under genetic control for PL (Heideman and Bronson 1991). Myers *et al.* (2005) proposed that the onset of breeding of PL in northern Michigan may be influenced by gene flow from southern populations, where this species typically begins breeding in March (Brown 1964; Baker 1983). Similarly, the onset of breeding for PMG may be influenced by gene flow from northern populations, which begin breeding in April or May (Millar *et al.* 1979).

In this study, PL began breeding earlier and ceased breeding later than PMG in all years except 2011, when PMG began breeding earlier. Analysis of ground temperature and capture records suggests that differences between species in the date of onset of breeding were not due to differences in temperature. The number of captures was not correlated with spring temperature at capture sites (Figure 4-6), but temperature varied little between sites (Figure 4-5). These observations support the hypothesis that breeding season length may be a species-specific niche difference where PL and PMG co-occur.

There is phenotypic variation in the responsiveness of individuals to photoperiod (Heideman *et al.* 1999), and natural populations of PL consist of a mixture of genetically determined phenotypes that are intermediate between absolutely photoresponsive and absolutely non-responsive (Heideman and Bronson 1991). Comparisons of the length of interval between the first and last recorded births and estimates of population-wide dates of onset and cessation of breeding suggest that there were fewer PMG than PL that bred either very early or very late. A possible explanation for this is that there is less phenotypic plasticity in the responses to environmental cues regulating breeding in PMG than there is in PL.

Peromyscus with longer breeding seasons have a greater annual reproductive growth than those with short breeding seasons (Millar *et al.* 1979); it is thus possible that differences in population growth between PL and PMG are influenced by breeding season length. Over the course of this study, PL bred for 24 days longer than PMG on average. PMG experienced the shortest breeding season and lowest abundance in 2012, at the same time that PL experienced the longest breeding season and greatest abundance. Further, PL bred for nearly 50 days longer than PMG in 2012, which was the largest difference in breeding season length between species – this coincided with the largest difference in abundance observed in this study.

A longer breeding season was not always associated with greater abundance, however. PL bred for the same amount of time in 2010 and 2011 (approximately 130 days), but its abundance was greater in 2011 than 2010. PL bred for 21 days longer than PMG in 2010, but no differences in abundance were observed that year. In contrast, PL and PMG differed in breeding season length by only 5 days in 2011, yet their abundance differed strongly. The overall length of the breeding season is thus not a consistent predictor of patterns of abundance, suggesting that the effect of

breeding season length on population growth is mediated by other factors. What could cause a longer breeding season to result in increased population growth in some years but not others?

For populations in which YOY breed in their natal year, an early onset of the breeding season maximizes total reproduction because mature YOY tend to dominate breeding in late summer (Havelka and Millar 2004) and early-born YOY are more likely than those born later to have litters of their own (Sharpe and Millar 1991). Myers *et al.* (2005) observed that PL increases faster and to a greater maximum in years following short and mild winters than in years following long and harsh ones. In this study, spring and overall PL abundance were highest in 2012, which was preceded by the mildest and shortest winter experienced by mice (Chapter 2). Reproductive output of PL YOY females was the highest in 2012 (Chapter 3), perhaps the result of successful early reproduction by their overwintered parents.

Early onset of breeding, however, is not always advantageous. Newborn mice suffer decreased growth rates at low temperatures and require greater maternal care in the nest (King 1968; Harland and Millar 1980). Breeding females must balance this need with longer bouts of foraging outside the nest to meet the energetic requirements of lactation (Millar and Innes 1985; Millar *et al.* 1990). Spring breeding begins following sudden rises in temperature that coincide with increasing photoperiod (Jameson 1953; Sheppe 1963; Brown 1964); however, once breeding has begun, further declines in temperature in the early spring may not cause cessation of reproduction (Sadleir 1974). An increase in temperature in the early spring may thus cause breeding to begin too early, resulting in reduced maternal survival and reproductive success.

I was not able to assess failed early reproduction; however, some trends observed during this study indirectly suggest that this occurred in 2010. The breeding season of 2010 was preceded by a relatively harsh and long winter (Chapter 2), and, consistent with the predictions of Myers *et al.* (2005), both spring and overall PL abundance were low. Based on the timing of the first known birth, I estimated that PL began breeding on April 18, 2010. This was nearly identical to the onset of breeding in 2012 (Table 3-2); however, spring conditions in 2012 were mild whereas conditions in early 2010 were colder. In 2010, female PL that established residency appeared on the grid later than female PMG, but the opposite trend was found for males (Chapter 3), suggesting that a sex-specific process was responsible. These observations suggest that PL may

have begun breeding in 2010 under harsher conditions, resulting in both failed reproduction and increased mortality of overwintered females. This might explain the absence of a numerical advantage for PL even though it bred for 21 days longer than PMG.

4.5.2   SUCCESSFUL EARLY BREEDING MAY CONFER A COMPETITIVE ADVANTAGE

I proposed in Chapter 3 that the high density of adult PL may have led to reproductive inhibition of YOY PMG. Here, I suggest that the density of breeding adult female PL could have negatively impacted YOY PMG in 2012. PMG stopped breeding on July 31 in 2012, nearly one month earlier than in previous years. The short breeding season for PMG in 2012 may have been caused by the lack of reproduction by PMG YOY females (Chapter 3). Because no PMG YOY females on the study grid bred in 2012, after OW females disappeared from the grid in early August, it is possible that no further reproduction occurred. These patterns suggest that some factor caused reduced reproductive rates and may have suppressed reproduction in PMG YOY females, which led to a shortened breeding season.

Both species occurred at high spring abundance in 2012, possibly due to enhanced overwinter survival conferred by a mild winter. The first recorded PL birth occurred on March 23, more than two weeks before the first recorded PMG birth (Table 3-2); similarly, population-wide onset of breeding for PL was more than a week before PMG. Early breeding in mild conditions may give YOY PL a competitive advantage over YOY PMG. When early breeding is successful, early-born young can become independent and establish territories when densities are low (Sharpe and Millar 1991), and may then be able to exclude later-born young from establishing territories in preferred habitats. These two species are known to be territorial and defend a core home range (Dooley Jr. and Dueser 1996). The victor in aggressive contests is often the resident rather than the intruder (Wolff *et al.* 1983); however, larger size is also advantageous (Garten 1976; Bowers and Smith 1979). Early-born young may have an advantage over late-born young in aggressive contests because they are the residents, and because they have more time to grow to a larger size. A later onset of breeding may thus confer a disadvantage when winters are mild and early breeding is successful.
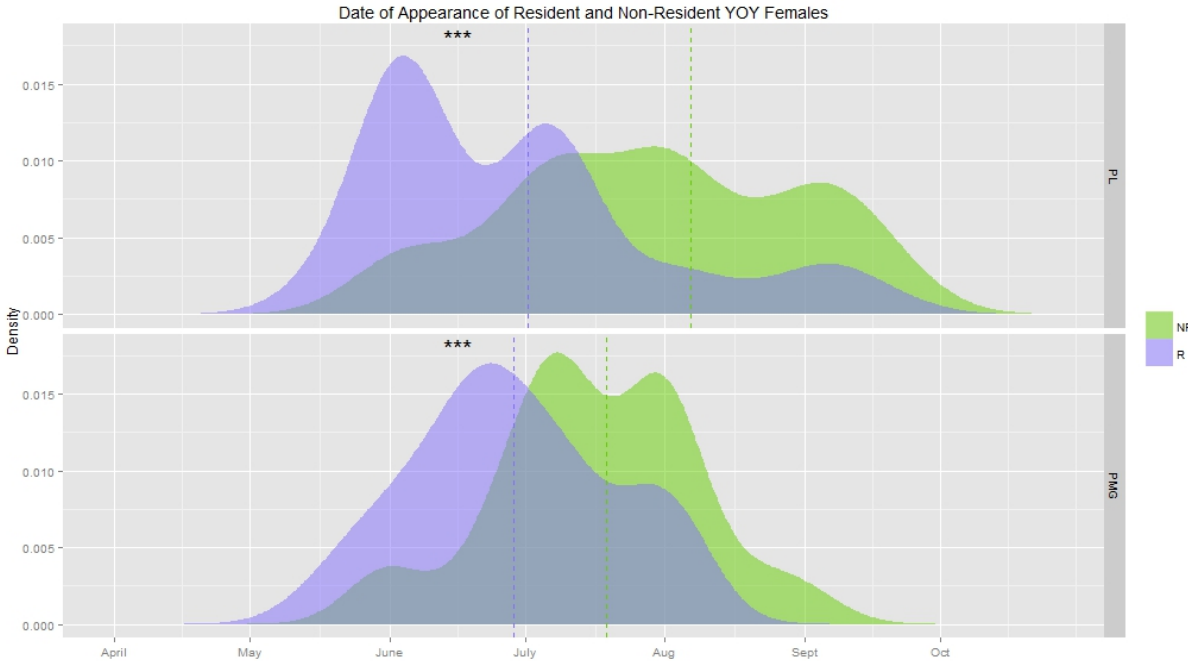
Figure 4-8: Seasonal distribution of the date of first appearance of resident and non-resident YOY female PL and PMG. Mean dates of first appearance of residents (R; purple) and non-residents (NR; green) are marked with vertical dashed lines. Significance of differences between R and NR YOY females is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

There is some evidence from this study that supports this hypothesis. First, YOY females that appeared early on the grid were more likely to become residents (persist longer than 14 days) and thus to establish territories than YOY females that appeared later (Figure 4-8). This was found for both PL (t=-5.27, P=5.9E-07) and PMG (t=-2.85, P=0.006). A second line of evidence suggests that the species that begins breeding (successfully) earlier tends to establish territories before the species that begins breeding later (Figure 4-9). PMG began breeding earlier than PL in 2011, and PMG residents appeared on the grid earlier than PL residents (P=0.002). PL began breeding earlier than PMG in 2012, and PL residents tended to appear on the grid earlier than PMG residents (P=0.1).

Figure 4-9: Probability density function of the distribution dates of first appearance of resident PL and PMG in (A) 2010, (B) 2011, and (C) 2012. Mean FD is marked with dashed vertical lines. Significance of differences between species in FD is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

I compared mean non-adult body weights of female YOY PL and PMG (Table 4-7) to assess whether size differences were present between early- and late-breeding YOY. In 2012, PL began breeding earlier than PMG, and female YOY PL were significantly heavier than female YOY PMG (P=0.02). In 2011, on the other hand, PMG began breeding earlier than PL, and female YOY PMG tended to be heavier than female YOY PL (P=0.06). Taken together, these three lines of evidence suggest that (1) YOY are more likely to establish territories if they are born early and thus appear on the grid early, (2) successful early breeding may be associated with

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establishing territories early, and (3) successful early breeding may allow early-born YOY to grow larger than those that are born later, which could confer a competitive advantage.

TABLE 4-7: WEIGHT OF FEMALE YOY

	PL			PMG			STATISTICS		
	MICE	WEIGHT	SE	MICE	WEIGHT	SE	DF	T	P
2010	11	13.30	0.54	18	13.41	0.65	26.85	-0.13	0.894
2011	47	13.45	0.27	24	14.73	0.61	32.06	-1.93	0.062[+]
2012	81	14.83	0.40	6	11.44	1.04	6.59	3.06	0.020*

Table 4-7: Comparison of non-adult weights of female YOY PL and PMG. An average non-adult weight was calculated for each individual; mean non-adult weights were compared between species. Significance of differences in mean non-adult weight between PL and PMG is marked (+: 0.05<P<0.1; *: P<0.05; **: P<0.01; ***: P<0.001).

4.5.3   THE IMPACT OF BOT FLY INFESTATION ON REPRODUCTIVE OUTPUT

Evidence indicates that bot fly infestation enhances survival of white-footed mice (Wecker 1962; Goertz 1966; Hunter *et al.* 1972; Burns *et al.* 2005), possibly at the cost of reproductive success. Parasitized males have considerably compromised gonadal development, reflecting a diversion of energy from reproduction into survival (Wecker 1962; Timm and Cook 1979; Burns *et al.* 2005). Infested females have fewer litters and fewer total offspring than uninfested females (Burns *et al.* 2005). During this study, bot fly infestation was low in 2010 and 2011 (1-3% of mice were infested), but was significantly higher in 2012 (10-35% infestation; Table 4-6).

The seasonal distribution of PL births in 2012 differs from patterns in other years and from patterns in PMG (Figure 3-2). While there was a general pattern of two seasonal groupings of births (early and late summer), the late summer grouping exhibits two peaks in births (Figure 4-4), suggesting that reproductive output may have been somewhat reduced in late July and August. The prevalence of bot fly infestation was significantly greater in 2012, particularly for PL (Table 3-6). Further, the timing of the apparent reduction in PL births coincided with the

interval of time over which infested individuals were trapped, which lasted from July 10 – September 18.

Population fluctuations of mice may have a time-lagged effect on the infestation prevalence of bot flies. Burns *et al.* (2005) noted that the rate of infestation was higher in years following years of peak mouse density, and lower following years of low mouse abundance. This hypothesis is supported by results from this study, though a more long-term study is required for verification. I found that bot fly infestation was the highest in 2012 (Table 4-6), which was the only year in this study that followed a year of high abundance.

Infested mice may employ life history strategies that decrease current reproduction to promote future reproduction (Forbes 1993; Perrin *et al.* 1996; Richner 1998; Richner and Tripet 1999). Infested juveniles may delay the date of first reproduction (Agnew *et al.* 2000), and infested adults may shift the order of litter sizes within their life cycle (Cole 1954). These life history shifts can have negative impacts on population dynamics by lengthening generation time (Cole 1954). In this study, I found that the prevalence of bot fly infestation was significantly higher in PL than in PMG (Table 4-6). Following years of high PL abundance, unequal rates of parasitism could cause reduced reproduction in PL, and may possibly slow the process of faunal turnover.

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CHAPTER 5.

SPATIAL RELATIONSHIPS AND SOCIAL INTERACTIONS IN A COMMUNITY OF *PEROMYSCUS* IN NORTHERN MICHIGAN

5.1   SUMMARY

Climate-induced ecological replacement of the 'northern' *P. maniculatus gracilis* by the 'southern' *P. leucopus* has been documented with long-term studies in the Great Lakes Region (Long 1996; Myers *et al.* 2005). The importance of biotic interactions in shaping species responses to climate change (Tylianakis *et al.* 2008; Gilman *et al.* 2010; Urban *et al.* 2012; Zarnetske *et al.* 2012) suggest that if *P. leucopus* and *P. m. gracilis* are competitors where they co-occur, ecological replacement may also be affected by interspecific competition. Few studies have investigated interspecific interactions of these two species in communities where they are syntopic in the Great Lakes Region.

It is possible that social interactions (both within and between species) are reflected in the spatial distribution of individuals. In this chapter, I characterize the distribution of *P. leucopus* and *P. m. gracilis* across the study grid, then use modified versions of the nearest neighbor method (Skellam 1952) to analyze temporal patterns in spatial relationships. I assess (1) within-species variation in the spacing of males and females to assess the effect of social interactions on spatial relationships, and (2) differences in the spacing between *P. leucopus* and *P. m. gracilis* captures to investigate whether spatial relationships are consistent with a hypothesis of interspecific competition. Differences between species in habitat associations are also investigated as a possible cause of spatial relationships.

Identification of 'preferred' and 'avoided' sites revealed substantial non-overlap in usage of the grid. These differences, however, could be due to differences between species in habitat preferences; *P. leucopus* tended to be found more often than expected at sites with large trees, while *P. m. gracilis* was most often captured at more densely vegetated sites. Analysis of nearest interspecific neighbor distances (NIN) suggests that spacing patterns of *P. leucopus* and *P. m. gracilis* may be influenced by overall density. The association of greater NIN with periods of high total mouse density (but not with lower densities) raises the possibility that competition may be occurring in this community, even in light of differences in habitat associations.

The distributions of male and female mice observed here are consistent with observations that the spacing between female mice is approximately regular during the breeding season (Metzgar 1971; Fairbairn 1977; Harland *et al.* 1979), but aggregated during the rest of the year (Metzgar 1979; Mihok 1979). The temporal variation in the spatial distribution of female mice, the stronger effect observed for breeding females, and the relatively weaker effect observed for males suggest that females (of both species) in this community maintain breeding territories through social interactions.

5.2   INTRODUCTION

Climate-induced ecological replacement of the 'northern' *P. maniculatus gracilis* by the 'southern' *P. leucopus* has been documented with long-term studies in the Great Lakes Region (Long 1996; Myers *et al.* 2005). Gradually warming winters over the last 30-40 years in this area have facilitated northward range expansion of *P. leucopus*, and communities in which *P. leucopus* and *P. m. gracilis* co-occur have become characterized by strong numerical dominance of *P. leucopus* (Myers *et al.* 2009).

Regular variation in climate may promote stability within communities by ameliorating effects by superior competitors (Post 2012). In the absence of competition, many cold-adapted species can persist in environments even after their optimal habitat disappears because their absolute rates of population growth remain positive; with competition, these species become extinct once

better adapted competitors arrive (Urban *et al.* 2012). Coexistence of *P. leucopus* and *P. m. gracilis* close to the northern range boundary of *P. leucopus* may have been maintained by their different winter adaptations and the frequency of mild versus harsh winters (Wolff 1996). This balance, however, has been upset by recent climatic warming in the northern Great Lakes region (Myers *et al.* 2005).

Recent empirical studies suggest that competition can facilitate climate-induced extinctions (Sinervo *et al.* 2010; Jankowski *et al.* 2010) by lowering fitness and population abundances (Urban *et al.* 2012). Competition at range boundaries may explain observations that species adapted to warmer climates generally colonize warming areas faster than resident species disappear (Kelly and Goulden 2008). It is possible that *P. m. gracilis* would be able to persist in areas that are becoming increasingly warm if *P. leucopus* were not also increasing in abundance; the combination of sub-optimal environmental conditions and increased density of *P. leucopus* may lead to ecological replacement.

The role of interspecific interactions in the replacement of *P. m. gracilis* by *P. leucopus* has not previously been investigated, perhaps due to uncertainty regarding the importance of such interactions to population dynamics in communities where these species co-occur. If interspecific competition affects population growth, then it is likely that competition will influence how population abundances respond to climate change. Do co-occurring *P. leucopus* and *P. m. gracilis* compete in northern Michigan?

Despite the difficulties of detecting competition with field experiments (Connell 1983; Schoener 1983), indirect tests for density dependent effects are possible. Regulation of annual population growth is hypothesized to be mediated by social interactions, particularly among breeding females (Harland *et al.* 1979). Available territories in which to breed may be a sex- and season-specific limiting resource for *Peromyscus* (Harland *et al.* 1979; Lusk and Millar 1989). Resident females exclude other females from their home ranges during the breeding season (Nicholson 1941; Metzgar 1971, Harland *et al.* 1979), resulting in a spatial distribution that is approximately regular during the breeding season (Metzgar 1971; Fairbairn 1977; Harland *et al.* 1979) but aggregated during the rest of the year (Metzgar 1979; Mihok 1979).

The maintenance of spatial relationships necessitates social interaction such as mutual avoidance (reported in *Clethrionomys*; Viitala and Hoffmeyer 1985) or overt aggression (Dooley Jr. and Dueser 1996). *P. leucopus* is reported to be more aggressive than *P. m. gracilis* (Stah 1978; Long 1996); it is thus possible that *P. m. gracilis* actively avoids *P. leucopus* rather than engaging in aggressive contests. If this is true, the spatial patterns that arise from avoidance should be detectable in the capture locations of mice.

In this chapter, I use location information from trapping records and assess temporal patterns in the spatial distribution of male and female *P. leucopus* and *P. m. gracilis* to find evidence of sex- and season- specific social interactions. I compare the distributions of capture locations and assess the degree to which locations of high trap success were shared between species, and investigate the distances between interspecific captures to assess whether *P. leucopus* and *P. m. gracilis* were further apart or closer together than expected by chance. Possible differences in habitat associations are also investigated as a cause of non-overlapping use of the grid.

5.3   METHODS

I monitored a syntopic population of *P. leucopus* (PL) and *P. m. gracilis* (PMG) in the Pigeon River State Forest in northern Michigan from April to October for three consecutive years. Individual mice were tagged with unique identification numbers. The location of each capture was recorded, and mice were released at their capture locations after processing. Please refer to Chapter 2 for a complete trapping protocol. To detect seasonal changes in the distribution of mice, I divided trap records into three temporal groups - spring (SP, April 1-June 20), summer (SU, June 21-August 15), and fall (FA, August 16-November 1). These groups were used in all analyses in this chapter.

Because the number of traps set and the sites at which traps were set varied, simulations were used to generate null expectations of the proportion of captures (number of captures divided by number of times a trap was set) and nearest interspecific distances under the assumptions that mice were equally likely to be trapped at every location and that capture locations were

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randomly spaced. All statistical analyses and simulations were run in R, version 3.02 (R Development Core Team 2013).

5.3.1   SPATIAL DISTRIBUTION OF PL AND PMG

How are PL and PMG distributed across the grid, and do these patterns change over time? I constructed heat maps of the locations at which mice were trapped to better visualize and assess temporal changes in the centers of activity. At each location, trap success was calculated as the number of captures divided by the total number a trap was set at that location. To smooth the data and make visual comparison of spatial distribution easier, I used a locally weighted polynomial regression (LOESS) to extrapolate over areas that were not trapped.

Sites at which mice were trapped more ('preferred' sites) or less often ('avoided' sites) than expected by chance were identified by comparing the observed trap success at a site to a null distribution. Null expectations of the proportion of captures were generated by simulation. Simulations referenced the number of mice that were caught; locations of 'captures' were then randomly chosen from the traps that were set. Each day in a temporal grouping was simulated 1000 times, and the number of successes (mice caught) and failures (no mice caught) at each trap were recorded.

Chi-squared analysis was used to compare observed trap success to null expectations and to compare the proportion of 'preferred' sites that were common to both species. Fisher's Exact test was used in lieu of Chi-squared analysis when the number of observed captures was low.

5.3.2   HABITAT ASSOCIATIONS

While I found no difference between species in the relationship between the number of captures and spring ground temperature at capture sites (Chapter 4), non-overlapping use of the grid could be the result of different habitat preferences rather than competition alone. To test this hypothesis, vegetation and habitat sampling was conducted in summer 2012 at 110 sites (Figure 5-1).
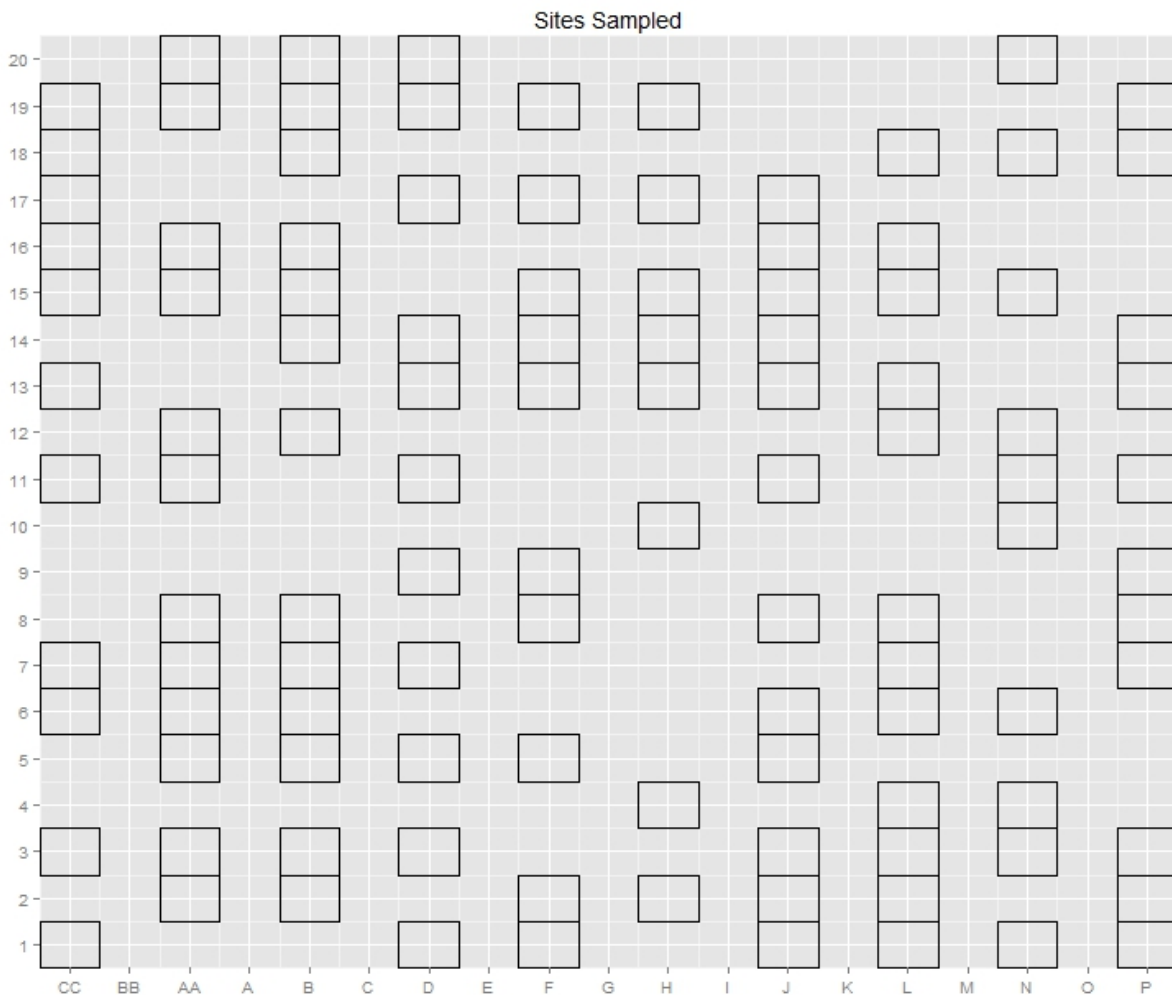
Figure 5-1: Sites at which vegetation and habitat sampling were conducted in summer 2012. A total of 110 out of 400 sites were sampled.

Both PL and PMG are known to prefer habitats where downed woody debris (Barry and Francq 1980; Planz and Kirkland 1992) and herbaceous ground cover (M'Closkey and Lajoi 1975; Dueser and Shugart 1978) are abundant. Habitat selection is probably influenced by the availability of food resources and predator avoidance strategies (Bowers and Smith 1979; Kaufman *et al.* 1983). Habitat measurements were thus chosen to characterize the density of vegetation (Vis, Saplings, Open/Shrub/Grass), the structure of ground cover (DWDA, DWDT), and the availability of resources including food and nest sites (DBHA, DBHT). At each sampled site, 9 measures of habitat characteristics were recorded (Table 5-1).

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TABLE 5-1: HABITAT CHARACTERISTICS MEASURED AT 110 SITES

NAME	DEFINITION	DESCRIPTION
VIS	VISIBILITY	• Distance at which half of a pre-defined object (a 4'x4' posterboard painted with colored squares) held at chest height becomes obscured
GRASS	GRASS COVERAGE	• Percent of the ground in a 1m radius covered by grass
SHRUB	SHRUB COVERAGE	• Percent of the ground in a 1m radius covered by herbaceous plants
OPEN	LEAF LITTER	• Percent of the ground in a 1m radius that was covered only with leaf litter
DWDT	TOTAL DOWNED WOODY DEBRIS	• Total diameter (cm) of downed woody debris (DWD) within a 1m radius of the center of a site; all pieces of DWD greater than 5cm in diameter were counted.
DWDA	SIZE OF DOWNED WOODY DEBRIS	• Average diameter (cm) of downed woody debris (DWD) within a 1m radius; all pieces of DWD greater than 5cm in diameter were counted.
SAPLINGS	NUMBER OF SAPLINGS	• Number of saplings (trees of DBH<10cm and height <2m) present within a 5m radius of the center of a site
DBHT	TOTAL AMOUNT OF TREE MATERIAL	• Total DBH (diameter at breast height, measured in centimeters) of trees in a 5m radius.
DBHA	SIZE OF TREES	• Average DBH (diameter at breast height, measured in centimeters) of trees in a 5m radius.

Table 5-1: 9 habitat characteristics were measured at each of 110 sampled sites in summer 2012.

Habitat associations of PL and PMG were calculated as the average value of each measured habitat characteristic at sites at which mice were trapped more than expected by chance ('preferred' sites). If a preferred site was not among the sampled sites, the habitat measures of the closest sampled trap or traps were used. Two-sample t-tests were used to compare mean habitat measures of preferred sites of PL and PMG to each other and to mean measures at all other sampled sites (the 'grid mean').

5.3.3   NEAREST NEIGHBOR DISTANCE

One commonly used method in the statistical determination of distribution patterns is the nearest neighbor method (Skellam 1952; Clark and Evans 1954), in which the distance from each individual to its nearest neighbors is compared to an expected distance to quantify the degree that

individuals are clumped in space. I used a modified version of the nearest neighbor method to assess patterns in the spacing of PL and PMG and of males and females within species.

Is the observed average minimum distance between a PL and PMG capture different than expected by chance? The distance to the nearest interspecific neighbor (NIN) was calculated for each day as the mean of the distances from each capture to its nearest neighboring capture of the other species. To assess patterns on a broader temporal scale, I averaged data from multiple days into a seasonal NIN. Seasonal NIN was then compared to a null distribution, which was simulated as described below under the assumption that mice are neither closer together nor further apart than expected by chance.

Simulations referenced the number of mice that were caught; locations of 'captures' were then randomly chosen from the traps that were set, and each 'capture' was assigned a species identity. The distance between each capture and the closest capture of the other species was determined. For each season, the mean of simulated minimum distances (one for each day falling within the season) was taken. This process was repeated 1000 times. PL and PMG were considered to be further apart than expected if the observed average minimum distance between a PL and PMG capture was greater than the simulated value more than 95% of the time.

5.4   RESULTS

5.4.1   SPATIAL DISTRIBUTION OF PL AND PMG

Trap success was localized in some areas rather than spread evenly throughout the grid (Figure 5-2). Usage of the grid changed both seasonally within years and between years. Areas in which trap success of PL was high were often not the same areas in which trap success of PMG was high, suggesting some degree of non-overlapping usage of the grid.
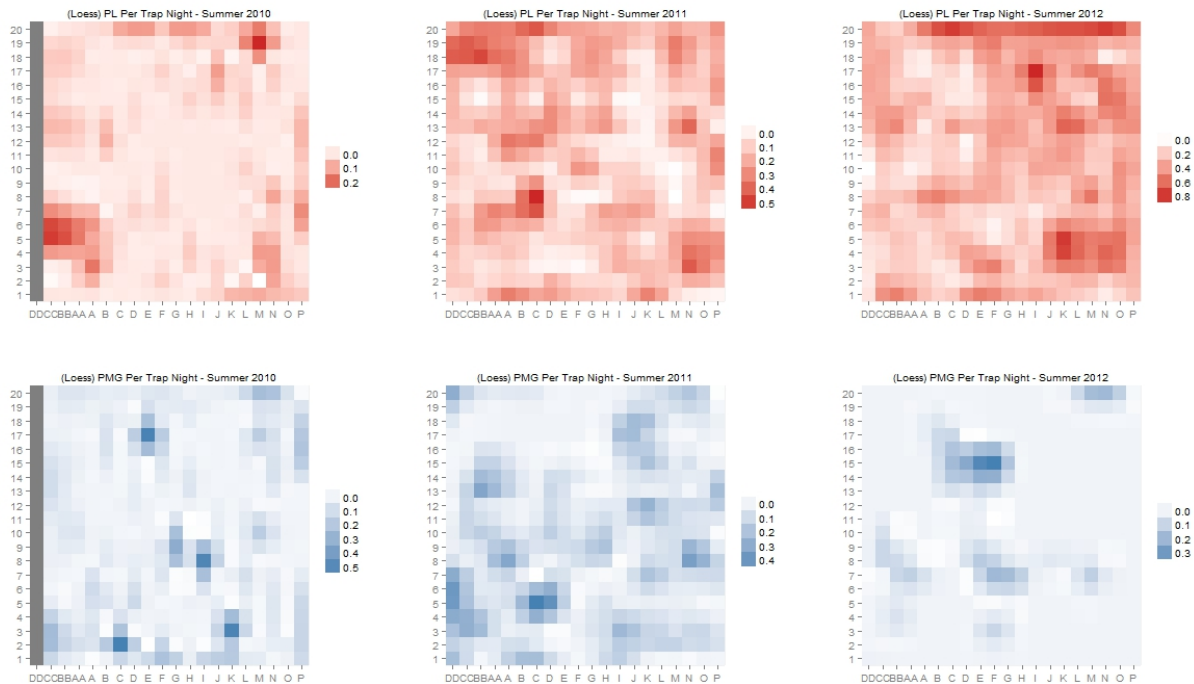
Figure 5-2: Heat maps of LOESS estimations of trap success at individual trap sites for PL (top) and PMG (bottom) in the summers of 2010 (left), 2011 (middle) and 2012 (right). Darker colors indicate areas of higher trap success.

Overall, PL was found more often than expected ('preferred') a total of 293 sites, while PMG was found more often than expected at 174 locations. Preferred sites rarely overlapped; during the same season, PL and PMG were both found more often than expected at only 4 sites (Table 5-2).

PL was found less often than expected ('avoided') 35 sites. Perhaps owing to low PMG numbers, I was not able to identify sites that PMG avoided. The proportion of sites that were avoided by PL and also preferred by PMG (7 out of 35 sites) was significantly greater than the proportion of sites that were preferred by PL and also preferred by PMG (χ^2=28, P<0.0001).

TABLE 5-2: NUMBER OF PREFERRED SITES

SEASON	TOTAL TRAPS	FEMALES			MALES			REPRODUCTIVE FEMALES		
		PL	PMG	SHARED	PL	PMG	SHARED	PL	PMG	SHARED
SP2010	400	8	3	0	6	8	0	6	5	0
SU2010	360	10	12	1	13	12	1	8	9	0
FA2010	200	5	1	0	5	2	0	2	0	0
SP2011	400	8	3	0	5	7	0	5	0	0
SU2011	400	14	20	0	10	15	0	19	10	1
FA2011	200	10	6	0	5	1	0	0	3	0
SP2012	400	24	10	1	21	5	0	19	5	0
SU2012	400	21	9	0	25	8	0	14	9	0
FA2012	200	7	3	0	10	3	0	4	0	0
SP2013	200	3	1	0	4	1	0	2	1	0

Table 5-2: Number of preferred sites (sites at which more captures were made than expected) for PL and PMG. During each season, the number of sites preferred by PL and PMG females, males, and reproductive females are listed. The number of individual sites that were preferred by both species in the same season (Shared) is also listed.

5.4.2 NEAREST NEIGHBOR DISTANCES

I used modified versions of the nearest neighbor method (Skellam 1952) to analyze temporal patterns in the spatial distribution of mice. I assessed (1) within-species variation in the spacing of males and females to assess the effect of social interactions on spatial relationships, and (2) variation in the spacing between PL and PMG captures to investigate whether spatial relationships were consistent with a hypothesis of interspecific competition. Null expectations were simulated as described above.

5.4.2.1 WITHIN-SPECIES VARIATION IN THE SPACING OF MALES AND FEMALES

For both species, I tested the hypothesis that mice were neither further apart nor closer together than expected at random. Differences between males and females in spatial relationships may reflect the effect of social interactions between individuals. I therefore investigated the spatial

relationships among males, females, and reproductive females. Mice were considered to be significantly further apart than expected if the observed distance to the nearest capture of the same gender (or reproductive status) was greater than the simulated value more than 95% of the time, and closer together than expected if the observed value was less than the simulated value more than 95% of the time.

PL: Female PL were either randomly spaced or closer together than expected during the spring, and were further apart than expected in the summer (Table 5-3). The spatial distribution of female PL in the fall varied among years; distribution was clumped in fall 2010, random in fall 2011, and regularly spaced in fall 2012. Reproductive PL females were further away from each other than expected in all seasons except for fall 2010 (random spacing) and spring 2011 (closer together than expected). Spatial relationships between PL males were more often random than for females; PL males were only further apart than expected in summer 2010.

TABLE 5-3: SPATIAL DISTRIBUTION OF FEMALES AND MALES - PL

	FEMALES		REPRODUCTIVE FEMALES		MALES	
SEASON	COMPARISON	P-VAL	COMPARISON	P-VAL	COMPARISON	P-VAL
SP2010	RANDOM	0.128	FURTHER APART	0.034	RANDOM	0.289
SU2010	FURTHER APART	0	FURTHER APART	0	FURTHER APART	0
FA2010	CLOSER TOGETHER	0.027	RANDOM	0.204	CLOSER TOGETHER	0.003
SP2011	CLOSER TOGETHER	0	CLOSER TOGETHER	0.007	RANDOM	0.155
SU2011	FURTHER APART	0.057	FURTHER APART	0	RANDOM	0.129
FA2011	RANDOM	0.331	FURTHER APART	0.012	CLOSER TOGETHER	0.002
SP2012	RANDOM	0.453	FURTHER APART	0.013	RANDOM	0.462
SU2012	FURTHER APART	0	FURTHER APART	0	CLOSER TOGETHER	0.054
FA2012	FURTHER APART	0	FURTHER APART	0.008	RANDOM	0.285

Table 5-3: Spatial distribution of PL females, reproductive females, and males. For each gender, comparisons are made between the observed distance to the nearest capture of the same gender and simulated distances under null expectations. The proportion of simulations that were more extreme than the observed value (P-VAL) are reported.

PMG: PMG females were further apart from each other than expected in 2010 (spring and summer) and randomly spaced in 2011 (summer and fall; (Table 5-4). PMG females were further apart than expected in summer 2012 but closer together than expected in fall 2012. In all seasons for which data were available, reproductive PMG females were further apart from each other than expected. Spatial distribution of PMG males was more often random than that of females. PMG males were further apart from each other than expected in summer 2010 and summer 2012, but were clustered in summer 2011 and fall 2012.

TABLE 5-4: SPATIAL DISTRIBUTION OF FEMALES AND MALES - PMG

| | FEMALES | | REPRODUCTIVE FEMALES | | MALES | |
SEASON	COMPARISON	P-VAL	COMPARISON	P-VAL	COMPARISON	P-VAL
SP2010	FURTHER APART	0.003	FURTHER APART	0.050	RANDOM	0.410
SU2010	FURTHER APART	0	FURTHER APART	0	FURTHER APART	0.003
FA2010	NA	NA	NA	NA	RANDOM	0.452
SP2011	NA	NA	NA	NA	RANDOM	0.298
SU2011	RANDOM	0.188	FURTHER APART	0.001	CLOSER TOGETHER	0.006
FA2011	RANDOM	0.245	FURTHER APART	0	NA	NA
SP2012	NA	NA	NA	NA	NA	NA
SU2012	FURTHER APART	0	FURTHER APART	0.012	FURTHER APART	0.085
FA2012	CLOSER TOGETHER	0.003	NA	NA	CLOSER TOGETHER	0.002

Table 5-4: Spatial distribution of PMG females, reproductive females, and males. For each gender, comparisons are made between the observed distance to the nearest capture of the same gender and simulated distances under null expectations. The proportion of simulations that were more extreme than the observed value (P-VAL) is reported.

5.4.2.2 DISTANCE TO NEAREST INTERSPECIFIC NEIGHBOR (NIN)

I tested the null hypothesis that PL and PMG captures are neither further apart nor closer together than expected at random. PL and PMG were considered to be significantly further apart than expected if the observed distance to nearest interspecific neighbor (NIN) was greater than the simulated value for at least 950 out of 1000 trials. Similarly, the species were considered to be clustered if observed NIN was less than the simulated value at least 95% of the time.

TABLE 5-5: DISTANCE TO NEAREST INTERSPECIFIC NEIGHBOR

SEASON	NIN - OBSERVED	NIN – SIMULATED (MEAN OF 1000)	COMPARISON	% < OBS	% > OBS
SP2010	100.35	116.22	RANDOM	0.87	0.13
SU2010	41.55	86.71	CLOSER TOGETHER	1***	0***
FA2010	81.03	71.27	RANDOM	0.23	0.77
SP2011	119.38	108.39	RANDOM	0.21	0.79
SU2011	48.49	48.65	RANDOM	0.50	0.50
FA2011	117.24	30.31	FURTHER APART	0***	1***
SP2012	167.25	63.66	FURTHER APART	0***	1***
SU2012	95.55	31.54	FURTHER APART	0***	1***
FA2012	88.45	36.46	FURTHER APART	0***	1***
SP2013	151.87	100.52	FURTHER APART	0.06[+]	0.94[+]

Table 5-5: Distance to nearest interspecific neighbor (NIN) for 10 seasons. For each season, comparisons are made between observed NIN and simulated NIN, and the proportion of simulated values that are greater or less than observed values are noted. Significance of differences between observed NIN and simulated NIN is marked (+: $0.05 < P < 0.1$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$).

Results are summarized in Table 5-5. There was considerable variation among years in the spacing of PL and PMG. PL and PMG were significantly further apart than expected at random in all seasons during 2012, fall 2011, and spring 2013. In summer 2010, in contrast, the spatial distribution of PL and PMG was clumped. Random spacing between PL and PMG was observed in spring and fall 2010, and spring and summer 2011.

5.4.3   HABITAT ASSOCIATIONS

It is possible that different habitat preferences explain why PMG was found more often than expected at some sites that PL was found to avoid. Sites at which mice were found more often than expected ('preferred' sites) differed from sites for which no preference was shown in all 10 habitat measures (Table 5-1), but to varying degrees. Little variation was found in the habitat associations of either species among years; however, habitat use varied seasonally within years.

PL: Sites preferred by PL most often differed in the amount (DWDT) and size (DWDA) of downed woody debris and in the amount (DBHT) and size (DBHA) of trees (Table 5-6).

PL males preferred sites with smaller pieces of downed woody debris, fewer trees and saplings, and sites that had less coverage of leaf litter than the grid-wide mean. Sites preferred by PL males in summer tended to have greater visibility than in either spring or fall (df=113, t=2.2, P=0.029).

PL females preferred sites with larger trees and smaller pieces of downed woody debris than the grid-wide mean. Sites preferred by PL females in the summer tended to have more (df=18, t=2.2, P=0.037) and larger pieces (df=26, t=2.4, P=0.023) of downed woody debris than sites preferred during spring or fall; sites preferred in spring tended to have fewer saplings than in summer or fall (df=46, t=2.2, P=0.034).

Sites at which reproductive PL females were found most often differed from the grid-wide mean in most habitat characteristics measured, and most of these differences were observed in the spring. Reproductive PL females were found at sites with less total and smaller pieces of downed woody debris, more and larger trees, less grass coverage, and fewer saplings than the grid-wide mean. Sites preferred in summer had larger trees than sites preferred in the spring or fall (df=40, t=2.1, P=0.046).

TABLE 5-6: HABITAT ASSOCIATIONS OF PL

		PREFERRED		ALL OTHER SITES		STATISTICS		
	SEASON	MEAN	SE	MEAN	SE	DF	T	P
FEMALES								
DBHA (CM)	Summer	20.23	2.98	12.52	1.20	13.46	2.4	0.031
DWDA (CM)	Spring, Fall	4.76	0.80	7.31	0.61	62.73	-2.54	0.013
NE FEMALES								
DWDT (CM)	Spring	15.88	3.82	33.97	4.78	93.45	-2.96	0.004
DWDA (CM)	Spring	4.18	0.75	7.40	0.59	54.92	-3.38	0.001
SAPLINGS (#)	Spring	7	1.28	10.36	0.91	15.61	-2.13	0.049
DBHT (CM)	Spring, Summer	66.17	14.12	25.39	2.67	7.51	2.84	0.023
DBHA (CM)	Spring, Summer	26.42	4.18	12.23	1.13	8.06	3.27	0.011
GRASS (%)	Fall	1.67	1.67	14.62	1.90	105	-7.70	7.9E-12
MALES								
DWDA (CM)	Spring, Summer	5.14	0.74	7.26	0.64	73.75	-2.17	0.033
DBHT (CM)	Spring	13.80	2.99	29.39	3.01	23.16	-3.66	0.001
SAPLINGS (#)	Summer	4.90	1.40	11.32	0.97	39.56	-3.77	0.0005
OPEN (%)	Summer	49.33	5.47	64.35	2.79	45.01	-2.45	0.018

Table 5-6: Habitat associations of PL females, reproductive females, and males. The season during which associations were found is reported. Mean habitat characteristics of sites at which PL were found more often than expected were compared to mean characteristics of all other sites (for which no preference was shown). Only significant differences between preferred and all other sites are reported (P<0.05).

PMG: Sites at which PMG was found more often than expected differed from the grid-wide mean in the amount of trees (DBHT), the degree of visibility (Vis), the proportion of ground coverage by shrubbery (Shrub), and the number of saplings (Saplings; Table 5-7).

PMG males were found most often at sites with fewer saplings and trees, less shrub coverage, and more coverage by leaf litter; sites preferred in the fall had fewer trees than in either spring (df=26, t=3.3, P=0.003) or summer (df=29, t=2.7, P=0.011).

PMG females preferred sites with fewer saplings, less grass coverage, more shrub coverage, and lower visibility than the grid-wide mean. Sites at which PMG females were found most often in

summer and fall tended to have lower visibility (df=30, t=-2.5, P=0.017) and more saplings (df=16, t=-4.2, P=0.0007) than in the spring.

Reproductive PMG females preferred sites with fewer trees, fewer but larger pieces of downed woody debris, and lower visibility than the grid-wide mean; sites preferred in summer were associated with the lowest visibility (df=12, t=2.4, P=0.036).

			TABLE 5-7: HABITAT ASSOCIATIONS OF PMG					
	PREFERRED			ALL OTHER SITES		STATISTICS		
	SEASON	MEAN	SE	MEAN	SE	DF	T	P
FEMALES								
SAPLINGS (#)	Spring	2.40	1.60	10.51	0.89	6.85	-4.43	0.003
GRASS (%)	Summer	7.96	2.71	15.17	2.13	61.24	-2.09	0.041
SHRUB (%)	Summer, Fall	36.48	5.34	23.37	2.41	37.23	2.24	0.031
VIS (M)	Summer, Fall	4.54	0.72	7.76	0.50	27.43	-3.69	0.001
NE FEMALES								
DBHT (CM)	Spring, Summer	10.91	3.72	29.77	3.02	18.77	-3.92	0.0009
DWDT (CM)	Summer	19.59	4.86	32.51	4.51	40.92	-1.95	0.050
VIS (M)	Summer	5.04	0.97	7.63	0.49	20.43	-2.38	0.027
DWDA (CM)	Fall	10.37	0.56	6.82	0.53	7.18	4.58	0.002
MALES								
SAPLINGS (#)	Spring	4.25	1.66	10.61	0.91	11.84	-3.36	0.006
SHRUB (%)	Summer	15.56	4.24	26.84	2.51	30.38	-2.29	0.029
OPEN (%)	Summer	73.89	5.67	57.95	2.82	26.20	2.52	0.018
DBHT (CM)	Fall	8.49	4.90	28.92	2.91	5.49	-3.58	0.014

Table 5-7: Habitat associations of PMG females, reproductive females, and males. The season during which associations were found is reported. Mean habitat characteristics of sites at which PL were found more often than expected were compared to mean characteristics of all other sites (for which no preference was shown). Only significant differences between preferred and all other sites are reported (P<0.05).

Differences between species (Table 5-8): Sites preferred by PL females did not differ from sites preferred by PMG females except in summer 2012, when sites preferred by PL females were associated with a greater quantity of downed woody debris, more trees, and greater visibility.

The strongest differences between reproductive PL and PMG females also occurred in 2012. Reproductive PL females were associated with sites with more trees, smaller pieces of downed woody debris, and greater visibility than reproductive PMG females.

In comparison with sites at which PMG males were found most often, sites preferred by PL males were associated with smaller pieces of downed woody debris, more trees, more saplings, and greater visibility.

TABLE 5-8: DIFFERENCES BETWEEN PL AND PMG IN HABITAT PREFERENCES

	PL		PMG		STATISTICS		
	MEAN	SE	MEAN	SE	DF	T	P
FEMALES							
DWDT (CM)	36.36	5.35	19.69	5.58	36.20	2.16	0.038
DBHT (CM)	36.38	5.07	19.12	5.13	37.25	2.39	0.022
VIS (M)	8.39	0.90	4.54	0.72	44.06	3.35	0.002
NE FEMALES							
DWDA (CM)	5.15	0.53	7.73	0.85	34.40	-2.59	0.014
DBHT (CM)	36.09	3.48	19.81	2.93	155.2	3.58	0.0005
VIS (M)	8.08	1.11	5.04	0.97	30.98	2.07	0.047
MALES							
DWDA (CM)	5.35	0.41	7.18	0.72	34.14	-2.23	0.032
DBHT (CM)	22.23	4.12	9.76	3.06	26.53	2.43	0.022
SAPLINGS (#)	11.81	1.26	6.85	1.73	51.63	2.32	0.024
VIS (M)	9.43	1.25	5.32	0.91	32.14	2.66	0.012

Table 5-8: Differences in habitat preferences between PL and PMG females, reproductive females, and males.

Mean and standard errors of habitat characteristics of preferred sites are reported. Means were compared using two-sample t-tests; statistics are listed. Only significant differences between species are reported ($P<0.05$).

Comparison of sites preferred and avoided by PL (Table 5-9): When compared to sites at which PL was found more often than expected, sites avoided by PL had less grass coverage, less downed woody debris, and a greater proportion of open ground covered only by leaf litter.

TABLE 5-9: COMPARISON OF PREFERRED AND AVOIDED SITES - PL

HABITAT	PREFERRED		AVOIDED		STATISTICS		
	MEAN	SE	MEAN	SE	DF	T	P
DWDT (CM)	36.60	3.80	24.24	3.93	-2.26	109.76	0.026
GRASS (%)	15.09	1.62	8.47	1.92	-2.64	52.84	0.009
OPEN (%)	48.28	5.27	72.92	9.42	2.28	18.24	0.035

Table 5-9: Differences in habitat characteristics between sites 'preferred' and sites 'avoided' by PL. Mean and standard errors of habitat characteristics of preferred and avoided sites are reported. Means were compared using two-sample t-tests; statistics are listed. Only significant differences between preferred and avoided sites are reported (P<0.05).

Comparison of sites avoided by PL and sites preferred by PMG: Sites avoided by PL did not differ significantly in any habitat measure from sites preferred by PMG (data not shown).

5.5   DISCUSSION

5.5.1   SPATIAL DISTRIBUTION OF MALES AND FEMALES

Peromyscus populations are characterized by relatively low density and relatively small annual fluctuations in numbers (Terman 1968), suggesting that population growth is controlled (Harland *et al.* 1979). Although weather (Fuller 1969; Myers *et al.* 2005) and food resources (Bendell 1959; Fordham 1971) influence abundance, controls on annual population growth are often hypothesized to be mediated by behavior (Harland *et al.* 1979). Resident females may exclude other females from their home ranges (Nicholson 1941; Metzgar 1971; Harland *et al.* 1979), and

males may display aggressive behavior towards juveniles and impact their survival (Sadleir 1965). Social interactions may be reflected in the spatial distribution of individuals, because the maintenance of spatial relationships (such as a core home range) necessitates behaviors such as mutual avoidance (Lusk and Millar 1989) or overt aggression (Dooley Jr. and Deuser 1996).

Investigations of the spacing of individuals in *Peromyscus* populations have largely focused on females, probably because of their role in reproduction. Results from this study (Table 5-3; Table 5-4) are consistent with observations that the spacing between female mice is approximately regular during the breeding season (Metzgar 1971; Fairbairn 1977; Harland *et al.* 1979), but aggregated during the rest of the year (Metzgar 1979; Mihok 1979). For both species, females were further apart from each other than expected in all summers during this study. In the spring and fall, in contrast, clumped or random distributions of females were sometimes observed.

The distribution of males, both PL and PMG, tended to be more random than that of females. This may be due to the role of females in reproduction (Lackey *et al.* 1985; Burt 1940). In polygynous mating systems, in which males invest more energy in competition for resources than in paternal care (Wolff 1989), males may be less strongly influenced than females by seasonal changes in population dynamics and environmental conditions (Trivers 1972). Available territories in which to breed may be a sex- and season-specific limiting resource for *Peromyscus* and other rodents (Bujalska 1973; Harland *et al.* 1979); breeding females tend to maintain small exclusive home ranges (Metzgar 1971), but males have a higher propensity to explore new areas (Schug *et al.* 1991).

The distribution of breeding females was more often regularly spaced than the distribution of all females (non-breeding and breeding), suggesting that the maintenance of regular spacing had a greater influence on breeding females. The temporal variation in the spatial distribution of female mice, the stronger effect observed for breeding females, and the relatively weaker effect observed for males suggest that females in this community maintain breeding territories through social interactions.

5.5.2   SPATIAL RELATIONSHIPS BETWEEN PL AND PMG

PL and PMG are extremely similar morphologically and ecologically (Horner 1954; Wolff 1985; Long and Long 1993). They are often difficult to distinguish in the field (Feldhamer *et al.* 1983; Myers *et al.* 2005). They exhibit broad niche overlap (Wolff and Hurlbutt 1982), both in allopatry and sympatry. Due to these similarities in morphology, diet, and habitat use, PL and PMG have been the subject of numerous investigations and it possible that they are competitors where they co-occur.

There is conflicting evidence in the literature regarding the role of interspecific competition in communities of *Peromyscus* from different geographic areas and amongst different sub-species. Master (1977), using a combination of field and laboratory experiments, found that interspecific competition played a dominant role in habitat selection of PL and *P. maniculatus bairdii* (a short-tailed grassland subspecies) in southeastern Michigan. Interspecific territoriality has been reported in a community of co-occurring PL and *P. maniculatus nubiterrae* (a long-tailed forest-dwelling subspecies similar to PMG) in Virginia, in which individuals competed for nest sites and defended core home ranges (Dooley Jr. and Dueser 1996). It has been hypothesized, however, that co-occurring PL and PMG interact ecologically as a single species with neutral population dynamics (Wolff 1985), and the victor in aggressive contests is often based on residency (i.e. resident or intruder) rather than on species identity (Wolff *et al.* 1983). It is unknown whether co-occurring PL and PMG compete in the Great Lakes Region.

The exclusion of one species from the niche of another is difficult to demonstrate (Connell 1983; Schoener 1983). Direct tests for competition typically involve removal experiments, in which enclosures are built around study plots and species densities within are manipulated and monitored (e.g. Brown and Munger 1985; reviewed in Connell 1983). In this case, enclosures were impractical because of their required size, because *Peromyscus* are adept at climbing (M'Closkey 1975), and because the populations under study are on public land where the construction of such structures would not be permitted. Another approach is to decrease populations of one species on experimental plots through continuous trapping and removal. I tested this approach during the summer of 2009 and found it to be impractical due to the speed at which new immigrants re-colonized plots.

If interspecific competition occurs in this community, it is possible that interspecific territoriality or avoidance is reflected in the spatial relationships between individuals. The distribution of PL and PMG across the grid varied seasonally and between years (Figure 5-2). Identification of 'preferred' and 'avoided' sites (sites at which captures were more or less numerous than expected by chance, respectively) revealed substantial non-overlap in usage of the grid.

Analysis of nearest interspecific neighbor distances (NIN) suggests that spacing of PL and PMG varied seasonally, and most variation occurred between years rather than within years (Table 5-5). Spacing patterns of PL and PMG may be influenced by overall density – in the latter part of 2011 and all of 2012, when mice were the most abundant, interspecific captures were further apart than expected. In 2010 and early 2011, on the other hand, spacing of PL and PMG was random, except for summer 2010 when PL and PMG were clumped. The association of greater NIN with periods of high total mouse density (but not with lower densities) raises the possibility that competition may be occurring in this community, even in light of differences in habitat associations (discussed below).

5.5.3   HABITAT ASSOCIATIONS OF PL AND PMG

Both PL and PMG are found in deciduous woodland areas, especially where herbaceous cover is moderate and logs and branches are abundant (Long 1996). Typical habitat attributes includes a canopy (if only of brush) and woody debris (Barry and Francq 1980). Both species are omnivorous (Wolff *et al.* 1985; Lackey *et al.* 1985), and both are nocturnal foragers (Madison 1977). Despite these similarities, there is some evidence that PL and PMG prefer different microhabitats. Reports from single species populations suggest that PL may show a greater preference for habitats with diverse ground cover than PMG (Drickamer 1990). PMG is associated with dense hardwood forests and also bogs and swamps (Dice 1925; Hooper 1942). PL in Michigan is reported to prefer oak-hickory woods with a diverse understory (Allen 1938; Burt 1940; Getz 1961), and may also be more likely than PMG to inhabit less forested areas, such as brushy prairies and wooded ravines (Long 1968, 1973).

I compared habitat characteristics of sites preferred by PL, sites avoided by PL, and sites preferred by PMG (analyses were unable to identify sites that PMG avoided). Sites that PL avoided had less DWD and consisted of greater ground coverage by leaf litter (and consequently had less grass and herbaceous cover) than preferred sites (Table 5-9). Sites avoided by PL did not differ significantly in any habitat measure from sites preferred by PMG. These results support the observation (Drickamer 1990) that PL prefer habitats with an abundance of diverse ground cover.

Forest-dwelling PL and PMG both preferentially use protected rather than exposed microhabitats (Kaufman *et al.* 1983; Travers *et al.* 1988; Drickamer 1990). In this study, both species were found more often than expected at sites that had fewer saplings (very small trees with DBH<10cm and height >2m) than the grid-wide average. Saplings on the grid often grew close together, had very few lateral branches, and had leaves only on their topmost branches. Because of these characteristics, sites at which there were many saplings were often sparsely vegetated with herbaceous cover. Visibility at these sites was generally high because there were no leaves between the ground and the tops of the saplings. The number of saplings found at a site was positively correlated with the visibility at the site (F=10.76, P=0.001); thus, the preference for sites with fewer saplings may indicate a preference for densely vegetated and protected habitats.

Similarly, large trees provide both nest sites and food resources (Long 1996), and they are included in the preferred habitat dimensions of both PL and PMG (Kaufman *et al.* 1983; Drickamer 1990). In this study, average tree size (DBHA) and vegetation density (Vis) were highly and inversely correlated (P=0.007; Table 5-10), indicating that large trees were often not surrounded by dense vegetation. This suggests that mice may have to choose between microhabitats containing large trees and those that are densely vegetated.

TABLE 5-10: CORRELATIONS BETWEEN HABITAT CHARACTERISTICS

HABITAT CHARACTERISTIC		HABITAT CHARACTERISTIC		STATISTICS	
NAME	DESCRIPTION	NAME	DESCRIPTION	F	P
DBHA	LARGER TREES	VIS	GREATER VISIBILITY	7.52	0.007
SHRUB	MORE SHRUB COVERAGE	DWDT	LESS TOTAL DWD	2.98	0.087
SHRUB	MORE SHRUB COVERAGE	OPEN	LESS LEAF LITTER	113.20	1.6E-18
SHRUB	MORE SHRUB COVERAGE	GRASS	LESS GRASS COVERAGE	6.59	0.012
SAPLINGS	MORE SAPLINGS	VIS	GREATER VISIBILITY	10.76	0.001

Table 5-10: Correlations between habitat characteristics measured in this study.

Sites preferred by PL contained significantly larger trees than those preferred by PMG (Table 5-8). PMG, on the other hand, was captured more often than expected at sites with lower visibility but fewer trees (Table 5-7). Further, while both species were found more often than expected at sites with fewer saplings, sites preferred by PL contained significantly more saplings (and consequently less foliage) than sites preferred by PMG. These results suggest that PL and PMG may select habitats based on different criteria. PL may prefer sites with large trees over those that are densely vegetated but without trees, while PMG may prefer densely vegetated sites over those with trees. Habitat selection is hypothesized to be related to the suitability of different combinations of microhabitat features in providing resources such as food and nest sites, or protection from predators (Kaufman *et al.* 1983; Travers *et al.* 1988). It is thus possible that differences in microhabitat associations reflect differences in food selection, nest site requirements, or predator avoidance strategies. It is also possible that habitat preferences are the same, but one species is restricted to sub-optimal habitat by the other.

It has been hypothesized that the partitioning of microhabitats between males and females is a strategy that maximizes reproductive success (Bowers and Smith 1979). In this study, differences in habitat associations were observed between males and reproductive females within species (Table 5-6; Table 5-7). Habitat associations found in this study suggest that reproductive females may select sites that are characterized by dense vegetation at a height of at least several inches above ground. This may come at the expense of having less DWD available (Table 5-10).

Males, in contrast, were found more often than females at sites where above-ground cover was less abundant.

5.6   CONCLUSION

The importance of biotic interactions in shaping species responses to climate change (Tylianakis *et al.* 2008; Gilman *et al.* 2010; Urban *et al.* 2012; Zarnetske *et al.* 2012) suggest that if *P. leucopus* and *P. m. gracilis* are competitors where they co-occur, ecological replacement may also be affected by interspecific competition. Though there is some evidence of interspecific territoriality (Dooley Jr. and Dueser 1996) and microhabitat partitioning (Wilson 1968; Geluso 1971; Master 1977; Holbrook 1978), it has also been hypothesized that co-occurring *P. leucopus* and *P. maniculatus* interact ecologically as a single species with neutral population dynamics (Wolff 1985). Few studies have investigated interspecific interactions in communities where these species are syntopic in the Great Lakes Region.

It is possible that social interactions (both within and between species) are reflected in the spatial distribution of individuals across the study grid. Results from this study (Table 5-3; Table 5-4) are consistent with observations that the spacing between female mice is approximately regular during the breeding season (Metzgar 1971; Fairbairn 1977; Harland *et al.* 1979), but aggregated during the rest of the year (Metzgar 1979; Mihok 1979). The temporal variation in the spatial distribution of female mice, the stronger effect observed for breeding females, and the relatively weaker effect observed for males suggest that females (of both species) in this community maintain breeding territories through social interactions.

The distribution of *P. leucopus* and *P. m. gracilis* across the grid varied seasonally and between years (Figure 5-2). Identification of 'preferred' and 'avoided' sites revealed substantial non-overlap in usage of the grid. These differences, however, could be due to differences between species in habitat preferences; *P. leucopus* tended to be found more often than expected at sites with large trees, while *P. m. gracilis* was most often captured at more densely vegetated sites. Analysis of nearest interspecific neighbor distances (NIN) suggests that spacing patterns of *P.*

leucopus and *P. m. gracilis* may be influenced by overall density. The association of greater NIN with periods of high total mouse density (but not with lower densities) raises the possibility that competition may be occurring in this community, even in light of differences in habitat associations.

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ENVIRONMENTAL CONDITIONS AND SOCIAL INTERACTIONS MAY MEDIATE ECOLOGICAL REPLACEMENT OF *PEROMYSCUS MANICULATUS GRACILIS* BY *PEROMYSCUS LEUCOPUS* IN NORTHERN MICHIGAN

6.1   INTRODUCTION

One of the major challenges in ecology is to predict how environmental change affects fluctuations in abundance of species in a community (Ives 1995; Kareiva *et al.* 1993; Gilman *et al.* 2010). Changes in abundance, however, depend not only on the direct effects of environmental conditions on reproductive success, but also the indirect effects of interspecific interactions that can serve as biotic multipliers of climate change (Tylianakis *et al.* 2008; Urban *et al.* 2012; Zarnetske *et al.* 2012). Under directional environmental change, niche or life history differences between species can become sources of competitive advantages (Brown *et al.* 2001; Tilman and Lehman 2001; Zavaleta *et al.* 2003) and can lead to rapid changes in community structure (Ernest *et al.* 2008). Variation in the responses of species to shifting climate regimes is ubiquitous in nature and can often shift competitive balances within communities to favor some species over others (Tylianakis *et al.* 2008).

Climate-induced ecological replacement of the 'northern' *P. m. gracilis* by the 'southern' *P. leucopus* has been documented with long-term studies in the Great Lakes Region (Long 1996; Myers *et al.* 2005). Gradually warming winters over the last 30-40 years in this area have facilitated northward range expansion of *P. leucopus*, and communities in which *P. leucopus* and *P. m. gracilis* co-occur have become characterized by strong numerical dominance of *P. leucopus* (Myers *et al.* 2009). I conducted a three year field study of syntopic *P. leucopus* and *P.*

m. gracilis in northern Michigan. I documented abundance, survival, and reproductive traits to provide a detailed examination of population dynamics in a community undergoing faunal turnover. Abundance of *P. leucopus* and *P. m. gracilis* differed strongly in two out of three years; community structure shifted from roughly equal abundance in 2010 to strong numerical dominance of *P. leucopus* in 2011 and 2012 (Chapter 2). Data on short-term population fluctuations, such as those observed in this study, may be useful in predicting long-term responses of population densities to directional environmental changes (Ives 1995).

Niche or life history differences can facilitate coexistence when the environment is temporally heterogeneous (Caceres 1997; Adler *et al.* 2006), but can lead to rapid changes in community structure when environmental change is directional (Ernest *et al.* 2008). In order to cause changes to abundance and community structure, differences between species must result in differential reproductive success. It is thus necessary to determine how species differences interact with environmental conditions to cause temporal fluctuations in reproductive success that ultimately facilitate replacement. If these trait differences are responsible for replacement, the mechanisms by which they lead to changes in abundance should be reflected in within-species variation in reproductive success.

In this chapter, I provide a summary and synthesis of results from my three year field study. *P. leucopus* and *P. m. gracilis* have been the subject of numerous investigations, and the ecological replacement of *P. m. gracilis* by *P. leucopus* has been established with long-term studies in the Great Lakes Region (Long 1996; Myers *et al.* 2005). Differences between species in traits, the processes that result in changes in reproductive success, and the role of interspecific interactions in replacement in communities where these species co-occur, are not well understood. I first identify traits in which *P. leucopus* and *P. m. gracilis* differ, then discuss the mechanisms by which these differences might facilitate ecological replacement by assessing short-term fluctuations in survivorship and reproductive patterns. Lastly, I indirectly assess the role of interspecific interactions in replacement by discussing whether observed patterns in *P. leucopus* and *P. m. gracilis* abundance are likely to be caused by environmental fluctuations alone.

6.2   DIFFERENCES BETWEEN SPECIES

How do *P. leucopus* and *P. m. gracilis* differ in niche or life history traits? Extreme morphological and ecological similarities between these two species have been noted by many authors (Horner 1954; Wolff and Hurlbutt 1982; Feldhamer *et al.* 1983; Wolff 1985; Long and Long 1993); however, few studies have provided a detailed examination of population dynamics from communities in which climate-induced replacement is occurring. Below, I discuss different aspects of their ecology and life histories that might influence replacement.

6.2.1   WINTER ADAPTATIONS

There is evidence that *P. leucopus* and *P. maniculatus* are adapted to different environmental conditions. *P. maniculatus* may be superior to *P. leucopus* in winter adaptations including the use of torpor, nest building, food storage, and lower food consumption (Wolff and Durr 1986; Tannenbaum and Pivorun 1988; Pierce and Vogt 1993), and thus may have an ecological advantage in boreal areas (Long 1996). *P. leucopus* may be more vulnerable than *P. maniculatus* to cold winters (Howard 1951), particularly to low temperatures and deep frosts (Madison *et al.* 1984; Long 1973). Direct comparisons of winter adaptations were beyond the scope of this study. Nonetheless, if *P. leucopus* and *P. m. gracilis* differ in winter adaptations, differences between species in winter survival are expected under harsh and mild conditions.

When winters are harsh, a greater proportion of *P. m. gracilis* should survive to the following spring than *P. leucopus*. In Michigan, winter survival of *P. leucopus* is enhanced when winters are mild and survival reduced when winters are harsh (Myers *et al.* 2005). The winter of 2011-2012 was the mildest experienced by mice during this study (Chapter 2); it was thus expected that a greater proportion of *P. leucopus* would overwinter in 2011-2012 than in 2010-2011. Nevertheless, the proportion of *P. leucopus* that overwintered did not differ significantly between years, and the proportion of *P. leucopus* and *P. m. gracilis* that survived the winter of 2010-2011 or 2011-2012 also did not differ (Chapter 3). There was, however, a non-significant trend for a greater proportion of mice to survive the winter of 2011-2012 than the previous winter; this raises the possibility that winter survival of both species is enhanced when conditions are mild.

Analyses comparing winter survival, however, were inconclusive due to the low numbers of overwintering mice, especially of *P. m. gracilis*. Further, all three winters during this study were characterized by lower than average snowfall and earlier than average dates of ice break-up (Chapter 2). It is thus possible that the winter conditions experienced by mice during this study were not harsh enough to cause enhanced survival of *P. m. gracilis* over *P. leucopus*. If this is the case, environmental conditions in this area may have already warmed sufficiently so that conditions under which *P. m. gracilis* is favored have become rare.

6.2.2   LENGTH OF BREEDING SEASON

Photoperiod is a primary cue for the initiation of spring breeding for *P. maniculatus* (Price 1966; Millar and Herdman 2004) and *P. leucopus* (Whitaker 1940; Heideman *et al.* 1999). Spring breeding is stimulated by increasing photoperiod and is mediated by temperature such that breeding begins following sudden rises in temperature that coincide with increasing day length (Sadleir 1974). Similarly, the cessation of breeding in higher latitude populations is thought to be closely tied to declining temperature, perhaps due to the increased cost of maintenance at lower temperatures (Sadleir *et al.* 1973) and energy requirements of lactation (Harland and Millar 1980).

Though the onset and cessation of breeding may be regulated by the same types of environmental cues, responsiveness to these cues may be under partial genetic control (Heideman and Bronson 1991). Myers *et al.* (2005) proposed that the onset of breeding of *P. leucopus* in northern Michigan may be influenced by gene flow from southern populations, where this species typically begins breeding in March (Brown 1964; Baker 1983). Similarly, the onset of breeding for *P. maniculatus gracilis* may be influenced by gene flow from northern populations, which begin breeding in April or May (Millar *et al.* 1979).

In this study, *P. leucopus* began breeding earlier and ceased breeding later than *P. m. gracilis* in all years except 2011, when *P. m. gracilis* began breeding earlier (Chapter 4). These observations support the hypothesis that breeding season length may be a species-specific niche difference where *P. leucopus* and *P. m. gracilis* co-occur.

6.2.3   OVERWINTERED FEMALES

Differing patterns of survival of overwintered (OW) *P. leucopus* and *P. m. gracilis* were observed in all three years of this study (Chapter 3). Mean persistence time of OW *P. leucopus* females was significantly longer than that of OW *P. m. gracilis* females. OW *P. leucopus* and *P. m. gracilis* males, in contrast, did not differ in this respect. Further, losses of OW *P. m. gracilis*, both males and females, were concentrated over a period of approximately 60 days in the spring, while losses of OW *P. leucopus* were more evenly distributed throughout the spring and summer.

Reproductive output by overwintered females is often a large contributor to overall reproduction for both *P. leucopus* and *P. m. gracilis* (Lusk and Millar 1989), in part due to increased litter size relative to young-of-year mice (Lackey 1978; Millar 1982; Myers and Master 1983; Havelka and Millar 2004). OW females produce more litters on average than young-of-year (YOY) females in some populations (Harland *et al.* 1979); however, the contribution of OW females to population growth may be constrained by their survivorship in the spring and summer (Millar *et al.* 1979). Though capable of producing up to 4 litters during a single season (Baker 1983), few overwintered individuals survive the entire length of summer and realize their full reproductive potential (Havelka and Millar 2004).

Differences between *P. leucopus* and *P. m. gracilis* in the persistence of OW females resulted in significant differences between species in the relative contribution of OW and YOY females to total reproduction. OW *P. leucopus* females produced more litters and thus contributed more to population growth than YOY *P. leucopus* females in all years of this study. Population increases in *P. m. gracilis*, on the other hand, appeared to depend equally on reproductive output of OW and YOY females, and reproduction by YOY may compensate for the relatively early loss of OW females from the population. *P. m. gracilis* OW and YOY females did not differ in the per-capita number of litters in any year except in 2012, when no *P. m. gracilis* YOY bred. Differences between *P. leucopus* and *P. m. gracilis* in the patterns of survival (and consequently in the potential reproductive output) of overwintered mice may constitute a life history difference between these species that has not been previously reported.

6.3   MECHANISMS OF REPLACEMENT

Shifts in community structure are ultimately caused by differences in reproductive success of the species that make up the community. Total annual reproductive output of a species consists of reproduction of OW and YOY females. For each of these cohorts, reproductive output is influenced by traits such as the abundance of breeding individuals, the rate at which they reproduce, their length of persistence on the grid, winter survival, and the age at first reproduction; reproduction is additionally influenced by abiotic conditions such as the length of winter, and by the length of the breeding season (Figure 6-1).
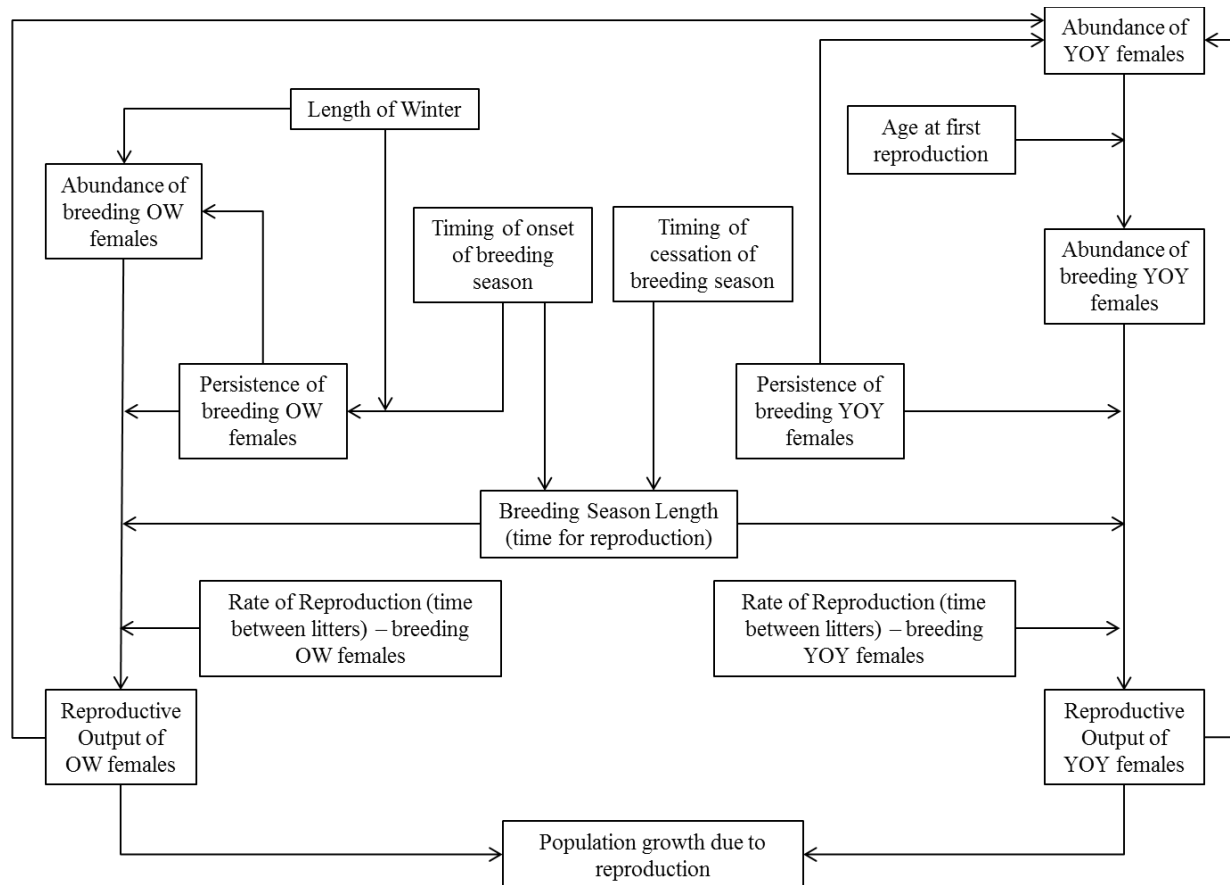

Figure 6-1: Conceptual model of the factors that influence population growth due to reproduction. Factors influencing reproduction are represented in boxes, and the effect of each factor (either directly on another factor or indirectly on another effect) is indicated with directional arrows.

There was some evidence that mild winter conditions enhance winter survival of both *P. leucopus* and *P. m. gracilis* (Chapter 3). Enhanced winter survival increases the abundance of breeding OW females in the spring, indirectly affecting the abundance of YOY females later in the season. While OW females dominate reproduction in spring and early summer, late-summer litters are typically produced by YOY females (Millar *et al.* 1979; Havelka and Millar 2004). Much of the difference between potential and observed reproductive output in some *Peromyscus* populations is attributable to survival (Schug *et al.* 1991), so that females that survive longer have proportionally more litters than short-lived females (Millar *et al.* 1992).

The age at which reproduction begins significantly impacts population growth via reproduction, effectively shortening generation time (Cole 1954). The frequency with which breeding females have litters is also an important contributor to differences in reproductive output. Individuals that reproduce quickly during a short life may be equally as successful as those that live a long time and reproduce at a slower rate, depending on the survival and reproduction of offspring (Stearns 1976).

Breeding season length can influence total annual reproductive output by modifying the length of time during which reproduction occurs. Comparisons of allopatric populations of *P. leucopus* and *P. maniculatus* that experience different breeding season lengths suggest that basic reproductive characteristics such as frequency of litters, litter size, and age at first reproduction are not significantly different (Millar *et al.* 1979). Consequently, it has been suggested that *Peromyscus* with short breeding seasons have a lower annual reproductive output than *Peromyscus* with longer breeding seasons (Millar *et al.* 1979).

6.3.1   DIFFERENCES IN SURVIVAL AND REPRODUCTION

Examination of within-species fluctuations in survival and reproduction may shed light on the mechanisms by which species differences result in changes in abundance. For both species, neither the persistence of OW mice nor the reproductive output of OW females differed between years (Chapter 3). Year-to-year within-species variation in survival and reproduction of YOY,

however, was observed: female YOY *P. leucopus* persisted longer in 2012 than in any other year; nevertheless, the rate of reproduction (estimated as the time between litters) by this cohort did not differ between years. In contrast, persistence of YOY *P. m. gracilis* females was similar each year, but reproductive output (estimated as the number of litters per female) of YOY *P. m. gracilis* females was reduced in each successive year, with *P. m. gracilis* YOY females reproducing at a slower rate in 2011 than in 2010 and not at all in 2012.

Taken together, results suggest that the relative importance of survival and reproductive rate to population growth is different for *P. leucopus* and *P. m. gracilis*. Increases in abundance of *P. leucopus* during this study appear to be explained by changes in winter survival and persistence of breeding females. For *P. m. gracilis*, in contrast, year-to-year variation in population growth may occur mainly due to changes in the reproductive patterns of YOY females.

6.3.2 HOW DO SPECIES DIFFERENCES AFFECT REPLACEMENT?

Analyses from this field study indicate that co-occurring *P. leucopus* and *P. m. gracilis* differ consistently in breeding season length and in the survivorship of OW mice after the start of the breeding season. Differences between species in the age at first reproduction, and reproductive rate and persistence of YOY females, were additionally observed in some years (Table 6-1). Though I found no significant differences in winter survival of the two species, comparisons of physiology and winter adaptations indicate that *P. m. gracilis* may have an advantage over *P. leucopus* in surviving harsh winters (Wolff and Durr 1986; Tannenbaum and Pivorun 1988; Pierce and Vogt 1993; Howard 1951; Madison *et al.* 1984; Long 1973), and that *P. leucopus* has enhanced survival when winters are mild (Long 1996; Myers *et al.* 2005). How do differences between species lead to changes in reproductive output under conditions of increasing warming?

TRAIT	*P. LEUCOPUS*	*P. M. GRACILIS*
	DIFFERENCES BETWEEN SPECIES	
PERSISTENCE OF OW FEMALES	Longer average persistence Losses spread evenly in spring and summer	Shorter average persistence Losses concentrated in spring
CONTRIBUTION OF OW AND YOY TO REPRODUCTION	Greater contribution of OW	Equal contribution of OW and YOY
BREEDING SEASON LENGTH	Begins breeding earlier (2010, 2012) Ends breeding later (all years) Longer breeding season (all years)	Begins breeding later (2010, 2012) Ends breeding later (all years) Shorter breeding season (all years)
	VARIATION WITHIN SPECIES	
PERSISTENCE OF YOY FEMALES TIME BETWEEN LITTERS - YOY AGE AT FIRST REPRODUCTION	Persisted longest in 2012	Most frequent litters in 2010 No YOY bred in 2012

Table 6-1: Differences observed between *P. leucopus* and *P. m. gracilis* in survival and reproduction.

6.3.2.1   INCREASES IN *P. LEUCOPUS* ABUNDANCE

Increases in the population growth rate of *P. leucopus* may be explained by the effect of environmental conditions on overwinter survival and spring/summer persistence (Figure 6-2). Many of the increases in *P. leucopus* abundance observed during this study may be due to changes in survivorship. Average persistence time of YOY females was the greatest in 2012 and led to increased reproductive output of this cohort. A longer breeding season lengthens the time for potential reproduction. In this study, the breeding season of *P. leucopus* extended for 24 days longer than that of *P. m. gracilis* on average; *P. leucopus* began breeding earlier than *P. m. gracilis* in two out of three years and ceased breeding later than *P. m. gracilis* in all years (Chapter 4). Because most late-season reproduction is attributed to YOY females (Harland *et al.* 1979), a later cessation of breeding could contribute to the differences between species in YOY reproductive output observed in 2011 and 2012. A longer breeding season, however, was not consistently associated with greater reproductive output in *P. leucopus* (Chapter 4), suggesting

that the degree to which population growth is affected by breeding season length is mediated by other factors.
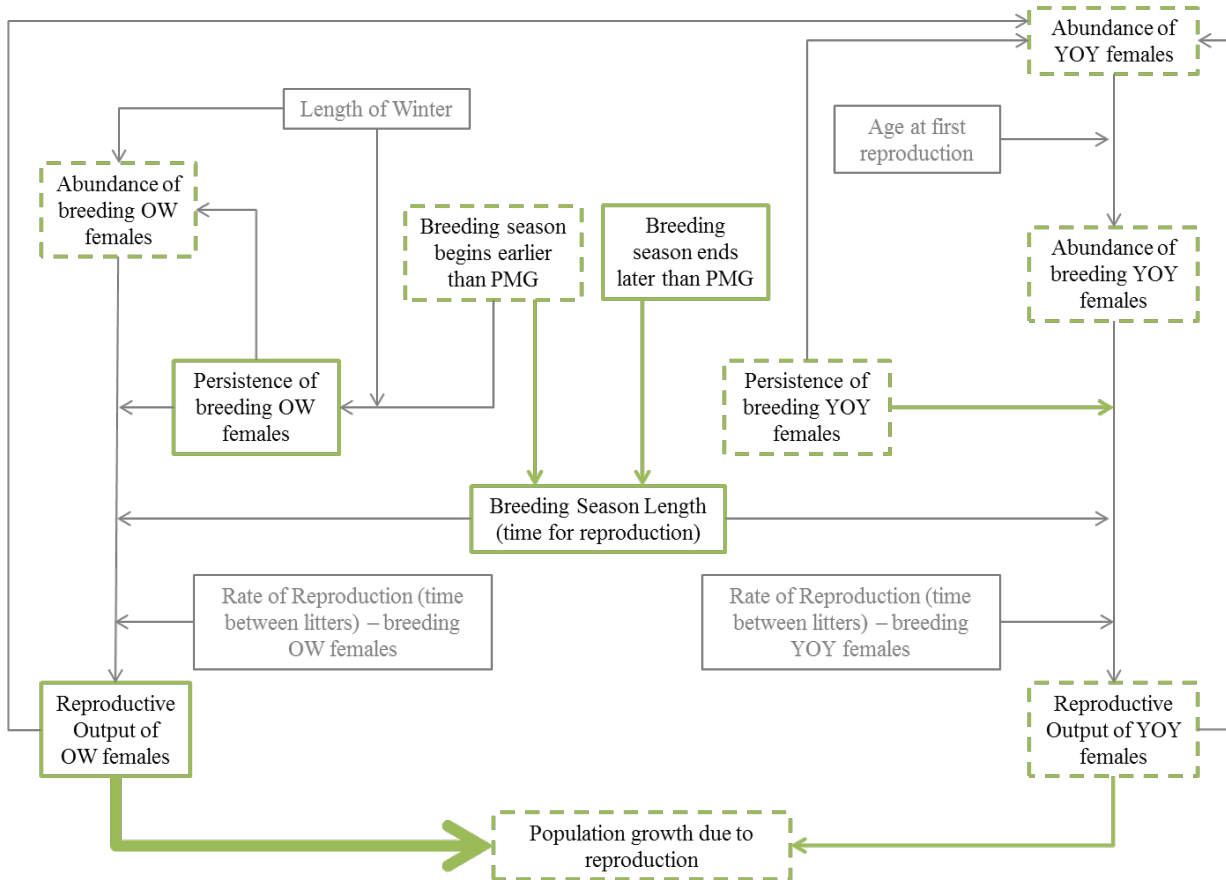

Figure 6-2: Factors influencing reproductive output for *P. leucopus*. Green boxes indicate traits in which *P. leucopus* differed from *P. m. gracilis*. Green arrows indicate observed effects (e.g., increased persistence of breeding YOY females was observed to contribute to reproductive output of YOY females, and reproduction of OW females contributes more to total reproduction than reproduction by YOY). Solid boxes and arrows represent traits or effects that were observed in all years, while dotted lines indicate that differences were observed in some (but not all) years. Gray boxes and text indicate traits that did not differ between species; gray arrows represent effects that were not directly observed by this study.

Reproduction by OW females should be most sensitive to the timing of the onset of breeding because their abundance is highest in the spring. The severity and length of winter could be an important factor in determining whether an earlier onset of the breeding season results in enhanced population growth. If breeding begins too early in the spring, e.g. if conditions are

harsh due to a long winter, both failed reproduction and increased mortality of OW females may result (Hayward 1965; Sadleir *et al.* 1973; Harland and Millar 1980). There was some indirect evidence that *P. leucopus* began breeding too early in 2010, and mortality of overwintered females could explain the relatively low numbers of *P. leucopus* in that year (Chapter 4). In 2011, *P. leucopus* began breeding later than in 2010, and because the winters preceding these years were similar in length and harshness (Chapter 2), a later onset of breeding by *P. leucopus* in 2011 may have resulted in fewer failed reproductive events and lower spring mortality of breeding OW females. Similarly, in 2012, mild spring conditions may have facilitated successful early breeding. This resulted in increased *P. leucopus* abundance in 2011 and 2012.

Due to the greater contribution of OW females to reproduction than YOY, any factors that influence the abundance, persistence, or rate of reproduction of OW females may result in disproportionately large changes in reproductive output in *P. leucopus*. The advantages conferred to *P. leucopus* when winters are mild are thus twofold, leading to both increased abundance of breeding females in the spring and early reproduction and lower spring mortality of breeding females. The relative contribution of OW females to reproduction and the effect of winter conditions on survival and persistence of OW females may explain why abundance of *P. leucopus* is so sensitive to winter conditions (Myers *et al.* 2005).

6.3.2.2 DECREASES IN POPULATION GROWTH RATE OF *P. M. GRACILIS*

Decreases in abundance of *P. m. gracilis* may be explained by slowed reproductive rate of YOY and delays in the age at first reproduction (Figure 6-3); this species may not be as heavily influenced by changes in reproduction by OW females. Though the evidence is inconclusive, it is possible that winter survival in both species is enhanced when conditions are mild, leading to a greater abundance of breeding females in the spring. Because of the relatively smaller contribution of OW females to reproduction in *P. m. gracilis*, however, the effect of environmental conditions on winter survival may have a smaller impact on population growth in this species than on *P. leucopus*. *P. m. gracilis* OW females produced fewer litters on average than *P. leucopus* OW females in all years during this study, and this was due to differences in their patterns of spring and summer survival. Losses of *P. m. gracilis* OW females were

concentrated in the spring and few survived to late summer; these individuals had less time for potential reproduction.
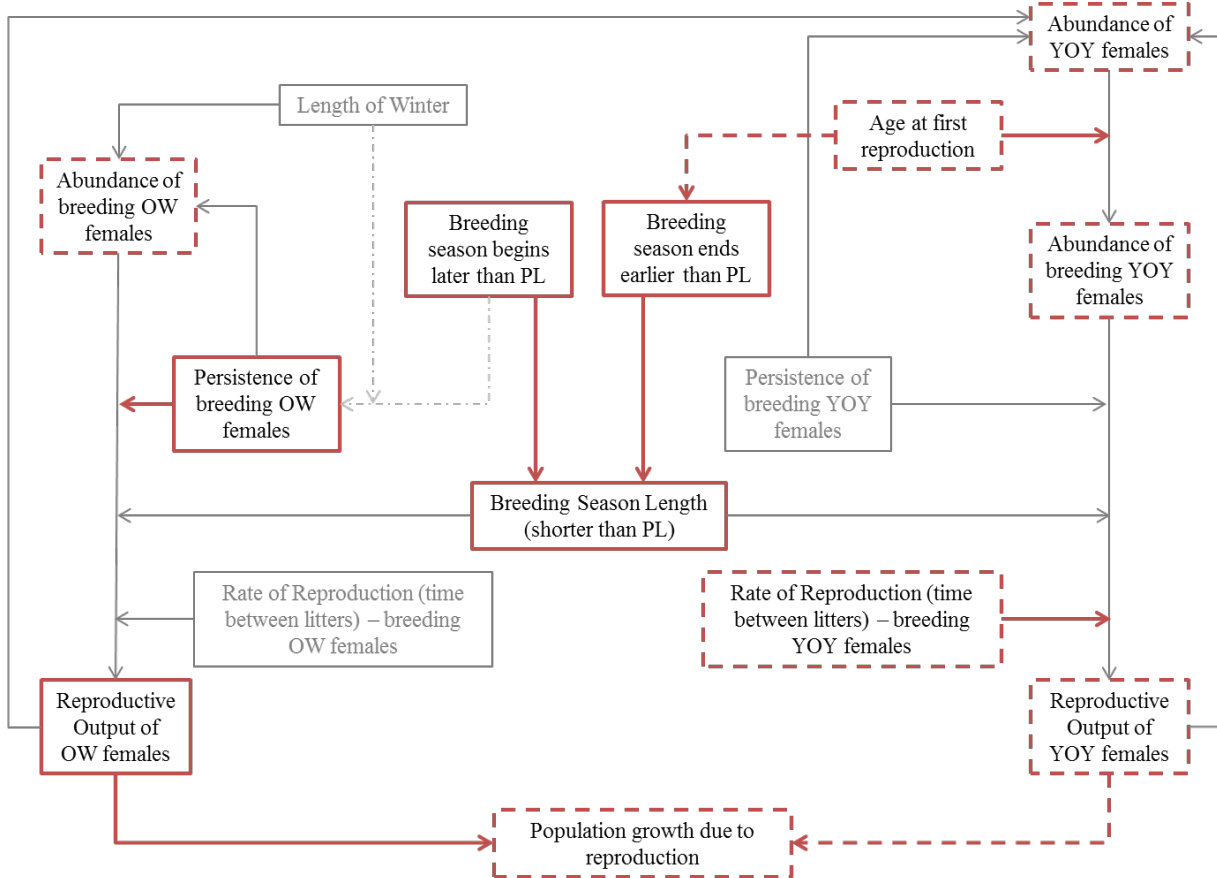

Figure 6-3: Factors influencing reproductive output for *P. m. gracilis*. Red boxes indicate traits in which *P. m. gracilis* differed from *P. leucopus*. Red arrows indicate observed effects (e.g., reduced persistence of OW females relative to *P. leucopus* resulted in decreased reproductive output of OW females). Solid boxes and arrows represent traits or effects that were observed in all years, while dotted lines indicate that differences were observed in some (but not all) years. Gray boxes and text indicate traits that did not differ between species. Gray arrows represent effects that were not directly observed by this study; dotted gray arrows indicate that no effect was observed – neither the timing of the onset of the breeding season nor the length of winter affected persistence of OW *P. m. gracilis* females in this study.

The relationship between environmental conditions, the timing of the onset of breeding, and reproductive output of OW females is not clear for *P. m. gracilis*. Though there was some variation in the timing of the onset of the breeding season, average persistence of OW *P. m. gracilis* females was not different across years, nor was their reproductive output. The onset of

breeding by *P. m. gracilis* in northern Michigan may be influenced by gene flow from more northern populations (Heideman *et al.* 2009; Myers *et al.* 2005) which begin breeding in April or May (Millar *et al.* 1979). It is possible that a later onset of breeding in this species reduces the chances of breeding too early, so that spring survival of OW *P. m. gracilis* females is not as sensitive as OW *P. leucopus* females to environmental conditions.

The breeding season of *P. m. gracilis* was consistently shorter than that of *P. leucopus*, suggesting that potential population growth is lower for *P. m. gracilis* because there is less time for reproduction. Cessation of breeding is typically regulated by responses to photoperiod and temperature (Sadleir 1974; Heideman *et al.* 1999), but can sometimes occur earlier than expected for other reasons (Canham 1969). In 2012, *P. m. gracilis* experienced the shortest breeding season of any year during this study, and this coincided with slowed population growth and reduced reproduction. No *P. m. gracilis* YOY females in the study grid bred in 2012 and OW females disappeared from the grid by early August (Chapter 3); this suggests that the breeding season was shortened due to the lack of reproduction in YOY females.

Year-to-year variation in population growth of *P. m. gracilis* may occur mainly due to changes in the reproductive patterns of YOY females (Chapter 3). Disparities in population growth of *P. leucopus* and *P. m. gracilis* were observed during this study in 2011 and 2012, and each of these years was characterized by reduced reproduction by *P. m. gracilis* YOY. Both slowed reproduction (in 2011) and delayed onset of first reproduction (in 2012) were observed. The age at first reproduction may influence population growth more than either longevity or the number of litters produced (Cole 1954), and small changes in this trait have the potential to greatly impact population abundance. Approximately 70% of YOY females bred in their natal year during this study, except in 2012 when no *P. m. gracilis* YOY females bred.

The relatively larger contribution of YOY females to reproduction may make *P. m. gracilis* more sensitive than *P. leucopus* to fluctuations in reproduction by YOY in their natal year. Breeding by YOY may typically compensate for the relatively early loss of OW females. The lack of reproduction by YOY females in 2012 resulted in a shortened breeding season, reduced annual reproductive output, slowed population growth, and contributed to the large disparity in abundance observed in that year.

6.3.3 ROLE OF INTERSPECIFIC COMPETITION IN REPLACEMENT

The role of interspecific competition in the replacement of *P. m. gracilis* by *P. leucopus* has not previously been investigated, probably due to uncertainty regarding the importance of such interactions to population dynamics in communities where these species co-occur (Master 1977; Wolff *et al.* 1983; Wolff 1985; Dooley Jr. and Dueser 1996). It is possible that replacement results as both species independently respond to changes in the environment (Wolff 1996; Myers *et al.* 2005). Recent empirical studies, however, suggest that competition can facilitate climate-induced extinctions (Sinervo *et al.* 2010; Jankowski *et al.* 2010; Urban *et al.* 2012), and competition at range boundaries may explain the disappearance of cold-adapted species from sub-optimal environments where they would typically be able to persist at low abundance (Kelly and Goulden 2008). It is possible that *P. m. gracilis* is able to persist in areas that are becoming increasingly warm if *P. leucopus* were not also increasing in abundance; the combination of sub-optimal environmental conditions and increased density of *P. leucopus* may lead to ecological replacement.

Elucidating the role of interspecific interactions in the replacement of *P. m. gracilis* by *P. leucopus* is difficult. The duration of this field study was not long enough for an accurate assessment of the effect of environment on abundance or reproductive success, and it is unknown whether these two species compete in this area.

6.3.3.1 DO CO-OCCURRING *P. LEUCOPUS* AND *P. M. GRACILIS* COMPETE?

The importance of biotic interactions in shaping species responses to climate change (Tylianakis *et al.* 2008; Gilman *et al.* 2010; Urban *et al.* 2012; Zarnetske *et al.* 2012) suggest that if *P. leucopus* and *P. m. gracilis* are competitors where they co-occur, ecological replacement may also be affected by interspecific competition. There is some evidence of interspecific territoriality (Dooley Jr. and Dueser 1996) and microhabitat partitioning (Wilson 1968; Geluso 1971; Master 1977; Holbrook 1978) in syntopic communities of *P. leucopus* and PM. Are *P. leucopus* and *P. m. gracilis* competitors in northern Michigan?

Analyses presented in Chapter 5 suggest that some patterns observed in the spatial distribution of mice are consistent with the existence of interspecific competition. Analysis of nearest interspecific neighbor distances (NIN) suggests that spacing patterns of *P. leucopus* and *P. m. gracilis* may be influenced by overall density – in the latter part of 2011 and all of 2012, when mice were the most abundant, interspecific captures were further apart than expected. In 2010 and early 2011, on the other hand, spacing of *P. leucopus* and *P. m. gracilis* was random, except for summer 2010 when *P. leucopus* and *P. m. gracilis* were clumped. The association of greater NIN with periods of high total mouse density (but not with lower densities) raises the possibility that competition may be occurring in this community.

Identification of sites at which *P. leucopus* and *P. m. gracilis* were found more or less often than expected by chance revealed substantial non-overlap in usage of the study grid. Differences in the use of space, however, could be due to differences between *P. leucopus* and *P. m. gracilis* in their habitat preferences; and indeed, *P. leucopus* was found more often than expected at sites with large trees, while *P. m. gracilis* was most often associated with sites with more dense foliage. Results from this study were thus inconclusive regarding the existence of interspecific competition in this community.

6.3.3.2 CAN ENVIRONMENTAL CONDITIONS EXPLAIN POPULATION GROWTH PATTERNS?

It has been hypothesized that co-occurring *P. leucopus* and *P. maniculatus* interact ecologically as a single species with neutral population dynamics (Wolff 1985) and that fluctuations in abundance within these communities may be due to differing environmental optima rather than to interspecific interactions (Wolff 1996). Can increases in abundance of *P. leucopus* and decreases in abundance of *P. m. gracilis* that are characteristic of faunal turnover be explained without invoking interspecific interactions?

Environmental conditions could explain much of the fluctuations in *P. leucopus* abundance. Due to the relatively large contribution of OW females to reproduction than YOY females in *P. leucopus*, mild conditions that allow for enhanced winter survival of OW females may result in disproportionately large increases in reproductive output in this species. *P. leucopus* may

consistently begin breeding earlier in the spring than *P. m. gracilis*; short winters may result in more favorable breeding conditions which facilitate successful early reproduction and lower mortality of breeding females. An additional source of increases in *P. leucopus* population growth in 2012 was the enhanced persistence of YOY females, which led to increased reproductive output by this cohort; the connection between this phenomenon and environmental conditions is unclear.

Reproduction by YOY mice was responsible for much of the year-to-year variation in population growth of *P. m. gracilis*. *P. m. gracilis* YOY females reproduced at a slower rate in 2011 than in 2010, and did not reproduce at all in 2012. OW *P. m. gracilis* females, however, did not differ in reproductive output between years (Chapter 3), suggesting that a cohort-specific process was responsible. What might cause *P. m. gracilis* YOY females to be unsuccessful, but have little effect on the breeding of OW females? OW females begin breeding in the spring when densities are low, and few (of either species) survive until fall. In contrast, *P. m. gracilis* YOY females do not begin breeding until June, when abundance of both species is higher; and reproduction in the late summer and fall, when abundance typically peaks, is dominated by YOY females. Differences in the timing of breeding events between OW and YOY females suggest that these cohorts may experience different abiotic (spring vs. summer/fall climate) and biotic (low vs. high abundance) breeding conditions.

One explanation for reduced reproduction of *P. m. gracilis* YOY is that this species suffers reduced reproduction when temperatures are too warm. Laboratory experiments suggest that there is an optimal temperature range between which the number and frequency of litters is maximized, and that the optimal range may differ for 'northern' and 'southern' populations (Bronson and Pryor 1983). All three summers of this study were characterized by temperatures that were warmer than the historical average (Table 6-2). It is possible that environmental conditions in summer 2011 and 2012 were outside of the optimal range of *P. m. gracilis* and resulted in reduced reproduction by YOY. Because I was not able to examine weather conditions at a finer temporal scale, and because sample sizes of *P. m. gracilis* tended to be low in all years, I was unfortunately unable to more thoroughly test this hypothesis.

TABLE 6-2: SUMMER TEMPERATURE AND PRECIPITATION

YEAR	TEMPERATURE (°F)		PRECIPITATION (IN)	
	MEAN	DEVIATION	MEAN	DEVIATION
2010	67.77	1.37	3.38	0.12
2011	66.3	0.97	3.46	0.27
2012	67.17	3.1	3.14	-0.04
HISTORICAL	64.93		3.21	

Table 6-2: Average summer temperature and precipitation obtained from a weather station in Gaylord, MI, 25 miles SSW of the Pigeon River Grid. Long-term historical averages of summer (June-August) temperature and precipitation are compared to yearly means for each summer.

Though the effect of climate cannot be ruled out, density-mediated interspecific social interactions provide a plausible mechanism that could result in reduced reproduction by YOY *P. m. gracilis* females, enhanced persistence of YOY *P. leucopus* females, and have little effect on the breeding of OW females. Reproductive output has been found to be inversely proportional to population density in *P. leucopus* (Burt 1940; Manville 1949), and high densities can cause *P. maniculatus* to cease breeding earlier than normal (Canham 1969; Sadleir 1974). Reduced reproduction by YOY *P. m. gracilis* females was observed during years of high *P. leucopus* abundance (2011 and 2012), but not when *P. leucopus* abundance was lower (2010).

Social interaction among breeding females is thought to be an important regulator of population growth in *P. leucopus* and *P. maniculatus* (Harland *et al.* 1979; Lusk and Millar 1989). Resident females actively exclude other females from their home ranges during the breeding season, resulting in season-specific spatial distributions of individuals (Nicholson 1941; Metzgar 1971, Harland *et al.* 1979). Spacing between adult female mice is approximately regular during the breeding season (Metzgar 1971; Fairbairn 1977; Harland *et al.* 1979), but aggregated during the rest of the year (Metzgar 1979; Mihok 1979).

Results from this study are consistent with reported patterns of the spatial distribution of individuals – for both *P. leucopus* and *P. m. gracilis*, the average minimum distance between females was greater than expected in the summer and fall, but was not different from random in

the spring; the same pattern was not observed for males (Chapter 5). The maintenance of spatial relationships is associated with social interactions such as overt aggression (Lusk and Millar 1989; Dooley Jr. and Dueser 1996). Social interactions among females may thus play an important role in population regulation and lie at the root of the low success of *P. m. gracilis* YOY. Reproductive inhibition of YOY females of both *P. leucopus* and *P. maniculatus* has been experimentally demonstrated in natural populations and may be mediated by density of breeding adults (Lusk and Millar 1989; Terman 1993).

6.3.3.3 SHIFTS IN COMPETITIVE DOMINANCE

Variation in the responses of species to climate change (Gilman *et al.* 2010) may shift competitive balances to favor some species over others (reviewed in Tylianakis *et al.* 2008). Changes in climate can also alter the nature of the interactions between species (Suttle *et al.* 2007; Pennings *et al.* 2003). It has been suggested that co-occurring *P. leucopus* and *P. m. gracilis* exhibit neutral dynamics with stochastic changes in abundance, and that they interact as a single species (Wolff 1996). Although climate-induced shifts from neutral interactions to competitive dominance have not been previously reported, it is possible that this phenomenon facilitates the replacement of *P. m. gracilis* by *P. leucopus*.

Available territories in which to breed may be a sex- and season-specific limiting resource for which females compete (Bujalska 1973; Harland *et al.* 1979). The identity of the victor in aggressive contests tends to depend on residency status (resident or intruder) rather than species identity (Wolff *et al.* 1983), and larger size is also advantageous (Garten 1976; Bowers and Smith 1979). This suggests that neither species is inherently a better competitor, but rather that competitive advantages are conferred to individuals that are able to establish territories early.

P. leucopus and *P. m. gracilis* may differ in their responses to environmental cues that regulate the onset of breeding, and results from this study indicate that *P. leucopus* may consistently begin breeding earlier than *P. m. gracilis* in the spring. The effect of an earlier onset of the breeding season on population growth may be mediated by environmental conditions such that the rate of population growth is inversely related to the length and severity of winter. Successful early breeding in mild conditions can lead to a numerical advantage by lengthening the time for

potential reproduction, but may also confer a competitive advantage by allowing young to establish territories early. Both the lack of reproduction by *P. m. gracilis* YOY females and increased persistence of *P. leucopus* YOY females may result from this competitive advantage. Breeding by OW females, on the other hand, would not be affected because these individuals have already established territories before the breeding season began.

Early-born young can become independent and establish territories when densities are low (Sharpe and Millar 1991) and have more time to grow to a larger size than late-born young, thus giving them a further advantage in aggressive contests. Results from this study support the hypothesis that successful early breeding leads to a competitive advantage (Chapter 4). For both species, YOY females that appeared early on the grid were more likely to establish territories than those that appeared later. The species that began breeding earlier tended to establish territories earlier than the species that began breeding later. YOY females of the early breeding species were also significantly heavier than YOY females of the later breeding species. Taken together, these results suggest that increasingly warm winters may shift the competitive balance within the community to favor *P. leucopus* by allowing this species to consistently establish territories before *P. m. gracilis*.

6.4   CONCLUSION

Understanding the mechanisms by which directionally changing climate regimes alter community structure is critical to accurately predict how global climate change will continue to impact natural communities. The biological mechanisms by which *P. leucopus* increases in abundance while *P. m. gracilis* declines are not well known, and the influence of interspecific interactions on replacement in communities of co-occurring *P. leucopus* and *P. m. gracilis* has not previously been investigated. I conducted a three year field study of syntopic *P. leucopus* and *P. m. gracilis* in Michigan's northern Lower Peninsula, an area in which climate-induced ecological replacement is occurring. Analyses of data collected during this field study have

sought to identify differences between species and examine the mechanisms by which warming climatic conditions facilitate ecological replacement of *P. m. gracilis* by *P. leucopus*.

P. leucopus and *P. m. gracilis* differ consistently in breeding season length (Chapter 4) and in the survivorship of overwintered mice (Chapter 3). Losses of OW *P. m. gracilis* were concentrated over a shorter period of time than OW *P. leucopus*; this resulted in differences between species in the relative contributions of OW and YOY females to annual reproductive output. Due to the greater contribution of OW females to total reproduction in *P. leucopus*, processes that affect the survival of OW females have a more important effect on population growth in this species than is the case for *P. m. gracilis*. Environmental conditions can explain much of the observed increases in abundance of *P. leucopus* via effects on winter survival and spring/summer persistence of OW females.

Results from this study suggest that interspecific social interactions might mediate the decline of *P. m. gracilis* in northern Michigan. Slowed population growth of *P. m. gracilis* during this study was associated with reduced reproductive rates in YOY females and delayed onset of first reproduction, while reproduction by OW females did not differ between years (Chapter 3). Density-mediated interspecific social interactions provide a plausible mechanism that could result in this pattern. Evidence for the existence of social interactions between females was found in the pattern of temporal variation in the spacing of females (Chapter 5). Social interactions between females at high densities can cause both reduced reproductive output and delayed onset of first reproduction (Canham 1969; Sadleir 1974; Lusk and Millar 1989). YOY females may be more likely than OW females to experience negative density-dependent effects on reproduction because population density is higher in the late summer than in the spring, and because by that time few OW females remain alive.

The effect of social interactions on reproduction may be mediated by changes in climate. Several analyses support the hypothesis that increasingly warm winters shift the competitive balance in this community by facilitating successful early breeding and allowing YOY *P. leucopus* to establish territories earlier than *P. m. gracilis* (Chapter 4). Early-born young were more likely to establish territories and were heavier on average than those born later; both larger size and residency status make an individual better able to win aggressive contests. Because *P. leucopus*

tends to begin breeding earlier in the spring than *P. leucopus*, and early spring reproduction is more successful in years following mild winters, YOY *P. m. gracilis* may be at a significant disadvantage when winters are mild due to the difficulty of establishing territories. OW females, on the other hand, were not similarly affected because their reproduction was concentrated during periods of low density (i.e., the spring) and because their territories were already established.

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