ABSTRACT

FACTORS AFFECTING THE NEGATIVE DENSITY AREA RELATIONSHIP OF THE WHITE-FOOTED MOUSE (*PEROMYSCUS LEUCOPUS*)

By Shawn M. Wilder

Several investigators have documented a negative density-area relationship (i.e. higher population densities in smaller fragments) for *Peromyscus leucopus* (the white-footed mouse). The purpose of this thesis is to investigate if high densities of *P. leucopus* are consistent among seasons and if higher densities may be due to greater reproduction, as a result of higher food availability, in small than large fragments. Observations of nest box use suggest that relative density and reproduction in small and large fragments differ among seasons. Higher densities in small than large fragments were only documented during the fall season. Observations of foraging patch use combined with reproductive data suggest that greater food availability in the edge may allow greater reproduction and thus contribute to higher densities in small fragments. Dense edge vegetation may be the primary contributor to greater food availability, although there is some evidence that there may be fewer competitors in small fragments.

FACTORS AFFECTING THE NEGATIVE DENSITY-AREA RELATIONSHIP OF THE WHITE-FOOTED MOUSE (*PEROMYSCUS LEUCOPUS)*

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DEDICATION

This thesis is dedicated to my parents, Michael and Joanne Wilder, who introduced me to nature when I was young and who have always provided support and encouragement.

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CHAPTER 1:

GENERAL INTRODUCTION

Deforestation that occurred primarily during the 19th century reduced forested habitat in the eastern U.S. to a fraction of its original coverage, with remnants and regrowth in some areas existing as forest fragments in an agricultural and urbanized matrix (Cummings and Vessey 1994). Fragmentation may influence the abundance and distribution of species in a number of ways. While the density of many mammal species does not vary with fragment area (Bowers and Matter 1997, Connor et al. 2000), some mammals have a positive density-area relationship, which increases their probability of extinction as fragment area decreases (Bowers and Matter 1997). However, other species such as *Apodemus sylvaticus* (the wood mouse) and *Peromyscus leucopus* (the white-footed mouse) show a negative relationship between population density and fragment area (Yahner 1992, Bowers and Dooley 1993, Bowers and Matter 1997, Mossman and Waser 2001, Anderson et al. in press). Nupp and Swihart (1996), summarizing data from their own and eight other published studies, found that *P. leucopus* can reach densities in small fragments that are an order of magnitude higher than densities in contiguous forest.

The negative relationship between *P. leucopus* density and fragment area may have negative impacts on plants and animals because of the ecological role of this species. *P. leucopus* can be a significant predator of passerine bird nests (Keyser et al. 1998, Schmidt et al. 2001), as well as the seeds of many plant species (Meiners and Stiles 1997, Ostfeld et al. 1997). Manson and Stiles (1998) reported that *P. leucopus* was the most abundant seed predator at their site and consumed the “vast majority” of predated seeds. But seeds were not chosen in proportion to their relative availability; some species of seeds were consumed more frequently than others (Manson and Stiles 1998). Selective seed predation can alter the vegetative community through differential recruitment rates of plants (Manson and Stiles 1998). The generalist diet of this species may also make it a significant competitor with other species of small mammals (Schmidt et al. 2001, Kurta 1995). *P. leucopus* is also an important prey item for raptors (Colvin and Spaulding 1983), snakes (Durner and Gates 1993), and mammals (Morris and Davidson 2000). Thus, understanding the response of *P. leucopus* to fragment area may increase our understanding of the effects of fragmentation on plant and animal communities.

Three hypotheses have been proposed to explain higher densities of *P. leucopus* in smaller fragments: 1) lower emigration rates, 2) lower predation rates, and 3) factors that result in greater food availability (i.e. lower competition and greater primary and secondary production) (Nupp and Swihart 1996). Lower emigration, or lack of emigration, has been referred to as a “fence effect” (see Krebs et al. 1969). The sharp junction of forest and field may act as a “fence” by inhibiting dispersal of individuals. However, demographic data do not support this hypothesis (Nupp and Swihart 1996, Anderson et al. in press). Additionally, evidence of dispersal from small fragments (Cummings and Vessey 1994) and rapid recolonization of small fragments that have been experimentally extirpated (Middleton and Merriam 1981, Krohne and Hoch 1999) provide evidence against this hypothesis.

Lower predation rates in small fragments are also unlikely to explain high densities, especially if interpatch distances are small relative to the high vagility of predators (e.g. hawks, Leary et al. 1998; owls, Zimmerman et al. 2001). Furthermore, some evidence suggests that predation rates by some larger mammals (e.g. raccoons, opossums, and canids) and raptors (e.g. hawks and owls) may be higher in small fragments and fragmented landscapes relative to contiguous forest (Loman 1991, Oehler and Litvaitis 1996, Donovan et al. 1997, Keyser et al. 1998, Dijak and Thompson 2000 Chalfoun et al. 2002).

The hypothesis that food availability is greater in small than large fragments has received support from demographic data collected from live trapping studies (Nupp and Swihart 1996). Greater food availability in small fragments may be the result of fewer competitors, higher food production in the edge, or both. Many competitors of *P. leucopus* (e.g. *Sciurus niger, S. carolinenesis,* and *Tamias striatus*) have relatively large area requirements and thus may not be able to sustain populations in some small fragments. If competitors become locally extinct in a fragment, then there may be more food available for *P. leucopus*. Greater cover, richness, and diversity of shrub and herbaceous plants in edge than interior habitat may result in greater food availability in the edge due to higher primary and secondary production (Ranney et al. 1981, Matlack 1994, Murcia 1995, Jokimaki et al. 1998). Animals in edge habitat may also have access to food resources contained in the agricultural matrix (Wolf and Batzli 2002). Greater food production in the edge may result in greater food availability overall in small patches because the proportion of a fragment composed of edge habitat increases as fragment size decreases (Laurance and Yensen 1991). However, despite indirect support from demographic data, no study has investigated if food availability may be higher in small than large patches and how higher food availability may contribute to higher densities of *P. leucopus*.

The purpose of this thesis is to investigate the negative density-area relationship of *P. leucopus* and to explore whether greater reproduction, as a result of higher food availability, may be one factors contributing to high population densities in small fragments. Chapter 2 investigates if there is seasonality in the effects of fragmentation on *P. leucopus*. Much research suggests that the density and reproduction of *P. leucopus* may be seasonal (Rintamaa et al. 1976, Wolff 1985, Krohne et al. 1988, Terman 1993, Kesner and Linzey 1997, Lewellen and Vessey 1998a, b). Yet studies of the effects of fragment size and edge commonly use data from a single season or combined over several seasons. Chapter 3 combines data on foraging patch use with reproduction in nest boxes to explore if greater food availability may allow greater reproduction in small than large fragments. Chapter 4 uses *Ixodes scapularis* (deer tick) prevalence on *P. leucopus* as an indirect way to investigate relative use of fragments by *Odocoileus virginianus* (white-tailed deer, a potential competitor of *P. leucopus*). I conclude in Chapter 5 by tying the chapters together and discussing general conclusions and important findings of this research.

Chapter 2:

Seasonal Effects of Fragmentation on the Density and Reproduction of White-Footed Mice (*Peromyscus leucopus*)

ABSTRACT

Past studies of the effects of fragment size and edge habitat on *Peromyscus leucopus* (the white-footed mouse) have used data from a single season or combined over several seasons. I used nest boxes to observe seasonal changes in the effects of fragmentation on the density and reproduction of *P. leucopus*. Relative density changed from lower, to similar, and then higher in small than large fragments. While large fragments displayed the typical bimodal pattern of litter production, small fragments maintained a relatively constant number of litters among spring, summer, and fall. Reproductive effort also differed among seasons, changing from higher in large than small fragments during the spring, to similar between size classes in the summer and fall. Although there was no difference between habitats in density, litter production, and reproductive effort during spring and summer, all were significantly higher in edge than interior habitats during the fall. My results suggest that including seasonality in the study of the effects of fragment size and edge may provide greater insight into how fragmentation affects population dynamics of temperate species of animals.

Several investigators have reported a negative density-area relationship for the generalist rodent *Peromyscus leucopus* (the white-footed mouse; Nupp and Swihart 1996, 1998, Krohne and Hoch 1999, Mossman and Waser 2001, Anderson et al. in press). Nupp and Swihart (1996), summarizing their own data and the results of eight other studies, found that *P. leucopus* may reach densities in small fragments that are an order of magnitude higher than densities in contiguous forest. Numerous investigations have also been conducted on relative population density in edge and interior habitats. Some studies have found higher (Cummings and Vessey 1994, Sekgoroane and Dilworth 1995, Bayne and Hobson 1998, Manson et al. 1999, Wolf and Batzli 2002, Anderson et al. in press) and others no difference between (Heske 1995, Nupp and Swihart 1996, Pasitschniak-Arts and Messier 1998) densities of *Peromyscus* in edge than interior. Thus, fragment size and edge may have important impacts on populations of *P. leucopus*.

Most studies of the effects of fragment size and edge on *P. leucopus* have been conducted in a single season (i.e. spring, summer, fall, or winter) or using data combined over several seasons. However, the density and reproduction of *P. leucopus* may vary among seasons. Populations of *P. leucopus* may show substantial intraannual fluctuations in density (Lewellen and Vessey 1998a). Low-density populations in the spring, which may result from high winter mortality, may increase by several-fold during the summer to reach fall peaks in density (Krohne et al. 1988, Kesner and Linzey 1997, Lewellen and Vessey 1998a). Reproduction may also be seasonal and consist of a spring and fall peak in litter production separated by midsummer and winter lulls (Rintamaa et al. 1976, Wolff 1985, Terman 1993). Long-term studies (e.g. $\geq$ 20 years) have confirmed that seasonal patterns in density and reproduction are consistent among years (Lewellen and Vessey 1998a, Merritt et al. 2001).

Biotic and abiotic factors may be important for seasonality in *P. leucopus* populations (Lewellen and Vessey 1998a, b, Kesner and Linzey 1997, Merritt et al. 2001). The diet of *P. leucopus* may vary dramatically depending on the seasonal availability of certain food items (Hamilton 1941). While arthropods may form the majority of food items consumed in the spring, seeds and berries predominate in the diet in the fall (Martell and Macaulay 1981, Wolff et al. 1985, Wolff 1996b). The availability of seasonal food items may affect reproduction and population density in current and subsequent seasons (e.g. fall mast may affect spring population densities, Wolff 1996b). Weather may also be important during certain seasons. Increases in the severity of winter weather by exposure to wind in edge habitat may have negative impacts on the survival of *P. leucopus* (Sealander 1951, Pierce and Vogt 1993, Wolff 1996a). Thus, the importance of particular factors for populations of *P. leucopus* may vary among seasons.

While removing seasonal variability (e.g. by only studying a species during one season or combining data from several seasons) may increase power to detect an effect of fragmentation, such analyses implicitly assume that there is no interaction between season and fragmentation. If fragmentation affects a biotic or abiotic factor important during a particular season, then there may be seasonal effects of fragmentation on *P. leucopus* populations. The purpose of this study was to test the assumption that there are no seasonal differences in the effects of fragment size and edge habitat on the density and reproduction of *P. leucopus*.

METHODS

Study Area

This study was conducted in 3 small (1 – 2 ha) and 3 large (15 - 100 ha) forest patches within 10 km of Oxford, Ohio. Isolation (i.e. distance to the nearest forested area) of study fragments ranged from 50 to 500 m. Vegetation in the fragments consisted of secondary-growth, deciduous forest dominated by oaks (*Quercus* spp.), beech (*Fagus grandifolia*), maple (*Acer* spp.), and hickory (*Carya* spp.) with an understory of honeysuckle (*Lonicera maackii*), blackberry (*Rubus* spp.), wild rose (*Rosa multiflora*), stinging nettle (*Urtica dioica*), other herbaceous species, and saplings. There was no difference in basal area of hard mast trees, basal area of all trees, and number of trees per hectare between small and large fragments in this study area (Anderson et al. in press). The matrix surrounding fragments primarily consisted of agricultural row crops such as corn and soybeans and in some fragments included mowed pasture and fields.

Data Collection

Plywood nest boxes (15 x 15 x 15 cm) with two 2.5 cm openings and a pivoting lid, were provisioned with polyester fiberfill for bedding. In each patch I placed 15 edge and 15 interior nest boxes (*n* = 180). Boxes were hung at 1.5 m on trees spaced 15 - 20 m apart. Vegetation studies have documented significantly higher shrub and herbaceous species abundance, diversity, and cover within 10 – 15 m from the abrupt edge relative to areas greater than 20 m from the abrupt edge (Ranney et al. 1981, Matlack 1993, Burke and Nol 1998, Gehlhausen et al. 2000, Anderson et al. in press). Thus, edge boxes were placed within 5 m and interior boxes approximately 50 m from the abrupt transition from field to forest.

Between May and October of 2002, I checked nest boxes during 10 periods spaced 2 to 4 weeks apart. During each period, all nest boxes were processed within several consecutive days. At first capture, individuals $\geq$ 8 g were anesthetized with isoflourane and injected with a passive integrated transponder (PIT tag, AVID

Identification Systems) subcutaneously in the interscapular area. For each mouse found in a box, I recorded nest box location, identification number, sex, weight, and the number of offspring of females. After data collection, individuals were immediately placed back in the nest box where they were found.

Data Analysis

If I had sampled the entire area of small patches I would not have been able to distinguish if area, edge, or both contributed to differences between small and large patches because the proportion of a patch composed of edge habitat increases as fragment size decreases (Laurance and Yensen 1991). However, sampling a constant proportion of edge and interior allowed me to detect differences between small and large patches using a 2-factor design that tests for area effects, and edge effects separately.

I used the number of individuals in each time period, which is likely to be proportional to population size (Slade and Blair 2000), as an estimate of relative density. I assumed that nest boxes did not attract individuals from distant areas of a woodlot because evidence suggests that *P. leucopus* are territorial (Wolff et al. 1983). Population estimates (e.g. MNKA, CAPTURE, Jolly-Seber) were not used because we were only interested in relative density and because population estimates require data from multiple capture sessions, which would have decreased our resolution for comparing seasonal changes in density (Slade and Blair 2000).

I was interested in relative population size at each time period (i.e. including new individuals and recaptures) and if there were consistent differences in relative population size over time. There was a low probability of observing the same litter more than once due to the relatively long length of the inter-check interval (2-4 weeks) compared with the time until weaning (approximately 3 weeks) and because female *P. leucopus* with litters may frequently change nest sites (Sharpe and Millar 1990, Jacquot and Vessey 1998, Havelka and Millar 2000). For number of individual *P. leucopus*, about 30 % of individuals were observed during two or more time periods, so I tested if there were any significant differences between habitats or patch size classes in the proportion of individuals observed 1, 2, 3, or $\geq$ 4 times. A 3-factor ANOVA with number of observations, patch size, and habitat (i.e. edge or interior) as fixed effects revealed no significant size or edge effects in the proportion of mice recaptured (df = 1, 28 or 3, 28; all $F \leq 1.31$; all $p \geq 0.29$). Thus, the observation that about 70 % of all individuals were only captured once and that there were no differences in recaptures between sizes or habitats suggest that multiple captures did not bias the effects of size or edge.

Data were organized into three seasons: spring breeding (checks 1-4), reproductive lull (checks 5-6), and fall breeding seasons (checks 7-10), because of the bimodal nature of *P. leucopus* reproduction in this area (Rintamaa et al. 1976). The cutoff dates for seasons were based on data from other investigators that suggest the spring breeding season is from April through June, the reproductive lull is during July and August, and the fall breeding season is from September through November (Rintamaa et al. 1976, Wolff 1985). Data on *P. leucopus* density and number of litters were analyzed among all 10 time periods. Patterns in density and number of litters are described for each season based on post hoc differences within time periods within each season. Data on reproductive effort (i.e. the number of females with litters divided by the total number of individual adult females) were summed among time periods and compared among the three seasons. The data were analyzed with a 3-factor ANOVA with season, size, and habitat as fixed effects. Fragment size was tested using fragment identification nested within fragment size as an error term, and time and time by size interactions were tested using fragment identification by time interaction nested within fragment size as an error term. A Tukey post hoc analysis was conducted on least squares means to generate p-values for all possible pairwise comparisons.

Survival was calculated as the proportion of individuals captured in the spring that were recaptured in the fall. Data on litter size were pooled across time periods to ensure adequate sample sizes to estimate mean litter size for each habitat of each fragment. Survival, mean litter size, the proportion males, mean male weight (female weight was not used because it may vary with pregnancy status), and the magnitude of population fluctuations (maximum – minimum number of individuals captured) were analyzed using a 2-factor ANOVA with size, and habitat as main effects. A Tukey post hoc test was conducted on least squares means in each ANOVA test to generate p values for all possible pairwise comparisons. ANOVAs were used because all data sets fit the assumptions of normality (all Kolmogorov-Smirnov $p \geq 0.12$) and homogeneity of variances. Results are reported as mean ± 1 SE.

RESULTS

Density

There was significant seasonal variation in the density of *P. leucopus* among the edge and interior of small and large fragments (Table 1, Figure 1). There was a size by time interaction (Table 1) indicating that for a period in the spring there was a higher density of *P. leucopus* in large than small patches (Figure 1a). There was also a significant interaction between habitat and time (Table 1), which indicated that for most of the year there was no difference between edge and interior habitats but during the fall there was higher density in the edge (Figure 1b). However, overall analyses indicated densities of *P. leucopus* were significantly greater in small than large fragments and edge than interior habitats.

The seasonal effects of fragmentation on abundance resulted in a greater mean magnitude of yearly population fluctuations (maximum – minimum abundance in a habitat) in small (34.7 ± 1.9) than large patches (23.3 ± 3.5, size effect: $df = 1, 4$; $F = 15.33$; $p = 0.017$). Population fluctuations did not differ by habitat (habitat: $df = 1, 4$; $F = 3.51$; $p = 0.134$, size by habitat interaction: $df = 1, 4$; $F = 3.51$; $p = 0.134$).

There was no effect of season, size, or habitat, separately or in any combination, on the proportion of males in patch populations ($df = 1, 20$ or $2, 20$; all $F \leq 2.64$; all $p \geq 0.10$) or mean male weight, an index of relative condition ($df = 1, 20$ or $2, 20$; all $F \leq 1.78$; all $p \geq 0.20$). There was also no effect of patch size ($df = 1, 4$; $F = 1.52$; $p = 0.28$) or habitat ($df = 1, 4$; $F = 0.11$; $p = 0.76$) on survival.

Reproduction

There were trends towards seasonal differences in the production of litters among fragment sizes and habitats (size x time and habitat x time; Table 1). The effect of edge on litter production was largest in the fall, with no significant difference between edge and interior habitats for the rest of the times sampled (Figure 2b). Overall, a greater number of litters was found in nest boxes in edge than interior habitats, although there was no effect of fragment size (Table 1, Figure 2).

The pattern of litter production differed among fragments (Figure 2a). Large patches displayed the typical bimodal pattern (Rintamaa et al. 1976, Wolff 1985, Terman 1993) of litter production with spring and fall peaks separated by a midsummer lull (Figure 2a). However, for small patches, post hoc analysis of all possible pairwise comparisons of the 10 checks revealed no significant fluctuation in litter production throughout the year, although the number of litters at the last check was marginally greater than at the first check (check 1 vs. check 10: $df = 40$; $t = 1.89$; $p = 0.066$, all other comparisons, $n = 44$: $df = 40$; all $t \leq 1.58$; all $p \geq 0.123$).

There were significant season, and season by size effects in reproductive effort (i.e. the proportion of adult females, $\geq$ 18 g, with litters) (Table 1, Figure 3). The pattern of reproductive effort changed from greater in large patches during the spring, to no differences during the lull, and then to greater in the edge of small and large patches during the fall (Figure 3). Litter size was not affected by fragment size ($df = 1, 4$; $F = 0.46$; $p = 0.53$), habitat ($df = 1, 4$; $F = 2.23$; $p = 0.21$), nor the interaction of fragment size and habitat ($df = 1, 4$; $F = 0.10$; $p = 0.76$).

DISCUSSION

There were seasonal differences in the effects of fragmentation on the abundance and reproduction of *P. leucopus*. Overall, I confirmed the negative density-area relationship of *P. leucopus* reported by other investigators (Nupp and Swihart 1996, 1998, Krohne and Hoch 1999, Mossman and Waser 2001, Anderson et al. in press); however, the relationship changed from a positive relationship in the spring, to no relationship for a brief period in the summer, and then a negative relationship in the fall. This suggests that higher population densities in small than large fragments that have been reported based on data from a single season or combined over several seasons may not be consistent among seasons.

The small and large patches also exhibited different seasonal patterns of litter production. While large fragments displayed the typical bimodal pattern of litter production (Rintamaa et al. 1976, Wolff 1985, Terman 1993), I observed relatively constant reproduction throughout the spring, summer, and fall in small fragments. Some investigators have tested if food quantity or quality (Wolff 1986), density (Terman 1993), reproductive inhibition (Terman 1987), or water availability (Nelson 1993) are responsible for the midsummer cessation of reproduction in *P. leucopus*. Given the lower spring density of populations in small than in large fragments, the data suggest that population density may be one factor contributing to the bimodal nature of *P. leucopus* reproduction (Terman 1987, 1993). However, experimental manipulation of spring densities in small patches would provide a more direct test of this hypothesis.

The effect of edge habitat on *P. leucopus* density and reproduction also varied among seasons. While in some seasons there was no effect of edge, other seasons showed substantial differences between edge and interior habitats. Population density, number of litters, and the proportion of females producing litters were all significantly greater in edge than in interior habitats during fall, but were not different between habitats in spring or summer. Thus, data collected in identical locations may suggest either no effect or a positive effect of edge habitat depending on the season in which the data were collected. Seasonal changes in the effect of edge may help to explain why past studies conducted during a single season or using data combined from multiple seasons (e.g. Heske 1995, Wolf and Batzli 2002) have produced conflicting results regarding relative densities in edge and interior habitats.

Seasonal changes in food abundance and weather, which are factors that may affect population size in *P. leucopus* (Lewellen and Vessey 1998a, b, Merritt et al. 2001), may help explain the observed patterns of density and reproduction. Higher abundance of food in the edge in the fall may result in the greater density and reproduction.

Contrary to this positive effect in the fall, there may be a negative effect of exposure to more extreme abiotic conditions in the edge than the interior in the winter. An edge effect in temperature may penetrate relatively deep into a forest (e.g. 40 m or more compared with the 15 m effect on shrub and herbaceous vegetation; Davies-Colley et al. 2000) and result in high mortality of *P. leucopus*, a species that is relatively poorly adapted to survive harsh winters (Sealander 1951, Pierce and Vogt 1993, Wolff 1996a). Higher winter mortality in the edge would be especially pronounced in small patches, whose deepest interior locations may be $\leq$ 50 m from the edge. The lower per capita litter production of females in small patches in the spring supports the cold winter edge hypothesis because initiation of breeding in *P. leucopus* may be delayed by low spring temperatures (Millar and Gyug 1981, Millar and Innes 1985). Thus, the conflicting seasonal effects of food and weather on population abundance may result in seasonal differences in the effects of fragmentation.

Despite significant advances in our understanding of the effects of fragment size and edge habitat on *P. leucopus* (Nupp and Swihart 1996, Morris and Davidson 2000, Mossman and Waser 2001, Wolf and Batzli 2002, Anderson et al. in press, this article), there have been relatively few investigations into seasonality in the response of this seasonal species to fragmentation. Yet this study highlights the need for more studies investigating the effects of season on the response of *P. leucopus* and other temperate resident species to fragmentation. Further studies are needed to confirm if the patterns I observed are consistent among years. Further investigation is also needed into the effects of fragmentation on food availability, temperature, and other factors may provide insight into why there may be seasonal changes in the response to fragment size and edge habitat. Such studies investigating seasonal difference in the effects of fragmentation may provide greater insight into the population dynamics of numerous species of animals in forest fragments in seasonal environments.

TABLE 1. Results of a 3-factor analysis of variance used to test for time (or season), size, and habitat (i.e. edge vs. interior) effects in A.) the number of *Peromyscus leucopus*, and number of litters, and B.) reproductive effort (i.e. the proportion of females producing litters) in nest boxes.

A.

		Mice			Litters		
Source of Variation	**df**	**Mean square**	**F**	**P**	**Mean square**	**F**	**P**
Size	1	104.53	5.44	0.080	< 0.01	0.01	0.934
Error a	4	19.23			1.07		
Time	9	108.85	5.70	< 0.001	1.21	1.70	0.126
Size x Time	9	88.87	4.65	< 0.001	1.66	2.32	0.036
Error b	36	19.10			0.71		
Habitat	1	53.33	5.41	0.025	5.21	5.48	0.024
Habitat x Size	1	1.20	0.12	0.729	< 0.01	0.01	0.926
Habitat x Time	9	24.44	2.48	0.024	1.71	1.80	0.099
Habitat x Time x Size	9	13.50	1.37	0.234	0.43	0.46	0.894
Error c	40	9.85			0.95		

B.

		Females with Litters		
Source of Variation	**df**	**Mean square**	**F**	**P**
Size	1	< 0.01	0.02	0.888
Error a	4	0.19		
Season	2	0.55	7.59	0.014
Size x Season	2	0.39	5.35	0.033
Error b	8	0.07		
Habitat	1	0.10	1.00	0.337
Habitat x Size	1	< 0.01	0.02	0.892
Habitat x Season	2	0.06	0.63	0.551
Habitat x Season x Size	2	0.03	0.31	0.742
Error c	12	0.10		

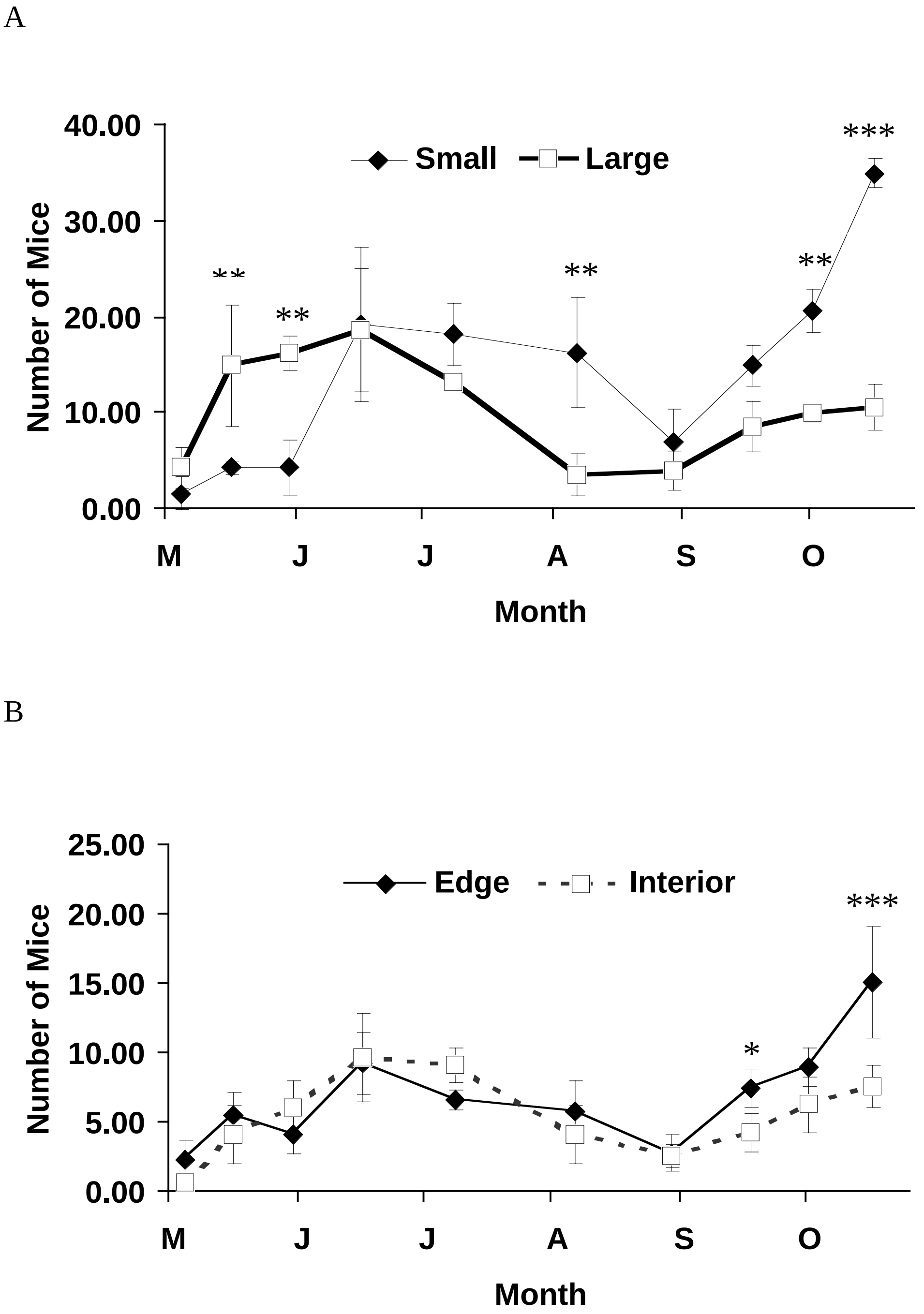


FIGURE 1. Comparisons of the number of individuals $\geq$ 8 g found in nest boxes for: a) small and large patches, and b) edge and interior habitats. Probability values for comparisons at each time period were calculated using a Tukey post hoc analysis: *: $p < 0.10$, **: $p < 0.05$, ***: $p < 0.01$.

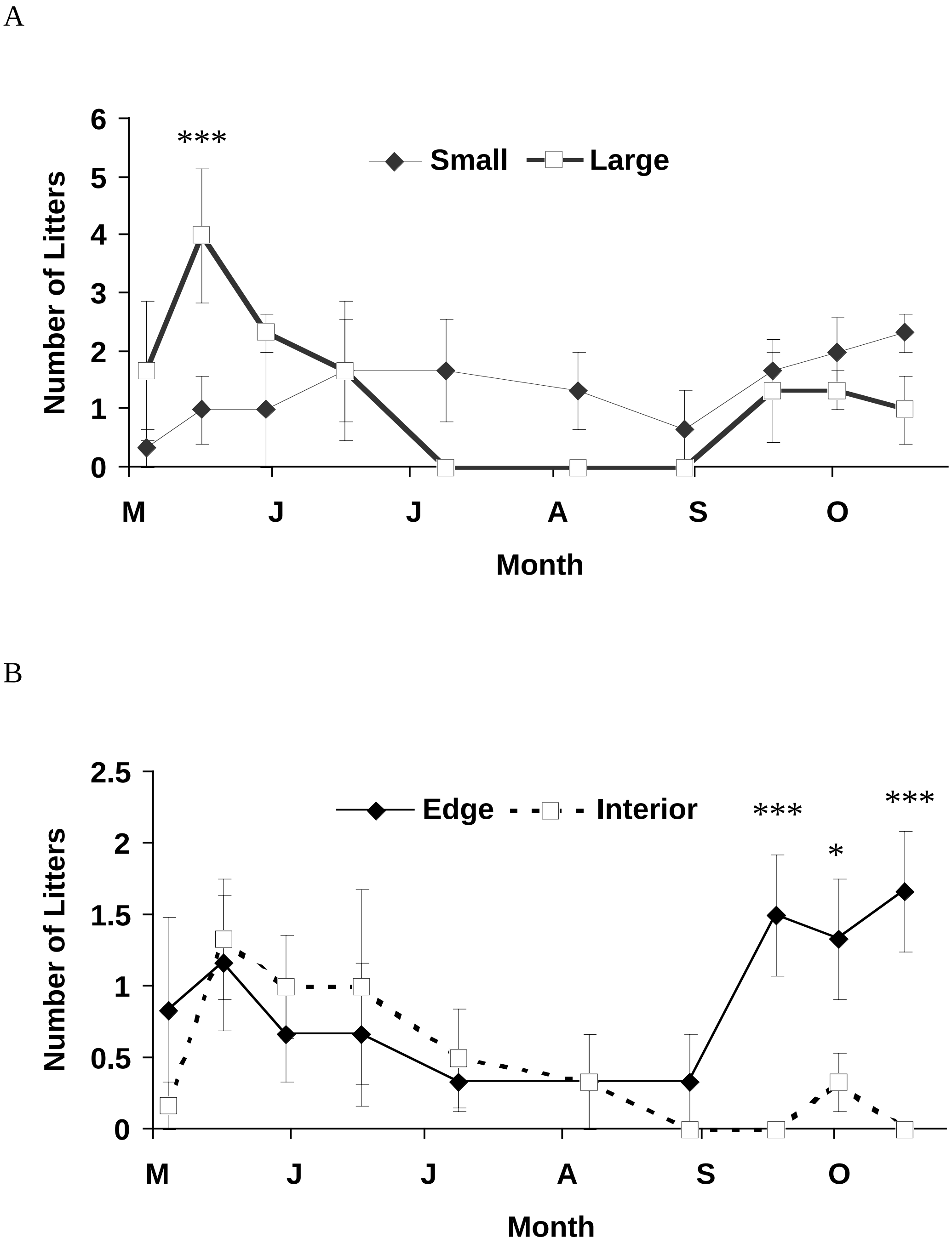
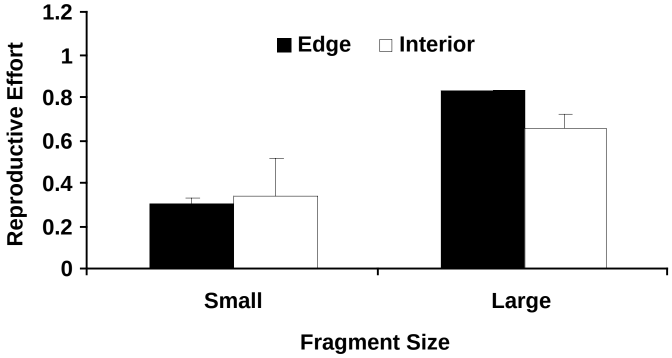
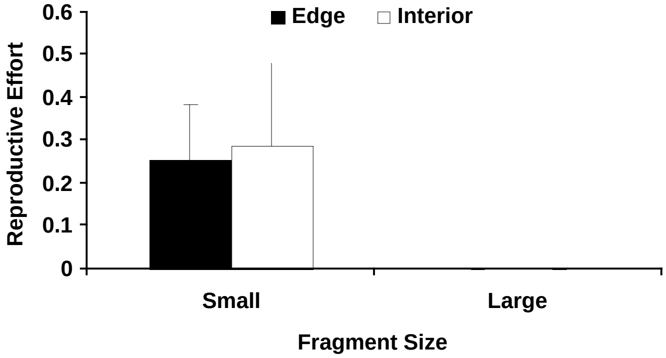


FIGURE 2. Comparisons of the number of litters in nest boxes for: a) small and large patches, and b) edge and interior habitats. Probability values for comparisons at each time period were calculated using a Tukey post hoc analysis: *: $p < 0.10$, **: $p < 0.05$, ***: $p < 0.01$.

A. SPRING BREEDING SEASON



B. REPRODUCTIVE LULL



C. FALL BREEDING SEASON

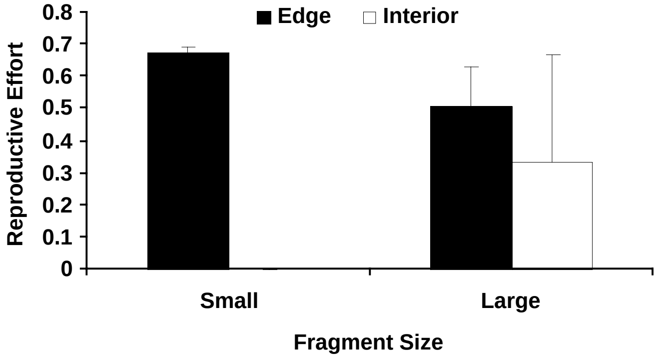


FIGURE 3. Comparisons of the proportion of adult females with litters in small and large patches, and edge and interior habitats during the: a) spring breeding season (significant size effect), b) reproductive lull (significant size effect), and c) fall breeding season (significant habitat effect).

Chapter 3:

Foraging, Reproduction, and the Negative Density-Area Relationship of a Generalist Rodent

ABSTRACT

While many species show positive relationships between population density and patch area, some species consistently show higher densities in small than large patches. Few studies have examined why certain species have negative density-area relationships. Greater reproduction as a result of higher food availability may be one factor contributing to higher densities of small generalist rodents in small than large forest fragments. I examined food resource use by *Peromyscus leucopus* (the white-footed mouse) using seeds in foraging trays and found equal giving-up densities (GUDs) for seed patches located in edge and interior habitats. Equal GUDs in edge and interior are consistent with higher food availability in edge habitat given that edge has higher cover than interior. In addition, examination of nest boxes showed that there was a greater number of litters and higher proportion of females producing litters in edge than in interior habitat. GUDs and *P. leucopus* densities were also higher in small than large fragments, which suggest that competitive release may also result in greater food availability in small fragments.

The relationship between animal population density and patch area has been the subject of considerable research for several decades (MacArthur et al. 1972, Bowers and Matter 1997, Bender et al. 1998, Connor et al. 2000, Bowman et al. 2002). Recent reviews suggest that the presence and direction (i.e. positive or negative) of a density-area relationship may depend on a number of factors including the degree of patch isolation (Bowers and Matter 1997), diet specificity (Bender et al. 1998), and taxon (Connor et al. 2000). While neutral or positive density-area relationships are often predicted and observed, some small generalist rodents (e.g. *Apodemus sylvaticus* and *Peromyscus leucopus*) consistently show negative density-area relationships (Bowers and Matter 1997). Populations of species such as *Peromyscus leucopus* (the white-footed mouse) can reach up to 10-fold higher densities in small than large fragments (Nupp and Swihart 1996). Yet, few studies have provided direct evidence regarding the mechanisms that may contribute to higher population densities in small than in large fragments. Studies of these mechanisms may provide insight into the factors that may contribute to consistently observed effects of fragmentation on the density of certain taxa.

High food availability may allow populations to reach high densities (Vessey 1987, Boutin 1990). Small rodents may have viable populations in fragments that are smaller than those necessary for large interspecific competitors (Nupp and Swihart 2000). Generalist rodents, in particular, may benefit from the loss of other species through density compensation by expanding their niche breadth to incorporate foods once consumed by locally extinct competitors (MacArthur et al. 1972). In addition, generalist species may benefit from the increase in the proportion of a fragment composed of edge habitat as fragment size decreases (Laurance and Yensen 1991). Forest edge habitat may have a greater diversity, abundance, and cover of shrub and herbaceous plant species that may provide greater primary (e.g. seeds, fruits, and berries) and secondary (e.g. invertebrates) production than interior vegetation (Murcia 1995, Jokimaki et al. 1998). Generalists in edge habitat may also have access to a variety of food resources in the surrounding matrix habitat such as agricultural crops, or primary and secondary production in grasslands (Wolf and Batzli 2002). This greater food availability may contribute to higher population densities of generalist rodents through enhanced reproduction. Vessey (1987) reported that in 9 of 13 studies, increased breeding was implicated as a factor contributing to higher densities of generalist rodents following food supplementation. A review by Boutin (1990) also suggests that food supplementation and its effect on enhanced breeding may contribute to higher population densities.

In a fragmented agricultural landscape, I compared food resource use and reproductive rates of *P. leucopus* in the edge and interior of small and large forest fragments. I combined data on giving-up densities in seed patches and reproduction in nest boxes to test the hypothesis that enhanced reproduction as a result of higher food availability may explain higher densities of *P. leucopus* in small than large fragments. In addition, I explore whether higher food availability and enhanced reproduction may result from density compensation, greater food production in the edge, or both.

METHODS

Study Area

This study was conducted in 3 small (1 – 2 ha) and 3 large (15 - 150 ha) forest fragments within 10 km of Oxford, Ohio. Isolation of study fragments ranged from 50 to 500 m, as measured by distance to the nearest forested area. The matrix surrounding fragments primarily consisted of row crops such as corn and soybeans, but some fragments were bordered by pasture or fields. A complete description of the study area is available in Anderson et al. (in press).

Foraging Behavior

Previous studies have used the abundance of food items in a habitat as a measure of food availability. However, the abundance of food items collected by an investigator may not match the availability of food as perceived by an animal (Hutto 1990, Kelley 1996). Thus, I used food consumption in foraging trays as a relative measure of food availability among habitats.

The marginal value theorem (MVT) suggests that the average harvest rate in a habitat will determine the threshold at which a forager will leave any particular patch within the habitat (Charnov 1976, Stephens and Krebs 1986). Brown (1988) extended the applicability of the MVT by incorporating foraging costs into a model of patch use based on the density of resources remaining in a food patch (i.e. giving-up density, GUD). The explicit nature of the costs in Brown’s (1988) model has allowed numerous investigators to examine the effects of a single factor on GUDs in rodents (predation risk, Abrams and Dill 1989; energetic costs, Brown et al. 1994; food availability, Olsson et al. 2002). Thus, assuming *P. leucopus* behaves according to the MVT and all other costs (e.g. metabolic, missed opportunity, and predation risk costs) are equal among sites, GUDs may be used as a relative measure of food availability among habitats (Brown 1988, Tuen and Brown 1996, Olsson et al. 2002).

Response to Food Addition:

Davidson and Morris (2001) observed that *P. maniculatus* behaves according to the MVT by documenting higher GUDs following food addition. I conducted a food addition experiment in my study area to confirm the findings of Davidson and Morris (2001) for *P. leucopus*. I used 2 types of trays in this experiment. One of the trays contained a plexiglass lid (OPEN) and the other contained an opaque lid (COVERED), which allowed us to examine the effects of cover on GUDs. The use of the two types of trays also allowed us to test the prediction of Brown et al. (1992) that the difference between paired OPEN and COVERED trays may be greater in areas with greater food availability.

A 5 x 5 grid with 20 m spacing was set up deep in the interior (i.e. approximately 60 to 140 m from the abrupt edge) of a large forested area. At each grid point I placed 1 of each of the types of trays (32 x 16 x 8 cm) within 1 m of each other with each tray containing 4.0 g of millet mixed into 1 L of sand. A 2.5 cm radius opening was created at each end of the trays to restrict use of trays to rodents as small as *P. leucopus*. Observation of footprints and a concurrent live trapping study indicated that *P. leucopus* was the only species of rodent using the trays (*unpublished data*). After 1 night, used trays were sieved of remaining millet and replaced with 4.0 g of millet. Food addition to the 5 x 5 grid area was conducted by distributing 300 mL of millet within 1 m of 12 randomly selected stations. The following day, used trays were again sieved of remaining millet. Millet was dried at 70^{o} C for 24 hours, cleaned of debris (e.g. discarded husks, feces, and vegetation), and weighed to the nearest 0.1 g to compare GUDs before and after food addition.

Effects of Habitat and Cover

To compare GUDs in the edge and interior habitats of small and large forest patches, I assumed that there would not be any major differences in temperature or foraging efficiency between trays and thus no major difference in energetic costs (Brown et al. 1994). Missed opportunity costs, the cost of not engaging in other activities that may enhance fitness, may be relatively low compared to other costs (see Brown et al. 1994) and are also not likely to differ between habitats. Predation costs, however, may differ between habitats due to differences in vegetative cover or structure (Thorson et al. 1998). Thus, I measured vegetation complexity to investigate if differences in cover between areas contributed to observed differences in GUDs. I counted the number of 0.5 m sections on a 3 m vertical pole that contacted vegetation at each point in a 9 x 8 grid. I divided the number of sections contacting vegetation by the total number of sections to calculate a proportion vegetative complexity for edge ($\leq$ 15 m) and interior (15 – 70 m) habitats. I based my definition of edge habitat on previous investigations that have suggested that microclimate (i.e. light penetration and soil moisture) and understory vegetation (i.e. shrub cover and vegetation complexity) may reach interior levels within 15 m of the abrupt transition from field to forest (Ranney et al. 1981, Burke and Nol 1998, Anderson et al. in press). There was no effect of fragment size on vegetative complexity (df = 1, 4; F = 0.79; p = 0.425), which suggests there should be no difference in cover and, hence, no difference in perception of predation risk between small and large fragments. Thus, if there was no difference in food availability, my null prediction for comparisons of GUDs between fragment sizes was equal GUDs. There was significantly greater vegetative complexity in edge than in interior habitat (df = 1, 4; F = 91.2; p = 0.0007), which suggests that there is greater cover in edge habitat. Thus, assuming *P. leucopus* responds to greater cover with lower GUDs as do other rodents (Morris and

Davidson 2000, Brown et al. 1994), my null prediction (i.e. if there was no difference in food availability) for comparisons of GUDs between edge and interior habitats was significantly lower GUDs in edge habitat. No difference in GUDs between edge and interior habitats may indicate that, in addition to greater cover, there is higher food availability in the edge and that cover and food have relatively equal importance (i.e. the lowering of GUDs by greater cover is counteracted by the elevation of GUDs by higher food availability). If GUDs are higher in edge habitat, then higher food availability may have a greater influence on GUDs than greater cover.

I measured foraging tray use among habitats with 5 stations (each with 1 OPEN and 1 COVERED tray) spaced 20 m apart at 10 m from the abrupt edge and 5 stations at 50 m from the abrupt edge in each small and large fragment (*n* = 120 trays). All trays were run simultaneously beginning 26 August 2002 for a 1 night acclimation period followed by 1 night of data collection. Millet was sieved from used trays, dried at 70^{o} C for 24 hours, cleaned of debris, and weighed. Analysis of variance (ANOVA) was used to analyze GUDs in a split-split-plot design (Proc GLM, SAS Institute). Fragment size was tested among fragment identification number, habitat was split within size, and tray type (i.e. OPEN or COVERED) was split within habitat.

Density and Reproduction

Plywood nest boxes (15 x 15 x 15 cm), each with two 2.5 cm openings, were provisioned with polyester fiberfill for bedding. In each fragment, I placed 15 edge and 15 interior nest boxes (*n* = 180). Boxes were hung at a height of 1.5 m on trees spaced 15 - 20 m apart. Since my vegetation data and those of other investigators (Ranney et al. 1981, Gehlhausen et al. 2000) suggest that the effect of edge on vegetation extends 15 m into a fragment, edge boxes were placed within 5 m and interior boxes about 50 m from the abrupt transition from field to forest.

Nest boxes were inspected 4 times between 29 August and 20 October 2002. During each inspection period, all nest boxes were checked within several consecutive days. At first capture, all individuals $\geq$ 8 g were anesthetized with isoflourane and injected with a passive integrated transponder (PIT tag, AVID Identification Systems) subcutaneously in the interscapular area. For each mouse found in a box, I recorded nest box location, identification number, sex, weight, and, for females, number of offspring. I used the total number of individuals captured as a relative measure of population density (Slade and Blair 2000, Wolf and Batzli 2002, Anderson et al. in press). All data sets were normally distributed; thus, I tested for the effects of fragment size and habitat on density and reproduction using a 2-factor nested ANOVA (Proc Mixed, SAS Institute). A Tukey post hoc test was conducted on least squares means to generate probability values for pairwise comparisons.

RESULTS

Foraging Behavior

Food addition resulted in a highly significant increase in GUDs in both OPEN (paired t-test: $n = 8$; $t = 10.09$; $p < 0.001$) and COVERED trays (paired t-test: $n = 10$; $t = 8.28$; $p < 0.001$), as predicted if *P. leucopus* behaved according to the MVT. Food supplementation did not affect the difference between OPEN and COVERED trays (paired t-test: $n = 6$; $t = 1.58$; $p = 0.175$).

A total of 83 of 120 trays (69 %) were used during my foraging experiment in the edge and interior of small and large forest fragments. There was a trend towards higher

GUDs in small than large fragments (Table 1, Figure 1). There was no effect of habitat or habitat by size interaction on GUDs. GUDs were significantly lower in COVERED relative to OPEN trays. There was no interaction between cover, fragment size, or habitat in any combination.

Density and Reproduction

A total of 246 mice $\geq$ 8 g were tagged during this study. There were significantly more mice in small than large fragments (Figure 2a; $F_{1,4} = 10.15$, $p = 0.033$). There were also more mice in the edge than interior of fragments ($F_{1,4} = 19.54$, $p = 0.012$), which may contribute to higher densities in small fragments, which have a greater proportion of edge habitat than large fragments. There was no interaction between fragment size and habitat in the number of mice ($F_{1,4} = 0.17$, $p = 0.70$).

There was no effect of fragment size on the number of litters in nest boxes ($F_{1,4} = 0.83$; $p = 0.413$). However, significantly more litters were found in the edge than interior (Figure 2b; $F_{1,4} = 14.70$, $p = 0.019$). This effect was substantial as 29 of 31 litters (94 %) were found in nest boxes in edge habitat. One reason for a greater number of litters in the edge may have been a greater number of females in nest boxes in edge habitat ($F_{1,4} = 20.74$; $p = 0.010$). In addition, the mean proportion of females that produced litters was greater in edge than in interior habitat (mean $\pm$ 1 SE; edge: 0.29 ± 0.05, interior: 0.08 ± 0.05; $F_{1,4} = 8.93$, $p = 0.040$).

DISCUSSION

No difference in GUDs between edge and interior habitats provides evidence that both cover and food availability are greater in edge habitat and that each have equal influences on GUDs, assuming other costs are equal. The combination of greater cover and higher food availability may have contributed to the substantially higher reproduction I observed in edge habitat (Figure 2b). Edge habitat had a greater density of nesting females, number of litters, and proportion of females producing litters. Similarly, Wolf and Batzli (2002) trapped a greater number of juvenile *P. leucopus* per reproductive female in the edges than interiors of forest fragments in Illinois. While they could not distinguish between juveniles that immigrated to the edge and those that were born in the edge, my nest box data provide direct evidence that the number of litters born in edge habitat is greater than in the interior. Since there is a greater proportion of edge habitat in small than large fragments, greater reproduction in the edge may explain overall higher population densities of *P. leucopus* in small forest fragments. A greater structural complexity of shrub and herbaceous plants in edge than interior may have provided greater cover and enhanced food availability in edge habitat (Murcia 1995, Jokimaki et al. 1998, Gehlhausen et al. 2000, Cadenasso and Pickett 2001).

An alternative explanation for no difference in GUDs between edge and interior habitats is that there is no difference in cover and food availability among habitats. However, there was significantly greater structural complexity of vegetation in edge habitat and *P. leucopus* in my study sites showed a strong and consistent response of lower GUDs in trays with greater cover (Figure 1). Thus, assuming there was sufficient power to detect any differences that may have existed, there is support for my use of lower GUDs in edge than interior habitats as a null prediction if there were no differences in food availability among habitats.

There was a trend towards higher GUDs in small than large fragments. This suggests that density compensation, which predicts higher food availability in small than large fragments due to a size effect, is another factor contributing to the negative density-area relationship of *P. leucopus* in my study area. Rosenblatt et al. (1999) and Nupp and Swihart (2000) have documented fewer species of potential competitors of *P. leucopus* (e.g. *Tamias striatus, Sciurus* spp., and *Odocoileus virginianus*) in small fragments. Also, potential competitors were rarely observed in small patches during my study (Wilder, *personal observation*). Higher food availability due to fewer competitors may explain why there was a size effect of higher *P. leucopus* densities. There was not, however, a size effect in reproduction, which may indicate that the increase in food availability was not great enough to affect reproduction or that another resource (e.g. cover or availability of nesting sites) was limiting reproduction.

Predation risk is another factor that may affect GUDs in edge and interior habitat. Morris and Davidson (2000) reported that weasel predation in the edge may have resulted in higher GUDs and lower survival and litter success in the edge than interior of a forest fragment in Ontario, Canada. However, weasels (*Mustela frenata*) have not been observed in my study landscape and I have no evidence of weasels (weasels, their scat, or partially consumed *P. leucopus*) in nest boxes as was found by Morris and Davidson (2000). Thus, in the absence of this specialist predator, my data suggest that edge is higher quality habitat than interior.

In addition to higher reproduction, several other factors may contribute to higher densities of *P. leucopus* in small fragments. While risk of predation as perceived by vegetation cover may not differ among fragments, lower predation pressure in small than large fragments may contribute to higher population densities. However, for most aerial and terrestrial predators in my study area, the low isolation of my forest fragments (i.e. 50

– 500 m) relative to the high vagility of some predators (e.g. hawks, Leary et al. 1998; owls, Zimmerman et al. 2001) may result in relatively equal predation pressure among fragments. To evaluate this hypothesis more information is needed on the use of small and large fragments by a variety of aerial and terrestrial predators, and their predation rates on *P. leucopus*.

Movement of animals through the matrix habitat may also affect population density in a fragment. Reduced emigration in small fragments has also been suggested as a factor that may elevate densities. Krebs et al. (1969) described a “fence effect” in which populations of some rodent species in enclosures may reach abnormally high densities due to a lack of emigration. However, demographic data suggest that populations in small fragments do not fit the predictions of enclosed populations with reduced emigration (Nupp and Swihart 1996). Bowman et al. (2002) recently argued that immigration behavior of ground-dispersing animals may often lead to the prediction of higher densities in small than in large fragments. If animals move randomly through matrix habitat, then the greater linear dimension of small fragments relative to their area may intercept a greater number of immigrants per unit area than large fragments. Although further research is needed to evaluate this hypothesis, the relatively low numbers of *P. leucopus* observed in matrix habitat would suggest that greater immigration is not likely to be a major factor contributing to substantially higher densities in small than large fragments (Cummings and Vessey 1994, Anderson et al. in press). Thus, while I cannot dismiss the potential contributions of lower predation, lower emigration, and higher immigration, I conclude that higher reproduction in edge habitat due to greater cover and availability of food resources is an important factor contributing to higher population densities in small than in large fragments.

TABLE 1. Split-split-plot ANOVA used to compare GUDs of *Peromyscus leucopus* among fragment sizes, habitats, and tray types (OPEN vs. COVERED).

Source of Variation	df	Mean square	F	P
Size	1	22.058	4.77	0.094
Error a (Size)	4	4.626		
Habitat	1	0.269	0.13	0.735
Habitat x Size	1	0.434	0.21	0.669
Error b (Habitat)	4	2.047		
Type	1	5.875	21.8	< 0.001
Type x Size	1	0.031	0.12	0.736
Type x Edge	1	0.51	1.89	0.174
Type x Size x Edge	1	0.022	0.08	0.775
Error c (Type)	67	0.27		

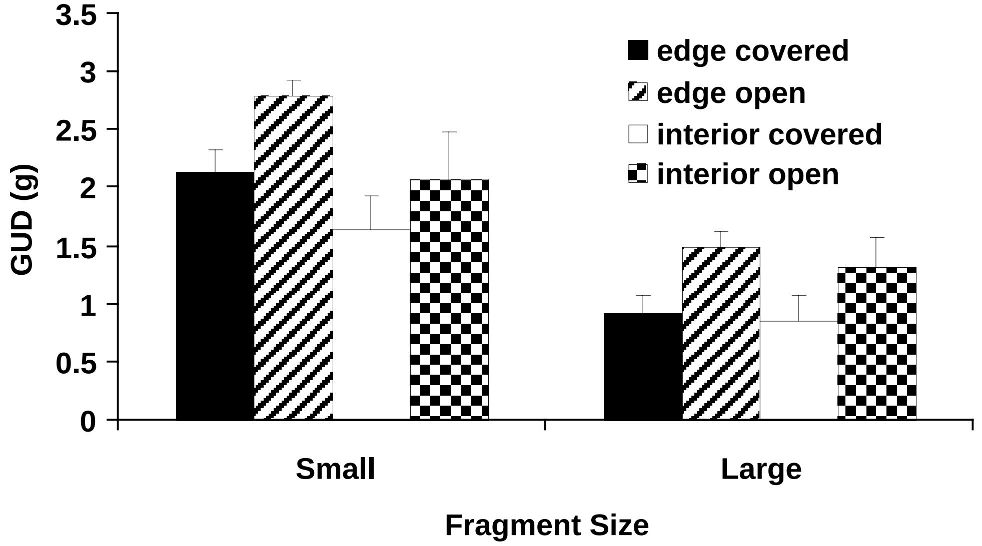
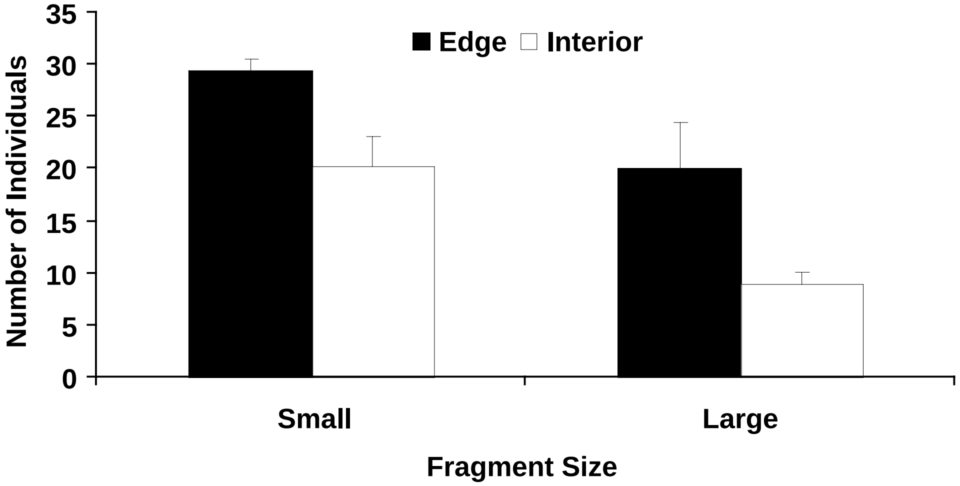


FIGURE 1. Mean (+ 1 SE) dry mass (giving-up density, GUD) of seeds remaining in artificial trays following a night of foraging.

A. MICE



B. LITTERS

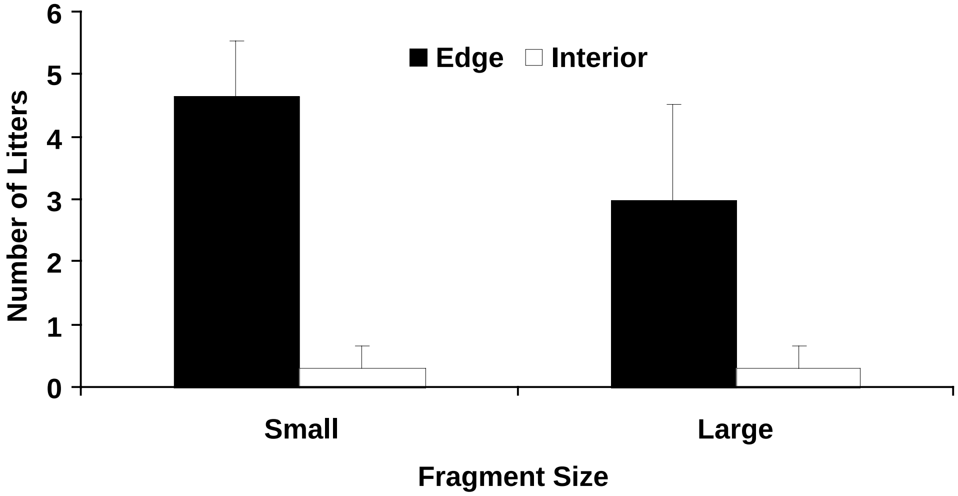


FIGURE 2. Mean (+ 1 SE) number of individual A) mice $\geq$ 8 g, and B) litters observed in nest boxes between 29 August to 20 October 2002.

Chapter 4:

Prevalence of the Deer Tick (*Ixodes scapularis*) on White-Footed Mice (*Peromyscus leucopus*) in Forest Fragments

ABSTRACT

The effects of fragmentation on the distribution of mammalian ectoparasites are not well understood. I examined *Ixodes scapularis* (deer tick) abundance using prevalence on *Peromyscus leucopus* (white-footed mouse) in small and large forest fragments in an agricultural landscape. My results indicate that *I. scapularis* may be less abundant in small than large fragments. Lower abundance of *I. scapularis* may result in lower parasite induced morbidity and mortality for *P. leucopus* in small fragments.

Despite a relatively large literature on the effects of fragmentation on the distribution and abundance of many species (e.g. Andren 1994; Fahrig and Merriam 1994; Bowers and Matter 1997), few studies have considered the effects of fragmentation on an obligate parasite such as *Ixodes scapularis* (formerly *I. dammini*; the deer tick). *I. scapularis* has a three stage life cycle (larvae, nymph and adult) that requires a blood meal from a vertebrate host before molting to the next stage (Ostfeld et al. 1995). Each blood meal is obtained from a separate host and host preference varies ontogenically, with juveniles (larvae and nymphs) having a generalized preference for an avian or mammalian host and adults having a specific preference for *Odocoileus virginianus* (white-tailed deer - Ostfeld et al. 1996a). The effects of fragmentation on host species would likely influence the abundance and distribution of *I. scapularis*.

The effects of fragmentation on *I. scapularis* are of interest because this species can serve as a vector of Lyme disease (Ostfeld et al. 1996b). During a blood meal, *I. scapularis* may become infected from its host with *Borrelia burgdorferi*, the spirochete that causes Lyme disease (Ostfeld et al. 1995). *Peromyscus leucopus* (the white-footed mouse) is an important host in this regard because it is often the most abundant and competent reservoir of *B. burgdorferi* in forested habitats (Donahue et al. 1987). Once an *I. scapularis* is infected, any subsequent host that it parasitizes can become infected (Ostfeld et al. 1995). The nymph may be the most dangerous stage for humans because of the ability to transmit *B. burgdorferi* (obtained during a larval blood meal), small size and generalized choice of mammalian hosts (Ostfeld et al. 1995). Thus, the abundance of juvenile *I. scapularis* attached to *Peromyscus leucopus* in a particular area may indicate the risk of Lyme disease to humans.

The abundance of juvenile *I. scapularis* may also indicate the abundance or intensity of use of an area by *O. virginianus*. After engorging on a final blood meal on *O. virginianus*, adult *I. scapularis* drop from the host and lay eggs that will overwinter and hatch into larvae the next summer. Correlational studies have observed lower juvenile *I. scapularis* abundance in areas with fewer *O. virginianus* (Wilson et al. 1985; Duffy et al. 1994). Experimental studies have confirmed that reduction or eradication of *O. virginianus* results in lower abundance of host-seeking, juvenile *I. scapularis* (Daniels et al. 1993; Stafford 1993) and fewer juveniles attached to *P. leucopus* (Wilson et al. 1988; Deblinger et al. 1993). Thus the abundance of juvenile *I. scapularis* on *P. leucopus* may be an indicator of the intensity of use of an area by *O. virginianus* the previous fall.

I tested the prediction that *I. scapularis* prevalence on *P. leucopus* would be lower in small (1 - 2 ha) than large patches (15 - 100 ha) in an agricultural matrix because of the lower probability that *O. virginianus* would inhabit such small patches.

METHODS

I measured the abundance of *I. scapularis* in fragments by examining prevalence on *P. leucopus* (Wilson et al. 1985, 1988; Deblinger et al. 1993). *P. leucopus* were trapped in 3 small (1 - 2 ha) and 3 large (15 – 100 ha) forest fragments within 10 km of Oxford, Ohio. Sherman live traps were placed in a grid with 10 m intervals extending 80 m (9 traps) along the edge and 70 m (8 traps) into the interior, for a total of 72 traps per fragment. Traps were baited with oats and checked the following morning for 2 consecutive days each trapping session. A total of 4 trapping sessions was conducted from May - July of 2002 for a total of 576 trap nights for each of the 6 fragments. For each capture, we recorded identification number, sex, weight, pelage, length (body and tail), and the presence of juvenile *I. scapularis* on the pinnae or face (where > 90 % of *I.*

scapularis attach - Ostfeld et al. 1993). Although I did not collect data on parasite load, the number of *I. scapularis* per *P. leucopus* appeared consistently low (i.e. $\leq$ 3 in this study compared with > 20 reported in other studies - Deblinger et al. 1993; Ostfeld et al. 1996b) and did not appear to vary among study sites. At 1st capture, individuals were anesthetized with isoflourane and injected with a passive integrated transponder (PIT tags, AVID Identification Systems) subcutaneously in the interscapular area. The use of PIT tags instead of ear tags avoided the artifact of higher infestation rates of *I. scapularis* on *P. leucopus* with ear tags (Ostfeld et al. 1993).

Only adult mice ($\geq$ 18 g - Cummings and Vessey 1994) were used in analyses to ensure that all mice had a similar period of exposure to *I. scapularis* in the habitat. I compared the proportion of individuals infected between the edge and interior of small and large fragments, since some evidence suggests that vegetative structure may influence *I. scapularis* abundance (Adler et al. 1992). Edge habitat was defined as the first 15 m of the forest closest to the matrix based on evidence that vegetative characteristics important to mice (e.g. shrub cover, density of saplings - Kaufman et al. 1983) reaches interior levels after 15 m (Ranney et al. 1981).

I included each mouse only once, as infected or not, and assignment of individuals to edge or interior was based on the proportion of captures in each habitat (Wolf and Batzli 2001). Thus, a mouse caught 1 of 3 times in the edge would be included as 0.33 mouse in the edge and 0.67 mouse in the interior. Individuals were classified as infected if a juvenile *I. scapularis* was attached to the mouse at any capture. I divided the number of infected adults by the total number of adults in a habitat (i.e. edge or interior) to yield the proportion of individuals infected with *I. scapularis* for each habitat of each fragment (i.e. prevalence).

Comparisons were made of the number of adult *P. leucopus* captured in small and large fragments to determine if there were differences in density that might affect infection rates. I also measured *I. scapularis* prevalence in adults that were caught multiple times (n = 2-8) or only once, and compared recapture rates between small and large fragments because different recapture rates may bias prevalence estimates.

Comparisons of prevalence were made using a 2-factor analysis of variance (Proc Mixed, SAS Institute) with fragment size, habitat, and size by habitat interaction or size, number of captures (single or multiple) and size by captures as fixed effects. The data did not violate the assumptions of normality and homogeneity of variances (Kolmogorov-Smirnov all $P > 0.15$; Levene's test all $P \geq 0.10$; respectively) for number of adults, recaptures, or the proportion of individuals infected. Independent sample t-tests were used to compare mean proportion and number of individuals recaptured between small and large fragments. All probabilities reported for statistical values are two-tailed.

RESULTS

There was a significantly lower proportion of adults infected with juvenile *I. scapularis* in small than large fragments ($F_{1,4} = 9.93$, $P = 0.035$; Figure 1). There was no effect of habitat (edge vs. interior; $F_{1,4} = 0.09$, $P = 0.78$) or size by habitat interaction ($F_{1,4} = 0.65$, $P = 0.47$) on the proportion of adults infected. When adults were separated by number of captures (i.e. single or multiple), there was still a significantly lower prevalence of *I. scapularis* on mice in small than large fragments regardless of whether they were caught once or multiple times ($F_{1,4} = 22.77$, $P = 0.009$; Table 1). *P. leucopus* that were captured multiple times had a significantly higher prevalence than individuals that were only captured once ($F_{1,4} = 31.79$, $P = 0.005$). However, there was no difference between small and large fragments in the number of adults or the proportion of adults captured multiple times ($df = 4$, $t = 1.635$, $P = 0.18$; $df = 4$, $t = -0.195$, $P = 0.86$; respectively). There was also no significant difference in the total number of individual adult *P. leucopus* captured in small and large fragments ($F_{1,4}$: 1.39, $P = 0.30$). There was no habitat effect or size by habitat interaction in the number of adults (all $F_{1,4}$: ≤ 4.68, all $P \geq 0.10$).

DISCUSSION

I documented a lower prevalence of *I. scapularis* in our small fragments. Although prevalence was affected by the number of captures, there was no difference in the number or proportion of recaptures between small and large fragments; thus, the patch size difference in prevalence was not the result of a bias in recapture rates in relation to patch size. Although prevalence was lower among *P. leucopus* in small patches, it is possible that *I. scapularis* loads (number of *I. scapularis* per *P. leucopus*) were higher in small fragments, which would make the impact of *I. scapularis* more similar between small and large fragments. However, to compensate for prevalence levels half of those in large fragments, loads would need to be substantially higher in small than large fragments. This did not seem to be the case as *I. scapularis* loads appeared to be low among all mice and did not vary noticeably among fragments.

Experimental studies documenting lower *I. scapularis* abundance the year after *O. virginianus* reduction or removal (Wilson et al. 1988; Daniels et al. 1993; Deblinger et al. 1993; Stafford 1993) suggest that a lower abundance of *I. scapularis* may indicate lower use of small fragments by *O. virginianus*. Lower use of small fragments by *O. virginianus*, a species that consumes large amounts of hard mast (McShea and Rappole 1992), may result in higher food abundance for other forest dwelling granivores and may help explain the well-documented observation of higher fall abundances of *P. leucopus*, a species that may rely heavily upon fall mast (McShea 2000), in small than large fragments (Nupp and Swihart 1996; Bowers and Matter 1997). McShea (2000) provided evidence for this hypothesis by documenting higher *P. leucopus* abundance in plots with *O. virginianus* exclusion compared to controls.

In addition to indicating fewer competitors, a lower proportion of *P. leucopus* infected with *I. scapularis* may result in a direct positive effect on *P. leucopus* abundance. *Ixodes* spp. have been documented to increase mortality rates in some rodent populations (e.g. *Clethrionomys rufocanus* - Viitala et al. 1986). Infection by *I. scapularis* may also result in transmission of *B. burgdorferi*, which has been documented to result in neurological damage in some *P. leucopus* (Burgess et al. 1990). Thus, the effects of fragmentation on parasites and pathogens may affect the abundance and distribution of host species.

Lower abundance of *I. scapularis* in small fragments may result in lower risk of infection with Lyme disease depending on the prevalence of *B. burgdorferi* in *I. scapularis* and *P. leucopus* in forest fragments. Prevalence of *B. burgdorferi* may be even lower than what would be expected based on the lower abundance of *I. scapularis* infecting *P. leucopus*. High winter mortality, sometimes an order of magnitude difference in fall and spring abundance (Lewellen and Vessey 1998), of *P. leucopus*, the predominant reservoir host, may result in stochastic extinctions of *B. burgdorferi* in small fragments if not all *P.leucopus* are infected. In addition, low rates of dispersal of *P. leucopus* (Cummings and Vessey 1994) may result in a limited ability to reestablish populations of *B. burgdorferi* in fragments. Thus, there may be relatively little risk of

Lyme disease to humans in highly fragmented (i.e. < 20 % forested habitat) agricultural landscapes. Further studies are needed to investigate parasite and pathogen transmission and effects on morbidity and mortality in fragmented landscapes.

Table 1. *Ixodes scapularis* prevalence for *Peromyscus leucopus* that were only captured once (single) and multiple times (but only included once in analyses; multiple) and the proportion of individuals captured multiple times in small and large fragments.

	Small (n = 3)		Large (n = 3)				
	$\bar{X}$	*SE*	$\bar{X}$	*SE*	*df*	*t*	*P*
Prevalence Single	0.058	0.03	0.285	0.025	4	2.20	0.092
Prevalence Multiple	0.348	0.118	0.817	0.076	4	4.54	0.011
Proportion Recaptured	0.591	0.08	0.612	0.071	4	-0.20	0.855

* *df*, *t*, and *P* values are reported for least squares means (single, multiple) and independent samples t-tests (proportion recaptured)

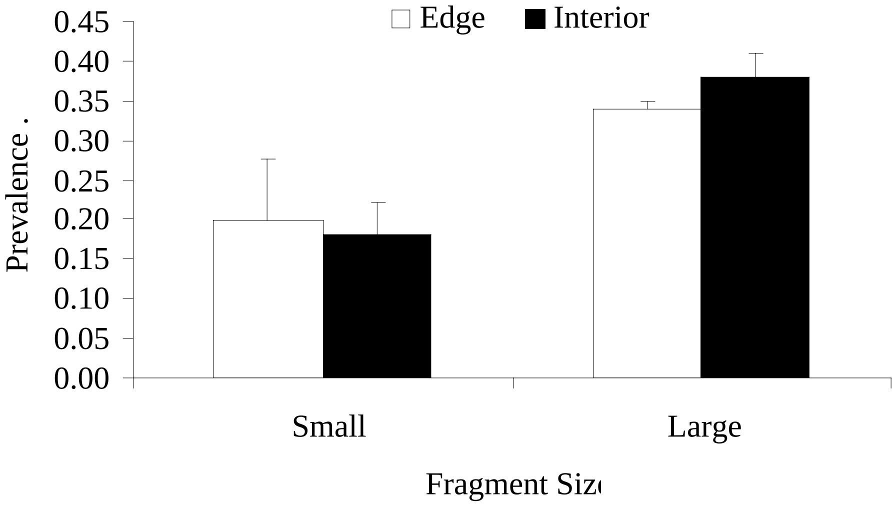


Figure 1. The proportion of *Peromyscus leucopus* infected with juvenile *Ixodes scapularis* (means ± 1 SE) in the edge and interior of small and large forest fragments.

Chapter 5:

General Conclusions

I observed seasonal effects of fragment size and edge on the density and reproduction of *P. leucopus*. This was not particularly surprising given that *P. leucopus* lives in a seasonal environment (Rintamaa et al. 1976, Lewellen and Vessey 1998a). However, little is known about the interaction between seasonality and fragmentation. Further research is needed to determine if the seasonal patterns I observed are consistent among years, and which abiotic and biotic factors may contribute to seasonality in the effects of fragmentation.

The foraging behavior and reproduction of *P. leucopus* in the fall suggest that edge effects of greater cover and food availability may be important for the negative density-area relationship. However, relatively little is known about how edge affects *P. leucopus*. Most studies of the effect of edge on *P. leucopus* have used live-trapping data and conjectured about what patterns of density or demographic data indicate about relative habitat quality (Wolf and Batzli 2002). However, density may not be an indicator of habitat quality (Van Horne 1983); thus, measures of reproductive success and juvenile recruitment are needed to gain more insight into the quality of edge habitat. Use of nest boxes and foraging trays in this study have provided support to the conjecture of past investigators that edge may be a high quality habitat for *P. leucopus* (Wolf and Batzli 2002, Anderson et al. in press).

An even more basic issue that has yet to be resolved is the depth of edge habitat. Depending on the study, reported depths of edge habitat range from 15 to 50 m or more from the abrupt forest-field junction (Wolf and Batzli 2002, Anderson et al. in press). While this is a relatively large distance, it is possible that the depth of edge for *P. leucopus* fluctuates by 50 m or more. Many factors (e.g. edge age, vegetation composition, and aspect) may vary and result in variations in the depth to which edge affects *P. leucopus*. In addition, there is likely to be separate edge depths depending on the factor under study. Anderson et al. (in press) and I argue that food availability and cover are likely to show an edge depth of approximately 15 m. However, other factors may have different edge depths. Predators of *P. leucopus* (e.g. medium sized mammals, snakes, hawks, and owls) are likely to perceive edge on a larger scale and, if they biased hunting with respect to edge, may result in edge depths of 50 to 100 m or more in predation pressure. Weather is also likely to have a deep depth of edge. In addition, depth of edge for temperature and wind exposure may vary with the season depending upon if leaves have fallen or not. Thus, while my data suggests that depth of edge is about 15 m for food availability, further research is needed to evaluate the depth that other factors affect animals from the abrupt forest-field junction of forest fragments.

Greater food availability due to competitive release may also contribute to the negative density-area relationship of *P. leucopus*. While it is difficult to directly quantify competitor abundance in small and large fragments, Chapter 4 provides some indirect evidence of fewer competitors. Lower *I. scapularis* prevalence on *P. leucopus* in small than large fragments suggests that fewer *O. virginianus* may visit small than large fragments. *O. virginianus* is a potential competitor of *P. leucopus* and may consume large amounts of mast, which is an important food source for *P. leucopus* in the fall (McShea et al. 1992, McShea 2000). A size effect in food availability, due to fewer *O. virginianus*, may help to explain why there was significantly more *P. leucopus* in small than large fragments based on fragment size. However, more direct data on *O. virginianus* movements in fragmented landscapes is needed to further examine this hypothesis.

This study has provided some insight into factors that may contribute to the negative density-area relationship of *P. leucopus*. However, this study has also generated many questions. It is not know to what extent immigration, emigration, and predation affect population densities in small relative to large fragments. Further investigations using new or different techniques should provide even greater insight into factors contributing to the negative density-area relationship of *P. leucopus*.

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