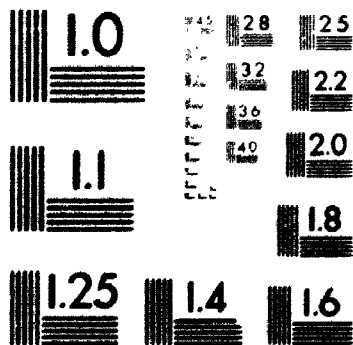


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Habitat distribution, spatial dynamics and reproduction of a
forest rodent (*Peromyscus leucopus*) in an agricultural
landscape

by
John Wegner

A Thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of

Doctor of Philosophy

Department of Biology
Ottawa-Carleton Institute of Biology
Carleton University
Ottawa, Ontario

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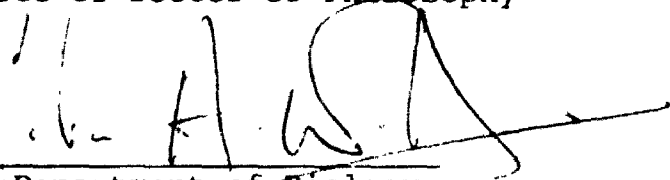
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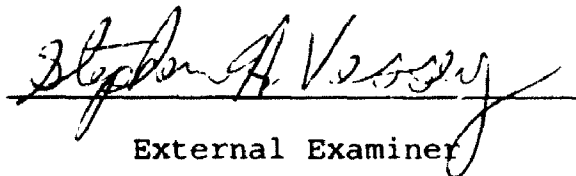
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Chair, Department of Biology



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External Examiner

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Abstract

I examined the distribution, abundance, movement patterns, and reproduction and recruitment of a woodland small mammal (*Peromyscus leucopus*) inhabiting agricultural landscapes in eastern Ontario. *P. leucopus* occupied forest in these landscapes, but also occurred in fencerows, corn fields and small grain fields. *P. leucopus* was rarely captured in hay fields. Minimum number known alive (mnka) were similar in woods and corn fields and lower in grain fields and fencerows. The pattern of population change over the snow-free season was similar in all habitats, but mnka decreased substantially in grain fields following harvest. Monthly turnovers of individuals was 75% in areas of up to 13.5 ha. Agricultural intensity had little effect on number of mice, but did influence the relative use of fencerows by *P. leucopus*. On low-intensity farms many more mice were captured in fencerows than in crop fields.

Reproductive condition and habitat in which movement occurred were the most frequent predictors of scale of movement for mice, but characteristics of the mice rarely explained more than 15% of the variation in the spatial scale of movement of *P. leucopus*. The scale of movement by mice in the agricultural landscape of eastern Ontario was greater than virtually all those reported in the literature. This trend was consistent for all indices of movement used. In addition to the larger scale of movement by *P. leucopus*, the variation among individuals was large. I propose that the *P. leucopus* population is composed of mice in two behavioral categories: stay-at-home and nomadic and that the nomadic behavioral type dominates in agricultural landscapes. The most likely explanation of the shift in scale of movement by *P. leucopus* in agricultural mosaics of eastern Ontario is a combination of the effect of forest fragmentation and the geographical context.

P. leucopus produced litters in all habitats except hay fields. Litter size was similar in all habitats where mice occurred, but fewer litters were found in grain fields and fencerows. Juvenile recruitment was similar among woods, corn, and grain. No juvenile recruitment occurred in fencerows. Adult recruitment was half as much in corn fields as in woods. Although most novel habitats can support reproduction, reproduction probably is currently lower than it was before habitat fragmentation occurred.

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First and foremost, I would like to thank Gray Merriam for his able assistance over the last 22 years (not all of it spent on this thesis, although at times it has seemed like it!). He is the type specimen for mentor. Gray has created an intellectual climate in the basement of the Tory building that is rivalled by none. The spirit of intellectual cooperation that has existed in the windowless bowels of Tory make it difficult to acknowledge all of the people who have contributed to this thesis, but I'll try.

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In the word of the Grateful Dead: "Lately it occurs to me what a long strange trip it's been."

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General Introduction

Landscapes of eastern North America were formerly forested (Curtis 1956, Scott 1979, White 1985). As European settlement proceeded across the landscape two important processes occurred in parallel: habitat fragmentation and the introduction of novel habitat types.

As the land was cleared for agriculture and human settlements, the once continuous forests were fragmented (Curtis 1956). The total amount of forest in any one area declined dramatically. The net result of this reduction was that individual forest patches became much smaller in area and forest patches became more isolated as barriers were inserted (Harris and Silva-Lopez 1992, Noss and Csuti 1994). This habitat fragmentation presented challenges for the organisms that once inhabited the forested landscape (Wilcove et al. 1986). As the total amount of forest decreased, the amount of traditional habitat available decreased and the total population size of many species presumably declined. For those patches of forest that remained, populations of organisms became more isolated from one another. The isolation of forest patches lowers the probability of a rescue effect (sensu Brown and Kodric-Brown 1977) and local populations that suffered extinctions would be recolonized less frequently. If the extinction of forest populations exceeded the recolonization rate of patches from which populations have disappeared, then the species may go extinct

in the whole region.

Not only did agricultural activity fragment the forest, but it also inserted new habitats into the landscape. These new habitat types are primarily the annual and perennial crop fields, but also include fencerows and farm buildings. These new habitat types on the one hand could act as barriers for the movement of organisms or could provide a substitute habitat for displaced forest organisms.

The response of organisms to these two processes then could be: to go extinct and disappear from the landscape, to maintain populations in the remnant patches in the landscape, or to adapt to the modified landscape by using the novel habitat types. Which response occurs for a particular species depends on a number of factors. Perhaps two of the most important factors are the movement scale of the species prior to fragmentation and the behavioral flexibility of the species - particularly with respect to habitat choice. If the distances between appropriate habitat patches (scale of habitat fragmentation) were larger than the scale of daily activity of the species or larger than the dispersal distance for the species, that species probably would go extinct unless the species modified the spatial scale of its activities as fragmentation proceeded. If a species had specific habitat requirements that could be fulfilled only in forest or if it refused to use novel resources as they became available, the species might also disappear from the landscape as the amount

of acceptable habitat in the landscape declined.

This study was designed to investigate three aspects of the individual and population dynamics of a woodland rodent (*Peromyscus leucopus*). First, I asked the question: what is the impact of substituting agricultural fields for forest on the habitat distribution of *P. leucopus*? Have the mice remained forest dwellers, or have they expanded their behavioral repertoire to include the novel habitats provided by agriculture? To answer this question I compared the number of mice found in the different habitat types and the demographic distribution of those individuals. Second, has the insertion of agricultural habitats into the forested landscape of eastern Ontario influenced the spatial scale of activity of *P. leucopus*? Fragmenting habitats may increase the spatial scale of movements for organisms inhabiting the fragmented landscape (Lord and Norton 1990, Taylor 1993, Ims et al 1993 and Henein 1995). In the agricultural landscapes of eastern Ontario, most of the forest has been removed and the woody vegetation remains as isolated forests and fencerows surrounded by various types of agricultural crops. Has this change in the distribution of forest influenced the scale at which the mice operate? For this question, I quantified the spatial scale of activity of mice in eastern Ontario and compared that spatial scale with that in other locations. The final question addressed here is what is the impact of agricultural activity on the reproduction of *P. leucopus*? If

these mice use agricultural habitats, are these habitats productive from a population perspective? Agricultural fields may function merely as a population sink - absorbing organisms from the more productive forests. To assess this, I investigated the habitat-specific natality and recruitment rates for *P. leucopus* in the various landscape elements in the agricultural mosaic.

Synthesizing the results of these three studies will allow me to evaluate the overall impact of habitat fragmentation and replacement of forest by agricultural crops on the distribution and dynamics of this forest rodent.

**Chapter 1. Spatial distribution of a woodland rodent in
 an agricultural landscape**

Introduction

Fragmentation of forests by clearing for agriculture has had a significant impact on the distribution of some forest dwelling species. Woodland species have had to respond not only to decreases in forest patch size, but also to the introduction of novel habitat types. In this chapter, I present some of the responses of a forest dwelling small mammal to this new agricultural landscape about 150- 200 years after forest fragmentation began.

This chapter presents data on the ecology of the white-footed mouse (*Peromyscus leucopus*) in farm landscapes that are a mosaic of woodlots, hay, pasture, corn, and cereal grains overlaid by a gridwork of fencerows. Three questions about the survival of these mice in farmland are discussed. 1. What is the habitat distribution of *P. leucopus* in agricultural landscapes? 2. Is there one or more than one mouse population in this mosaic landscape (i.e. do mice move among the habitat types they occupy)? 3. What is the spatial scale over which demographic units of mice function in this mosaic?

P. leucopus has been found most commonly in wooded habitat throughout its range (Baker 1968, Barry and Franco 1980, Polgar and Barrett 1983, Seagle 1985). *P. leucopus* has been characterized by arboreal behaviour (M'Closkey 1975,

Madison et al. 1984, Graves et al 1988) and trees and shrubs are important indicators of its habitat (Horner 1954, Dueser and Shugart 1978, Newton et al. 1980, Stah 1980, Kaufman et al. 1985). Although considered a woodland species, it has often been called a habitat generalist (Choate 1973, Kantak 1983, Ormiston 1983, Buckner and Shure 1985, Yahner 1986, Adler and Wilson 1987) because it occupies a variety of wooded habitats.

Few authors have found *P. leucopus* outside woodlots. Madison (1977) showed that radio-tagged *P. leucopus* rarely moved more than 10 m from the forest edge. Wegner and Merriam (1979) found that *P. leucopus* rarely penetrated more than 10 m into adjacent pastures from forests or wooded fencerows. Hansen and Batzli (1978) suggested that *P. leucopus* may move up to 30 m into farm fields. Getz and Brighty (1986) found that *P. leucopus* were restricted to uncultivated habitats in Illinois farmland. Yahner (1983) reported that these mice rarely used crop fields or farm buildings.

P. leucopus has been captured infrequently in habitats other than woods and few studies have investigated their population dynamics in non-forested areas. Pearson (1959) found that until old fields were 46 years old *P. leucopus* were not common, and even then densities in old fields were half of those in forests. Others have captured small numbers of *P. leucopus* regularly in various types of grassy fields (Blair 1948, Whitaker 1966, M'Closkey and Lajoie 1975, Adler and

Wilson 1987, Clark et al. 1987). Adler and Tamarin (1984) found this species commonly in grassland but on an offshore island (Muskeget, Maine) and Adler et al (1984) argued that grassland contained only dispersers, a view held earlier by Burt (1940).

Reports of *P. leucopus* using agricultural fields also are uncommon. Linduska (1942) reported a few individuals near the edge of a field of stoked corn but assumed they had strayed from a nearby wooded fencerow. Whitaker (1966) reported a few captures near the edges of corn fields. Lackey (1978) found *P. leucopus* in corn and rice milpas in Mexico, but did not find them in Michigan crop fields. Balcomb et al. (1984) reported three *P. leucopus* killed in corn fields by carbofuran. Fleharty and Navo (1983) found no *P. leucopus* in Kansas corn fields, but reported them in grassy strips between crop fields. Turner and Stains (1967) found this species occupying an unharvested corn field when the surrounding forest was flooded. This was the only report of extensive use of an agricultural field by *P. leucopus*.

My study was initiated when repeated visual records followed by preliminary trapping and track registry indicated much more use of corn and cereal grain fields by *P. leucopus* than was suggested by the literature.

Methods

Study area

Populations were studied on farmland subject to low and intermediate intensities of agriculture. Study areas were within 60 km south of Ottawa, Canada. Individual farms were 50 - 100 ha and sampling was done on a per farm basis to control for agricultural intensity (Gladkina and Skalinov 1988). Intensity was defined by the combination of the amount of the farm under cultivation and the amount of woody vegetation in the fencerows surrounding the crop fields. Thus, a low-intensity farm had a small area under cultivation and wide, woody fencerows and medium intensity farms had a large proportion of the farm under cultivation and little woody vegetation in fencerows. Two low and two medium intensity farms were sampled. Crops on any one farm included pasture, hay, corn, and spring grains (barley, oats, and spring wheat). Fencerows and woods adjacent to crop fields were also studied. Typical fencerow dominants included *Fraxinus americana*, *Crataegus* spp., and *Spiraea* spp. and forest dominants included *Acer saccharum*, *Fagus grandifolia*, *F. americana*, *Tilia americana*, and *Carya cordiformis*.

Live-trapping

Sherman-type live-traps were provided with sunflower seeds and dacron wool. Traps were set 20 m apart in fencerows bounding each agricultural field. A rectangle of traps was placed 20 m inside each field and woods. An additional trap-

line bisected the field along the long axis with traps 20 m apart. This design gave equal numbers of traps in each field and its fencerows. Samples in intermediate intensity farms included two grain fields, and one each of corn and hay. Samples in low intensity farms included two grain fields, and one each of corn, hay and woods. Results are presented as average for each habitat type.

Traps were open for four consecutive nights in each location. For each trap unit (fencerows plus crop field), fencerows were trapped first then traps were moved to the lines in the field. Each field and its fencerows were trapped monthly from May to November (6 sessions) during 1986, which sampled the complete breeding season. Individuals not previously captured were marked with a unique numbered tag. Each morning tag number, location, sex, age, weight, and reproductive condition were recorded for all captures. Other species captured by live-trapping were: *Microtus pennsylvanicus*, *Zapus hudsonius*, *Tamias striatus*, and *Blarina brevicauda*.

Results are given as minimum number known alive (mnka). Since trappability exceeded 90%, this is a meaningful index of population size (Hilborn et al 1976). Because field size varied, results were standardized to equalize sampling effort per area. All results are given for the modal field size of 4.5 ha (40 traps x 4 nights = 160 trap-nights/month).

Rate of change of individuals in trapped samples was

reported as turnover rate calculated as [(individuals captured at time 1 but not at time 2)+(individuals not captured at time 1 but captured at time 2)] **divided by** [(total individuals captured at time 1)+(total individuals captured at time 2)]. Turnover of 1.00 means that the two monthly samples had no individuals in common.

My trapping design differs from most small mammal trapping, which is commonly done in rectangular 7 x 7 grid of traps spaced 7-10 m apart. Such grids each sample less than 0.5 ha and were inappropriate for this study since fencerows are linear landscape elements and best sampled by lines of traps. To estimate the spatial scale at which mice use farmland requires sampling the whole of each field. Preliminary sampling indicated that *P. leucopus* moved through farmland on a scale larger than the 50-70 m dimension of the usual grid. Even if *P. leucopus* operated at the spatial scale reported in the literature (75 m home range diameter (Stickel 1968)), 20 m spacing would place at least 3 traps in most home ranges.

Nest boxes

Nest boxes were used by Nicholson (1941) and Morris (1986, 1989, 1991) to assess natality and natal habitat choice by *P. leucopus* and Goundie and Vessey (1986) used them to assess survival and dispersal of young mice. Nest box data are reported here to demonstrate habitats used outside of the breeding season when live-traps were avoided by mice and when

trap mortality would be high due to cold. In addition, nest boxes do not artificially truncate the movement of a mouse and they are capable of multiple captures including family units.

Nest boxes were 15 x 15 x 17 cm, had a hinged lid, a 20 mm opening for mice, and were made of 10 mm fir plywood. Dacron wool bedding was supplied and changed as needed.

In 1987, nest boxes were placed in fencerows and fields in the same sampling pattern used for live-traps, but with 50 m spacing. Three of each of corn, hay, grain, and woods were sampled; fields sampled were different than those used for live-traps. Boxes were placed on the ground in all habitats. Boxes were checked fortnightly during the breeding season and monthly, weather permitting, during the rest of the year. All captures were treated as for live-trap captures. Results are reported as the total for each habitat type.

Results

Habitat distribution

P. leucopus were trapped most frequently in fields of small grains, corn and woods (Table 1.1). The seasonal patterns of abundance were similar among all habitats through September ($\chi^2 = 18.98$, $df=16$, $p=0.27$), rising from spring lows to peaks in August. Captures decreased in corn after harvest (September), but continued high in woods through October. Mice occurred in crop fields in May just after cultivation and seeding. No mice remained in grain fields in

October during the period when the fields were ploughed. Hay was the least used habitat and only exceeded 1 mnka/160 trap-nights during peak dispersal in September. Interestingly, numbers of mice in fencerows were never high, but were relatively constant with numbers far below those found in the woods.

Based on nest box data, ploughed grain and corn fields were used by as many, or more, mice as used the woods in late autumn (November, Table 1.2). Total number of mice in mid-winter (January) were too low for analysis despite reasonable sampling effort (Table 1.2). Approaching the end of winter (March) mice were still using nest boxes in corn fields, occurred rarely in grain fields, but were not observed in woods. Relative use was the same in the tree habitats at early snow melt (April, Table 1.2). These data indicate continued presence in all farm patches, except hay and pasture, throughout the winter.

Movement among landscape elements

Of mice caught in live-traps more than once, 44% were caught both in crop fields and their surrounding fencerows and thus cannot belong to distinct subpopulations; 39% were caught only in fencerows and 17% only in crop fields.

Of the 349 individuals live-trapped, nearly 40% were captured only once (Table 1.3). I have no evidence of large population fluctuations (Table 1.1) as a potential cause of this frequency of single captures.

Turnover of individuals was estimated in three contiguous fields on an intermediate agricultural farm. Turnover of individuals in trapped monthly samples did not differ among habitat types or patch locations in any consistent pattern (Table 1.4). All monthly turnover rates are high (Table 1.4), many samples turned over completely and there was no temporal pattern over the breeding season. Grain and corn fields had slightly lower turnover rates on average than hay fields and fencerows.

Increasing the sample unit to include both the field and its surrounding fencerows did not decrease turnover rates (Table 1.5). Increasing the sample unit to include two adjacent fields and their fencerows, or even to include three adjacent fields and their fencerows, did not decrease turnover rates (Table 1.6).

Effects of agricultural intensity

Agricultural intensity had little effect on the number of mice (Table 1.7), but the proportion of captures in the fencerows compared to those in the crop field changed dramatically. On the low-intensity farm, captures in the fencerows equalled or exceeded captures in the crop field. The narrower fencerows on the medium-intensity farm had far fewer mice than did the crop fields.

Discussion

Forests of eastern North America were once continuous

(Curtis 1956, Whitney and Somerlot 1985). Fragmentation of eastern Ontario forests occurred more than 100 years ago as agricultural fields replaced forest. Significant amounts of forest remain, but crop fields dominate the landscape. Previously, small grains, hay and pasture were the dominant crops, but within the past 25 years grain corn has become an important cash crop. However, the intensity of agriculture in eastern Ontario is still distinctly lower than in many more intensively farmed regions such as southern Ontario or the mid-west of the United States. Getz and Brighty (1986) found that 75% of their study region in Illinois was annually cultivated for corn or soybeans. In our study area, corn was a rotational crop and occupied less than 25% of the mosaic. It is this recent agricultural landscape that *P. leucopus* is now using extensively in our study region.

P. leucopus is near the northern edge of its range in eastern Ontario and population densities here are lower than in more southerly forests. Smith and Speller (1970) found density to be 1/ha in eastern Ontario whereas most other studies in North America have reported densities an order of magnitude higher (Blem and Blem 1975, Madison 1977, Miller and Getz 1977, Hansen and Batzli 1978, Gottfried 1979, Adler and Wilson 1987, Vessey 1987, Krohne et al. 1988). Densities in my study woods peaked at 3.5/ha, which was similar to the peak density I found in corn fields (3/ha, Table 1.1). Therefore, although densities reported for *P. leucopus* in small grain and

corn fields were low, these are comparable to densities in woods. Populations fluctuated substantially between spring lows and peaks in autumn. This annual cycle is similar to that seen elsewhere (e.g. Vessey 1987, Krohne et al. 1988).

Most studies of *P. leucopus* have been done in forests. Few studies have put equivalent effort into sampling this species in farm fields. Getz and Brighty (1986) and Fleharty and Navo (1983) did sample fields in Illinois and Kansas, but neither found *P. leucopus* in agricultural fields. They did, however, find *P. maniculatus* commonly in fields.

In this study, *P. leucopus* was captured commonly in all farm fields except hay and pasture. The mice used farm fields throughout the reproductive season. Although their use of small grain fields declined after harvesting when hay or grasses began to dominate the field vegetation, they continued to use corn fields even after ploughing and probably through the winter.

On low-intensity farms the relative use of fencerows compared to adjacent crop field was almost equal. However, at intermediate farming intensity where fencerows were narrower and had less woody vegetation, the mice used crop fields more intensively than adjacent fencerows. I would expect that this relative increase in importance of the crop fields might be further extended under high-intensity agriculture in our region.

The question of whether the populations in woods or in

fencerows are distinct from those in crop fields can be addressed together with the question of the operational spatial scale for mice in this agricultural landscape. These questions can be explored using the turnover rates based on the individual identities of mice in the sample and on frequencies of capture of marked individuals.

Movement of individuals through the agricultural landscape (as indexed by the number of captures per individual) is quite high. The majority of individuals were captured only once or twice (average = 3.13, Table 1.3). This frequency of capture is not, however, atypical for this species. Although sampling frequency, duration, and intensity make comparison difficult, 3.13 is well within the range found in other studies (e.g. 1.4, Rose and Walke 1988; 2.9, Adler and Wilson 1987; 5.9, Wolff 1985a).

Because the capture frequency is in the middle of the range of literature values, individuals in this study were probably sampled with about the same intensity (probability of capture) as others have done. The probability of capture may depend on the behaviour of mice toward traps, the area sampled relative to the area used by individuals, and the amount of time spent by individuals in the area trapped. Assuming no effective differences in the trap response and because I sampled for the same durations as used by most studies but used a much larger area in each trap session and in the analysis - my results show higher mobility by the mice than do

other studies with the same capture frequency.

The scale over which these mice move may be larger than that found in most other studies (Tables 1.4, 1.5, 1.6). If mice in this study were moving over a spatial scale less than the total trapped area, then the turnover of individuals should decrease when the trapped area equals the spatial scale of the mice. The turnover did not differ at any of the spatial scales studied (Tables 1.4, 1.5, 1.6). A minimum of 67% of all individuals within a field (4.5 ha) turned over monthly and this rate did not differ substantially at the largest spatial scale trapped (3 fields = 13.5 ha). This implies movement of individuals over a very large spatial scale. Only Krohne et al. (1984) have a operating spatial scale for *P. leucopus* that might be comparable, and this applied only to dispersers. This study brings into question the distinctions among dispersers, transients and residents when *P. leucopus* is living in agricultural mosaics. High turnover rates imply that animals that constantly move through landscape units dominate in this agricultural landscape.

My results clearly demonstrate that *P. leucopus* occupies agricultural fields in the fragmented farmland of eastern Ontario. Minimum number known alive was equivalent in the traditional habitat of woods and the novel habitat of corn fields. Thus *P. leucopus* has responded to forest fragmentation by expanding its distribution into agricultural fields. Turnover of individuals in patches also implies that

the spatial scale of movement by *P. leucopus* may have increased as this species has expanded into these novel habitat types. A spatial scale of 13.5 ha was insufficient to encompass a single demographic unit, and the scale of activity of individual mice will answer the question of whether the movement patterns of this species have been affected by habitat fragmentation.

Table 1.1 Summer use of landscape elements indexed by minimum number known alive (mnka). Standardized for 40 traps (4.5 ha field size, 800 m of fencerow).

Month	Grain	Corn	Hay	Fencerow ¹	Woods
May	1	1	0	1	0
June	6	3	1	1	3
July	12	5	1	5	5
August	11	14	1	4	16
September	4	13	4	4	8
October	0	1	1	4	11

¹ = average of fencerows for the 3 field types.

Table 1.2 Winter use of landscape elements indexed by use of nest boxes.

	Total no. nest boxes	Grain		Corn		Fencerow		Woods	
		n^a	I^b	n	I	n	I	n	I
November	474	4	11	6	27	10	1	2	16
January	237	2	2	3	1	5	0	1	0
March	180	1	1	3	13	4	1	1	0
April	417	3	0	6	5	9	0.5	2	0

^a = number of patches x number censuses.

^b = individuals/ 100 nest boxes.

Table 1.3 Recapture frequencies as an index of permanency of individuals in the trappable population^a in fields, fencerows and woods.

Captures per individual	Number of individuals	Frequency (%)
1	129	39.96
2	75	21.49
3	43	12.32
4	33	9.46
5	19	5.44
6	12	3.44
7	7	2.01
8	8	2.29
9	5	1.43
10	2	0.57
11	6	1.72
12	3	0.86
13	1	0.26
14	2	0.57
15	2	0.57
16	0	0.00
17	1	0.29
18	1	0.29
Total	349	100.00

^a = approximately 30 ha actually trapped.
(Mean \pm sd = 3.13 \pm 2.97 captures/individuals).

Table 1.4 Turnover of individuals between monthly sessions in three contiguous trap grids (see Methods for turnover calculation). Sample trapped from individual fields (F) separated by surrounding fencerows (FR).

	Grain			Hay			Corn					
	F1	FR1	F2	FR2	F3	FR3	F1	FR1	F2	FR2	F3	FR3
May-June	0.75	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
June-July	0.70	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.71	1.00	1.00	1.00
July-August	0.77	1.00	1.00	1.00	0.86	1.00	0.67	1.00	0.71	1.00	1.00	1.00
August-September	0.94	0.88	1.00	1.00	1.00	1.00	0.92	1.00	1.00	1.00	1.00	1.00
September-October	1.00	0.64	1.00	1.00	0.68	1.00	0.86	1.00	1.00	1.00	1.00	1.00

Table 1.5 Monthly turnover of individuals as in Table 1.4 except samples are fields and their surrounding fencerows taken together.

	F1 + FR1	F2 + FR2	F3 + FR3
May-June	0.88	1.00	1.00
June-July	0.65	1.00	0.71
July-August	0.73	0.88	0.68
August-September	0.83	0.90	0.92
September-October	0.73	0.76	0.86

Table 1.6 Monthly turnover of individuals as in Table 1.4 except samples are two adjacent fields taken together with their surrounding fencerows and three adjacent fields taken together with surrounding fencerows.

	$(F1+FR1) + (F2+FR2)$	$(F1+FR1) + (F2+FR2) + (F3+FR3)$
May-June	0.85	0.73
June-July	0.77	0.82
July-August	0.59	0.56
August-September	0.85	0.84
September-October	0.74	0.77

Table 1.7 Effect of agricultural intensity on minimum number known alive (mnka) live-trapped in fields and in fencerows (FR) of those fields.

Intensity	Corn						Grain									
	Low		Medium		Low		Medium		Low		Medium					
	July	August	July	August	July	August	July	August	July	August	July	August				
FR	6.00	7.00	1.18	4.72	7.74	5.16	3.56	4.45	5.55	8.88	4.56	13.68	1.54	3.08	12.18	11.31
Both	1.08	0.79	0.26	0.35	5.03	1.68	0.29	0.39								

Chapter 2. Spatial scale of movement of a woodland rodent (*Peromyscus leucopus*) in an agricultural landscape

Introduction

The white-footed mouse (*Peromyscus leucopus*) historically has been considered a woodland species or a species associated with woody vegetation, but it is also characterized as a habitat generalist (See literature review in Chapter 1). Recently, it has been found in agricultural fields (Chapter 1, Wegner and Merriam 1990, Cummings and Vessey 1994).

Understanding the movement of organisms as they are affected by habitat fragmentation is imperative, but data are remarkably scarce (Wiens 1995). Use of space by a species is an important part of its life history. Home range size (Burt 1943) and other measures of use of space have been studied extensively for white-footed mice. Although determining home range size is difficult, knowledge of it is important for understanding the social organization of *Peromyscus* (Wolff 1989). Here, I report the spatial scale at which mice operate in an agricultural landscape that was once continuous forests and was cleared for agriculture approximately 150 years ago. My study differs from previous studies on the spatial scale of white-footed mice in two important ways. First, most studies of home range size for *P. leucopus* have been in forests (e.g. Stickel 1946, Metzgar 1973, Madison 1977, Wolff 1985b, Wolff et al 1983). Second, these studies rarely included more than

one habitat (i.e. only forest) in their sample. Exceptions are Blair (1940) who studied mice in forest and grassland in Michigan and Hirth (1959) who studied mice in three seral stages of old field succession. There is one final difference between my study and most published research: my research is at a larger spatial scale.

The purpose of this study is four-fold: 1. to characterize the use of space by *P. leucopus* in an agricultural landscape (near the northern edge of its range); 2. to explain variation in the spatial scale of movement by mice in this landscape; 3. to assess the impact of habitat fragmentation on the spatial scale of *P. leucopus* by comparing my results to the ecological literature; and 4. to evaluate which measure of space use is most appropriate for *P. leucopus* in agricultural landscapes.

Methods

Study area

Study areas were within 60 km south of Ottawa, Canada on farmland with low and intermediate intensities of agriculture. Individual farms were 50 - 100 ha and sampling was done on a per farm basis to control for agricultural intensity (Gladkina and Skalinov 1988). Crops included pasture, hay, corn, barley, oats, and spring wheat. Fencerows and woods adjacent to crop fields were also studied. Typical fencerow dominants included *Fraxinus americana*, *Crataegus* spp., and *Spiraea* spp.

and forest dominants included *Acer saccharum*, *Fagus grandifolia*, *Fraxinus americana*, and *Tilia americana*.

Live-trapping

Sherman-type live-traps were provided with sunflower seeds and dacron wool. Traps were 20 m apart in fencerows bounding each agricultural field. Crop field samples consisted of a rectangle of traps inset 20 m from the fencerow in the field parallel to the field boundary. Trap spacing was 20 m. An additional line of traps, 20 m apart, bisected the field along its long axis. This design within the crop field gave equal numbers of traps in a field and its surrounding fencerows. This sampling design was developed to document the distribution of mice in non-traditional habitats (Chapter 1, Wegner and Merriam 1990). Fields were chosen to obtain samples of habitat types on a farm. The selected fields were not always adjacent and thus maximum distances that could be recorded varied among study sites. The average trap grid was 4.5 ha and the largest contiguous trapped area was ca. 18 ha. The largest detectable movement distance was > 2 km.

In 1985, sampling began in June and continued until the end of October (first snowfall). In 1985, 2 grain fields, and 1 each of corn, hay, and woods were trapped. In 1986, each field and its fencerows was trapped monthly from May to November 1986 (6 sessions). A total of 4 grain fields, 2 corn fields, 2 hay fields, and 1 woods were sampled. For each sample unit (fencerows plus field), fencerows were trapped

first then traps were moved to the lines in the field. In each location, traps were open for four consecutive nights. Individuals not previously captured were marked with a unique numbered tag. Each morning tag number, location, sex, age, weight, reproductive condition and presence of a parasitic fly larvae (Diptera: Cuterebridae) were recorded for all captures. Traps were set for a total of 20,600 trap-nights. A total of 358 individuals were captured 1107 times.

Nest boxes

I used nest boxes as an alternate way of assessing the spatial scale of mice. Nest boxes have the advantages that they do not artificially truncate the movement of a mouse and that they are capable of multiple captures including family units. Nest boxes were made of 10 mm fir plywood that were 15 x 15 x 17 cm, with a hinged lid, and a 20 mm opening. Dacron wool bedding was supplied and changed as needed.

Boxes were placed in fencerows and fields in the same sampling pattern used for live-traps, but with 50 m spacing between nest boxes. Boxes were checked bi-monthly in 1987 during the breeding season and monthly, weather permitting, during the rest of the year. In 1988 nest boxes were checked weekly. Total number of nest box visits was 1287 in 1987 and 4860 in 1988 for a total of 6047. A total of 356 mice were captured 994 times. In 1987, nest boxes were placed in 6 locations; 4 of the samples (2 corn fields (and fencerows), 1 grain field (and fencerows) and 1 woods) were contiguous with

a total area of 31 ha and the other 2 corn fields (and fencerows) were 0.7 km away and had an area of 6.5 ha. In 1988, nest boxes were also in 6 locations; 4 contiguous samples (3 of the 1987 locations plus an added woodlot (1 corn field (and fencerows), 1 grain field (and fencerows), 2 woodlots) which covered an area of 37 ha and the two smaller corn fields (and fencerows) used in 1987 0.7 km away. Maximum possible distance between nest boxes within 4 contiguous plots was 1025 m in 1987 and 950 m in 1988. The largest possible movement distance in both years between the 2 sets of fields was 2350 m. All captures were treated as for live trap captures.

Data analysis

Many different measures have been suggested for providing an index of space use. The criteria used for choosing among the indices were that several authors had measured the index for white-footed mice, that the indices include both linear measures and areal ones, and that the indices provided a reasonable estimate of the spatial scale of organisms. Five different measures were selected; three of the measures are linear measures and two are areal measures of home range. The indices of spatial scale used in this study were:

1. Average distance between captures (ADBC). DAVIS (1953) suggested this index to get around some of the problems of other estimators. Stickel (1954) discussed this measure as a possible index of home range size.

Brant (1962) used it in his study of *Peromyscus maniculatus* in California. Ostfeld et al. (1985) used it successfully as an estimate of home range size in a study of California voles.

2. Longest single movement (LSM). Although no one else has applied it to *P. leucopus*, LSM was selected to compare with other measures. Henein (1995) found it a useful measure of spatial scale of *Tamias striatus*.

3. Observed range length (ORL). ORL is the maximum distance between any two capture locations for an individual. Stickel (1954) first suggested ORL as an index of home range size for white-footed mice and it was favored by her in her review of *Peromyscus* home ranges (Stickel 1968). Kikkawa (1964) used ORL because each animal was captured too few times to estimate home range. It was used by Read (1984) in his study of nomadic dasyurids in Australia to give an index to approximate the maximum movement distance of an animal.

4. Minimum area polygon (MAP). Stickel (1954), in her review of home range estimators, suggested that MAP underestimates home range, but its ease of use has made it the most often cited measure of home range. MAP or modified versions of MAP are the most often reported index of spatial scale of *P. leucopus* (see Table 2.8).

5. 95% Confidence Ellipse (95 % ellipse) was developed to make the home range estimator more probabilistic and to

recognize that home ranges are not circular as suggested by Hayne (1949) in his center of activity index (Koepl et al. 1975; Jennrich and Turner 1969).

Other methods discussed in the literature that did not fit my criteria were: center of activity (Hayne 1949, White 1964, Dixon and Chapman 1980); and number of different trap stations where an animal is captured (Metzgar 1973, Metzgar and Sheldon 1974).

For calculating the indices, trap locations were translated to x,y coordinates, and SAS (1990) was used to calculate: distance moved between sequential captures (this provide the basis for ADBC and LSM); average distance between captures (ADBC); longest distance between two captures (LSM); and observed range length (ORL) ADBC, LSM and ORL were calculated for all individuals captured two or more times and also for individuals captured five or more times.

Home range was also estimated using the tw techniques mentioned above: minimum area polygon (MAP) and 95% confidence ellipses (95% ellipse) (Jennrich and Turner 1969). Calculation of home range size was done using SAS programs provided by G. White (an older version of the SAS program is found in White and Garrott 1990).

Krohne (1986) suggested that a minimum of 9 captures was needed for accurately estimating MAP for *P. leucopus*, whereas Stickel (1954) maintained that a minimum of 12 captures was necessary for home range size. At the extreme, Mares et al.

(1980) found that 20 captures were necessary to represent the home range size of *Tamias striatus*. If Mares et al.'s criterion were applied to my data, no home range calculations could be done. Using Khrone's criterion, in both his samples and mine, would exclude approximately 95% of all individuals captured. Wegner and Merriam (1990) showed that turnover of individuals in agricultural landscapes was very high (67 - 100% per month) and that turnover rate was not reduced significantly by tripling the size of trap grids up to 12 ha. The small number of captures per individual is an index of the openness of the population and I decided to reduce the minimum number of captures of individuals included in the analysis. Forty percent of the individuals live-trapped and 58% of the individuals in nest boxes were excluded from analysis because they were only captured once. Preliminary analysis showed a relationship between number of captures for an individual and the indices. Therefore, data for statistical analysis were weighted by the maximum number of captures (CAFMAX). Estimates of home range size were based on those individuals captured five or more times. To assess the effect of the number of captures on the estimates of spatial scale of movement by *P. leucopus*, I calculated the percent change in the estimate of spatial scale for *P. leucopus* for all indices as capture number increased beyond five captures. Following the method used by Krohne (1986), I calculated the percent change in value of the index for each individual as the number

of captures for that individual was increased by one. Then I averaged the percent change for all individuals captured that number of times.

For each measure of spatial scale, means and standard deviations were calculated for each combination of sex/age/reproductive condition and for movements within each habitat type. Calculations were done separately for live trap and nest box data.

Three measures of spatial scale of movement of mice for statistical analysis were made: 1. distance between two sequential captures ; 2. average distance between captures (ADBC); and 3. observed range length (ORL). All animals with multiple captures were include in the analysis. Too few individuals were captured five or more times to include home range size in the analysis.

For the live-trap data for distance between two sequential captures, all movements equal to zero were omitted from the analysis to conform to the assumption of normal distribution of observations. For the nest box data, data were log-transformed to normalize them.

Independent variables included in the analysis were; SEX; AGE; habitat (HAB); reproductive condition (REPCON); presence of cuteribrid (BOT), date (JULIAN), time between captures (TIME); and sex and age nested within reproductive condition (REPCON(SEX*AGE)). Average distance between captures and observed range length were weighted by the maximum number of

captures for an individual (CAPMAX). Type III analysis of variance was used for all analyses (SAS 1990).

Results

There was no consistent pattern of significance among all of the analyses for the measures of spatial scale (Table 2.1 (See Appendix 2 for complete results for each analysis)). However the two variables that were most frequently significant were habitat in which the movement occurred and the reproductive condition of the animal. Scheffe's test distinguished between pairs of classes of reproductive condition and habitat only for distance between sequential captures for nest box data (Appendix 2.2). For this comparison, scrotal males moved farther than did non-scrotal males. In habitat comparisons for the same data set, mice in grain fields and woods moved farther than did mice in corn fields. None of the analyses accounted for more than 16 percent of the variation in the movement data (Appendix 2).

Table 2.2 summarizes the results for the five measures of spatial scale for male and female *P. leucopus*. These values are presented to illustrate general features and the elements of the variation of the pattern of movement of *P. leucopus*. Distribution of values for all indices were skewed. None-the-less, I've presented means and standard deviations for comparison with literature values. These values should be interpreted cautiously. Estimates of spatial scale are

sensitive to sample size (i.e. total number of observations for an individual), but I have calculated the estimates of spatial scale on the minimum number of captures (i.e. calculations for the three linear measures are based on all individuals with multiple captures and the two measures for home range are based on five or more captures per individual). There are three reasons for doing calculations based on small number of captures per individual. First, if some higher threshold of minimum captures is used, then few individuals would have the necessary number of observations. For example if greater than nine observations were used as the minimum criterion (Krohne 1986) for MAP, then fewer than 5% of all individuals would be used to estimate spatial scale. Second, estimates of spatial scale are still variable after 10 captures (Figure 2.1). Finally, in samples where turnover of individuals is between 67 and 100% per month, few captures should be expected per individual and those captures should underestimate the true spatial scale of those individuals on the sample unit.

Qualitative comparison of the estimates of spatial scale in Table 2.2 show that there is: no clear difference between the spatial scale of males and females (as the statistical analysis indicates, Table 2.1); large standard deviation for each estimate; and no clear difference between live-trapping and nest box for estimates of spatial scale of mice. This last conclusion comes despite the difference in sample spacing

between the two approaches (20 m for live-traps and 50 m for nest boxes) and the fact that live traps truncated the movement of mice whereas nest boxes did not.

Table 2.2 categorizes movements by males and females. None of the other ways traditionally used by small mammal ecologists for categorizing mice by age, reproductive condition (repcn), or habitat decreased the variation of the estimates (Tables 2.3 to 2.6). In addition, there was no consistent difference between the size of the estimates of spatial scale based on ≥ 2 captures or ≥ 5 captures. No other way of classifying the movements of these mice decreased the variation in the estimates.

The effect of number of observations on the estimates of spatial scale for live-trap data can be seen in Figure 2.1. For the three linear measures of spatial scale the average percent change decreased to less than 10% after seven captures. Variation in the estimates of size of home ranges remained between 10 and 20% over the whole spectrum of number of captures per individual. Average percent change in the size of the spatial scale indices increased dramatically for individuals captured 12 times. This large change in the size of the estimates of spatial scale was the result of the movements of two individuals. When these two individuals are removed from the calculations, percent change in the estimates drops to zero.

The 95% confidence ellipse home range method yielded a

larger estimate of home range size 82% of the time compared to the minimum area polygon method (Table 2.7). Male average home range 95% confidence ellipses for live-trapped animals were as large or larger than the modal field size (4.5 ha).

Table 2.8 summarizes estimates of the spatial scale for *P. leucopus* from the literature. Comparing these results with those tabulated in Table 2.2, ADBC and ORL for mice in farmland were larger than any previously published. For MAP, only 3 of the published estimates of home range size are greater than mine. One of these (Vessey 1987) used bivariate home range size and 95 % confidence limits (Vessey pers comm). As shown in this study, confidence ellipses tend to give larger home range size estimates than MAP does (Table 2.7).

Discussion

Determinants of spatial scale

Only a small amount of variation in the movements of *P. leucopus* is explained by the independent variables (7 % to 16 %, Appendix 2). Other studies have found that sex and age are important factors influencing movement patterns (e.g. Wolff 1993, Goundie and Vessey 1986). Wolff (1993) found that female mice are territorial during the breeding season and therefore moved smaller distances than males, and Goundie and Vessey (1986) showed that juvenile males dispersed farther than did juvenile females. In contrast, Sheppe (1966, could not show a correlation between home range size and age or sex.

Reproductive condition and habitat in which the movement occur were the two variables that were significant most often (four times each). For the analysis of the distance between sequential capture of individuals in nest boxes, the direction of the influence of these two variables was more clearly defined. Scrotal males move over a larger area than non-scrotal males (Appendix 2.2). Distances moved between two sequential captures were greater in grain fields and in woods than in corn. Interestingly, fencerows do not stand out as habitat where longer movements occur. Previously, I suggested that fencerows may act as corridors for mice in these agricultural landscapes (Wegner and Merriam 1979). If fencerows do act as corridors, it is not apparent in the distance moved by mice within them. This contradiction may be due to the difference in landscape composition between the 1979 landscape and the ones studied here. The earlier study was conducted in a landscape dominated by pasture which is similar to hay; a habitat in which mice rarely occur (Chapter 1). On the other hand, the present study was in a mixed agricultural landscape that included corn and grain fields. In a landscape dominated by hay and pasture with a few woods, white-footed mice may use the fencerows as movement pathways. Of the agricultural landscapes investigated in this study, fencerows become less important for providing connectivity because corn and grain fields also provide acceptable habitat for mice.

The spatial scale of movement of *P. leucopus* in farmland

The spatial scale of movement of mice in the agricultural landscape of eastern Ontario was larger than almost all of those presented in the literature (Tables 2.2 and 2.8). The larger spatial scale of mice reported here could be influenced by several factors.

P. leucopus is at the northern edge of its range in eastern Ontario. It may be that these mice are resource limited here. Miller and Getz (1977) found an inverse relationship between food availability and home range size, but Sheppe (1967) did not. Bowers and Dooley (1993) support the assertion that home range size may be geographically driven. In their study of mice in old field habitat they found similar home range sizes to those found by Wolff (1985b) in continuous forest in the same area.

The spatial scale of *P. leucopus* in other studies in the same geographic region is similar to that found in agricultural landscapes. Speller (1968) found males with 0.19 ha home range and females with 0.21 ha in a study in mixed forest, early successional habitat and old fields. Smith and Speller (1970) also working in eastern Ontario found home range sizes for *P. leucopus* of about 0.4 ha. Merriam and Lanoue (1990) found large scale movements by radio-tagged *P. leucopus* in one of the study areas used by me. Madison (1977) studying *P. leucopus* in a 2.3 ha isolated woodlot in New York found home range sizes for both males females of 0.1 ha.

Home range size also may be related to the habitat type or vegetation composition through which a mouse is moving. However, most studies of home range size in *P. leucopus* have been conducted in 'forest'. *P. leucopus* in successional habitats had no difference in home range size in habitat varying from old field to second growth forest (Hirth 1959). Adler and Wilson (1987) found similar ORL for mice in several different habitat types. In the heterogeneous agricultural landscapes of eastern Ontario, habitat often had an effect on the distance moved by mice (Table 2.1).

Home range size of mice also may have increased as a result of habitat fragmentation. Taylor (1993) showed this effect for a forest damselfly; Matthysen et al. (1995) found that nuthatches dispersed farther in fragmented landscapes. Yahner (1992) showed that *P. leucopus* population sizes increased following habitat fragmentation in managed forests in Pennsylvania.

Most investigations of the spatial scale of *P. leucopus* do not give the landscape context in which the mice occurred. This makes it difficult to distinguish between habitat effects and landscape effects. Thus, I was unable to add important information about landscape composition and configuration (Dunning et al. 1992) in Table 2.8. Two studies that did report the spatial scale of *P. leucopus* also state the landscape context: one study site in continuous forest in Virginia (e.g. Wolff et al 1983, Wolff 1985b) and the other

a 2 ha woodlot surrounded by agricultural fields in Ohio (e.g. Vessey 1987, Schug et al 1991). In continuous forest in Virginia home range size was an order of magnitude smaller than that found in the present study ($585 \text{ m}^2 \pm 33 (\text{SE } N=105)$). Home range sizes of *P. leucopus* in the isolated woodlot in Ohio were in the same order of magnitude (with similar amounts of variability) as those found in eastern Ontario, but with much greater fluctuations in population density in the woodlot than in the farmland of eastern Ontario. This comparison suggest that habitat fragmentation may be one of the factors influencing the movement patterns of *P. leucopus*.

The estimates of spatial scale of mice in agricultural landscapes will also be affected by the heterogenous distribution of acceptable white-footed mouse habitat. For example, including hay fields as part of home range or using straight line movements that cross hay fields may have an effect on the estimates of spatial scale. Home range size will be inflated by including hay fields in it, but linear measures of spatial scale will underestimate movement distance if mice do not cross hay fields. For analysis of movement data, I assumed that habitat was homogeneous and all equally accessible to *P. leucopus*.

Not only are the estimates of spatial scale presented in Table 2.2 larger than those reported in the literature; they are also more variable. The variation may be, in part, the result of the large scale of my study (and thus the potential

for detecting longer movements), but this is only a partial explanation. Behavioral differences within categories of mice (e.g. whether within sex (Table 2.2) or age (Table 2.3) or reproductive condition (Table 2.6) offer a more likely explanation.

Figs. 2.2 and 2.3 present the movement patterns of four mice. Mouse 399 (female) was caught in both years (Figure 2.2). Her first 11 captures, in 1985, were within 80 m of one another. In 1986, she moved 240 m to the other side of the field and remained within 80 m of that location for the rest of 1986. Over the course of 38 days mouse 731 (male) moved completely across the 18 ha trap grid; for an ORL of 540 m. Mouse 517 (female) was captured 11 times over 160 days (Figure 2.3). All of her captures were in two fencerows around a hay field; with an ORL of 240 m. Mouse 498 (male), on the other hand, had an ORL of 760 m in just 97 days. The movements in these two figures illustrate the amount of variation in the spatial scale of *P. leucopus*.

These examples illustrate the variation in patterns of movement by mice in agricultural landscapes of eastern Ontario. The variation could be represented by two alternate patterns of distribution. Stay-at-home mice only moved short distances such as mice 399 and 517 and operated at a small spatial scale. The majority of mice were of this stay-at-home type by Stickel and Warbach (1960) (79%) and Burt (1940). Nomadic mice either moved over a large area (mouse 498) or

flowed across the landscape (mouse 731) and thus operated at a larger spatial scale. Mice move their nests frequently (Stickel 1968) and this may be the behavioral basis for the nomadic strategy.

Other researchers have suggested behavioral types based on spatial dynamics of *Peromyscus leucopus*. Sheppe (1966) suggested three patterns of home range movement for mice: stable; shifting gradually; and moving abruptly and a combination of these behavioral types may influence the spatial pattern of mice in agricultural landscapes. There are various sorts of support for such behavioral flexibility. Myton (1974) suggested two types of home range for white-footed mice: most of the captures concentrated at the center of the home range; and captures spread evenly over a larger home range. At low densities, male mice abandon their home ranges and become vagrants searching for mates and thus move over a larger spatial scale (Wolff 1989, Nadeau et al. 1981).

What may be responsible for the larger spatial scale of mice reported in this study compared to the literature (Table 2.8) is a change in the proportion of mice in the population that are stay-at-home mice and nomads. This would also explain the large amount of variation in the estimators of spatial scale if there is still a mix of stay-at-home individuals and nomads in these agricultural landscapes.

Change from the stay-at-home to the nomadic behavioral types may be a function of the increased variability and

therefore lower predictability of habitat in agricultural landscapes. Sheppe (1966) showed that mice will move their home range to 'track' an artificial food supply. There is great within-year variability within any one crop field. For example, a 'corn field' goes from a ploughed field to a newly planted field with no cover to a mature corn field with substantial amounts of cover and food to a harvested field with smaller amounts of cover but still abundant food supply to a ploughed field all within 6 months. In addition, that 'corn field' may become a 'grain field' the next year and a 'hay field' the next year. This variation in potential habitat quality is in sharp contrast with the more constant nature of forested habitats.

Finally, the differences in the spatial scale between agricultural landscapes and other landscape types may be influenced by the sampling procedures used. Three factors may contribute to difficulties in cross study comparisons. Sample units used here were larger than normally used in studies of *P. leucopus*. Stickel (1954) stressed 'appropriate' grid size, but did not explain how to settle on the appropriate one. Bondrup-Nielson (1985) also discussed influence of grid size on estimates of home range - small grid increases edge effect in the grid. Faust et al. (1971) have shown that home range size can be a function of grid size, and Liro and Szacki (1987) suggested that in a heterogeneous landscape such as the agricultural one studied here a trap grid of several hectares

may be too small. In any case, most of the literature values for home range size for white-footed mice are substantially smaller than the ones used in this study and may have contributed to differences in spatial scale reported here.

Second, the sampling method may also provide bias. Sheppe (1967) found a bias in trapping estimates of home range comparing trapping and track registry of mice. He found that trapping may overestimate home range size due to increased movements following release from live traps, but Metzgar (1973) observed the reverse to be true. Douglas (1989) compared live trap vs radiotelemetry estimates of home range size and found that they give different results, but Wolff (1989) found similar home range sizes with these two techniques. Since live-trapping data and nest box data gave similar estimates of spatial scale (Table 2.2), the spatial scale of mice reported here is not an artifact of the sampling technique used.

Finally, trapping records may include forays outside a home range. However, Mohr (1947) found that although there are different ways of estimating home range size, all estimates tend to be of the same order of magnitude. Therefore all estimates have been combined in Table 2.8 and differences that do appear are considered real if they are at least an order of magnitude different.

Appropriate indices for assessing spatial scale

Home range estimators may not be appropriate for most

mice in the agricultural landscape of eastern Ontario because mice were highly nomadic (Chapter 1 turnovers of 67 to 100% per month). The behaviour of mice in these agricultural landscapes may be similar to Read's (1984) dasyurids in Australia, where he concluded that the whole population of these small mammals was made up of transients. If home range for these mice is constantly changing, the linear measures of spatial scale may be more appropriate than the areal ones for assessing spatial scale of mice. Home range sizes are inflated by including non-habitat in the area (i.e. hay field). Henein (1995) used linear estimates of spatial scale to partially solve this problem. Finally, the linear estimates of spatial scale are more appropriate because they are less sensitive to number of captures than are the home range estimates (Figure 2.1).

Summary

Mice move at a larger, more variable spatial scale in the landscapes studied here than those reported in the literature. Differences in spatial scale of mice may be due to a shift in the proportion of the mice in the landscape that exhibit stay-at-home and nomadic behaviours. Although some of variability in movement patterns of mice may be explained by characteristics of the mice (most notably reproductive condition and habitat in which movement occurs), the bulk of the variation remains unexplained by traditionally reported characteristics of mice. Additional research is necessary to

test the hypothesis that the two movement behaviours (stay at home and nomadic) occur in *P. leucopus* because this may be an important behaviour shift by this species that is necessary for its survival in agricultural landscapes.

Table 2.1 Summary of significant independent variables ($p \leq 0.05$) using analysis of variance for live-trap and nest box data. See Appendix for complete results. (Repcon = reproductive condition; ADBC = average distance between captures; ORL = observed range length).

Dependent variable	Live-traps	Nest boxes
log(distance between two sequential captures)	Date Time between captures Repcon Habitat	Habitat Repcon
log (ADBC)	n.s.	Habitat
log (ORL)	Habitat Repcon (sex*age)	Habitat Repcon (sex*age)

Table 2.2 Summary of Spatial Scale of *Peromyscus leucopus*.

A. Live-trap data. Data presented as mean \pm s.d. Based on ≥ 2 captures for ADBC, LSM, and ORL (male N=127, female N=97); and ≥ 5 captures for MAP and 95% ellipse (male N=32, female N=30)

Spatial measure	Male	Female
ADBC (m)	75 \pm 114	70 \pm 111
LSM (m)	121 \pm 156	106 \pm 126
ORL (m)	134 \pm 179	118 \pm 137
MAP (m ²)	8470 \pm 9766	5031 \pm 6037
95% Ellipse (m ²)	40755 \pm 41026	24827 \pm 30019

B. Nest box data. Data presented as mean \pm s.d. Based on ≥ 2 captures for ADBC, LSM, and ORL (male N=169, female N=187); and ≥ 5 captures for MAP and 95% ellipse (male no.=13; female no.=12).

Spatial measure	Male	Female
ADBC (m)	93 \pm 186	73 \pm 105
LSM (m)	119 \pm 209	101 \pm 183
ORL (m)	127 \pm 212	104 \pm 184
MAP (m ²)	16034 \pm 19300	4906 \pm 4613
95% Ellipse (m ²)	91558 \pm 137850	32685 \pm 34556

Table 2.3 Movements by mice in agricultural landscapes by sex and age. Based on ≥ 2 captures. ADBC= average distance between captures; LSM=longest single movement between two sequential captures; and ORL=maximum distance between any two captures. Abbreviations: f=female, m=male, adt=adult, sad=subadult, juv=juvenile.

A. Live-trapping data. Distance in metres (mean \pm sd; accuracy ± 10 m). Largest possible ORL=670m.

Sex	No.	Age	ADBC	LSM	ORL
f	71	adt	77 \pm 127	110 \pm 139	124 \pm 152
	18	sad	51 \pm 40	97 \pm 95	106 \pm 102
	8	juv	57 \pm 33	83 \pm 36	93 \pm 45
m	106	adt	77 \pm 121	122 \pm 162	134 \pm 189
	12	sad	86 \pm 93	71 \pm 62	158 \pm 143
	9	juv	43 \pm 34	145 \pm 143	96 \pm 77

B. Nest box data. Distance in metres (mean \pm sd; accuracy ± 25 m). Largest possible ORL possible = 975 m.

Sex	No.	Age	ADBC	LSM	ORL
f	61	adt	53 \pm 66	62 \pm 74	65 \pm 76
	29	sad	71 \pm 121	102 \pm 232	102 \pm 232
	97	juv	86 \pm 117	125 \pm 210	128 \pm 212
m	67	adt	97 \pm 201	124 \pm 211	133 \pm 213
	32	sad	77 \pm 203	94 \pm 208	103 \pm 214
	70	juv	97 \pm 165	126 \pm 210	131 \pm 213

Table 2.4 Movements by mice in agricultural landscapes organized by sex and age. Based on ≥ 5 captures. ADBC= average distance between captures; LSM=longest single movement between two sequential captures; and ORL=maximum distance between any two captures. Abbreviations: f=female, m=male, adt=adult, sad=subadult, juv=juvenile.

A. Live-trapping data. Distance in metres (mean \pm sd; accuracy ± 10 m). Largest possible ORL=670m.

Sex	No.	Age	ADBC	LSM	ORL
f	29	adt	84 \pm 91	113 \pm 111	126 \pm 128
	5	sad	48 \pm 30	66 \pm 49	78 \pm 64
	1	juv	46	63	63
m	31	adt	69 \pm 72	96 \pm 84	97 \pm 84
	3	sad	89 \pm 45	201 \pm 172	207 \pm 171
	0	juv	n.d.	n.d.	n.d.

B. Nest box data. Distance in metres (mean \pm sd; accuracy ± 25 m). Largest possible ORL possible = 975 m.

Sex	No.	Age	ADBC	LSM	ORL
f	5	adt	54 \pm 36	103 \pm 59	113 \pm 69
	1	sad	81	216	216
	6	juv	53 \pm 38	137 \pm 109	116 \pm 108
m	6	adt	64 \pm 30	215 \pm 164	230 \pm 160
	3	sad	98 \pm 53	206 \pm 81	267 \pm 101
	4	juv	129 \pm 93	321 \pm 326	375 \pm 293

Table 2.5 Movements by mice in agricultural landscapes organized by habitat. Based on ≥ 2 captures. ADBC= average distance between captures; LSM=longest single movement between two sequential captures; and ORL=maximum distance between any two captures.

A. Live-trapping data. Distance in metres (mean \pm sd; accuracy ± 10 m). Largest possible ORL=670m.

Habitat	No.	ADBC	LSM	ORL
Corn	55	65 \pm 58	104 \pm 91	111 \pm 94
Fencerow	121	73 \pm 134	115 \pm 148	130 \pm 161
Grain	33	96 \pm 119	127 \pm 207	141 \pm 260
Hay	1	31	45	45
Woods	14	55 \pm 32	125 \pm 94	141 \pm 91

B. Nest box data. Distance in metres (mean \pm sd; accuracy ± 25 m). Largest possible ORL possible = 975 m.

Habitat	No.	ADBC	LSM	ORL
Corn	158	90 \pm 174	107 \pm 203	110 \pm 204
Fencerow	18	85 \pm 127	97 \pm 134	100 \pm 135
Grain	45	115 \pm 88	151 \pm 114	168 \pm 125
Woods	134	62 \pm 134	101 \pm 215	104 \pm 215

Table 2.6 Movements by mice in agricultural landscapes organized by reproductive condition (repcon). Based on ≥ 2 captures. ADBC= average distance between captures; LSM=longest single movement between two sequential captures; and ORL=maximum distance between any two captures. Abbreviations: f=female, m=male, l=lactating, p=pregnant, s=scrotal, z=not reproductively active.

A. Live-trapping data. Distance in metres (mean \pm sd; accuracy ± 10 m). Largest possible ORL=670m.

Sex	Repcon	No.	ADBC	LSM	ORL
f	l	29	77 \pm 89	104 \pm 110	108 \pm 116
	p	18	48 \pm 45	83 \pm 73	91 \pm 80
	z	50	74 \pm 137	115 \pm 148	134 \pm 163
m	s	50	66 \pm 88	105 \pm 167	115 \pm 211
	z	77	81 \pm 128	131 \pm 148	146 \pm 156

B. Nest box data. Distance in metres (mean \pm sd; accuracy ± 25 m). Largest possible ORL possible = 975 m.

Sex	Repcon	No.	ADBC	LSM	ORL
f	l	11	61 \pm 97	67 \pm 96	67 \pm 96
	p	16	66 \pm 67	86 \pm 73	95 \pm 77
	z	160	74 \pm 109	105 \pm 195	107 \pm 196
m	s	24	112 \pm 163	154 \pm 181	167 \pm 182
	z	135	88 \pm 192	111 \pm 216	116 \pm 219

Table 2.7 Home range size (m^2) of mice in agricultural landscapes organized by sex and age (mean \pm s.d.). Based on ≥ 5 captures. MAP= minimum area polygon; 95% ellipse= 95% confidence ellipse. Abbreviations: f=female, m=male, adt=adult, sad=subadult, juv=juvenile.

A. Live-trap data.

Sex	No.	Age	MAP	95% Ellipse
f	19	adt	5382 \pm 6410	2618 \pm 32034
	5	sad	2810 \pm 1688	1512 \pm 7425
	1	juv	2560	18662
m	31	adt	8199 \pm 9970	37291 \pm 36051
	3	sad	11092 \pm 8673	74242 \pm 77703
	0	juv	-	-

B. Nest box data

Sex	No.	Age	MAP	95% Ellipse
f	5	adt	2945 \pm 3145	20211 \pm 23282
	1	sad	8900	64881
	6	juv	5875 \pm 5546	37715 \pm 42428
f	6	adt	5567 \pm 4439	29726 \pm 22170
	3	sad	23567 \pm 11716	105362 \pm 72854
	4	juv	26088 \pm 30903	173952 \pm 234018

Table 2.8 Summary of literature values for spatial scale of *Peromyscus leucopus*

A. Average distance between captures ADBC (m).

Female	Male	Both	Reference
		46	Turner and Stains 1967
22	28		Stickel 1968
21	23		Stickel 1968
25	32		Stickel 1968
70±111	75±114		This study: live-trap data
73±105	93±186		This study: nest box data

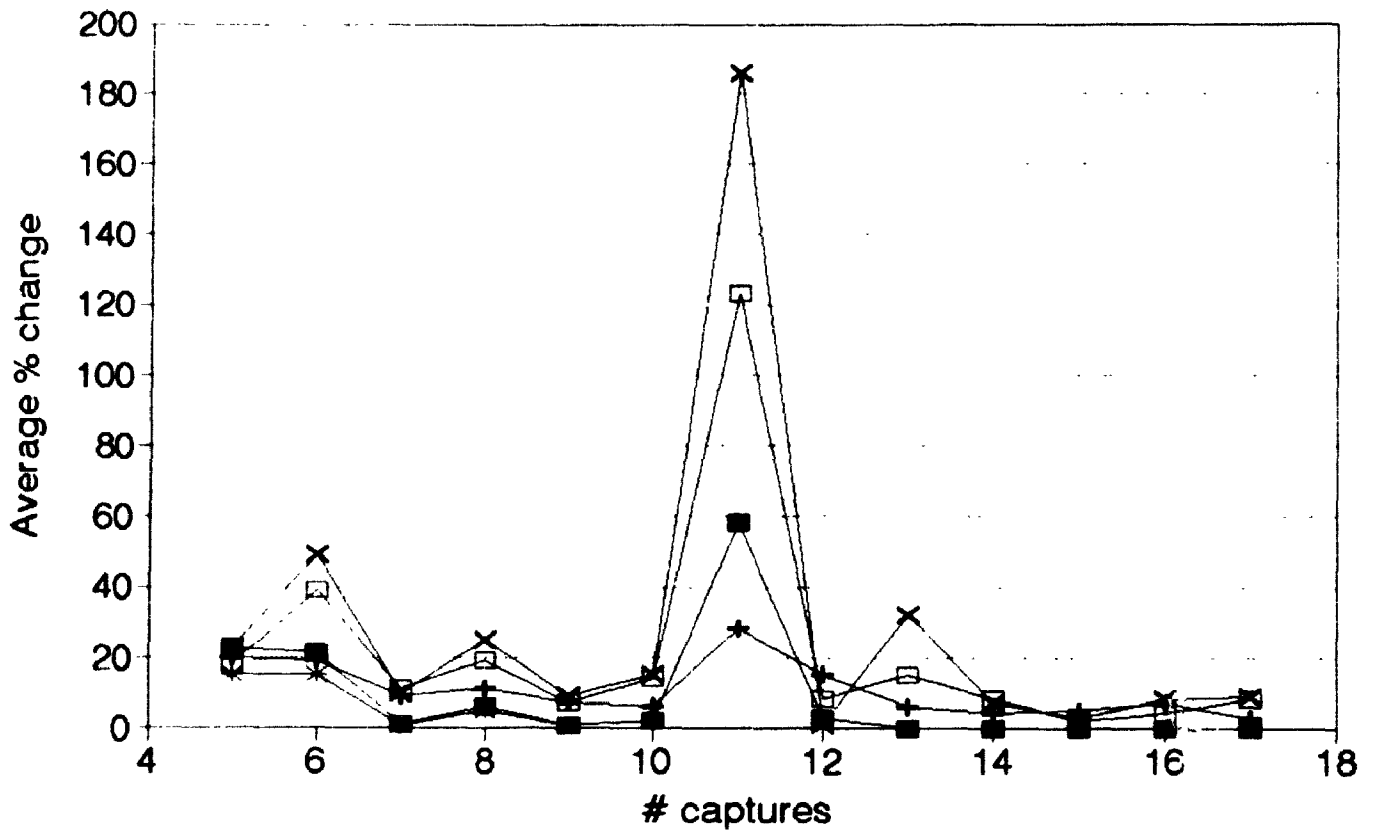
B. Observed range length ORL (m)

Female	Male	Both	Reference
43	57		Stickel and Warbach 1960
		61	Beer 1961
		42	Stickel 1968
74	70		Stickel 1968
53	65		Stickel 1968
104±13	79±12		Stickel 1968
	36±0.9		Stickel 1968
46 to 92	61 to 122		Stickel 1968
69.9	36.3		Adler and Tamarin 1984
11.4	19.8		Adler and Tamarin 1984
		31.8±17.7	Adler and Wilson 1987
		24.6±20.3	Adler and Wilson 1987
		25.6±13.8	Adler and Wilson 1987
		27.1±14.9	Adler and Wilson 1987
		23.0±10.1	Adler and Wilson 1987
118±137	134±179		This study: live-trap data
104±184	127±212		This study: nest box data

Table 2.8 C. Home range size (ha). All methods combined.

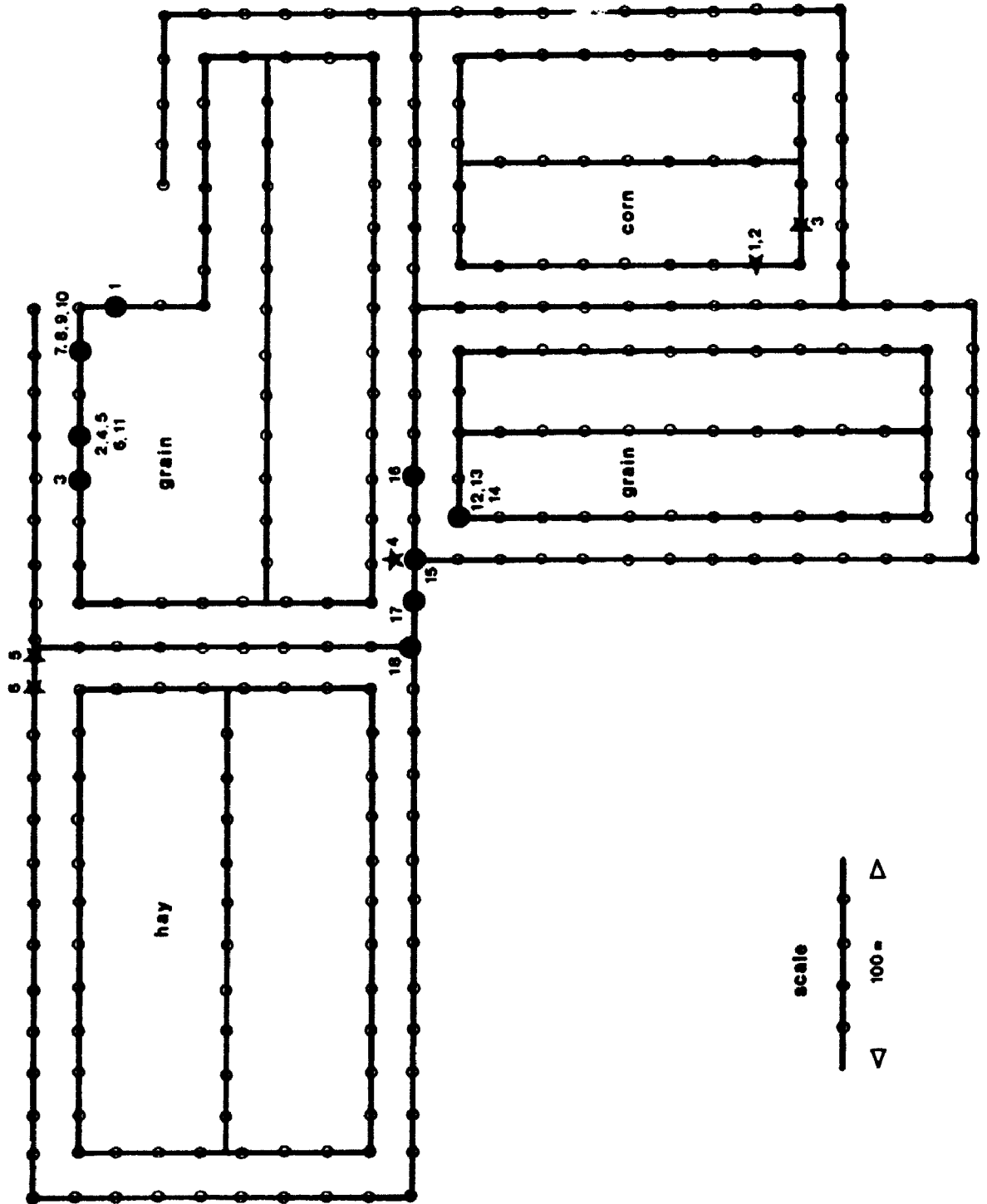
Female	Male	Both	Reference
		0.32±0.06	Blair 1940
0.08	0.11		Burt 1940
		0.06	Fitch 1958
		0.08	Beer 1961
		0.15	Sheppe 1966
0.21	0.19		Speller 1968
0.09	0.06		Stickel 1968
		0.06	Stickel 1968
		0.08	Stickel 1968
		0.12	Stickel 1968
0.10	0.11		Stickel 1968
0.08	0.08		Stickel 1968
0.39	0.4		Smith and Speller 1970
		0.30	Metzgar 1971
0.13	0.73		Myton 1974
0.91	1.26		Mineau and Madison 1977
0.24±.24	0.24±.14		Madison 1977
0.023	0.027		Wolff et al. 1983
0.29±.17	0.29±.15		Madison et al. 1984
		0.024	Cranford 1984
		0.1	Lackey et al. 1985
		0.059±.003	Wolff 1985b
1.37	1.56		Ormiston 1985
0.01 to 4.5	0.01 to 1.5		Vessey 1987
0.053	0.186		Schug et al. 1991
0.50±.61	0.85±.98		This study: live-trap MAP
0.49±.46	1.6±1.9		This study: nest box MAP

Figure 2.1 Average percent change in estimates of space use as number of captures increases.



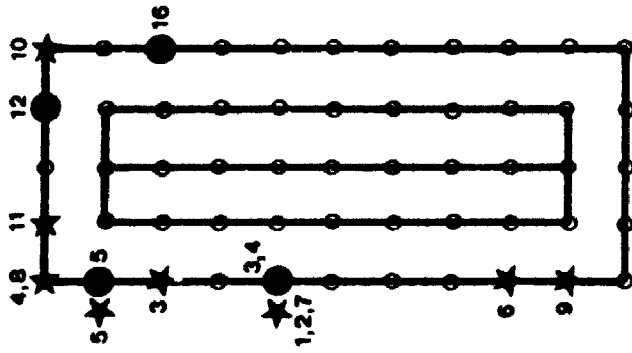
■ ORL + ADBC * LSM
 □ 95% Ellipse × MAP

Figure 2.2 Illustration of the movement patterns of mice.
Mouse 399 = ● . Female captured 18 times over
310 days. Mouse 731 = ★ . Male captured 6
times over 38 days. Open circles represent
trap sites. Numbers are the order of capture
for each mouse.

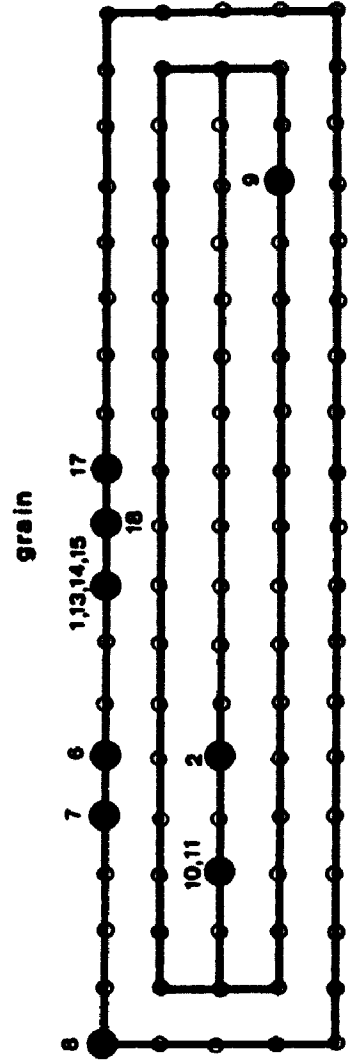
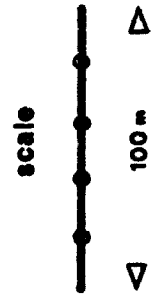


scale
 100 m

Figure 2.3 Illustration of movement patterns of mice.
Mouse 517 = ★ . Female captured 11 times over
160 days. Mouse 498 = ● . Male captured 18
times over 97 days. Open circles represent
trap sites. Numbers are the order of capture
for each mouse.



hay



grain

Appendix 2

Analysis of variance for analysis of relationship between measures of spatial scale and independent variables.

Appendix 2.1 Analysis of variance for distance between two sequential captures for live trap data. (All movements where distance equals zero have been removed to satisfy assumption of normality).

Source	DF	Type III SS	Mean Square	F value	Pr>F
SEX	1	17.1394	17.1394	3.60	0.0583
AGE	2	23.5767	11.7884	2.48	0.0850
HAB1	3	45.4945	11.3736	2.39	0.0499
HAB2	3	28.6622	7.1655	1.50	0.1993
REPCON	3	47.1853	11.7963	2.48	0.0432
BOT	3	33.7539	11.2513	2.36	0.0703
TIME	1	29.9093	29.9093	6.28	0.0125
JULIAN	1	32.7151	32.7151	6.87	0.0090
$R^2 = 0.129125$					

Appendix 2.2 Analysis of variance of distance between two sequential captures (log(DIST)) for nest box data.

Source	DF	Type III SS	Mean Square	F Value	Pr>F
SEX	2	1.2923	0.6461	1.09	0.3372
AGE	2	0.9874	0.4937	0.83	0.4355
HAB	3	10.8059	3.6020	6.08	0.0005
REPCON	3	9.6949	3.2316	5.45	0.0011
TIME	3	2.5448	0.8483	1.43	0.2333
JULIAN	1	0.7798	0.7798	1.32	0.2521

R' = 0.1003

Scheffe's test for variables: (Comparison of pairwise differences at p=0.05)

1. REPCON
 - Scrotal > nonscrotal
2. HAB Comparison
 - Grain > Corn
 - Woods > Corn

Appendix 2.3 Analysis of variance for log(ADBC) weighted by maximum number of captures/individual for live-trap data.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SEX	1	1.4271	1.4271	2.95	0.0876
AGE	2	1.1045	0.5522	1.14	0.3216
HAB	4	1.6536	0.4134	0.85	0.4924
REPCON(SEX*AGE)	5	5.2858	1.0572	2.19	0.0577

R² = 0.1042

Appendix 2.4 Analysis of variance for log(ADBC) weighted by maximum number of captures/individual for nest box data.

Source	DF	Type III SS	Mean Square	F Value	Pr>F
SEX	1	0.5067	0.5067	0.75	0.3870
AGE	2	1.4606	0.7303	1.08	0.3402
HAB	3	10.5925	3.5308	5.23	0.0015
REPCON(SEX*AGE)	6	3.0767	0.5128	0.76	0.6023

R' = 0.0743

Appendix 2.5 Analysis of variance for log(ORL) weighted by maximum number of captures/individuals for live-trap data.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SEX	1	1.5585	1.5585	1.94	0.1653
AGE	2	0.0944	0.0472	0.06	0.9429
HAB	4	7.9925	1.9981	2.49	0.0450
REPCON(SEX*AGE)	5	14.3418	2.8683	3.57	0.0042

$R^2 = 0.1577$

Appendix 2.6 Analysis of variance for log(ORL) weighted by maximum number of captures/individual for nest box data.

Source	DF	Type III SS	Mean Square	F Value	Pr>F
SEX	1	1.3347	1.3347	1.34	0.2475
AGE	2	4.4270	2.2135	2.23	0.1096
HAB	3	11.5988	3.8662	3.89	0.0094
REPCON (SEX*AGE)	6	13.3331	2.2222	2.23	0.0396

R² = 0.0865

Chapter 3. Natality and recruitment of *Peromyscus leucopus* in an agricultural landscape

Introduction

Peromyscus leucopus is a generalist species traditionally associated with forested habitats (Chapter 1). *P. leucopus* has expanded its habitat repertoire in eastern Ontario to include agricultural habitats such as corn, grain, and fencerows (Chapter 1). Mice occupying these habitats could be vagrants in search of woody cover, part of a population sink (sensu Pulliam and Danielson 1991), or be a productive part of the mouse population. Morris (1986, 1989, 1991) studied the reproductive success of *P. leucopus* in an agricultural landscape near London, Ontario, but he evaluated fitness only among animals inhabiting the traditional wooded habitat types: forest, forest edge, and fencerow. He concluded that litter size did not differ among the three habitats, but that the forest contributed a greater proportion of recruits than either of the other two habitats. The contribution of novel habitat types to natality and recruitment into the *P. leucopus* population has not been assessed.

This study was designed to evaluate the contribution to natality and recruitment of each of the habitat types in which *P. leucopus* occurred in an eastern Ontario agricultural landscape. The evaluation required measuring several components: number of litters produced, average litter size, proportion of females in breeding condition, number of

juveniles weaned per litter, number of adult mice recruited, and the proportion of successful litters. Taken together natality and recruitment can be used to evaluate the role of agricultural habitats for the survival of *P. leucopus* and thus to assess the impact of forest fragmentation on the population dynamics of *P. leucopus* in agricultural landscapes.

In summary, the purpose of this study was to compare the number, size, and temporal distribution of litters in traditional forested habitats (woods and fencerows) with those in novel habitats (corn, grain, and hay), and to compare population recruitment of mice occupying novel habitats with that in woods and fencerows.

Methods

Study area

Study areas were within 60 km south of Ottawa, Canada on farmland with low or intermediate intensities of agriculture. Crops included pasture, hay, corn, barley, oats, and spring wheat. Fencerows and woods adjacent to crop fields were also studied. Typical fencerow dominants included *Fraxinus americana*, *Crataegus* spp., and *Spiraea* spp.; forest dominants included *Acer saccharum*, *Fagus grandifolia*, *Fraxinus americana*, and *Tilia americana*.

Nest boxes

I used nest boxes for assessing natality. Nest boxes were made from 10 mm fir plywood and measured 15 x 15 x 17 cm,

with a hinged lid and a 20 mm opening for mice. Dacron wool bedding was supplied and changed as needed. Nest boxes have been used by Nicholson (1941) and Morris (1986, 1989, 1991) to assess natality and natal habitat choice by *P. leucopus*. Goundie and Vessey (1986) also used them to assess survival and dispersal of young mice.

Boxes were placed 50 m apart in fencerows. Within crop fields and woods, nest boxes were placed in a rectangle 20 m from fencerows (or the edge of the woods) with 50 m spacing between boxes. In addition, another row of boxes with 50 m spacing was placed along the length of the middle of the field. In 1987, three fields (and associated fencerows) each of corn, grain, and hay were sampled. Three woods were also sampled. All nest boxes were placed on the ground. Boxes were checked bi-monthly in 1987 during the breeding season and monthly, weather permitting, during the rest of the year. In 1988, two fields (and associated fencerows) of each of corn and grain were sampled. Two woods were also sampled. No litters were detected in hay fields in 1987 and in 1988 hay fields were not sampled. In 1988 nest boxes were checked weekly. Due to the low number of mice found in nest boxes placed on the ground in the woods and fencerows in 1987, additional nest boxes were placed in trees approximately 1.5 m from the ground in 1988. Total number of nest box samples was 1287 in 1987 and 4860 in 1988 for a total of 6047. Each mouse with an ear large enough to accept a monel fingerling

ear tag was tagged. Litters were defined by the presence of an adult lactating female in a nest box with young < 7 g; (weight of juveniles at independence is typically >9 g (Millar et al. 1979)). For each capture date, tag number, age, sex, weight, and location were recorded.

Results

The breeding season for *P. leucopus* extended from May to November, with the bulk of the litters being produced in the autumn (Figure 3.1). There was no evidence that the breeding season is bimodal for these mice. Grain fields, however, had a different seasonal pattern from other habitat types. All of the litters in grain fields were found in May.

White-footed mice produced litters in all but one of the habitats studied (Table 3.1). Mice rarely occupy hay fields in these agricultural landscapes (Chapter 1) and the lack of litters there is not surprising. There were no significant differences in the average litter sizes among the habitats in which litters occurred ($F=1.44$, $df=3$, $p=0.2$). There also was no difference in the frequency of litter size among habitats ($\chi^2=13.68$, $df=18$, $p>0.1$). The most frequent litter size was 4 (Figure 3.2).

P. leucopus travels over a large spatial scale (Chapter 2) and most individuals had the opportunity to move between habitats. Another way to classify litters, therefore, is to look at a female's habitat use before and at the time of

having a litter. This analysis requires multiple captures of the female; recapture information was available for the mothers of 23 of the 62 litters (Table 3.2). Most females in woods and corn and both fencerow mice had their litters in the habitat that they had occupied previously. Mice inhabiting grain fields exhibited a different pattern. All of the mice that occupied grain fields before giving birth moved to another habitat to have their litters and both females that had litters in grain fields came from other habitat types.

The potential of a habitat to support reproduction can be assessed by calculating either the number of litters present or the proportion of adult females in breeding condition (pregnant or lactating) in the habitat type. I used two methods to estimate the proportion of adult females in breeding condition. First, I used the proportion of adult females in a habitat type that were in nest boxes with litters. This will produce a minimum estimate of proportion of females in breeding condition. The second method included females with litters plus females that were designated as pregnant or lactating when captured in a nest box. This method always gives higher estimates of proportion of adult females in breeding condition (Table 3.3). Both methods were based on monthly totals of females during the breeding season (May to October). Habitat had a significant effect on the proportion of adult females in nest boxes with litters ($F=3.13$, $df=3$, $p=0.036$), but was not significant when all

pregnant and lactating mice were considered ($F=1.44$, $df=3$, $p>0.1$). A larger proportion of adult females were with litters in corn and fencerows and a smaller proportion were with litters in woods and grain fields.

Recruitment was difficult to determine for these mice because few individuals stayed on the study plots for very long. The average number of captures per individual was 2.8 ± 1.3 (sd). In addition, only 58 percent (155 of 268) of the juveniles in litters were large enough to ear-tag.

I developed three estimates of the contribution of each habitat type to recruitment. First, juvenile recruitment was estimated by looking at what proportion of the taggable littermates was caught again as juveniles without their mother. Adult recruitment was estimated as the proportion of the marked littermates that were captured as adults. Finally, I calculated the proportion of litters with one or more successful adult recruits to estimate overall recruitment success. Habitat differences for the various recruitment rates were tested following Morris (1989). Expected values for each of the three recruitment rates were calculated by multiplying the number of litters with marked young in a habitat by the empirical recruitment rate for all habitats combined.

There were no significant differences among habitats for the number of juveniles weaned (Table 3.4 A; $\chi^2=4.68$, $df=3$, $p>0.1$). Corn and woods weaned a similar proportion of

individuals tagged as littermates (53 and 58 percent respectively). All habitats that recruited juveniles had the same number of juvenile recruits per litter (Table 3.4 A). No juveniles were successfully weaned from fencerow litters.

Habitat type, however, did influence the number of adults recruited (Table 3.4 B, $\chi^2=10.54$, $df=3$, $p<.05$). The woods litters were substantially more successful in recruiting adults. Since none of the fencerow juveniles from tagged litters appeared as weaned individuals, fencerow litters did not appear to contribute to adult recruitment. Although there were fewer marked littermates in grain fields than in fencerows, grain field litters contributed the same number of recruits per litter as did woods litters.

There was no difference between habitats in the proportion of litters that recruited one or more juveniles into the population (Table 3.4 C $\chi^2 = 5.36$, $df=3$, $p>0.1$). Two thirds of all woods litters recruited one or more individuals into the adult population, whereas fewer than 30 percent of corn litters produced an adult recruit.

Not all of the adult recruits remained in the habitat in which they were born. One female born from a woods litter was recruited as an adult in a grain field and one male born in the woods appeared in a corn field as an adult. Woods were not the only habitat to supply recruits to other habitats. One male born in corn was recruited in grain. Grain litters produced two individuals that were recruited into woods; one

male and one female.

Female recruitment accounted for a small fraction of the total number of adult females in each habitat. To compare the amount of in situ recruitment versus the number of females immigrating into a habitat type, I divided all adult females into one of three categories: 1. females known to be recruited from litters in that habitat type; 2. females first captured as juveniles or subadults in the habitat; and 3. females first tagged in the habitat type as adults (Table 3.5). I considered the first two categories as an estimate of in situ recruitment and the third group of females to represent immigration. There is no significant difference among habitats in the amount of in situ recruitment ($\text{Chi}^2=5.143$, $\text{df}=3$, $p>0.1$). Juvenile recruitment from within a habitat patch type accounted for at most 53 percent of the total number of adult females in that habitat.

Discussion

Total number of litters was similar in woods and corn fields. A lack of differences between these two habitats may in part be due to difficulties getting mice to use nest boxes in the woods. In 1987, I placed nest boxes on the ground in all habitats. Morris (pers. comm.) found this an adequate technique in southern Ontario. Others, however, have placed nest boxes in trees (Goundie and Vessey 1986, Wolff and Durr 1986, Rose and Walke 1988). In 1988, I placed nest boxes at

a height of 1.5 m in trees in woods and fencerows and the number of litters recorded increased dramatically. Comparing 1988 results alone, there were 17 litters in woods (15 in tree boxes) and 8 in corn fields. Therefore, litter frequency in woods may in fact be higher than it is in corn fields.

Habitat did not influence litter size (Table 3.1). Litter size among all habitats was 4.65 ± 1.40 (mean \pm standard deviation). Although not statistically different, the smaller number of litters and smaller litter size in grain fields may indicate a trend toward a smaller total number of offspring in that habitat. Morris (1989) reported no difference in litter size among woods, woods edge and fencerow habitats in southern Ontario. Litter size among the three habitats in his study was 4.29 ± 1.28 . There was no significant difference in litter size between his results and mine ($t=1.932$, $df=195$, $p>0.05$). Goundie and Vessey (1986) reported an average litter size of 4.2 ± 1.37 in an isolated woodlot in Ohio. Litter size in their woodlot did not differ significantly from the size reported in my study ($t=1.596$, $df=99$, $p>0.1$). Millar (1989) predicted that litter size for *P. leucopus* in eastern Ontario should be 5.0 based on an equation that predicts litter size in woods based on latitude and longitude. This prediction of litter size is also close to the one I found in the agricultural habitats (4.65). Litter size in *P. leucopus* is known to be variable over its range. The average size reported in the literature ranges from 3.4 in the southern part of its range

to 5.5 near the northern edge of its range (Millar 1989, Layne 1968). However there is little evidence that litter size varies among habitats within a geographic region (Millar 1989, Layne 1968). Therefore it is not surprising that litter sizes do not differ among habitats in my study.

Most authors report a bimodal breeding season in *P. leucopus* (Rintamaa et al. 1976, Wolff 1985a, Goundie and Vessey 1986, Morris 1989). For example, Morris (1989) found 26 litters between April and June, 8 litters in July and August, and 26 litters in September and October. The breeding season in eastern Ontario was not bimodal (Figure 3.1). There were few litters in the spring and early summer and the bulk of the litters observed were found in August and September. The distribution of litters in time varied by habitat. All of the litters observed in grain were present in May when the grain crop was newly planted and the crop was less than 15 cm tall. These litters may be associated less with grain fields than these results indicate. All of the grain fields used in this study had been corn fields in the previous year. Thus grain field litters could be related to presence of corn in the previous year. *P. leucopus* does occupy corn fields in winter (Chapter 1). The combination of a food supply (from waste corn) and sufficient ground cover (provided by the small grain crop) may make these grain fields better habitat in May for mice than corn fields alone. The rotation pattern of corn followed by small grains is a common one in eastern Ontario.

Recruits from these spring litters may be important for population survival because they provide additional adults to the population that may breed in the fall. Among the other habitats, corn consistently had the largest proportion of litters in all months. Excluding May, the proportional contribution of litters from woods was consistent over the breeding season (Figure 3.3).

Classifying litters based on nest box location (Table 3.1) or on the capture history (Table 3.2) gave similar results (i.e. litters were attributed to the same habitat by both techniques). Although mice in agricultural landscape may move over large areas (Chapter 2), females tended to have their litters in the habitat they had occurred in previously. The exception was litters found in grain fields. None of the females that had litters in grain fields were captured in grain fields before giving birth and all of the females that were caught in grain fields before giving birth had their litters in other habitats. Thus female mice in grain fields are more transient than females in other habitat types in the landscape.

The proportion of adult females with litters varied among habitats (Table 3.3). Woods and grain fields had a smaller proportion of females with litters than did corn fields and fencerows. Grain field females produced litters only in May and adult females found in this habitat were never with litters at other times during the breeding season. Woods

supported larger numbers of females in the fall, but a small proportion of those females were with litters. However, there was no difference in the proportion of females that were reproductively active in each of the habitat types.

The number of litters produced in each habitat (Table 3.1) was related to the total number of females in the habitat rather than differences in the proportion of females in the habitat that were breeding. Minimum number known alive (mnka) was similar in woods and corn and lower in grain and fencerows (Chapter 1). Therefore it is consistent that woods and corn should have more litters than grain and fencerows.

Although juvenile recruitment did not vary among habitats, adult recruitment did (Table 3.4). The number of recruits was highest in the woods and lowest in the fencerows where none of the marked individuals appeared in the population as adults. Recruitment was half as high in corn fields as in woods. These are minimum estimates of recruitment. The estimates are based on mice that were tagged in litters in nest boxes and were also captured as adults. Although the study area in 1988 was 30 ha, the large spatial scale at which mice operate in this landscape decreased the probability of recapturing individuals. On average, mice were captured in nest boxes 2.8 times each. Recruitment reported in the present study was higher than that reported by Morris (1989) in an agricultural landscape in southern Ontario. He found successful recruitment in woods interior to be 18 of 45

litters (0.4) and only 13 of 73 litters in woods edge (0.18). Woods recruitment in my study was substantially higher (0.67). Most of my nest boxes would have been considered by Morris to be edge nest boxes, which implies an even greater discrepancy between our results.

Recruitment of tagged females accounted for a small proportion of all the adult females found in a particular habitat type (Table 3.5). The majority of adult female mice were tagged for the first time as adults. Movement of females into a habitat type may be more important for explaining the number of individuals in that habitat than is the number of individuals recruited from within the patch.

In conclusion, although litter size and number did not differ substantially between woods and corn fields, successful recruitment of mice into the population was markedly greater in the woods. Therefore, substituting corn (and grain) for woods during habitat fragmentation has had a negative impact on the overall population size of *P. leucopus*. Effects of habitat fragmentation, however, were less than expected because *P. leucopus* used agricultural fields as breeding habitat. *P. leucopus* is currently taking advantage of the habitats created by agricultural activity, and mice living in corn fields are contributing to overall population growth. Although grain fields contributed recruits to the population, the recruitment they provided was insufficient to explain the number of individuals found in grain fields. Fencerows, while

producing almost four times as many litters as grain fields, contributed no mice to the population. Thus, grain fields and fencerows may be acting as population sinks and woods and corn fields may be acting as population sources in agricultural landscapes.

Table 3.1 Litter size in *P. leucopus*.

Habitat	Number of litters	Mean size	Standard Error	Minimum size	Maximum size
Woods	19	4.74	0.323	2	7
Corn	25	4.76	0.266	1	7
Fencerow	14	4.71	0.412	2	7
Grain	4	3.25	0.479	2	4
Hay	0	0	0	0	0

Table 3.2 Habitat(s) of marked females found with litters. Location of female before having the litter and habitat location of the nest box in which the litter occurred.

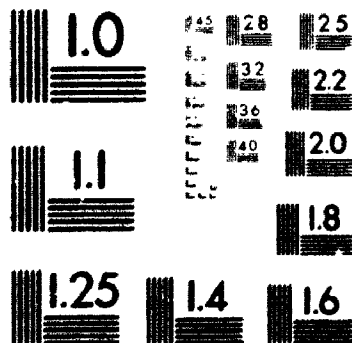
Habitat of litter	Habitat of female before litter was born			
	Woods	Corn	Fencerow	Grain
Woods	4			1
Corn		10		2
Fencerow			2	2
Grain	1	1		

Table 3.3 Monthly average (\pm S.D.) of the proportion of adult females reproductively active during the breeding season (May to October).

Proportion of females in breeding condition	Corn	Grain	Fencerow	Woods
Estimate based on no. females with litters	0.45 \pm 0.35	0.16 \pm 0.29	0.56 \pm 0.46	0.24 \pm 0.34
Estimate based on no. females in nest boxes + no. pregnant or lactating	0.78 \pm 0.34	0.41 \pm 0.49	0.70 \pm 0.43	0.55 \pm 0.46

2 OF/DE 2

PM-1 3 1/2" x 4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT



PRECISIONSM RESOLUTION TARGETS

Table 3.4 Recruitment of mice from litters.

A. Recruitment of juveniles

Litter habitat	No. litters with tagged littermates	No. littermates tagged	Juvenile recruits	No. juvenile recruits/litter
Woods	15	57	30	2.00
Corn	21	76	44	2.09
Fencerow	6	14	0	0.00
Grain	3	8	6	2.00

B. Recruitment of adults

Litter habitat	No. litters with tagged littermates	No. littermates tagged	Adult recruits	No. adult recruits/litter
Woods	15	57	17	1.13
Corn	21	76	10	0.48
Fencerow	6	14	0	0.00
Grain	3	8	3	1.00

C. Number of litters with one or more successful recruit

Litter habitat	No. of litters with tagged littermates	No. of litters with ≥ 1 recruit
Woods	15	9
Corn	21	6
Fencerow	6	0
Grain	3	2

Table 3.5 Sources of adult female recruitment in each habitat

Source of females	Woods		Corn		Fencerow		Grain	
	No.	%	No.	%	No.	%	No.	%
Known Recruits	11	11	5	5	0	0	1	3
1st captured as juv or sad	26	27	42	39	11	23	16	50
1st captured as adult	60	52	60	56	36	77	15	47
Total no. adult females captured	97		107		47		32	
Potential juvenile recruitment	38%		44%		23%		53%	
Potential adult immigration	62%		56%		77%		47%	

Figure 3.1 Seasonal distribution of
litters

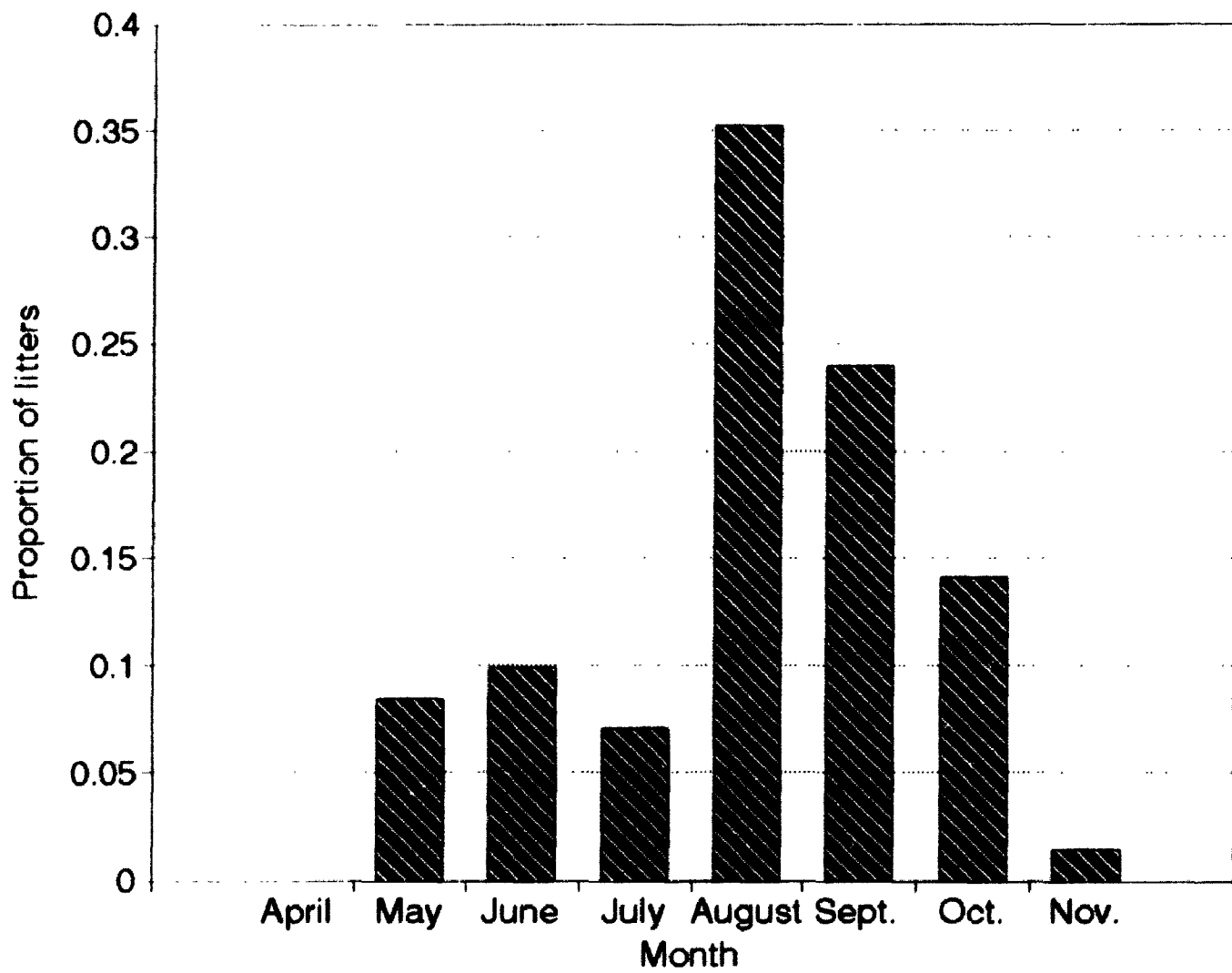


Figure 3.2 Litter sizes

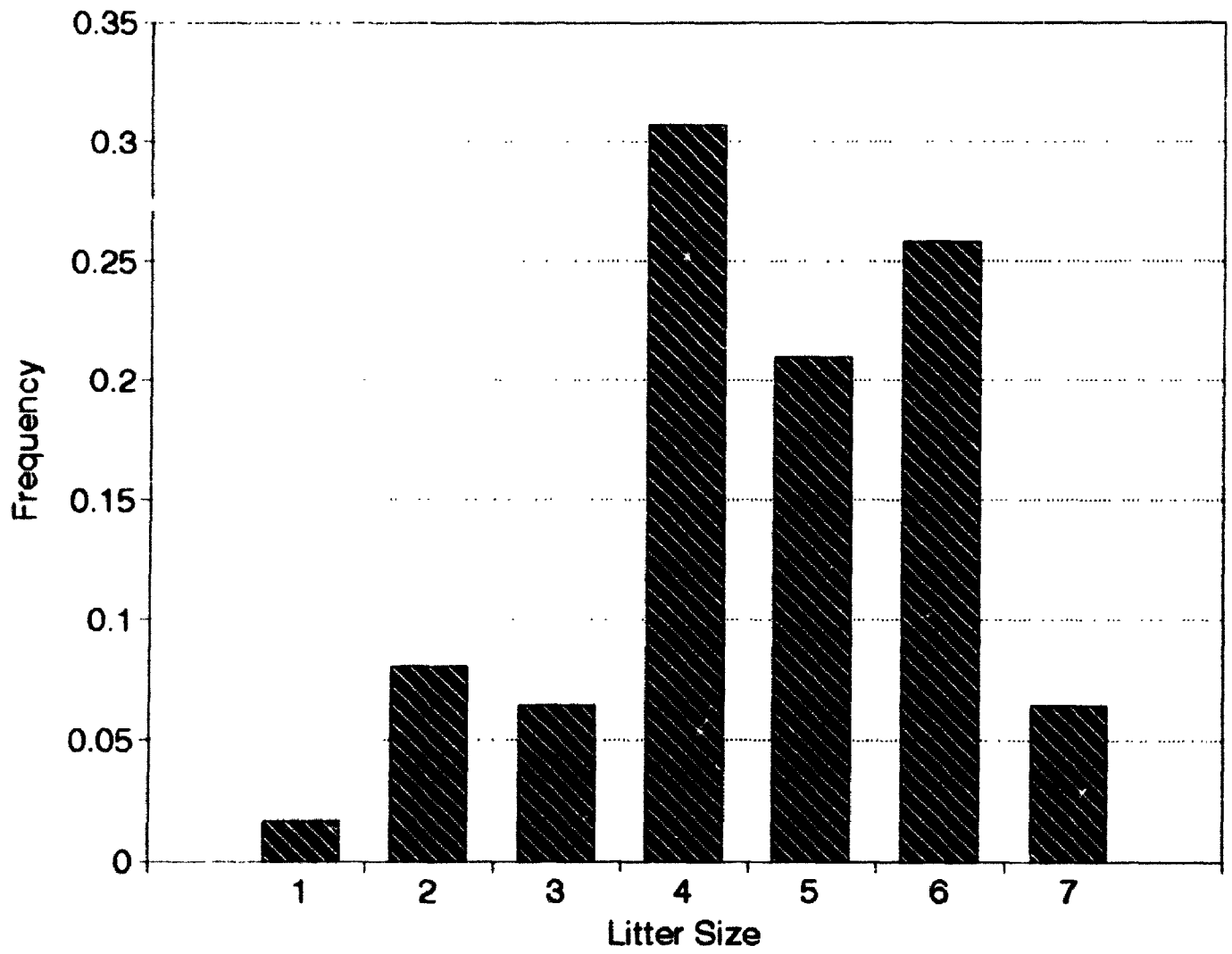
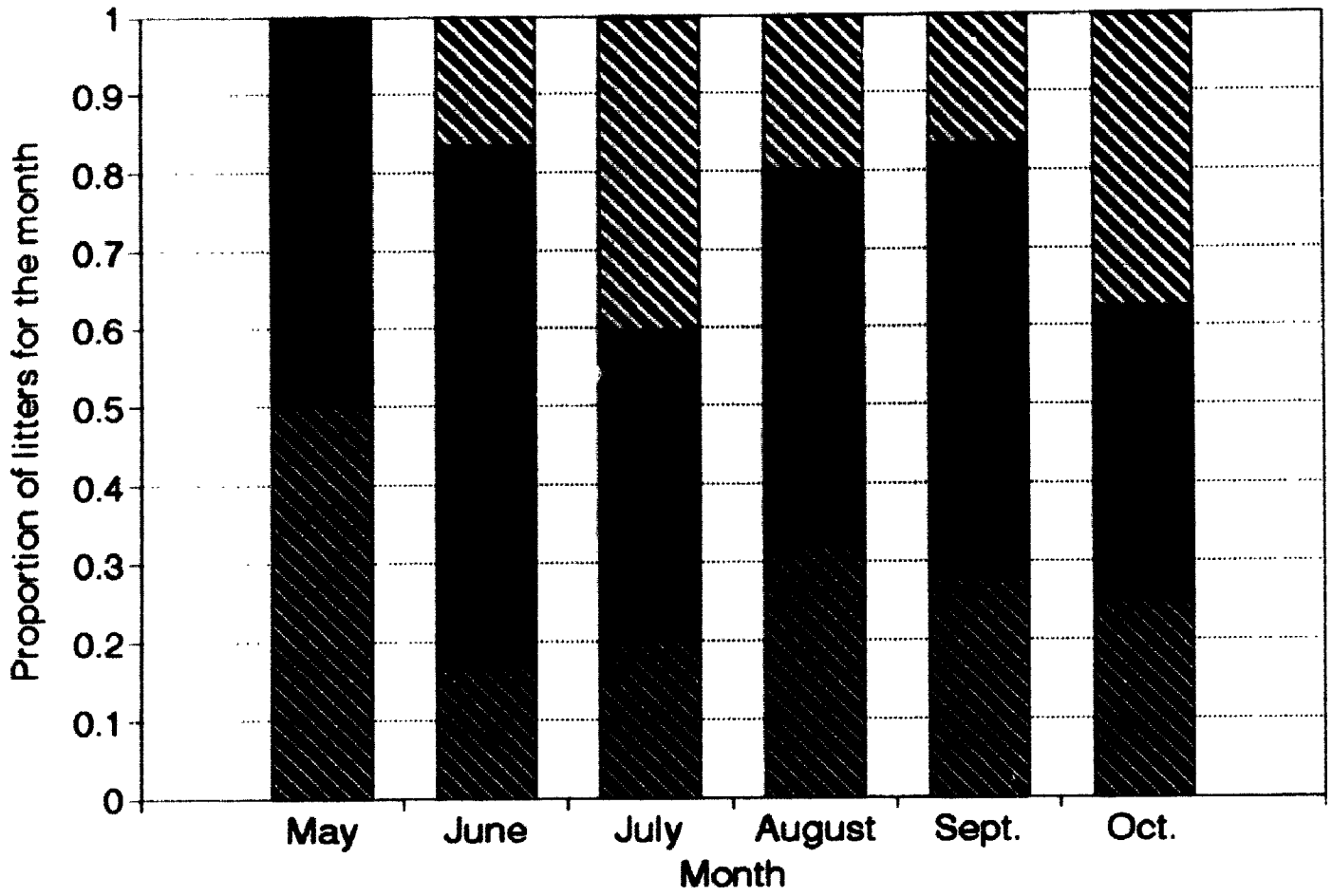


Figure 3.3 Proportion of litters occurring in three habitat types by month



General Discussion

The Operational Demographic Unit for *P. leucopus*

To interpret the spatial and temporal distribution of *P. leucopus* requires an appropriate operational demographic unit (ODU, Merriam in press) for the species. There are two general models have been used to describe the fundamental attributes of an ODU. The first model of an ODU assumes that it is demographically isolated. A change in the population size, viewed from this perspective, is explained entirely in terms of births and deaths. The other model of ODU is of a non-isolated demographic unit. Population dynamics in an open ODU are not explained by births and deaths alone. Population change depends on the sum of births minus deaths and immigrations minus emigrations.

In the agricultural landscapes of eastern Ontario, populations of *P. leucopus* are not isolated (Chapter 1). There are two pieces of evidence that show that *P. leucopus* populations are not closed demographic units. First, 44 percent of all mice captured more than once were captured in both fencerows and crop fields and the movement of mice from one crop field to another was not rare. Mice did not stay in a single vegetation type, but moved from one habitat to another. Second, the turnover per month of the number of individuals in a vegetation patch was very high (Chapter 1, Table 1.4, 1.5, and 1.6). Turnover varied from 56 to 100

percent per month within a habitat patch. The turnover rate did not change significantly as the sampling scale increased from a single crop field, to the crop field plus the surrounding fencerows, to three crop fields and their associated fencerows taken together. Thus, the operational demographic unit for *P. leucopus* is open in eastern Ontario agricultural landscapes. The number of individuals in a particular habitat patch is therefore dependent not only on births and deaths, but also on emigrations and immigrations.

Three categories of population models can be used to explain the dynamics of open demographic units. All three of these alternatives are for spatially- divided models (Fahrig and Merriam 1994). The source-sink model (Pulliam 1988, Pulliam and Danielson 1991) distinguishes between two patch types in the spatially-divided population. First, source patches produce offspring in excess of mortality. This excess production emigrates. Sink habitats provide acceptable habitat for a species, but these habitats produce fewer offspring than are necessary to replace mortality losses. In the extreme case, sink patches may provide resources for the survival of individuals, but provide insufficient resources for breeding. Sink habitats receive emigrants from sources. In some cases, sinks may act as refuges and can occasionally provide colonists to source populations (e.g. Henderson et al. 1985).

Metapopulations are another way of viewing spatially

divided populations (Levins 1970, Hanski and Gilpin 1991). In this model, all patches of acceptable habitat (local populations) are of equal quality (i.e. there are no sources and sinks) and all patches are equally accessible. Interpatch movements occur infrequently, but metapopulation survival depends on that movement of individuals between local populations because local populations go extinct and recolonization will re-establish local populations.

The third population perspective is of a panmictic, highly-connected population. This model combines aspects of source-sink and metapopulation models and has the following attributes. First, acceptable habitat patches may be of different quality. Second, patch accessibility is not equal, but interpatch movement is influenced by the spatial scale of the movements of the individuals and the habitat types through which individuals must travel. Few habitat types provide barriers to the movement of individuals. Interpatch movements are common and turnover of individuals in habitat patches is high. Finally, yearly variation in patch characteristics and patch quality blur the distinctions between source patches and sink patches (i.e. any habitat patch may act as both a source and as a sink both within and between years).

In farmland in eastern Ontario, *P. leucopus* populations are best represented by the panmictic population model. Turnover of individuals is high at all spatial scales investigated ranging from 4 ha to 15 ha (Chapter 1, Tables

1.4, 1.5, and 1.6) and no clear edges to the demographic unit could be found.

Adult recruitment from within a habitat patch compared to the immigration of females as adults in the habitat patch also will indicate the openness of the ODU (Table 3.5). Grain fields were the only habitat type where in situ recruitment accounted for the majority of adult mice captured. Among other habitat types in situ recruitment ranged from a low of 23 percent in fencerows to a high of 44 percent in corn fields (Table 3.5). That means that more than half the adults found in each habitat type except grain fields were caught for the first time as adults and therefore may be attributed to other habitat types. Based on this, there are no clear sources and sinks in the ODU. In fact, all of the patches are dependent on other patches for the adult females found in each patch type.

Clearly, the operational demographic unit for *P. leucopus* is open, with no clear boundaries. Mice move across the agricultural landscape at very high rates, and in all probability the majority of the mice are nomadic (Chapter 2). Mice either moved across the landscape and disappeared very soon after their first capture (Chapter 1, Tables 1.4, 1.5, and 1.6) or they moved at a larger spatial scale than has been previously reported for this species (Table 2.2).

The habitat template for *P. leucopus*

What has caused this shift in the scale of *P. leucopus* and led to the panmictic ODU for this species? Habitat provides the template in which organisms evolve (Southwood 1977, 1988). Normally, the distribution of patches within the template is dynamic as patches are continuously created and destroyed, but the overall structure of the template remains constant. A species must evolve a life history strategy that can match the pattern of the habitat template and the frequency of patch destruction within the template. Previously, the spatial and temporal pattern of the habitat template changed gradually and species were able to evolve new life history traits to survive in the new template. However, if the pattern of the template changes drastically, then species are more likely to be lost from the landscape. Clearing forest for agriculture and the associated habitat fragmentation has changed the spatial distribution and composition of patches in the template abruptly, and selection pressures have been very intense for new life history strategies for species. The amount of forest in the template has been reduced and novel habitats such as corn and grain have been inserted. The temporal dynamics of the template have also changed. Rather than consistent changes due to seasonal growth, as in forest, farmland has rapid and unpredictable changes at several time scales. These time scales range from farming activities that happen within one

year, such as ploughing, planting, spraying and harvesting, to crop rotation which takes place on the scale of 5 to 10 years. Crop rotation means that patches are destroyed more frequently than in forest and that the spatial distribution of patches in the template is also changing. Thus, both the spatial distribution of habitat patches and the temporal dynamics of the individual patches have changed as a result of forest fragmentation and the introduction of agriculture.

Adaptation of *P. leucopus* to the new habitat template provided by the agricultural landscapes of eastern Ontario has been two-fold. First, as a habitat generalist associated with woody vegetation (Chapter 1), *P. leucopus* already had behavioral flexibility for living in several different woody habitat types. With the introduction of crop fields to the habitat template, *P. leucopus* has expanded its behavioral repertoire of acceptable habitats to include novel habitats such as corn, grain, and fencerows (Chapter 1). The number of mice (minimum number known alive) inhabiting woods was similar to that found in corn and grain fields, and fencerows support only slightly fewer than woods (Table 1.1).

The habitat expansion of *P. leucopus* into agricultural fields may have kept the overall spatial distribution of habitat patches that mice can occupy similar to the spatial heterogeneity that existed in the unfragmented landscape (Middleton and Merriam 1983). Although mice now may have a similar spatial distribution to the pre-fragmented landscape,

productivity of these patches (in terms of mice production) may be substantially less. For example, corn fields were indistinguishable from woods with respect to the number of juveniles weaned per litter (Table 3.5), but adult recruitment in corn fields was half that in the woods. The difference in weaned juveniles and adult recruitment may be due to either higher dispersal rates of juvenile mice from corn fields or to higher mortality in corn. I cannot distinguish between these two alternatives, but the absence of an influx, into other habitats, of juveniles weaned in corn fields suggests that higher mortality was the most likely fate of disappearing juveniles.

P. leucopus has also increased its spatial scale as a result of changes in the habitat template (Chapter 2). This shift in spatial scale has occurred not only in the novel habitat patches in which *P. leucopus* occurs, but in woods as well.

P. leucopus may use one of two spatial strategies to survive: stay-at-home and nomadic (Chapter 2). Stay-at-home mice move relatively short distances and have small home ranges (Figure 3.2, mouse 399 and Figure 3.3, mouse 517). Nomadic mice move over a much larger scale and have large 'home ranges' because they move across the trap grids rapidly and disappear (Figure 2.2, mouse 731) or because they make large movements daily (Figure 2.3, mouse 498). The large variation in the measures of space use (Tables 2.2) indicates

the presence of both strategies in the agricultural mosaic and the predominance of nomadic mice contributed to the larger values of space use than reported in the literature (Table 2.8). These two behavioral types probably also occurred in continuous forest, but stay-at-home mice predominated. Perhaps the shift in strategies occurred because of the higher seasonal and yearly variability that occurs within crop fields. Mice move their nests often because they rapidly soil their nests (Wegner, pers. observation). These movements may have been the basis for the nomadic strategy. Instead of a mouse moving its nest a short distance to the next nest cavity, the individual is choosing to move larger distances.

The larger spatial scale for *P. leucopus* in fragmented landscapes is not apparent in other parts of its range (Table 2.8). *P. leucopus* is at the northern edge of its range in the Ottawa area and achieves smaller fall population sizes than farther south (Khrono et al. 1988). Food resources for *P. leucopus* may be more limited in forests at this latitude because species that produce large mast crops are uncommon here (Rowe 1972). Thus mice in small woodlots in eastern Ontario may have needed to forage outside woods to survive.

Summary

The impact of modification in the habitat template for *P. leucopus* been a strong force. This forest habitat generalist has become a habitat generalist as it has incorporated several non-forested habitats into its behavioral repertoire. As part

of this process, *P. leucopus* has also expanded its spatial scale as the majority of the mice became nomadic. As the spatial scale for the mice expanded and mice became more nomadic, the operational demographic unit for the mice became open until the ODU has become a panmictic one with no clear boundaries evident at the largest spatial scale of individuals studied here (30 ha).

The novel habitats into which the mice expanded are not just population sinks. Novel habitats act as breeding habitat for *P. leucopus*. The proportion of litters that produce one or more recruits is not different among all the habitats in which *P. leucopus* occurs. Total recruitment of adults from novel habitat types such as corn fields is significant, but is generally lower than for forest.

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