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Responses to habitat variation by small mammal individuals and populations at different spatial scales (Ontario).

Lawrence Anthony. Heidinga
University of Windsor

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RESPONSES TO HABITAT VARIATION BY SMALL MAMMAL INDIVIDUALS AND POPULATIONS AT DIFFERENT SPATIAL SCALES

by

Lawrence Heidinga

A Thesis
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ABSTRACT

Small mammal habitat selection was studied at different spatial and temporal scales at Point Pelee National Park, Ontario. At a relatively large scale, small mammals were censused in nine different locations over the 450 hectares of the park, and compared temporally for censuses performed in the same sites in 1971 and 1996. The nine locations represented a variety of habitats at different stages of ecological succession, and some of them changed significantly between 1971 and 1996. Habitat preferences observed for three rodent species in 1971 were used to predict which habitats in 1996 would contain populations of these species. Predictions were upheld in some cases, but population cycles and the extinction risk to small populations suggested reasons for unexpected absences. Another study examined responses of two rodent species to habitat variation at much smaller spatial (2.125 ha) and temporal (one summer) scales. In the first analysis, abundances of the two species varied with habitat type, and the relationship was similar at two spatial scales. In the second analysis, I found that home range size and overlap were not consistently affected by habitat type, and significant relationships were not always observed in the same habitats that were significant in the abundance regressions. One explanation for inconsistencies is that large-scale habitat cues affect initial home range placement, and home range size and overlap are adjusted afterward in response to local conditions.

ACKNOWLEDGEMENTS

My supervisor, Bob M'Closkey, was a major reason my stay at Windsor was worthwhile. From a practical point of view, I learned good science from him by example and through informal discussions. I also appreciated Bob's positive attitude, encouragement, and his confidence in my abilities. I am neither so old nor so confident that these did not increase my own confidence and positive attitude towards science and life. Doug Morris offered advice several times during my thesis and carefully reviewed a paper for me. More importantly he introduced me to theoretical ecology as an undergraduate, and excited me with the novel idea of thinking for myself. Hugh MacIsaac and Jan Ciborowski sometimes served as substitute advisors when Bob was on sabbatical. Steve Hecnar offered advice, was a sounding board for ideas, and was always ready to help me out in any way. My field assistants, Linda Walker and Kristen Kolar were great help (in spite of the bugs, poison ivy, thunder storms). Cyril Rodrigues and Peter Sale offered their time to sit as a committee member and chair my defense, respectively. The staff at Point Pelee, notably Tom Linke, as well as the other wardens and the naturalist staff helped me in a lot of different ways.

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Chapter I

GENERAL INTRODUCTION TO HABITAT SELECTION THEORY

Habitat selection is an important determinant of small mammal distribution and abundance at small spatial scales. Habitat selection can affect population regulation (Petit and Petit 1996; Morris 1988; Pulliam 1988), coexistence with competitors (Pimm and Rosenzweig 1981; Abramsky *et al.* 1992; Danielson 1992; Ward and Seely 1996), avoiding predators (reviewed in Lima and Dill 1990; see also Brown 1988; Moody *et al.* 1996; Abramsky *et al.* 1997), and responses to disturbance and temporal habitat change (Chapters 51-55 in Verner *et al.* 1986; Fox 1990; Morris 1990; Smith and Lindenmeyer 1992; Higgs and Fox 1993; Hakkarainen *et al.* 1997). Because habitat selection can affect so many aspects of an organism's life, assessing habitat selection for a species is often the first step towards its successful management (*e.g.* Verner *et al.* 1986).

Our understanding of habitat selection has been furthered by its solid grounding in evolutionary ecology, the basis of which is a simple maxim: individuals are expected to make decisions regarding the selection of habitats that maximize their fitness. There are two basic scales of habitat selection, individual and population, although population responses are emergent properties of individual responses.

Individual responses to habitat have been modeled using optimal foraging theory. Charnov's (1976) marginal value theorem predicts that individuals maximize energy intake, and therefore fitness, by assessing the energy gains of each patch in which they forage, with the missed opportunity costs of not foraging in other patches. However, the prediction of energy maximization is altered if foraging in some patches is associated with costs due to predation (Lima and Dill 1990; Moody *et al*. 1996), missed opportunities for reproductive activities (Brown 1988), metabolic costs (Brown 1988; Corp *et al*. 1997), defending territories (examples in Davies and Houston 1984), or travelling between patches (Rosenzweig 1981). For example, if an individual has to choose between a resource-rich habitat and a resource-poor habitat, it might be expected to choose the former. The actual choice of patch may, however, be unexpected if the resource-rich patch is associated with high predation costs, high travel costs between patches, or other costs. This example does not reflect the full complexity of individual models, but illustrates that organisms make decisions on the basis of many factors that can affect their fitness.

Population theories of habitat selection are largely based on the paradigm of the Ideal Free Distribution (IFD, Fretwell and Lucas 1970; see a history of theory development in Rosenzweig 1991). All individuals are assumed to be equal, and choose habitats on the basis of maximizing their fitness. Individuals are 'ideal' because they select the habitat where they will achieve maximum fitness, and are 'free' because they can choose habitats without incurring costs travelling between them. Most authors assume that the habitat characteristics that affect fitness are based on resource availability (*e.g.* Kennedy and Gray 1993; Rosenzweig 1991).

The IFD can be illustrated as in Figure 1.1, where fitness is plotted against density for habitats A and B. Fitness is a decreasing function of density because higher densities are expected to lead to lower resource levels, and fitness in this example is always higher in habitat A. An individual entering the system will assess current habitats and densities, and occupy the habitat where it will have the highest fitness. For densities lower than the threshold T (Fig. 1.1), individuals will only occupy habitat A where the fitness is higher than the highest possible fitness in habitat B. When density in habitat A exceeds the threshold, fitness is lowered to the point where some individuals can maximize their fitness by selecting habitat B. Because habitat selection changes with density, this is referred to as density-dependent habitat selection. If density is increased even more, individuals will divide themselves between the habitats such that their fitnesses are equal. Whenever fitnesses become unequal between habitats, it would pay for some individuals to switch from the low to high

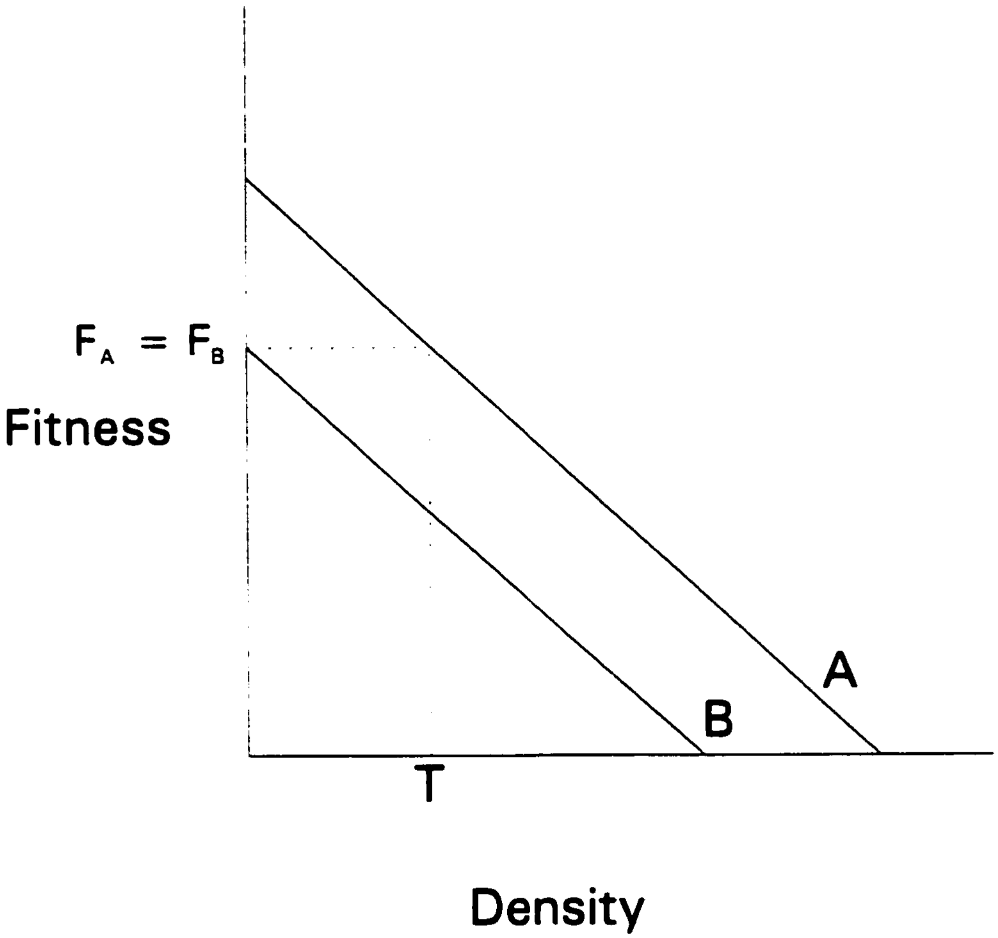

Figure 1.1 The Ideal Free Distribution (IFD). As density increases, fitness in habitats A (F_a) and B (F_b) decreases. Individuals that maximize their fitness will occupy only habitat A until density reaches threshold T. At that point $F_a = F_b$, and individuals will distribute themselves between the habitats such that fitnesses remain equal between habitats.

fitness habitat until fitnesses were again equal between habitats. Note also that density is always higher in the habitat with the highest fitness, and therefore is an indicator of habitat quality when the conditions for the IFD are valid.

There are many other habitat selection models to explain a lack of fit to the predictions of the IFD, most of which consider violations of the assumptions of the IFD. Fretwell and Lucas (1970) developed the ideal dominance distribution (IDD) that looks at differences between individuals in interference competitive ability. Through interference competition, *e.g.* hostile interactions, resident individuals can make it risky for new individuals to settle in a habitat, and this risk is expected to linearly increase with density. Therefore, a new individual has to assess fitness by looking at habitat suitability minus the potential fitness cost to initially settling in the habitat, which is represented by the dashed line in Fig. 1.2. Because densities are higher in the more suitable habitat, costs to settle there are also higher. Therefore, it will be beneficial for new individuals to occupy habitat B at lower densities than predicted by the IFD. The realized fitness of surviving residents will be higher in habitat A than habitat B, a fact used in field tests to separate the IDD from the IFD because the IFD predicts equal fitnesses between habitats.

As in the IFD, density in the IDD is always highest in

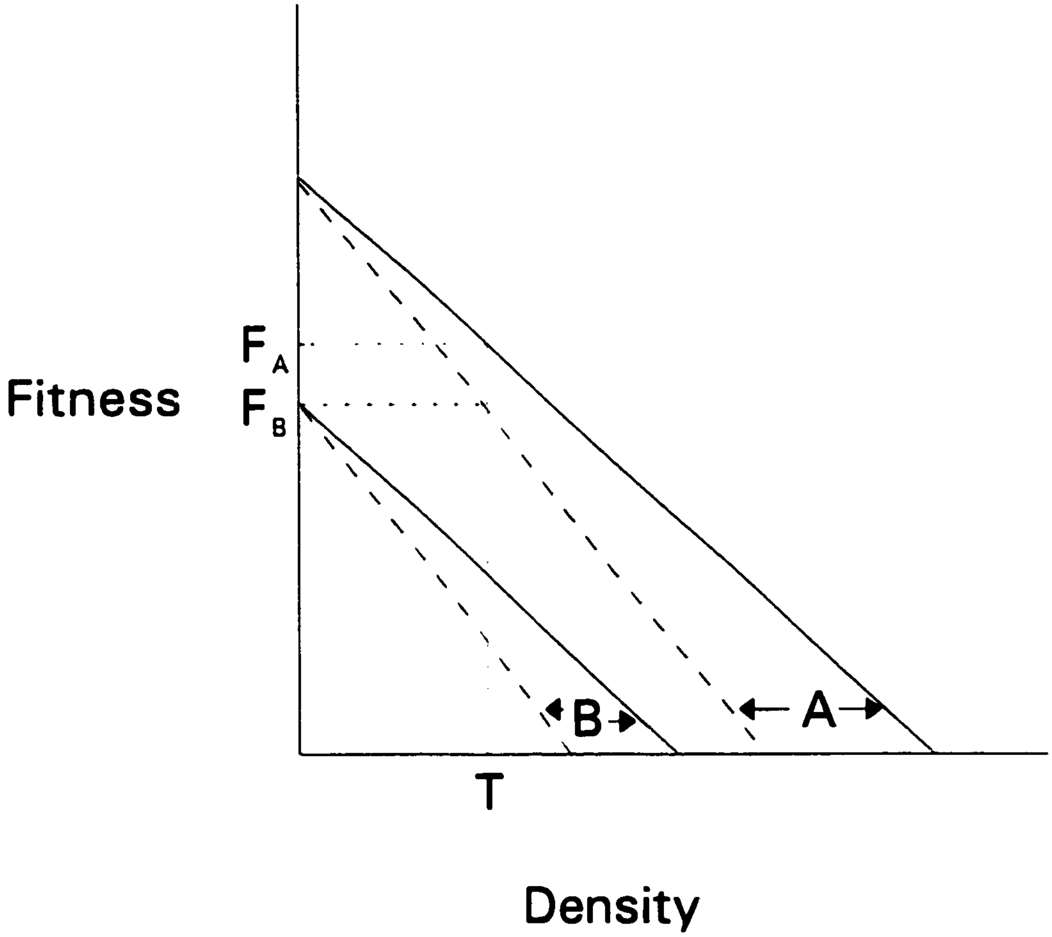

Figure 1.2 The Ideal Dominance Distribution (IDD). Solid lines represent fitness as a decreasing function of density. Initial settlement in a habitat incurs a risk due to hostile interactions with settled residents, which increases with density. Habitat selectors evaluate habitat fitness minus the risk to initial settlement, represented by the dashed lines. Because of the increased risk in habitat A, unsettled individuals will choose habitat B at lower densities than predicted by the IFD. Residents that survive the settlement process have a higher fitness in habitat A than habitat B ($F_a > F_b$).

the habitat of highest suitability, although other ways of modelling territoriality can lead to density sometimes being higher in a poor habitat (*e.g.* Van Horne 1983). For example, imbalances in contest competitive ability, such as when adults have an overwhelming advantage over juveniles, or when nest sites are limiting and easily defended (Pulliam 1988), can lead to a few individuals monopolizing the best habitat and forcing other individuals into the poor habitat. A special case of this is the source/sink phenomenon where population growth rate is negative in the sink habitat, but a population exists anyway because of immigration of individuals from the source habitat. In most cases, however, the types of unbalances in competitive ability should be recognizable in the field.

The predictions of the IFD have been often tested in lab experiments, with debatable support for its predictions (reviewed and debated by Kennedy and Gray 1993; Åström 1994; Gray and Kennedy 1994; Milinski 1994). Field tests of the IFD and IDD have directly or indirectly measured fitness and/or resource availability in different habitats to separate these two hypotheses. Few studies have found support for all of the predictions of the IFD (Wahlstrom and Kjellander 1995; Guillemette and Himmelman 1996), but many have found support for the IDD (Andrén 1990; Messier *et al.* 1990; Dhondt *et al.* 1992; Ens *et al.* 1992; Oksanen *et al.* 1992; Halama and Dueser 1994; Morris 1996; Petit and Petit

1996).

Other factors that invalidate the assumptions of the IFD are associated with particular scales of observation. Habitat preferences will likely be harder to discern at small spatial scales, particularly scales smaller than an average home range. If rich and poor habitat are juxtaposed at this scale, the travel and time costs of avoiding the poor habitat may be greater than the gains expected from only exploiting the rich habitat. That is, it takes the organism so long to travel around or over the poor habitat that the organism might as well use it because it is there anyway. Thus, individuals might use the poor habitat even when it was not expected on the basis of habitat quality alone (Rosenzweig 1981; Morris 1992; Åström 1994).

At large spatial scales, one could compare habitats that are well beyond any one individual's perceptual limits, and beyond the ability of the individual to assess and choose freely between the areas. One could compare two areas of the same habitat and find different densities and different fitnesses. At this scale of comparison, the habitats may experience uncoupled, stochastic population dynamics (Henschel and Lubin 1997), different environmental conditions, and different rates of dispersal (Fahrig and Paloheimo 1988; Caselle and Warner 1996), all of which can affect local densities and fitnesses regardless of habitat type. Individuals do not adjust densities to these differences via habitat selection because they either do not know the differences exist, or the travel costs are simply too great. The scale at which organisms select habitat will depend on the resource they are exploiting (Orians and Wittenberger 1991). Orians and Wittenberger (1991) found that choices made for nest site location by yellow-headed blackbirds were made at the scale of individual marshes, and not based on small-scale heterogeneity within the marsh.

Densities obviously can change through time even when habitat remains constant (see detailed discussion in Pimm 1991). Temporal variation may occur due to environmental variation (Wolda 1989; Ellner and Turchin 1995; Morris 1996; Lewellen and Vessey 1998), stochastic population dynamics caused by delayed density-dependence (May 1976), and changes in dispersal rates. Comparing densities in habitats between different times requires accounting for this variation. Morris (1990) provides a way that temporal variation and habitat change can both be accounted for, although it requires data to be collected in a specific way that no long-term studies have been able to achieve.

Obviously, invoking habitat selection to explain patterns in densities between habitats must be done carefully, and the conditions and assumptions of the predictions have to be made explicitly. If the conditions of the IFD or IDD are met, densities are expected to reflect habitat quality, but care is required because the relative densities can change. For instance, if all individuals occupy habitat A (density < T, Fig. 1.1), relative densities of the two habitats will be very different than at higher system densities where individuals occupy both habitats (see Morris 1994 for many types of density patterns). Van Horne (1983) also pointed out that densities estimated in one season may not reflect the actual quality of the habitat for the whole year.

The framework of habitat selection theory that I have outlined provides the foundation for the two projects in this thesis that look at very different scales of habitat selection. The first study (see Chapter II), takes place over fairly large spatial and temporal scales. The study compares small mammal censuses collected 25 years apart, from study sites spread over 450 ha. Habitat preferences are assessed from the first census in 1971, and then used to predict changes in small mammal abundance through time due to successional habitat change. As already discussed, deviations from these predictions may occur due to temporal variation caused by a variety of factors.

The second study (see Chapter III) looks at habitat selection of two rodents within 2.125 ha study plots in two ways. The first method assesses habitat selection from the viewpoint of the individual, as indicated by responses of home ranges to habitat variation. These results are compared to the response of combined individuals, as indicated by different numbers and captures of individuals at each station, or blocks of nine stations. I examined whether habitat preferences indicated by individual home ranges lead to predictable effects on combined-individuals indices.

Both of my studies assume that density is an indicator of habitat quality. Two studies have looked at habitat-specific fitness of the most common small mammal at Point Pelee, *Peromyscus leucopus* (white-footed mouse). Halama and Dueser (1994) found some support for the IDD, where fitness was greatest in the habitat with the highest densities. Morris (1996) collected a long-term data set over 12 years which contains large variation in density over the period, and his data also supported the IDD because fitness was higher in the habitat with the greatest density. These studies support the idea that even though territoriality probably does occur in this species (Wolff 1989), there is no suggestion that it is of the form where a few individuals will monopolize the best habitat and force high densities of subordinates into a suboptimal habitat.

Chapter II

CHANGES IN SMALL MAMMAL ABUNDANCE OVER 25 YEARS

SUMMARY

Small mammal abundances in nine locations at Point Pelee National Park were censused in 1971 and 1996. The locations represented a mix of habitat types and plant successional stages, some of which changed due to ecological succession between 1971 and 1996. Habitat preferences were assessed for three rodent species using observed abundances in 1971, and their response to habitat change was predicted for 1996. Habitat preferences accurately predicted the ubiquitous presence of *Peromyscus leucopus*, but population cycles provided a better explanation for unexpected absences of *Microtus pennsylvanicus* in 1996. Habitat loss was probably a major contributor to the extirpation of *P. maniculatus* at Point Pelee. The current status of non-rodent species is not well understood, although there is no indication that any of the species are in danger of local extirpation.

INTRODUCTION

The application of ecological principles is finding increased use in conservation and management (Primack 1993). Of current concern is the increased fragmentation of natural habitats due to human disturbance (Chapter 11, Heywood and Watson 1995), and protected areas often form important islands of habitat that need to be carefully managed. In order to institute management plans, it is mandatory to know both the current status of species and the recent trajectory of changes in their distribution and abundance. A full understanding of species might only come with knowledge at several organizational levels, including reproductive ecology and mating system structure, habitat requirements, determinants of local distribution and abundance, metapopulation dynamics, and the relative abundance and species richness of assemblages.

Small mammals are model organisms, capable of revealing the mechanisms and ecological correlates of diversity, abundance, and distribution. They are small (typically less than a few hundred grams), show rapid growth and development to maturity, often abundant, diverse, and are important functional elements in terrestrial food webs (*e.g.* Golley *et al*. 1975; Tamarin 1985; Kirkland and Layne 1989). Because of their cosmopolitan distribution, small mammals are found in virtually every seral stage in ecological succession, although abundance and diversity vary widely among stages (Rosenzweig and Winakur 1969; M'Closkey 1975; 1978; M'Closkey and Lajoie 1975). Numerous field studies have demonstrated a link between the physical structure of habitats and small mammal abundance and diversity (Price 1978; Morris 1979; Kotler 1984; Brown 1988). In addition, small mammals respond to changes in habitat structure during ecological succession because of the unique habitat requirements of each species (Connor 1953; Hirth 1959; Pearson 1959; Wirtz and Pearson 1960; Getz 1961a;b; Shure 1970; M'Closkey 1975; M'Closkey and Fieldwick 1975; Fox 1982; 1990; Price and Waser 1984). Successional changes during post-fire recovery of plant communities also provide a spectrum of community types to which small mammals respond (Clark and Kaufman 1990; Wirtz *et al.* 1988; Fox 1982; 1990; Price and Waser 1984).

This study examines changes in small mammal abundance and distribution at Point Pelee National Park through successional time. Point Pelee is an area of conservation concern because its small area and isolation from other natural habitats is likely to lead to small population sizes and little incoming colonizers, respectively. Small populations are at increased risk of extinction due to stochastic demographic and environmental variability (*e.g.* Goodman 1987; Lande 1993), and the lack of dispersal means that rescue of populations at risk of extinction is unlikely (conservation implications discussed in McCullough 1996). The reduced area at Point Pelee is even more pronounced because the available habitat is a complex mixture of different successional stages rather than a continuous distribution of one predominant habitat. Species associated with particular seral stages in ecological succession may be rare because of the low representation or availability of that habitat at Point Pelee.

This was the impetus for not only assessing the current abundance and distribution of small mammals at Point Pelee, but also for investigating factors that may have caused changes in abundance over the last 25 years. The original data were collected by Bob M'Closkey in 1971 (M'Closkey 1972; M'Closkey 1975; M'Closkey and Lajoie 1975) in nine different habitats that represented different successional stages. He had sufficient data for three rodent species to establish their habitat preferences, and then predict likely changes in abundance as habitats changed due to ecological succession. I tested these predictions by recording small mammal abundances in the same areas as M'Closkey, some of which had undergone successional changes in habitat. The predictions are outlined below to allow a full description of the habitats, habitat changes, and species preferences for these habitats. When the data did not support predictions based on habitat preferences, I assessed whether there was evidence for changes in density caused by other factors such as population cycles, environmental variation, fragmentation and disturbance. Five other small species were captured at Point Pelee, but the data from this study and others have not produced a good understanding of their biology and habitat preferences. The census data are presented for these species to see if any major declines in their abundance occurred or are expected.

HABITAT DESCRIPTIONS AND CHANGES

All habitats are located in Point Pelee National Park, Essex County, Canada (42°00' N, 82°31' W), a large sandspit extending into Lake Erie. Bob M'Closkey (1972; M'Closkey and Lajoie 1975) trapped small mammals in nine habitats in Point Pelee in 1971 (Table 2.1). Throughout the paper plot location is identified using the original, 1971 habitat type.

The grassland and asparagus/herbaceous habitats were old fields abandoned only 2 and 4 years before 1971, respectively. The grassland was dominated by wheat grass (*Agropyron trachycaulum*). Half the asparagus/herbaceous habitat was dominated by asparagus (*Asparagus officinalis*), and the other half by horseweed (*Erigeron canadensis*) and other herbs. The beach dune was a naturally occurring early successional habitat, with grasses and vines interspersed with occasional red cedar (*Juniperus virginiana*). The habitat mixture of red cedar, shrubs (staghorn sumac, *Rhus typhina*) and vines (riverbank grape, *Vitis riparia*) grew in an abandoned apple orchard. The marsh border habitat was composed of a variety of grasses and sedges. The last four habitats were all forest types named for the trees that dominated them: red cedar, hackberry (*Celtis occidentalis*), white pine (*Pinus strobus*) and climax deciduous. Climax deciduous forest includes some of the largest trees in the park, often red oak (*Quercus rubra*), chinquapin oak (*Quercus muehlenbergii*) and basswood (*Tilia americana*).

Table 2.1 A comparison of the habitats and dominant plants of lacations censused in 1971 and 1996.

1971		1996	
Habitat	Dominant Plant	Habitat	Dominant Plant
Grassland	wheat grass[a]	Grassland/ herbs/shrubs	Quack grass Goldenrod Grey Dogwood
Asparagus/ Herbaceous	asparagus horseweed	Poplar/ shrubs	Eastern Poplar Grey Dogwood
Beach Dune	vanilla grass riverbank grape	Shrubs	Grey Dogwood
Marsh border	grasses & sedges	Marsh Border	grasses & sedges
Cedar/shrub/ vines	Red Cedar sumac riverbank grape	Shrubs	Grey Dogwood
Red Cedar		Red Cedar	
Hackberry		Hackberry	
White Pine		White Pine	
Climax Deciduous		Climax Deciduous	

[a] see text for latin binomial

All of the early successional habitats had changed by 1996 (Table 2.1). The grassland had become a mixture of grasses, shrubs and herbs, dominated by quack grass (*Agropyron repens*), grey dogwood (*Cornus drummondi*) and goldenrod (*Solidago* spp.), respectively. There was also a fair amount of riverbank grape in this habitat. The asparagus/herbaceous community had changed into a stand of Eastern poplar (*Populus deltoides*) on one half, and grey dogwood on the other. The other two habitats that experienced major change were the beach dune and the cedar/shrub/vine habitat, which had both been overgrown by grey dogwood with occasional red cedar interspersed.

The marsh border had all but disappeared, perhaps due to rising marsh levels, but a small plot was established in similar habitat nearby (see Methods). The forest habitats had also remained relatively unchanged, and were still dominated by the same tree species.

HABITAT PREFERENCES AND PREDICTIONS

RODENT SPECIES

Habitat preferences for three rodent species were generated from the 1971 data collected by M'Closkey (1972; and Lajoie 1975), and compared with information attained from the ecological literature. Our knowledge of the habitat preferences of the three rodent species captured is based on qualitative habitat classification. Researchers have classified habitats using quantitative metrics of the habitat, but no one has established direct links between these measures and fitness/density that are broadly applicable to many populations and environments. This means that my predictions are crude and based on gross changes in habitat type rather than factors that directly affect individual fitness. Habitats are deemed suitable simply if they had a resident population in 1971 (indicated by an "X" in Table 2.2). All habitats in 1996 were comparable to at least one of the habitats in 1971 in habitat structure, therefore I could predict whether the 1996 habitat was suitable or not based on the 1971 data. The prediction of suitability is indicated by a checkmark in the 1996 column (Table 2.2), and mirrors the predictions made by M'Closkey (1972; and Lajoie 1975; and Fieldwick 1975).

The most widely distributed species of the three rodents was *Peromyscus leucopus* (white footed mouse), which was present in every habitat except the grassland habitat in 1971 (Table 2.2). This is consistent with its reputation as a habitat generalist, usually only absent from some grasslands and recently disturbed habitats (Beckwith 1954; Pearson 1959; Hirth 1959; Morris 1979; Adler 1986; Huntly and Inouye 1987; Cunningham 1990). The predictions are simple: Because *P. leucopus* will occupy all types of herbaceous, shrub and tree dominated habitats, all habitats in 1996 contained some suitable habitat, and all should contain a resident

Table 2.2 Habitats occupied by three rodent species in 1971 (X), and predicted to be occupied in 1996 (X). Wrong predictions are circled. The species are as follows: Pl, *P. leucopus*, Pm, *P. maniculatus*, and Mp, *M. pennsylvanicus*.

		Habitat Suitable?					
1971 Habitat	1996 Habitat	Pl		Pm		Mp	
		71	96	71	96	71	96
Grassland	Grassland/Shrubs/Herbaceous		X	X	X	X	X
Asparagus/Herbaceous	Shrubs/Forest	X	X	X		X	
Beach Dune/Prairie	Shrubs*	X	X			X	
Marsh Border	Marsh Border*	X	X			X	X
Cedar/Shrub/Vines	Shrubs	X	X				
Red Cedar	Red Cedar	X	X				
Hackberry	Hackberry	X	X				
White Pine	White Pine	X	X				
Climax Deciduous	Climax Deciduous	X	X				

* reduced trapping effort

population of this species.

Microtus pennsylvanicus (meadow vole) is known to occupy early successional habitats, especially grasslands, and to avoid shrubby and forested habitats (Beckwith 1954; Morris 1979; Adler 1986; Huntly and Inouye 1987; Cunningham 1990). M'Closkey found this as well, recording resident populations in the two grassy habitats, grassland and marsh border, as well as the asparagus/herbaceous habitat (Table 2.2). The predictions for this species are also simple: the only grassy and/or early successional habitats in 1996 were in the grassland/herb/shrub and marsh border habitat, therefore these are the only habitats expected to have resident populations.

The last rodent species, *Peromyscus maniculatus bairdii* (prairie deer mouse), was recorded in 1971 in the grassland and asparagus/herbaceous habitats by M'Closkey (Table 2.2). Other researchers have also found that this sub-species of deer mouse is an early successional species, the first to appear after a disturbance, and one of the first to disappear (Beckwith 1954; Hansen and Warnock 1979; Morris 1979; Fitch *et al*. 1984; Foster and Gaines 1991). In 1996, only one area contained potentially suitable habitat for *P. maniculatus*, the grassy and herbaceous areas of the grassland/herb/shrub habitat.

NON-RODENT SPECIES

There were five non-rodent species captured, but the general understanding of their habitat preferences is too limited to make predictions of habitat responses. Two shrew species were captured, *Blarina brevicauda* (short-tailed shrew) and *Sorex cinereus* (masked shrew), as well as one zapodid, *Zapus hudsonius* (meadow jumping mouse). Two larger mammals, *Mustela erminea* (short-tail weasels) and juvenile *Didelphis virginiana* (opossum), were captured. The data for these species will be examined to assess changes in status over the 25 year period, and when possible, explanations offered to explain changes.

METHODS

Eleven plots were trapped at Point Pelee in 1996 (Fig. 2.1). Plots were grids of stations, and stations were spaced 15 meters apart in all plots except the beach dune and marsh border, which had 10 meter spacing. The size and number of plots are not comparable with M'Closkey (1972). In several instances, I established one or two large plots that ran across several habitat boundaries, where M'Closkey had several small plots in the same vicinity. However, when the data were extracted by habitat for 1996 (discussed below), I had similar or greater trapping effort in all habitats except for the marsh border and beach dune habitats (Table 2.3; a trap-night is one trap set for one night). Both of these habitats were located on the east shore of the park (Fig. 2.1), which is no longer accessible by vehicle, therefore I

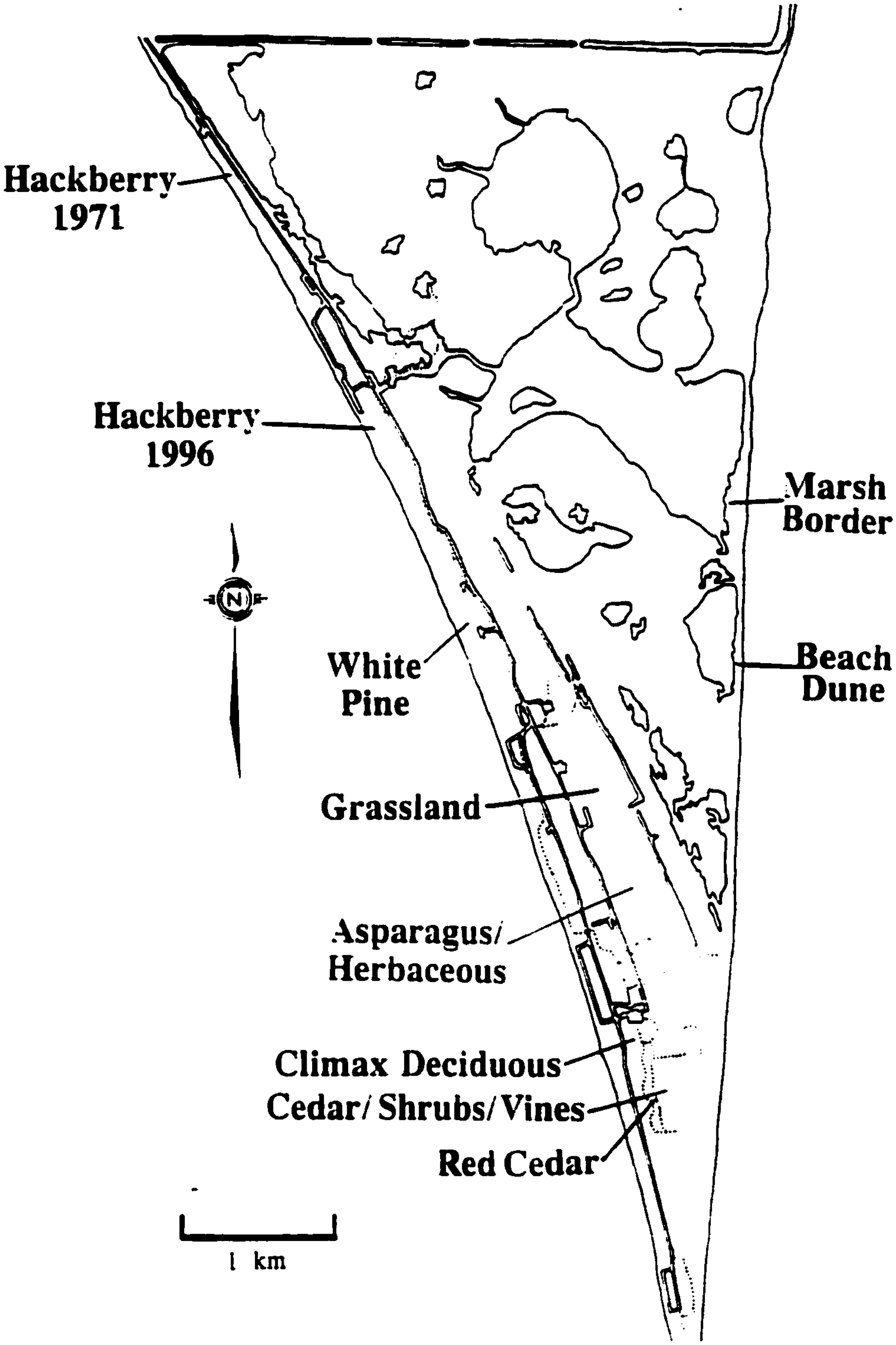

Figure 2.1 A map of habitats trapped in 1996. Changes in plot location between 1971 and 1996 are noted for the hackberry habitat.

Table 2.3 A comparison of trapping effort in nine areas censused in 1971 and 1996. A trap-night is one trap set for one night.

1971			1996		
Habitat	No. of Stations	No. of Trap-Nights	Habitat	No. of Stations	No. of Trap-Nights
Grassland	64	512	Grassland/ Herbs/Shrubs	198	2220
Asparagus/ Herbaceous	49	392	Poplar/ Shrubs	49	679
Beach Dune	119	952	Shrubs	80	160
Marsh Border	30	240	Marsh Border	16	32
Cedar/shrub/ Vines	29	232	Shrubs	35	455
Red Cedar	18	144	Red Cedar	10	130
Hackberry	18	144	Hackberry	42	546
White Pine	25	200	White Pine	29	377
Climax Deciduous	36	288	Climax Deciduous	64	832

was limited to only two nights of trapping in these habitats, with reduced plot sizes. In addition, disturbance by racoons was so high on these plots that I could not have continued trapping there.

M'Closkey (1972) had trapped each area two nights every two weeks from July 13 to September 1, 1971, and I had the same routine from June 12 to August 23 (Table 2.4). Logistic problems only allowed one night of trapping for several habitats in the third session (July 5). Previous to June 12, the schedule was altered to account for large numbers of bird watchers in certain areas of the park. Plots in low-impact areas were trapped 3-4 nights each from May 14 to May 23, and the heavily used areas were trapped from June 4 to June 7.

Plot locations were mostly in the same areas as trapped by M'Closkey (1972; Fig. 2.1), except the two hackberry plots which were flagged about 2 kilometers south of the original plot, but within the same continuous hackberry forest. In some cases I increased the replication of habitats, but always near to the original location and only if the habitat was continuous between plots.

When a plot was trapped, one Sherman live trap (8x8x25 cm), either folding or non-folding, was placed within 1.5 meters of each station in the evening, and collected after sunrise. Each trap contained a ball of cotton for warmth, rolled oats for food and bait, and a piece of potato for moisture.

Table 2.4 Trapping dates for study plots in 1996.

Plot	Trap Session					
	1	2	3	4	5	6
Grassland	May 22-25	June 12-15	June 25-28	July 9-12	July 23-26	Aug 6-9
Asparagus/ Herbaceous	May 24-27	June 14-15	June 27-28	July 11-12	July 25-26	Aug 8 -9
Beach Dune						Aug 15-16
Marsh Border						Aug 15-16
Cedar/Shrubs/ Vines	June 4-7	June 20-21	July 5	July 18-19	Aug 2-3	Aug 22-23
Red Cedar	June 4-7	June 20-21	July 5	July 18-19	Aug 2-3	Aug 22-23
Hackberry	May 16,22,23	June 18-19	July 3-4	July 16-17	July 21-Aug 1	Aug 20-21
White Pine	May 16,22,23	June 18-19	July 3-4	July 16-17	July 21-Aug 1	Aug 20-21
Climax Deciduous	June 4-7	June 20-21	July 5	July 18-19	Aug 2-3	Aug 22-23

All (for rodents) or some of the following information was recorded for every captured animal: species, age, tag number (i.d.), sex, sexual condition, weight, body length, and tail length. Animals captured for the first time were marked by clinching a monel steel fingerling fish tag in the right ear, which is stamped with a unique identification number. If the tag was torn out or illegible, the animal was retagged in the left ear. Shrews, mustelids and opossums were not tagged, measured, or sexed.

The age of an individual was determined by the degree of pelage change for *Peromyscus* spp. Individuals of *M. pennsylvanicus* less than 20 grams were classified as juveniles, and there was no protocol for the remaining species. Sexual condition was assessed for male rodents by the position of the testes as either abdominal, partly scrotal, or fully scrotal. Females were recorded as either perforate or imperforate by the condition of the vaginal orifice. Size and condition of the nipples show lactation, and the size of the animal sometimes, but not always, indicates pregnancy.

The mass of individuals was measured within 0.5 grams using a Pesola scale and weighing individuals in a plastic bag of known weight. Body length and tail lengths were measured to the nearest millimeter by stretching the animal over a small ruler. Other characteristics of the animal, such as the presence of parasites, wounds, or unusual characteristics were recorded in the notes.

Abundances are reported as either the total number of captures or densities calculated as the minimum number of residents alive (MNRA) metric per hectare. MNRA is simply the total number of individuals known to occupy an area not including those individuals captured only once. Habitat area was calculated as a proportion of total plot area:

$$PlotArea * \frac{No.ofHabitatStations}{TotalNo.ofPlotStations}$$

Stations were assigned to habitats subjectively by Bob M'Closkey in 1971 and myself in 1996. Densities are presented as averages for both 1971 and 1996 when replicates of habitat were available. Because densities varied throughout the summer, only data collected between July 27 and August 18 are compared between 1971 and 1996.

Additional censuses were performed in the grassland and asparagus/herbaceous habitats in years other than 1971 and 1996. M'Closkey and Lajoie (1975) trapped in the asparagus/herbaceous field in 1972, at which point the habitat had remained largely unchanged (Table 2.5). Doug Morris (1984) trapped in both the grassland and asparagus/herbaceous habitats in 1978 and 1979. The grassland habitat was still dominated by wheat grass in 1978, but shrubs had invaded a small area along an overgrown fence line, and there were also occasional white pine and black locust found on the plot. The asparagus/old field habitat had changed by 1978, and was

Table 2.5 Habitat Change over 25 years in the grassland and asparagus/herbaceous areas. Habitat types are based on the descriptions of M'Closkey (1972), Morris (1984) and this study. Brackets indicate invading species that were present in low numbers.

	Habitat	
Year	Grassland	Asparagus/Herbaceous
1971	Grassland	Asparagus/Herbaceous
1972	———	Asparagus/Herbaceous
1978	Grassland (herbs/shrubs)	Herbaceous/Brambles (saplings/shrubs)
1979	Grassland (herbs/shrubs)	Herbaceous/Brambles (saplings/shrubs)
1996	Grassland/Herbs/ Shrubs	Poplar/Dogwood
1997	Grassland/Herbs/ Shrubs	———

now dominated by goldenrod, wild strawberries (*Fragaria* spp.) and brambles (*Rubus* spp.). The last census was performed by myself in the grassland habitat in 1997 (Chapter III), and the habitat was the same as 1996. The data from these three sources were standardized by calculating the number of captures per unit effort. The number of captures for each species was summed for the entire trapping session, and then divided by the total number of trap-nights.

RESULTS

RODENT SPECIES

Some changes in presence/absence of the three rodent species, *P. leucopus*, *P. maniculatus*, and *M. pennsylvanicus*, did occur between 1971 and 1996 (Table 2.6). Values that are circled in Tables 2.2 and 2.6 indicate the predictions based on habitat preferences that proved wrong. *P. leucopus* was found in every habitat as predicted. *P. maniculatus* has apparently been locally extirpated from the park, and was not found in the grassland habitat in 1996 as predicted. Three individuals of *M. pennsylvanicus* were captured, but never recaptured. This suggests that they were likely transient or dispersing individuals and residents of a very small population, which is in contrast to predictions based on habitat preferences. Note that the marsh border data are biased because of the much reduced trapping effort there.

The additional data for the grassland and asparagus/

Table 2.6 A comparison of the number of captures and residents of three rodent species captured in nine areas in 1971 and 1996.

1971	1996	Number of Captures (MNRA/ha)					
		P. leucopus		*P. maniculatus*		*M. pennsylvanicus*	
Habitat	Habitat	1971	1996	1971	1996	1971	1996
Grassland	Grassland/Shrub/ Herbaceous	0	478(16)	12(4)	0[c]	44(16)	2(0[a])
Asparagus	Shrub/Forest	34(13)	134(18)	34(12)	0	4(5)	1(0[a])
Beach Dune	Shrubs	229(66)	63([b])	0	0	2(5)	0
Marsh Border	Marsh Border	10(7)	1(0[a])	0	0	5(2)	0
Cedar/Shrub/Vines	Shrubs	18(23)	89(37)	0	0	0	0
Red Cedar	Red Cedar	14(38)	37(83)	0	0	0	0
Hackberry	Hackberry	13(18)	249(103)	0	0	0	0
White Pine	White Pine	48(74)	124(56)	0	0	0	0
Climax Deciduous	Climax Deciduous	69(25)	215(48)	0	0	0	0

[a] no residents captured [b] not enough trap nights to calculate MNRA/ha.

[c] circles indicate populations absent where they were predicted

herbaceous habitats show that *P. maniculatus* probably disappeared from the park somewhere between 1972 and 1978 (Fig. 2.2 & 2.3), as Morris (1984) had no records in 1978 and 1979. Note that in these figures lines connect different censuses only to facilitate separating the data for different species, and are not to be interpreted as accurate interpolations of population size in non-census years.

Individuals of *M. pennsylvanicus* were recorded in at least one habitat in every census year (Fig. 2.2, 2.3), although there were only records of transients in 1996. The low numbers recorded in the grassland habitat in 1996 were followed by a large increase in abundance by the fall of 1997 (Fig. 2.2). *P. leucopus* began using the grassland habitat only in large numbers after 1979 when there was a large amount of shrub and herbaceous habitat (Fig. 2.2), but was found consistently in the asparagus/herbaceous field (Fig. 2.3).

NON-RODENT SPECIES

The data for *S. cinereus*, *D. virginiana* and *M. erminea* are useful only in that they record the presence of these species. Trap biases occur with these species because *S. cinereus* may often be too small to trip the trap mechanism, and *D. virginiana* and *M. erminea* are often too large to fit in these traps. *S. cinereus* and *D. virginiana* were not recorded in 1971, and were represented by only single captures in 1971. It is possible that *S. cinereus* was in the

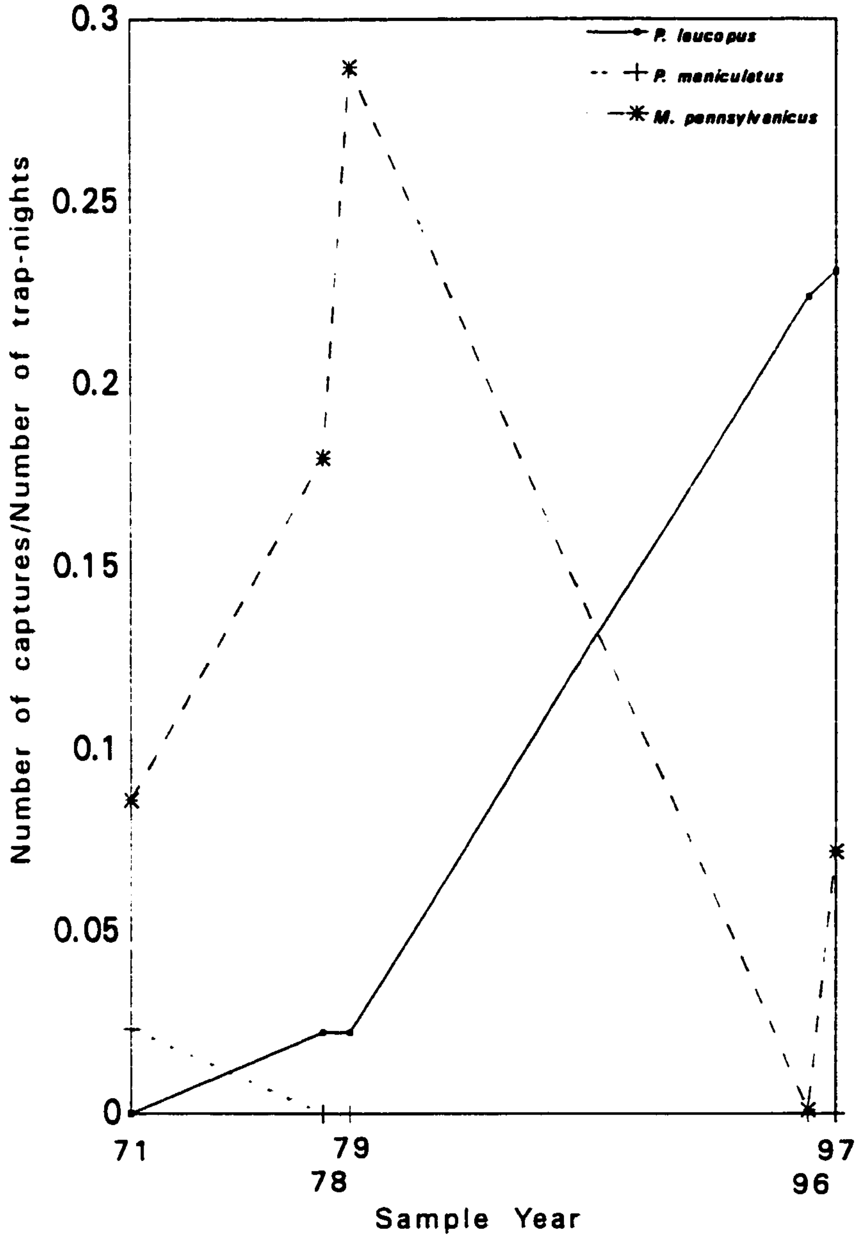

Figure 2.2 Changes in catch-per-unit effort for three rodent species in the grassland habitat in five different census periods. See text for data sources.

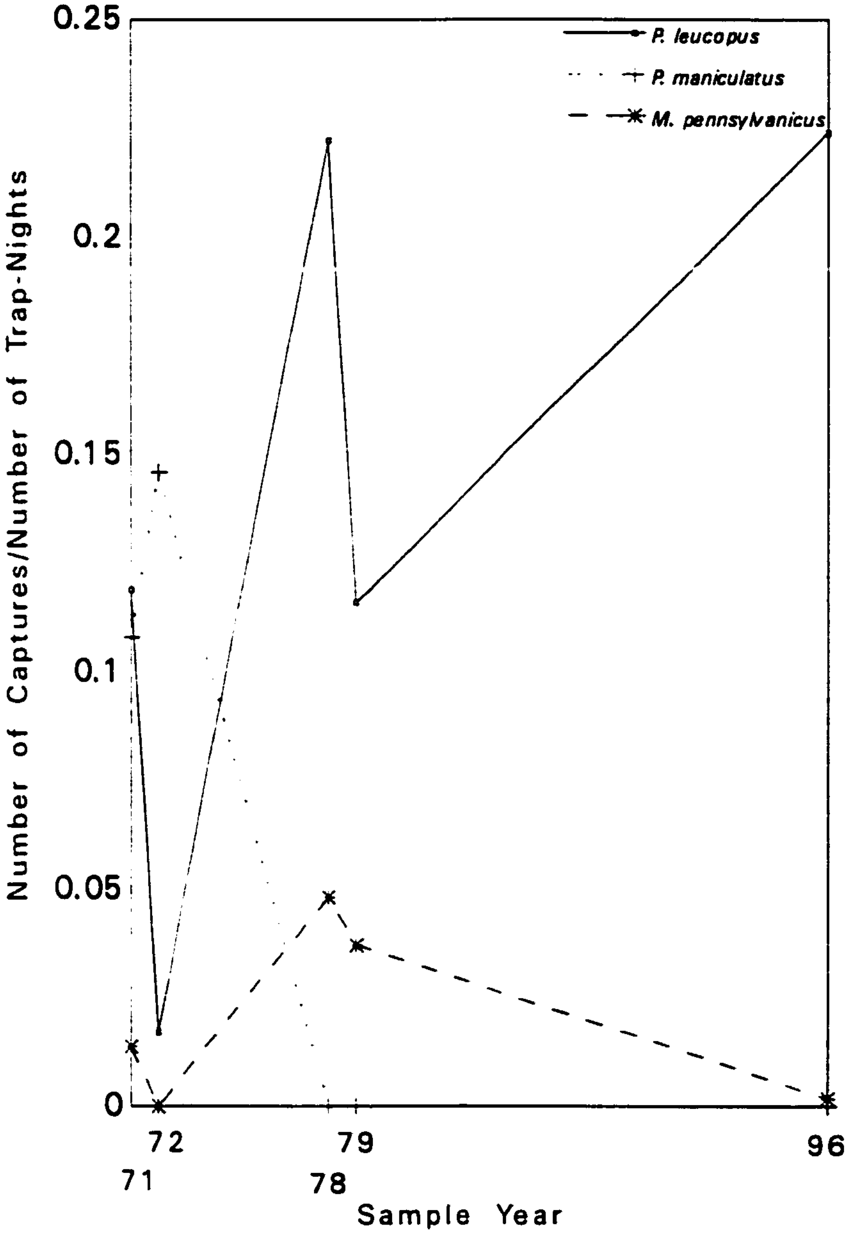

Figure 2.3 Changes in catch-per-unit effort for three rodent speciesin the asparagus/herbaceous habitat in five different census periods. See text for data sources.

park in 1971, but not recorded. *D. virginiana*, on the other hand, has only invaded southern Ontario and Point Pelee in the last few years (T. Linke, pers. comm.). *M. erminea* was captured in both censuses.

B. brevicauda was captured only in the marsh border and white pine habitats in 1971. No predictions were made from this observation because other researchers have found that *B. brevicauda* will occupy many habitats, a result I observed in 1996 (Table 2.7). The grassland and asparagus/herbaceous habitat data indicate that *B. brevicauda* can be quite common at times (Fig. 2.4, 2.5), depending on the habitat and the year.

Although there were only single records of *Z. hudsonius* in 1971 and 1996 (Table 2.7), the extra data for grassland and asparagus/herbaceous plots indicate that it has been present in low numbers throughout the 25 year period.

DISCUSSION

RODENT SPECIES

The three rodent species displayed a variety of responses to habitat change. It is not too surprising that *P. leucopus* was found in every habitat as predicted. As the most abundant and widespread small mammal species in the park, there would be no lack of colonists to occupy the grassland habitat as patches of herbs and shrubs invaded.

P. maniculatus, on the other hand, was not widespread,

Table 2.7 A comparison of the number of captures of five small mammal species in 1971 and 1996.

		Number of Captures									
		Zapus hudsonius		*Blarina brevicauda*		*Sorex cinereus*		*Mustela erminea*		*Didelphis virginiana*	
1971 Habitat	1996 Habitat	1971	1996	1971	1996	1971	1996	1971	1996	1971	1996
Grassland	Grassland/Shrub/ Herbaceous		1		12						1
Asparagus/ Herbaceous	Shrub/Forest				14						
Beach Dune	Shrubs						1				
Marsh Border	Marsh Border	1		2							
Cedar/Shrub/Vines	Shrubs				1						
Red Cedar	Red Cedar										
Hackberry	Hackberry				2						
White Pine	White Pine			3	1						
Climax Deciduous	Climax Deciduous				2			2	1		

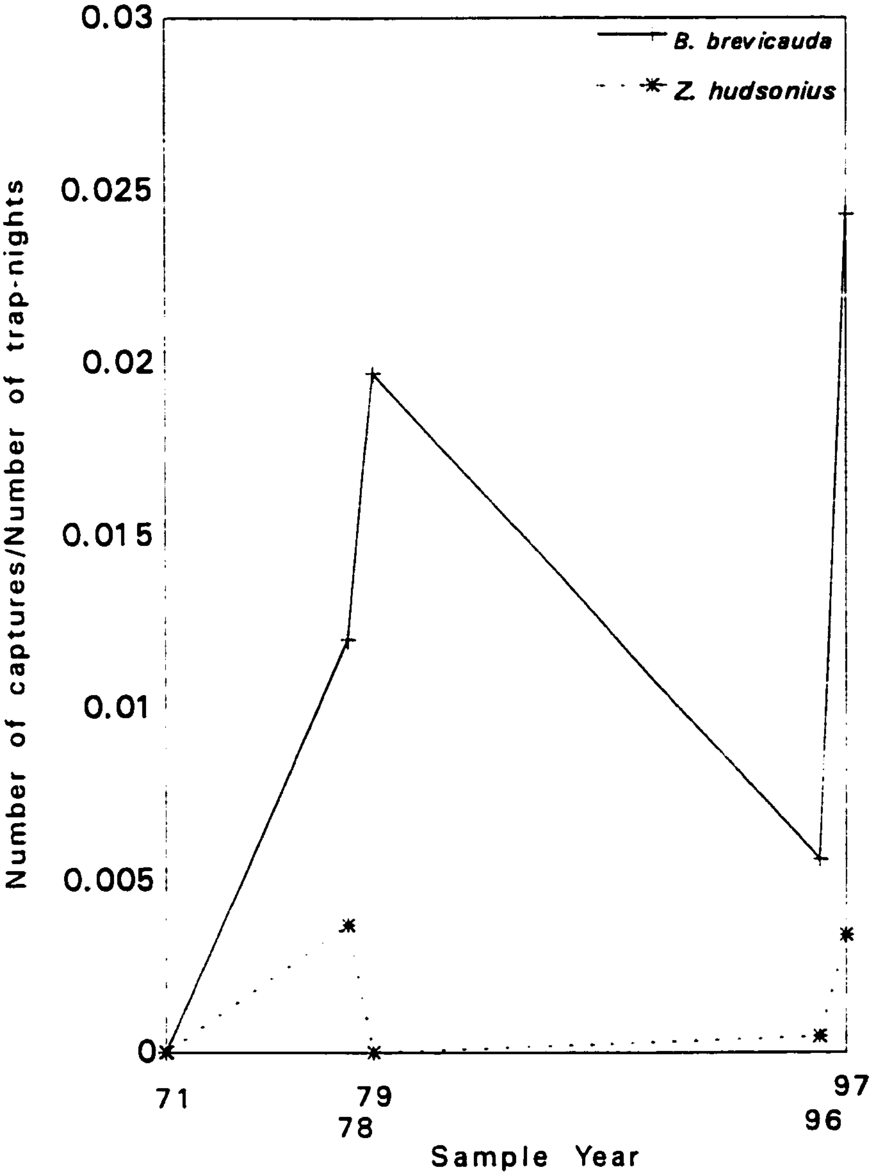

Figure 2.4 Changes in catch-per-unit effort for *B. brevicauda* and *Z. hudsonius* in the grassland habitat in five different census periods. See text for data sources.

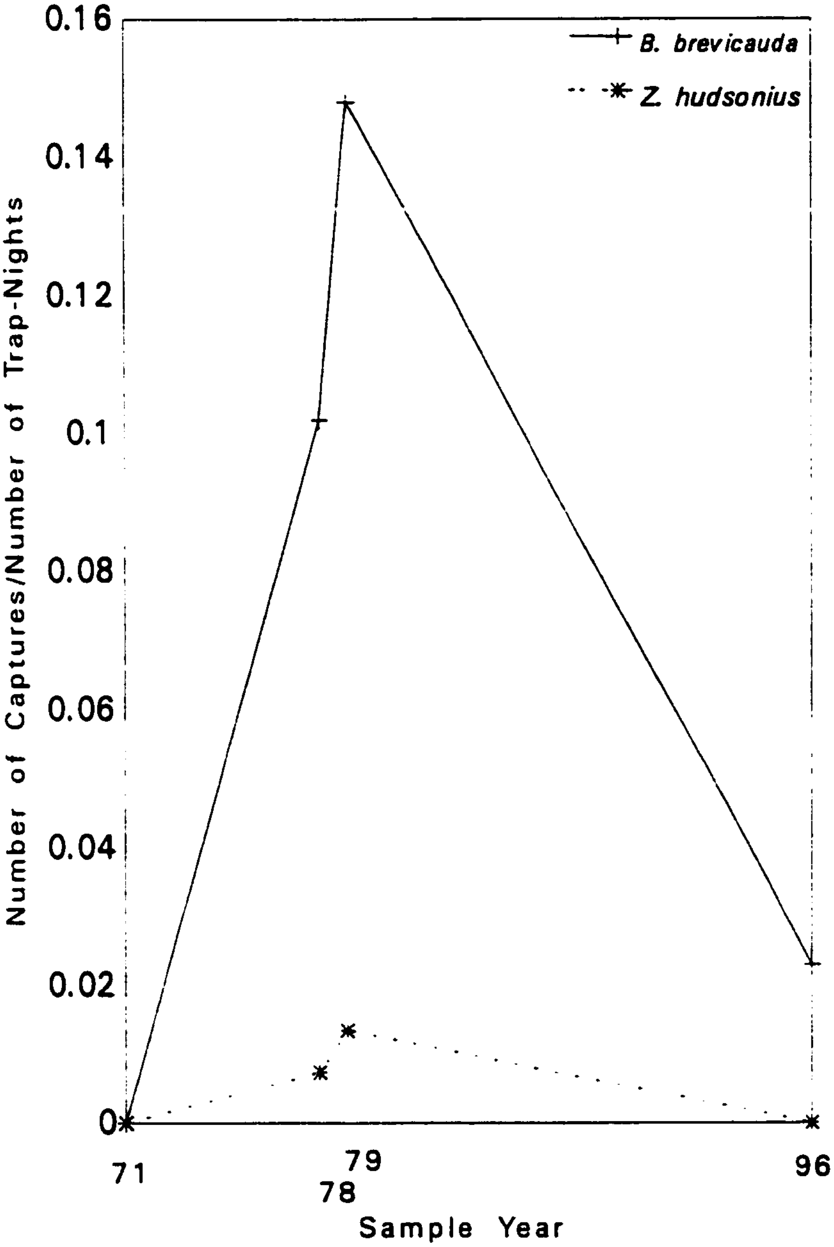

Figure 2.5 Changes in catch-per-unit effort for *B. brevicauda* and *Z. hudsonius* in the asparagus/herbaceous habitat in five different census periods. See text for data sources.

and not particularly abundant, and was apparently extirpated from the park by 1978. By 1978, the habitat where it had achieved its highest densities, the asparagus/herbaceous field, may have been unsuitable habitat because it had become colonized by different species of herbs, and also contained some shrubs. Although *P. maniculatus* had also occupied the grassland habitat, its densities had been very low there, and the small population would have been at risk of extinction due to environmental and demographic stochasticity. Alternatively, the grassland may have only been a sink habitat, supporting a population only because of its proximity to the asparagus/herbaceous habitat. In either scenario, however, it is the decline in habitat area that put the species at risk of extinction. While habitat suitability alone did not correctly predict presence or absence of this species, the decrease in the amount of habitat was indicative of the increase in extinction risk.

The data from 1996 taken alone would have suggested that *M. pennsylvanicus* was on a similar road to extinction as *P. maniculatus*, since no residents were captured. But even though *M. pennsylvanicus* is also considered a species that prefers early successional habitat, it is unlikely that it had the same risk of extinction as *P. maniculatus*. Spicer (1995) recorded populations of *M. pennsylvanicus* in the marsh habitat of Point Pelee, which covers an extensive area (1100 ha), and, therefore, there may be a large population of the species within the park. Furthermore, the rarity of *M. pennsylvanicus* in 1996 was not due to lack of habitat. In 1997, there was a dramatic increase in population size in the grassland area, and it is quite possible that 1996 was a low point in a regular cycle of abundance. A three-four year cycle in population size has been demonstrated by other researchers (*e.g.* Krebs *et al*. 1969), although the data are not available to explicitly demonstrate a similar cycle at Point Pelee.

The conservation emphasis for these three rodent species is obviously on the two species that use the less common, early successional habitats. Although I argued that there may be a large population of *M. pennsylvanicus* in the marsh habitat of the park, I do not believe this is reason to assume this species may persist in the long-term. Not much is known about the marsh habitat, and I suspect that population size might change if marsh levels fluctuate, and will definitely crash if the marsh is flooded for an extensive period. If this coincides with a small population during the population cycle, then there will be some years that extinction risk for this species could be quite high. Furthermore, habitat area for *M. pennsylvanicus* is expected to decrease over the next few decades as shrubs invade the remaining grassland habitat.

NON-RODENT SPECIES

It is difficult to make conclusions for the non-rodent species, even though two species, *B. brevicauda* and *Z. hudsonius*, were captured regularly. The major problem is that we do not fully understand the habitat preferences of these species. *B. brevicauda* will apparently use many different habitats, and researchers have shown that it may choose microhabitats based on insect and moisture availability (*e.g.* Merrit 1986). It seems unlikely that my general classification of habitats as forest, shrub, herbaceous, or grassland had anything to do with how *B. brevicauda* views its habitat.

Similarly for *Z. hudsonius*, little is known about its habitat preferences, and little was added. *Z. hudsonius* is known to prefer moist areas of habitat, which may explain why all of its captures were in close proximity to the marsh (pers. obs.; M'Closkey 1972).

Despite the gap in our knowledge of *B. brevicauda* or *Z. hudsonius*, it is comforting to know that populations have persisted for over 25 years in the park despite low numbers and fluctuations in population size. Unfortunately, we still do not know enough about these species to predict if the populations will persist into the future.

CONSERVATION IMPLICATIONS

Habitat loss is currently one of the most important causes of vertebrate extinctions (Reid and Miller 1989). However, proper design of reserves must also take into account habitat loss or change within the park due to ecological succession and disturbance (Pickett and Thompson 1978; Saunders *et al*. 1991; Fahrig and Merriam 1994).

At Point Pelee, it was the failure to recognize the role of disturbance in creating early successional habitats that led to habitat loss for *P. maniculatus* and *M. pennsylvanicus*. Early this century fire suppression was implemented, although early successional habitats persisted until the late 1960's because of agricultural activities within the park.

Currently, the park is experimenting with prescribed burns in recognition of the importance of disturbance and habitat renewal. For *P. maniculatus*, it is clear that the burns will have to be at least as large as the old asparagus/herbaceous field to maintain a large population, and burned frequently enough to maintain early successional habitat. It is entirely possible that *P. maniculatus* could colonize these burns, because there are likely populations in the agricultural areas directly outside the park's boundary. *M. pennsylvanicus* will also benefit from the burns, as continued disturbance will ensure persistence of suitable habitat outside of the marsh area of the park.

Chapter III

INDIVIDUAL AND COMBINED-INDIVIDUAL RESPONSES OF TWO SMALL MAMMALS TO SMALL SCALE HABITAT VARIATION

SUMMARY

An abandoned agricultural field contained a mixture of grass, herbaceous, vine and shrub habitats that formed small patches of habitat. The response of rodents *Peromyscus leucopus* and *Microtus pennsylvanicus* to this habitat was quantified in two ways. First, combined-individual responses were assessed by regressing abundances on habitat type to infer habitat quality. Second, individual responses, as measured by changes in the overlap and size of home ranges, were also regressed on habitat type. Abundance data indicated that *P. leucopus* preferred shrubs over vines, and avoided grassy areas, while *M. pennsylvanicus* avoided shrubs. Home ranges were affected by age and sex, but the effects of habitat were varied and difficult to interpret, probably because we do not understand how variables like density and resource availability interact to affect home ranges. The effects of habitat on combined-individual and individual analyses were not similar. Perhaps home range placement, which affects abundance, is based on large-scale habitat cues, and decisions on size and overlap are made subsequently based on the immediate habitat landscape.

INTRODUCTION

All organisms use space in their normal daily activities, including those related to harvesting resources and producing offspring. Predictable patterns in space use allow it to be studied by researchers as a tool to learn about the interaction between the organism and its environment. Patterns of space use can vary from simple, such as a sessile barnacle attached to a rock, or plant roots that can exploit small soil microspaces, to complicated travel patterns of mobile organisms with flexible behaviours and space use patterns. The study of the travel patterns of mobile organisms, has often relied on the concept of the home range, because in one metric all the travels resulting from many different individual behaviours, such as resource intake, predator avoidance, mating, and caring for young, are represented (Burt 1943). Closely related to the home range is the concept of the territory, that part of the home range that is defended against intruders. Home ranges and territories not only reveal information about individual behaviours, but form the basis for emergent, population patterns of space use.

Home ranges are often described using their size and overlap with neighbouring home ranges, because changes in size and overlap can affect important factors such as access to resources and mates. These changes in resources and other factors can be illustrated as costs and benefits to certain home range sizes (Davies and Houston 1984; Fig. 3.1), and suggest the existence of an optimum territory or home range size. Home range overlap is not understood as well as home range size, and most of the following overview focuses on home range size.

I classify factors that directly affect costs and benefits of changing home range/territory size into four groups: metabolic/ resource factors, reproduction factors, predation factors, and genetic factors. The examples listed below are for mammals, and are grouped by whether they show evidence that the factor has an effect, "for", or no effect, "against". The majority of examples are cited for their effects on home range size.

The influence of metabolic and/or resource factors are based on the simple idea that, all other things equal, a larger home range will contain more resources (*e.g.* McNab 1963). Therefore, individuals that need more resources should increase home range size. Or, if resource availability is decreased, individuals will have to travel further to satisfy their needs, and home range size will increase. For example, the amount of resources needed and home range size may increase for heavier individuals (for: Ostfeld and Canham 1995; against: Koskela *et al.* 1997; Tufto *et al.* 1996; Wauters *et al.* 1994), for pregnant or lactating females (for: Koskela *et al.* 1997; Tufto *et al.* 1996), and vary with temperature (for: Brooks 1993). Resource

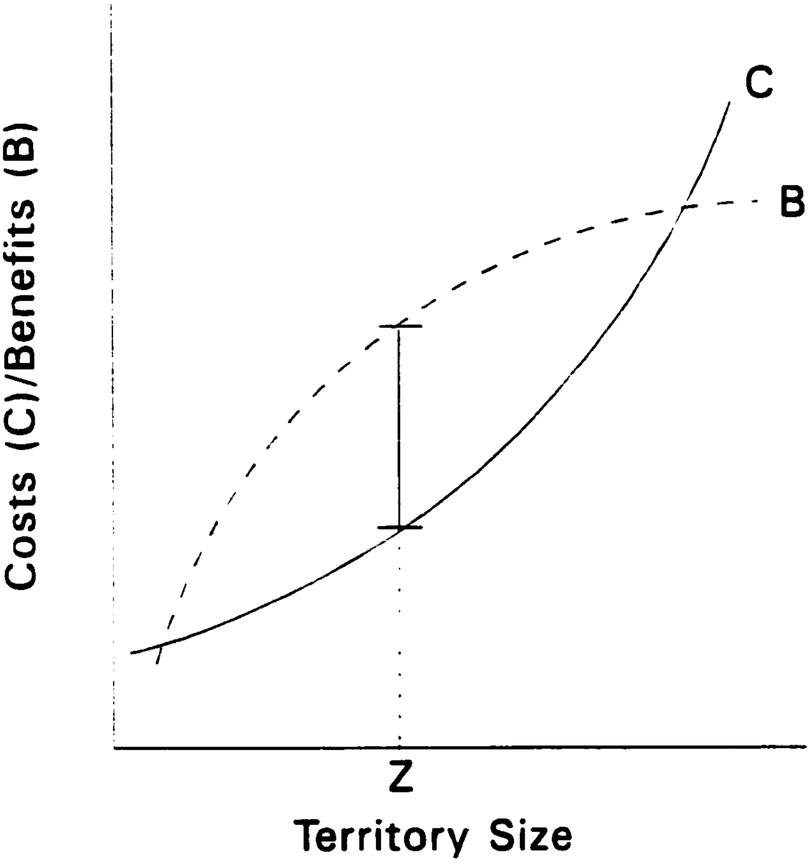

Figure 3.1 Hypothetical costs and benefits to defending a territory. Optimum territory size occurs when the difference between benefits and costs is at a maximum (Z). If the benefits were always less than the costs, than a territory should not be defended. Adapted from Davies and Houston (1984).

availability can be manipulated by food supplementation, and generally results in either no effect or a decrease in home range size (reviewed by Boutin 1990).

Reproductive factors, excluding those expressed through metabolism, are expected to be different for male and female mammals. Female mammals may defend their pups from infanticide by other females, and home ranges will decrease with increasing risk because smaller areas are easier to defend (for: Wolff and Cicarello 1991; Salvioni and Lidicker 1995; Fortier and Tamarin 1998; Wolff and Schauber 1996). Males are often thought to have large home ranges in order to access mates (for: Adler *et al.* 1987; Ims 1988; Nelson 1995), while females are expected to be passive in response to mate distribution (for: Ims 1988).

Not much information has been collected on the effects of predation and genetic factors on home ranges. Predation risks have been inferred from habitat differences in risk (Geffen *et al.* 1992; Tufto *et al.* 1996; Hubbs and Boonstra 1998), but there appears to be no consensus on how predation should affect home range size. For instance, Tufto *et al.* (1996) expected home ranges containing high risk habitats to be larger, Desy *et al.* (1990) expected home ranges to be smaller under predation risk, and both researchers found what they expected. This may be because Desy *et al.* (1990) were able to control densities but Tufto *et al.* (1996) were not, and the effect of higher predation risk may have been confounded in the latter study by lower densities in high risk habitats. Genetic factors are not a topic of discussion in this paper, but some authors have found that home range overlap is higher for related individuals than unrelated ones (*e.g.* Ims and Andreasson 1991).

All the factors discussed above can affect home ranges directly, but another set of factors affect home ranges indirectly by affecting the direct factors discussed above. Habitat, the focus of this chapter, is one such indirect factor, and different habitats are often associated with different resource availabilities and risks of predation. Density is another indirect factor, that may increase the costs to pup defence (Wolff 1989), increase access to mates (*e.g.* Nelson 1995), and decrease resource availability. The sex of the animal can determine the importance of access to mates, resource availability and pup defense (*e.g.* discussed in Ostfeld 1985). Age can affect home range size because juveniles weigh less, need fewer resources, may be less mobile, and have no need to access mates (for: Wauters *et al.* 1994). Landscape characteristics indirectly affect home ranges if they affect intruder pressure and the number of neighbours (Stamps *et al.* 1987), which in turn can affect pup defense and access to mates.

Mammal studies that have explicitly studied the relationship between mammal home ranges and habitat quality have found conflicting results. Habitats with increased resource availability either had no effect on home range size (Wauters *et al*. 1994) or decreased home range size (Bowers and Smith 1979; Tufto *et al*. 1996). Home range sizes in some studies depended on the distribution of the resource more than the quality (Kruuk and Parish 1982; Geffen *et al*. 1992). Blanford's foxes may have perceived variation in predation risks between habitats because the habitat with the highest resource levels also had more cover for predators, and was generally avoided (Geffen *et al*. 1992). Tufto *et al*. (1996) found evidence that home range sizes for roe deer increased when habitat of high predation was included, Desy *et al*. (1990) found the opposite by experimentally manipulating predation risk, and Hubbs and Boonstra (1998) found no effect of predation. Some experiments have altered habitat quality by habitat removal with variable results (Diffendorfer *et al*. 1995; Wolff and Schauber 1996; Andreassen *et al*. 1998). This variation is expected because the direction of the response is predicted to depend on the scale of habitat removal relative to home range size (Ims *et al*. 1993).

I wanted to examine and compare the effects of small-scale habitat heterogeneity on two rodent species, *Peromyscus leucopus* (white-footed mouse) and *Microtus pennsylvanicus* (meadow vole), at two levels of organization: 1) individual responses, using home ranges, and 2) combined-individual responses. It was the characteristics of my study site that originally prompted the idea that I could look at the effects of habitat variation at small spatial scales. The site was located in an abandoned agricultural field that had a mixture of grassy, herbaceous, vine, and shrubby habitats. I chose the site because the variation occurred at a small enough spatial scale that one home range of a small mammal could contain several different habitats. I had confidence that both study species could recognize these as different 'microhabitats' (habitats that vary at a scale smaller than a home range), because Morris (1984; 1987) showed obvious habitat preferences in small mammals when similar habitats occurred as larger, continuous tracts of 'macrohabitat'.

The two study species differ in habitat preferences. *P. leucopus* is considered a habitat generalist, preferring shrubby and forest habitats, while *M. pennsylvanicus* is specialized to grassland habitats (see Chapter II; species compared in: Beckwith 1954; Morris 1979; Adler 1986; Huntly and Inouye 1987; Cunningham 1990). This is reflected in their diets, which is biased to insects in *P. leucopus*, and monocot plants in *M. pennsylvanicus* (*e.g.* M'Closkey and Fieldwick 1975). Females of both species are considered territorial (Madison 1985; Wolff 1989), perhaps to prevent infanticide (Wolff and Cicarello 1991; Fortier and Tamarin 1998). Although it is unlikely that these two species never interact, studies done within the area have not found any evidence for significant interactions (Morris 1989; M'Closkey and Fieldwick 1975).

What is the effect of habitat on combined-individual responses of these two species? To answer this question I looked at how the number of individuals and number of captures (combined-individual response) were related to habitat type at two spatial scales: individual stations, and in 3 x 3 blocks of 9 stations (Fig. 3.2). As discussed in Chapter I, habitat preferences may be less obvious at small scales, because of increased variation in habitat use caused by individuals using poor habitats adjacent to, or mixed in with, good habitats. The explanation is that the costs to travelling over a poor patch without exploiting it are greater than the benefits gained from exploiting the richest patches only. At small spatial scales, poor patches will sometimes be next to other poor patches, and sometimes next to good patches, and there will be large variation in their use. This effect will also occur at larger scales, but it will be restricted to areas along the borders of habitats, and cause proportionally less variation in abundance. Therefore, it is predicted that habitat should explain more variation in the number of individuals and/or captures for larger scale (block) regressions. Morris (1987) found that large scale habitat variation affected densities more than small scale variation when he compared variance in density in plots of 135 stations against 3 x 3 blocks of stations.

This analysis assumes that abundances will be highest in the best habitats, that is, I assume that individuals follow

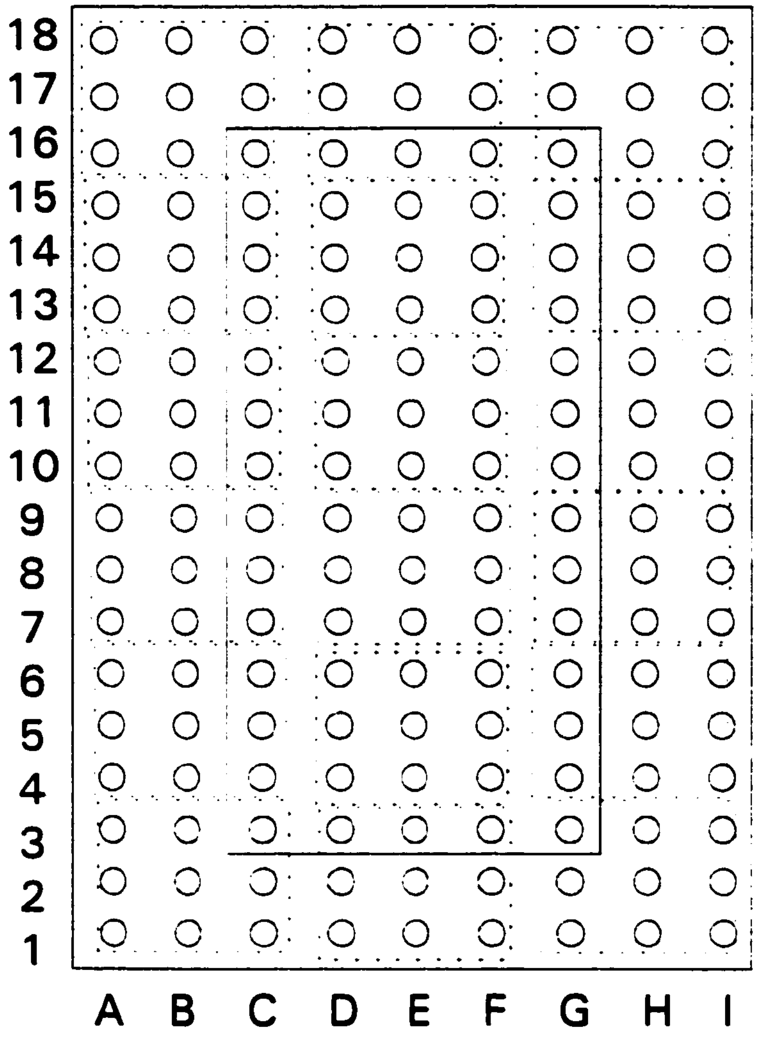

Figure 3.2 The design of plots included 9 x 18 stations (circles). Data were collected at the scale of stations and blocks of 3 x 3 stations (outlined by dashed lines). The boundary strip of the outer two rows is contained between the two solid lines, and home ranges that were entirely within this boundary strip were not included in data analyses.

either an ideal free distribution or ideal dominance distribution where density is higher in higher quality habitat (see overview in Chapter I, this study). Fitness data in two studies of *P. leucopus* supported the ideal dominance distribution (Morris 1996; Halama and Dueser 1994), and density was always higher in the high fitness habitat. There are no comparable studies for *M. pennsylvanicus*.

What is the effect of habitat on individual home ranges? Home ranges were characterized by their size and overlap with neighbouring home ranges, and then examined to see if the type(s) of habitat within the home range affected these characteristics. I have enumerated the following effects of habitat quality on home range size that could occur:

1. a) We might expect that habitat quality has no effect on home range size. Morris (1987) found that densities responded more to variation in macrohabitats rather than microhabitats, so perhaps if densities do not respond to this scale of habitat variation then neither will individual home ranges. However, unless there is a lot of unused space, changes in density necessarily imply that there have been changes in home range size and/or overlap, as the new individuals have to go somewhere.

b) Another explanation for no effect is that the home ranges are responding to a factor more important than resource availability, such as access to mates or prevention of infanticide. For instance, if access to mates is the most important determinant of home range size, home range size will not change in response to habitat unless access to mates also changes.

2. Higher quality habitats have more resources. In this case home range size is expected to decrease if the home range contains high quality habitat, because increased resource availability reduces the need to travel far for resources.

3. Higher quality habitats have higher densities. This is true because I define it as true for the purpose of this analysis. Increasing densities make the same predictions as increasing resources: home range size should decrease. Higher densities mean that mates are easier to access, requiring less travel. Increased density also results in increased intruder pressure, so smaller, better protected territories are necessary to prevent infanticide, for example. Note that without experimental manipulation, the effects of habitat density and resource availability on home range size cannot likely be separated (Davies and Houston 1984).

4. Higher quality habitats have lower predation risk. I do not deal with this prediction even though their are predators such as snakes (R.T. M'Closkey pers. comm.), owls and coyotes at the park (Heidinga and M'Closkey 1997). However, I am unable to deal with this question because I was unable to quantify predation risk in these habitats.

I have avoided discussing home range overlap in any detail, because how and why organisms vary overlap is not understood well. In general, changes in overlap are expected with changes in intruder pressure. At low intruder pressure, the defense of a territory is easy, and overlap is low. Increases in intruder pressure, such as would be expected with an increase in density, will lead to increases in overlap. Intruder pressure could become so large that it is no longer economically feasible to defend a territory.

Ostfeld (1985) argued that, if females have territories to defend resources, then territories should be easily defended when resources are widespread and densities are low, because intruder pressure will be low. However if densities are high, or resources are aggregated in such a way that females will be competing for the same resources in a small space, intruder pressure may become too high for territories to be economically feasible. Alternatively, other researchers have argued that females are territorial to defend young from infanticide (*e.g.* Wolff and Cicarello 1991). When intruder pressure increases, it seems more likely that females would reduce home range size rather than increase overlap. A smaller home range would make it easier to ensure that no individuals entered the territory and found the nest.

Male overlap may be determined primarily by female distribution. Ims (1987a) hypothesized that reproductive females aggregated in space and time would be easily defended, and allow males to establish territories. A subsequent test using grey-sided voles, however, showed that male territoriality was decreased and overlap increased when females were aggregated (Ims 1987b). Ims (1987b) speculated that he did not account for the increase in intruder pressure that occurred when all males were competing for females in a small area.

While the above discussion of overlap does offer some testable hypotheses, the problem is that in several scenarios the same problem can be solved by both changes in home range size and overlap. For instance, increased densities lead to increased intruder pressure, which increases the costs of defending the home range, and overlap is predicted to increase. However, the individual could decrease intruder pressure simply by shrinking home range size and keeping overlap the same. No one has answered the question of when an increase in density should lead to an increase in overlap, when it should lead to a reduction in home range size, and when both should change.

There is not much consensus in the literature on which factors should affect home ranges of *P. leucopus* and *M. pennsylvanicus*, although most expect that the response to density and resource availability to be affected by sex. Females are often expected to be more responsive to resources than males because they incur high metabolic costs during pregnancy and lactation, while males should be more responsive to female distributions (*e.g.* Ostfeld 1985; Ims 1987a). This idea was supported by the emigration of many male *P. leucopus* after female removal (Adler *et al.* 1987). However, food supplementation experiments showed that response to resources is not restricted to female *P. leucopus*, nor was the response consistent: sometimes both sexes were affected by food supplements, and sometimes neither (reviewed in Wolff 1989). Differences in sex were recorded by Bowers and Smith (1979) in another *Peromyscus* species, *P. maniculatus*, where females occupied the best microhabitats. However, in three out of eight trapping sessions, Morris (1984) found that there was evidence that male *P. leucopus* occupied the best microhabitats. There is certainly no consistent evidence that female *P. leucopus* are more responsive to resources than males.

Fortier and Tamarin (1998) recorded that *M. pennsylvanicus* females were completely unresponsive to food supplementation, but males reduced home range size. Both sexes in this study reduced home ranges in response to increased densities, and evidence suggested that females defended territories to prevent infanticide.

Because I can examine both individual and combined-individual responses in the same study system, I have the opportunity to compare the effects of habitat on these two levels of organization. In general, one might expect that emergent, population patterns are simply additive outcomes of individual behaviours. In that case, habitat would have similar effects on individuals and combined-individual parameters. This pattern is eroded whenever different mechanisms are important at different levels of organization (Wiens *et al.* 1993).

I have listed below the hypotheses and goals for this project. All predictions assume that habitat quality is indicated by higher densities. Although I list hypotheses for both home range size and overlap, I do not offer predictions as to whether one or both metrics should change in different situations. Part of the goal of the project, then, is to observe which of these factors the organisms change in response to habitat.

1. Non-Habitat Effects on Home Ranges

a) Prediction: Male home ranges for both species will be larger than females. This prediction is based mostly on previous empirical results, with the underlying idea that male home ranges need to be large to access mates.

b) Prediction: Adult home ranges will be larger than juvenile home ranges. Juveniles are smaller, require less food, and do not require access to mates.

c) Prediction: Heavier individuals should have larger home ranges because they need more energy.

2. Habitat Effects on Combined-Individual Responses

a) Prediction: Habitat effects should explain more variation in the number of individuals and captures of both species at large-scales than at small-scales. At small spatial scales, there is increased variation due to individuals using habitats they normally would not use at larger spatial scales.

3. Habitat Effects on Individual Responses

a) Prediction: Home ranges of both species that contain more high quality habitat will be smaller. The size decrease may be because higher quality habitats have higher densities, increased resource availability, or both.

b) Prediction: Overlap will increase with increasing density because intruder pressure increases with increasing density.

c) Goal: To compare the response of individuals with combined- individuals responses to habitats. Are the same habitats important in both analyses? Is it clear that the combined-individual response is the outcome of individual responses to habitat variation?

METHODS

STUDY SYSTEM

The study system was in an abandoned agricultural field in Point Pelee National Park in Essex County, Canada (42°00' N, 82°31' W). The field was abandoned in 1969, with only minor anthropogenic disturbance since then. There was obvious habitat variation in the field which included patches dominated by shrubs, vines, herbs, and grasses. Shrub species were dominated by rough-leaved dogwood (*Cornus drummondi*), vines were almost entirely riverbank grape (*Vitis riparia*), and herbs were dominated by poison ivy (*Rhus radicans*) and goldenrod (*Solidago* spp.). Grasses were dominated by quack grass (*Agropyron repens*) and bluegrass species (*Poa* spp.), although there were occasional patches of reed canary grass (*Phalaris arundinacea*) found in moist areas.

PLOT SETUP AND TRAPPING SCHEDULE

The two plots, designated as North and South, were grids with 162 stations, 9 stations wide by 18 stations long. I hoped this size would be large enough to minimize the number of home ranges that touched the plot edge, although size was limited by the number of stations I could trap alone. The number of plots and their shape was limited by the size and shape of the field. Stations were spaced at 12.5 meters, and each plot covered 2.125 hectares. The two plots were separated at their closest point by about 200 meters.

The North plot was trapped first in each of the three trapping sessions, spring, summer and fall of 1997 (Table 3.1). Originally I intended to trap each plot 12 nights over the course of 15 nights to avoid trapping on nights of extreme weather, but there were several exceptions. Heavy rains flooded part of the South plot after four days trapping in the first session, and I did not trap the ten days from May 29 - June 7. I resumed trapping the remaining eight days

Table 3.1 Trapping dates for two plots in 1997.

Session	Location	No. of Days Trapped	Trapping Dates
1	North	12	May 7 - May 21
	South *	4	May 24 - May 28
		8	June 8 - June 15
2	North	12	July 6 - July 19
	South	12	July 23 - August 5
3	North	10	September 3 - September 14
	South	9	September 18 - September 28

* discontinuous trapping due to flooding on plot

of the session on June 8 when all but three traps could be set out. The data for this session were treated like data from other sessions. Only 10 and 9 nights were accumulated for the North and South plots respectively during the fall session because of unacceptable levels of trap disturbance from several racoons. To account for the reduced trapping effort and for traps that had been disturbed, the number of captures and densities were divided by the total number of undisturbed trap-nights that occurred at a particular station.

VEGETATION ANALYSIS

Twenty-eight habitat variables were chosen on the basis of what other small mammal researchers have found useful (*e.g.* M'Closkey and Lajoie 1975, Morris 1984, Dueser and Shugart 1979), as well as some variables that reflect plant species common in my plots (Table 3.2). Habitat measurements were recorded from July 19 - 28, 1997, at each of the 324 stations at the time when the vegetation appeared to be near its peak biomass. These measuremements were used to separate habitats (described below). Although these habitats change seasonally, it is assumed that the classification of habitats would be consistent seasonally, even if the exact measures of variables were different.

Two variables, the basal area of all trees (basalArea) and the number of logs (logs) were measured within a 5 meter radius of the station (Table 3.2). Three variables were

Table 3.2 Habitat characteristics measured at each station in both plots. See text for details.

Variable Name	Description
Variables measured within 5 metre radius of station:	
BasalArea	-Summed basal area of all trees
Logs	-Number of logs within a 5 metre radius of the station
Variables measured within 3 metre radius of station:	
Shrubper	-Percent cover of all shrubs (excluding poison ivy & vines)
Vine>2m	-Percent cover of vines within 2 metres height of ground
Vine<2m	-Percent cover of vines above 2 metres height
Quadrat Variables:	
Dirt	-Percent cover of bare soil
Grass	-Percent cover of grass
Herb	-Percent cover of all herbs combined
Moss	-Percent cover of moss
OtherHerbs	-Percent cover of herbs other than poison ivy and goldenrod
Goldenrod	-Percent cover of goldenrod
Horsetail	-Percent cover of horsetail
PoisonIvy	-Percent cover of poison ivy (shrubby and herbaceous)
Grapevine	-Percent cover of riverbank grape
Wood	-Percent cover of dead wood
Moisture	-Moisture measured using garden moisture probe
Profile Variables:	
MeanX	- mean percent coverage of profile boards at height X cm, includes the following heights/variables: Mean0, Mean12.5, Mean25, Mean50, Mean100, Mean175
PropX	- (MeanX)/(sum of all Means) - this is the proportion of the profile board coverage at height X. It includes the following heights/variables: Prop0, Prop12.5, Prop25, Prop50, Prop100, Prop175

estimates of what percent shrubs or vines covered the ground within 3 meters of the station pin. Shrubper, the percent coverage of shrubs, excluded vines and shrubby poison ivy. Coverage of vines was broken into two groups based on whether they occurred above or below 2 meters from the ground (Vine<2m, Vine>2m) to reflect that some vines were mainly near the ground and others swarmed over shrubs.

Several variables were measured as percent coverage of a 50 cm x 50 cm quadrat. Two replicate quadrats were taken, one directly over the station, and the other 1 meter away in a randomly determined direction. Most of these variables are self-explanatory. Herbaceous plants were represented by four variables, with percent cover of goldenrod and poison ivy measured separately because of their dominance on the plots. The coverage of all other herbs was estimated in the "OtherHerbs" variable, and finally the total coverage of all herbs was measured in the "Herbs" variable. Because plants from the different categories may overlap and cover the same portion of ground, the Herbs variable was not usually the sum of the goldenrod, poisonIvy and otherHerbs variables.

Moisture was measured using the "Moisture Meter" (Continental Industries, Brampton, Ontario, Canada, L6T 4X3). This is a simple moisture probe used by gardeners, and gives moisture values between 0 and 10. The tip of the meter was inserted 10 cm into the ground and two measurements were taken within 25 cm of the station flag.

The last variables used profile boards to estimate the amount of vegetation at different heights from the ground. Metal plates with dimensions 10 cm x 20 cm were attached to a rod at six different heights from the ground (heights are to the bottom of the plate): 0 cm (bottom touching the ground), 12.5 cm, 25 cm, 50 cm, 100 cm, and 175 cm. The rod was placed directly at the station, and viewed face on from a distance of 1 meter away at the same height as one of the six profile boards. From this position, the percentage of the board blocked from view by vegetation was estimated. Three replicates at each station were recorded, each replicate at an angle of 120° from the other two, and the direction of the first replicate was determined randomly. The three estimates of cover at each height X were averaged into the variable MeanX for that height. To obtain the proportion of profile coverage that occurs at each height X, or PropX, the Mean for a given height is divided by the sum of MeanXs for all heights (values summed for that station only).

The number of habitat variables was reduced using Principal Components Analysis (PCA), and I retained the first three principal components (PC's). This number of PC's was a trade-off between including as much habitat variation as possible, and keeping the number of variables in the regression equations low. Habitat was represented by three numbers for each station, one value for each PC. To provide three similar measures of the habitat composition of blocks, plots and home ranges, the PC scores at each station within the area were summed for each PC separately *e.g.* for a block, nine values of PC1 were summed, nine values for PC2, and nine values for PC3.

TRAPPING PROTOCOL

One live-trap, baited with oats and a piece of potato, was placed at each station in the evening, and collected the following morning. Traps were collected each day to avoid vandalism and because traps were rearranged daily to control for variation in trap type. Each trap type was similar in the mechanism used to trap the small mammals, but differed in size. Folding Shermans had dimensions of 23 cm x 9 cm x 8 cm. Medium sized Shermans were non-folding, with dimensions 26 cm x 8 cm x 8 cm. The largest traps were non-folding, galvanized steel traps with dimensions 30 cm x 9 cm x 7.5 cm. Possible differences in capture success for trap types were accounted for by setting half the plot with folding Shermans, and the other half with the other two non-folding types, and then switching halves the next trap day. The two larger trap types were lumped together because there were not many galvanized traps, and not enough medium sized traps to cover half the plot.

For each captured individual of the two species of interest, the following information was collected before release: capture station, age, sex, sexual condition, tag number, and weight. Age for *P. leucopus* was determined by pelage colour. Juveniles are completely grey, sub-adults have varying degrees of brown pelage, and adults are completely brown. For the purposes of the data analysis, sub-adults and adults were combined into the adult category, and individuals that started the session with juvenile pelage were recorded as juveniles even if they ended the session with mature pelage. *M. pennsylvanicus* less than 20 grams were designated juveniles, although almost no juveniles were captured of this species.

Individuals captured for the first time were tagged in the right ear with either a monel steel fingerling fish tag (no longer sold), or #1005 size 1 monel tags (National Band and Tag Co., 721 York St., Box 430, Newport, KY, USA, 41072-0430). If an individual was captured with a deep tear in the right ear, they were recorded as recaptures, and tagged in the left ear.

HOME RANGE CALCULATION

All home range characteristics were calculated by a computer program I prepared (Appendix I). Home range sizes were calculated for each session separately. Size was estimated based on the minimum convex polygon (MCP) method (see Andreassen *et al.* 1993 for a review of this and other methods), and counting the number of stations contained within this polygon (Fig. 3.3). This measure corresponds well with my estimate of the amount of habitat in a home range, as habitat is measured at each station only.

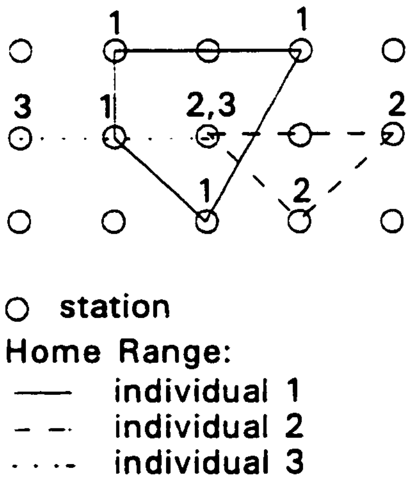

Figure 3.3 An example of how home range size and overlap were calculated. Capture points for individuals 1, 2, and 3 are indicated by the appropriate number above the station. Minimum convex polygons are drawn around the capture points and the number of stations within the polygon counted to measure home range size (individual 1, 6 stations, individual 2, 4 stations, individual 3, 3 stations). Home range overlap was measured by counting the number of stations within the home range shared with each neighbour, and summing the values for each neighbour. The home range of individual 1 overlaps with one station with individual 2, and two stations with individual 3, so total overlap is 3 stations.

Furthermore, home range size estimates are more robust if the home range is small or linear.

Biases can occur in measuring home range size because size generally increases with the number of captures (Andreassen *et al.* 1993). To account for this, the number of captures could simply be included as a predictor of home range size in the regressions described below. While this method is statistically valid, a significant effect of the number of captures indicates that area is underestimated. This will result in underestimates of overlap, and perhaps misconceptions of what habitats the home ranges contain. For *P. leucopus*, there were enough individuals with many captures that I decided to use only those individuals captured 7 or more times. For this subset of individuals, there was no significant correlation between home range size and number of captures (females: $r = 0.0462$, $p = 0.8247$; males: $r = 0.153$ $p = 0.296$). For *M. pennsylvanicus* there were few individuals captured more than five times, therefore the number of captures was included as a predictor in the home range size regressions. To account for biases in home range size caused by home ranges that touched the edge of the plot, I eliminated the home ranges of animals whose captures were contained entirely within the outer two stations of the plot (Fig. 3.2). This method was chosen because eliminating all individuals that simply touched the edges produced a bias in the data set, because the largest home ranges (usually male

P. leucopus) had the greatest probability of touching the plot edge.

Some home range data points among the sessions were not independent because the same individuals were captured in more than one session. When this occurred, one of the data points was chosen at random to be retained in the analysis, and the others were discarded.

Intraspecific home range overlap was measured for each individual by counting the number of stations that were shared with a neighbour's home range, and summing the values for each neighbour. In Fig. 3.3, individual 1 overlaps with individual 2 at one station, and twice with individual 3, so total overlap is three. This metric will be affected by both the number of neighbours and absolute overlap. Overlap was separated by sex as male-male and female-female overlap, and two measures of intersexual overlap. If the male was the target home range (*e.g.* individual 1 in the example above) and females overlapped this home range, male overlap with females was measured. For female home ranges as the target, female overlap with males was measured. To avoid confusion, note the order and meaning of the latter two variables because they can be very different values. If there are 6 females and 1 male, female overlap with the male could be very high, but male overlap with females is likely going to be low.

Some other measures of overlap use only the actual stations at which two or more individuals were caught, while my method includes all stations where the home ranges overlap whether there were joint captures on the station or not. Because I assumed when measuring home range size that all stations in the home range were being used, it is consistent to also assume this for my measure of overlap.

DATA ANALYSIS

General Population Trends

The number of different individuals captured during each session was counted separately. Because I have a minimum of 9 days trapping for each session and plot, it is reasonable to expect that I captured most individuals. This excludes individuals only captured once, which are considered transients. The values were summed separately for each sex of each species.

Non-Habitat Effects on Individual Responses

Two ANOVA's were performed to look for differences in home range size between sexes of each species (adults only), and between juveniles and adults of *P. leucopus*. Because juveniles were generally uncommon, there were only sufficient data to test age differences using the South plot in session 1, and the North plot in session 2.

Ideally the effects of age and sex should not have needed a separate analysis, and would have been included in the regressions that are described below. However, the number of home ranges used in the analysis was small, and the regressions were limited in the number of variables that they could handle, so I decided not to include any interaction terms. Because the literature review suggested that sex and age would potentially interact with many of the other predictor variables, rather than have to arbitrarily choose some interactions to include in the regression, I decided to run separate regressions for each sex. The only statistical comparisons of the effects of sex and age were therefore limited to the two ANOVA's described above.

Habitat Effects on Combined-Individual Responses

To test combined-individual responses towards habitats, the number of captures and number of different individuals were counted at two scales: by station and by block. Blocks are non-overlapping, contiguous groups of 9 stations (3 x 3, Fig. 3.2). The entire plot was 9 stations by 18 stations, containing 3 blocks by 6 blocks. At the scale of stations, the number of individuals and captures were divided by the total number of undisturbed trap nights, because disturbed traps were assumed to be unavailable for use. At the larger scale of blocks, the total number of captures and different individuals for each of the nine stations was summed for the entire block. Similarly, the habitat scores for blocks were the scores from each station in the block summed. These habitat values are then put into the regression equation as follows:

$$\text{Number of captures or individuals} = PC1 + PC2 + PC3 + SESS1 + SESS2 + LOC$$

PC1, PC2 and PC3 are the three habitat principal components, and LOC was a dummy variable to account for plot location. SESS1 and SESS2 were dummy variables to code for the appropriate session (only two variables, or n - 1 variables are used to account for three (n) categories). There were four different regressions with four different dependent variables run for each sex of each species (16 total): the number of captures at each station, the number of individuals at each station, the number of captures in a block, and the number of individuals in a block. There were 972 cases for the station data and 108 cases for the block data.

The main goal of our analysis was to compare the above regressions with the home range analyses to be described, therefore every attempt was made to make the regression equations as similar as possible. This meant that even though there were enough cases to examine interaction terms in the above regressions, they were not included because they could not be included in the home range regressions.

I did not transform the data unless it was absolutely necessary. Non-normality, heteroscedasticity, non-linearity and outliers tend to weaken multiple regression rather than invalidate the results (Tabachnick and Fidell 1989). In no case were data transformed for the home range regressions because there were no major violations of these assumptions. In contrast, the violation of assumptions for the station number of individuals and capture regressions were prominent because many stations recorded no captures for a particular session, species and sex. This preponderance of zeros created a J-shaped distribution with most of the cases in the tail perceived as outliers (over 40 outliers in one regression analysis). Attempts to transform the data using logarithmic, inverse and square root transformations were inadequate and typically resulted in worse distributions. The only satisfactory method appeared to be to dichotomize the data into stations with and without captures. While this did improve normality and reduce the number of outliers to acceptable levels, dichotomization had little effect on the results of the analysis. The relative weighting of variables was almost identical to the same analysis with untransformed data, and R^2 improved very little, suggesting that the large number of cases in the analysis made the regression robust to these violations of assumptions. Because the results were changed very little, only the analysis of the untransformed data is reported to make comparison between regressions simpler.

Habitat Effects on Individual Responses

The regressions used to examine home range characteristics are from the perspective of the individual. The habitat composition for each home range was determined by summing the values for each PC variable for every station in the home range. I intended to use these variables in the following four regressions for each sex of the two species:

home range size = PC1 + PC2 + PC3 + LOC + (SESS1 + SESS2 +
NUMOFCAPS)

female overlap = PC1 + PC2 + PC3 + LOC + (SESS1 + SESS2) +
HRSIZE

male overlap = PC1 + PC2 + PC3 + LOC + (SESS1 + SESS2) +
HRSIZE

weight = PC1 + PC2 + PC3 + LOC + (SESS1 + SESS2)

The PC, SESS and LOC variables are the habitat, session and plot location variables. Session variables are bracketed because they were not needed for *M. pennsylvanicus* for which only data from the third session was used. NUMOFCAPS is the number of times an individual was captured, and was only included in the *M. pennsylvanicus* regressions of home range size. HRSIZE, or home range size, was included in regressions of overlap because if home ranges were placed in the plot completely at random, then by chance alone large home ranges should have higher overlap than small home ranges.

Unfortunately, I was only able to run these regressions in their entirety for male *P. leucopus* (48 cases), because there simply were not enough cases to run the regressions for female *P. leucopus* (25 cases), and female (28 cases) and male (31 cases) *M. pennsylvanicus*. Tabachnick and Fidell (1989) suggest a minimum of 5 cases for every predictor variable as a rule of thumb, which would require 35 cases for the largest regression. When cases were limiting, I first analyzed the data without the habitat variables. Then the correlation matrix was examined to see if any of the habitat variables were significantly correlated with the dependent variable in question. If the number of significantly correlated habitat variables made the total number of variables too high, I deleted a variable from the initial regression. The variable with the least significance was chosen, but only if it was not significant at $p = 0.05$. In one case, all three habitat variables were significantly correlated with the dependent variable, and no variables in the original regression could be deleted because they were all significant. Here I chose the two habitat variables with the highest significance and entered them into the regression equation.

Some of the results suggested that the distribution of habitats may have affected home range size and overlap, for instance, habitat occurring in small clumps may be too small to support more than one individual. Moran's coefficient was calculated to measure the spatial autocorrelation of habitat values between adjacent stations and blocks. A separate calculation was performed for just the interior stations, that is, excluding the outer two rows of stations (Fig. 3.2), to better reflect the area that I chose home ranges from. A BASIC program was written based on information from (Griffith 1987) to calculate the coefficient for stations and blocks (Appendix II). Values close to one indicate positive autocorrelation, while values close to negative one indicate negative autocorrelation (Griffith 1987).

RESULTS

VEGETATION AND HABITAT CLASSIFICATION

The three habitat principal components (PC's), PC1, PC2, and PC3, explained a total of 48.4% of the variation in the habitat data (Table 3.3a). In order to interpret the PC's, all habitat measurements that scored greater than .30 absolute value are listed for each PC in Table 3.3b. For PC1, there were high negative values on four variables associated directly with shrubs: prop175, mean175, shrubper, and vine>2m (see Table 3.2 for variable descriptions). The high negative scores on dirt and moss suggest a shaded understory with few herbs. Prop0 and prop175 scored high negative values indicating that there was vegetation at shrub height and near the ground, with little in between. In contrast, positive values of PC1 are associated with thick vegetation occurring 50 cm and lower, as indicated by the

Table 3.3 Principal component (PC) statistics for the first three habitat PC's (A) Eigenvalues and percent variance explained, (B) PC scores greater than |0.30|.

PC	Eigenvalue	Variance Explained (%)
1	6.39	22.8
2	4.77	17.1
3	2.38	8.5

Table 3.3b:

PC1		PC2		PC3	
Variable	PC Score	Variable	PC Score	Variable	PC Score
Herbs	.32	Mean100	.80	Herbs	.39
Mean0	.72	Mean175	.36	Mean0	.33
Mean12.5	.80	Prop100	.80	Mean12.5	.37
Mean25	.90	Mean50	.65	Mean175	.52
Mean50	.65	Prop50	.60	PoisonIvy	.49
Prop25	.77	Grapevine	.34	Prop175	.35
Prop50	.60	Goldenrod	.35		
Grapevine	.37	Vine<2m	.42		
Goldenrod	.31				
Vine<2m	.30				
Dirt	-.60	Grass	-.50	Grapevine	-.65
Moss	-.36	Prop0	-.74	Vine<2m	-.59
Mean175	-.54	Prop12.5	-.90		
Prop0	-.43	Prop25	-.39		
Prop175	-.75				
Shrubper	-.77				
Vine>2m	-.41				

high values of mean0, mean12.5, mean25, and mean50. Specific plants do not score as high as the profiles, but there is some relationship with vines, goldenrod, and the total cover of herbs. In summary, PC1 separates shrubby from vine/herbaceous associations within 50 cm of the ground.

The second principal component, PC2, scored high negative values on grassy habitat (-.50). The proportions of vegetation at 0, 12.5 and 25 cm from the ground scored more importantly than their means because in grass dominated areas there was usually nothing registering on higher profiles. High positive values are found on mean50, mean100, prop50 and prop100, those sites where the majority of the vegetation occurs at 50-100 cm in height. The actual plant species at this height appear to be riverbank grape and goldenrod. This is similar to PC1, but higher above the ground. In summary, PC2 separates grassy habitat from vine/goldenrod associations 50-100cm from the ground.

The third habitat PC appears to separate vine from poison ivy/herbaceous associations. The weighting on grapevine is clear, no variables other than grapevine and vine<2m score lower than -.30. The weighting on herbs is also clear, scoring high on poisonIvy, herbs, and profile means at 0 and 12.5 cm from the ground. Profile scores at 175 cm were also high, suggesting that these herbaceous associations occurred under some shrub cover, although not the thick, shady shrub cover associated with PC1.

Plot totals for the three habitat PC's are shown in Table 3.4. The North plot had fewer shrubs (positive value PC1), more grass (negative PC2), and much more vine coverage than the south plot (negative PC3). The south plot obviously had more shrubs, more vine/goldenrod, and more poison ivy/herbaceous cover.

GENERAL POPULATION TRENDS

P. leucopus densities were fairly constant over the three sessions (Table 3.5). Density was higher on the South plot than the North, mainly because there were many more males on the South plot. Female densities were similar on both plots, but slightly higher on the North plot. Juveniles began emerging at the end of May (South, Session 1).

Densities of *M. pennsylvanicus* increased steadily throughout the summer on both plots (Table 3.5). Females generally outnumbered males.

NON-HABITAT EFFECTS ON HOME RANGES

P. leucopus

Male *P. leucopus* had larger home ranges than females (Table 3.6), and this difference was significant (Table 3.7). Plot location was marginally significant ($p = 0.060$), indicating larger home ranges in the North plot. There were no differences observed due to session.

Overlap with male home ranges was greater than overlap with female home ranges for both sexes (Table 3.6). I did not test if this difference was significant, because such a

Table 3.4 Plot PC scores summed by adding PC scores for each individual station. Total plot scores sum to zero because PCA scores have a mean of zero and standard deviation of 1. Plot interior scores are presented to better represent the area used for the home range analyses.

Location	PC	Total Plot PC Score	Plot Interior PC Score
North	PC1	15.85	13.46
	PC2	-32.90	-16.11
	PC3	-47.70	-27.09
South	PC1	-15.85	-13.16
	PC2	32.90	16.01
	PC3	47.70	30.77

Table 3.5 Number of residents recorded for two rodent species on two plots and three sessions.

			Number of Different Individuals					
			North			South		
Species	Age	Sex	Sess1	Sess2	Sess3	Sess1	Sess2	Sess3
P. leucopus	Adult	Male	23	27	26	24	38	34
		Female	23	16	22	17	17	18
	Juv	Male	0	11	2	13	1	2
		Female	0	10	2	14	2	4
M. pennsylvanicus	Adult	Male	4	12	31	1	12	19
		Female	14	19	37	9	12	36

Table 3.6 Mean home range sizes and overlap values for adults of two rodent species.

				Number of Stations (standard error)		
Species	Sex	Location	No. of Cases	Home Range Size	Female Overlap	Male Overlap
P. leucopus	F	North	13	5.92	2.07	7.53
				(.57)	(.78)	(1.12)
		South	12	5.50	.50	8.41
				(.41)	(.15)	(1.16)
	M	North	20	9.85	6.50	7.45
				(.71)	(.85)	(1.06)
		South	28	7.67	5.64	6.71
				(.56)	(.65)	(1.06)
M. pennsylvanicus	F	North	16	3.25	1.87	5.62
				(.44)	(.39)	(.74)
		South	12	3.33	1.00	2.75
				(.33)	(.17)	(.74)
	M	North	18	7.94	6.83	7.44
				(1.45)	(.98)	(.77)
		South	13	8.61	5.38	9.00
				(1.26)	(.85)	(1.64)

Table 3.7 An ANOVA testing for differences in home range size of adult *P. leucopus* due to the individual and interacting effects of sex, plot location, and session.

Source of Variation	Degrees of Freedom	Sum of Squares	F-Ratio	Sig. of F
Sex	1	76.72	9.90	0.003
Location	1	28.52	3.68	0.060
Session	2	.91	.06	0.943
Sex X Loc	1	9.15	1.18	0.282
Sex X Sess	2	6.91	.45	0.642
Loc X Sess	2	1.40	.09	0.914
Sex X Loc X Sess	2	22.06	1.42	0.249
Error	61	472.83		
Total	72	701.48		

test would require a null model to account for the fact that male home ranges are larger, and therefore are expected to overlap more with neighbouring home ranges regardless of their sex. The observed trend cannot be interpreted as either supporting or refuting intrasexual territoriality, a common interpretation in other studies.

Home range size was significantly larger for adult *P. leucopus* than juveniles (Table 3.8). This ANOVA used a subset of data for the times when juveniles were most common. There were no significant differences due to sex detected in this smaller data in contrast to the full data set analyzed in Table 3.7.

M. pennsylvanicus

Data for adult *M. pennsylvanicus* home range sizes were log-transformed due to significant heteroscedasticity in the data (Cochrans test, p = .000). Male home ranges were larger than females (Table 3.6), and this was statistically significant (Table 3.9). Plot location and session variables had no significant effect on home range size.

As with *P. leucopus*, intersexual overlap was greater than intrasexual overlap, for both male and female *M. pennsylvanicus*.

HABITAT EFFECTS ON COMBINED-INDIVIDUAL RESPONSES

A general indication of habitat preferences can be given by comparing the amount of shrubs (shrubper) and grass (grass) at stations with and without captures of *P. leucopus*

Table 3.8 An ANOVA testing for differences in home range size of *P. leucopus* due to age, sex and plot location. Session variables were not included because only data from South, session 1, and North, session 2, had sufficient numbers of juveniles to test.

Source of Variation	Degrees of Freedom	Sum of Squares	F-Ratio	Sig. of F
Age	1	39.06	6.83	.013
Sex	1	.34	.06	.807
Location	1	3.66	.64	.428
Age X Sex	1	15.24	2.66	.110
Age X Loc	1	7.90	1.38	.247
Sex X Loc	1	2.13	.37	.545
Age X Sex X Loc	1	4.41	.77	.385
Error	40	228.73		
Total	47	327.48		

Table 3.9 An ANOVA testing for differences in home range size of adult *M. pennsylvanicus* due to sex and location. Session variables were not included as only data from session 3 were used.

Source of Variation	Degrees of Freedom	Sum of Squares	F-Ratio	Sig. of F
Sex	1	7.15	32.66	.000
Location	1	.18	.82	.370
Sex X Loc	1	.00	.00	.966
Error	54	11.83		
Total	58	24.27		

or *M. pennsylvanicus*. *P. leucopus* preferred shrubs and avoided grasses. Stations with captures had an average (± standard deviation) of 33.2% (± 38.2) shrub coverage and 28.9% (± 31.8) grass coverage, while those without captures had less shrubs (6.85 ± 12.21) and more grass (57.3 ± 26.5). *M. pennsylvanicus* showed the opposite trend, occupying habitats with more grass (39.6 ± 31.8) and less shrubs (18.7 ± 27.7), but had no captures on stations with a lot of shrubs (42.3 ± 42.9) and little grass (27.7 ± 33.3).

The results for the density/capture regressions and home range regressions are shown in one table for each sex/species combination. The beta-coefficients, or standardized regression coefficients, are listed for each factor in the regression that was significantly different than zero. Beta-coefficients are not meant to be compared directly (quantitatively) between different regressions, but can be compared indirectly by looking at their relative importance in each regression.

P. leucopus

The abundance regressions using number of individuals and captures at stations and blocks show that male and female *P. leucopus* exhibited similar habitat preferences (Table 3.10a, b). More individuals and captures were recorded for both sexes at shrubby sites (negative PC1), and vine/goldenrod associations (positive PC2). Positive PC2 values also indicate avoidance of grassy areas, and is

Table 3.10 Beta-coefficients for those variables found to add a significant amount of variation to several abundance and home range regressions. (A) Male *P. leucopus*. (B) Female *P. leucopus*.

		Predictor Variable Beta-Coefficients							
Dependent Variables	R^2	PC1	PC2	PC3	Loc	Sess1	Sess2	Mean Weight	Home Range Size
Station Captures	.18	-.08	.36	-.12			.15	▬[a]	▬
Station Individuals	.19	-.16	.35	-.13			.11	▬	▬
Block Captures	.32	-.25	.23	-.25			.35	▬	▬
Block Individuals	.24		.29			-.20		▬	▬
Home Range Size	ns*								▬
Female Overlap	.64	-.28	.22						.64
Male Overlap	.41								.43
Weight	ns*							▬	▬

* not significant [a]variables not included in the regression

Table 3.10b:

Dependent Variables	R^2	PC1	PC2	PC3	Loc	Sess1	Sess2	Mean Weight	Home Range Size
				Predictor Variable Beta-Coefficients					
Station Captures	.13	-.16	.29	-.08	.10	.10	.06[m]	▬[c]	▬
Station Individuals	.12	-.20	.27	-.05[m]	.10			▬	▬
Block Captures	.23	-.21	.35		.26	.22		▬	▬
Block Individuals	.17		.39		.26[m]				
Home Range Size[a]	ns*	▬	▬	▬					▬
Female Overlap 1[a]	.51	▬	▬	▬	.50	.42[m]		-.45	.49
Female Overlap 2[b]	.76	-.63	▬	▬	.39	.26	▬		.24
Male Overlap[a]	.68	▬	▬	▬			.53		.54
Weight 1[a]	ns*	▬	▬	▬				▬	▬
Weight 2[b]	ns*		▬					▬	▬

m - marginally significant * not signficant [a]regression without habitat variables

[b]regression with habitat variables correlated with dependent variable

[c]variables not included in the regression

stronger in females than males at the scale of blocks. Conversely, the positive effect of vine cover on habitat selection seemed to be stronger in males than females, as it showed up in the male block captures regression but not the female. The number of individuals in blocks responded negatively in both sexes to grassy areas, but in contrast to block captures there was no significant effect of PC1 or PC2.

A consistent location effect was observed for female *P. leucopus*: numbers of individuals and captures were higher on the North plot than the South (Table 3.10b). Three regressions for males recorded that abundances were higher in session 2 than other sessions (Table 3.10a). Male densities were also higher for the entire plot in session 2 (Table 3.5), although the differences do not appear large.

The proportion of variance explained, or R^2 values, increased for the block regressions over the station regressions for both sexes (Table 3.10a, b). For males, this effect is attributable mostly to habitat, as other variables in the equation do not change much between regressions. For females there was also an increase in the variation explained by location and session 1, so less of the increase in R^2 is explained by habitat.

M. pennsylvanicus

Table 3.11 a & b show the regressions for male and female *M. pennsylvanicus*, respectively. The regressions of the number of individuals and captures show mainly an effect

Table 3.11 Beta-coefficients for those variables found to explain a significant amount of variation to several abundance and home range regressions. (A) Male *M. pennsylvanicus*. (B) Female *M. pennsylvanicus*.

Dependent Variables	R^2	Predictor Variable Beta-Coefficients PC1	PC2	PC3	Loc	Sess1	Sess2	Mean Weight	Home Range Size	No. of Captures
Station Captures	.17	.20			.07	-.37	-.31	▬[c]	▬	▬
Station Individuals	.20	.20			.07	-.42	-.35	▬	▬	▬
Block Captures	.40	.22				-.63	-.53	▬	▬	▬
Block Individuals	.53	.21				-.74	-.58	▬	▬	▬
Home Range Size 1[a]	ns[*]	▬[c]	▬	▬		▬	▬		▬	
Home Range Size 2[b]	.46	-.31[m]	.31[m]	-.36	▬	▬	▬		▬	.42
Female Overlap[a]	.46	▬	▬	▬		▬	▬		.62	▬
Male Overlap[a]	.28	▬	▬	▬		▬	▬		.49	▬
Weight	ns[*]					▬	▬	▬	▬	▬

m - marginally significant [*]not significant [a]regressions run without habitat variables

[b]regressions with habitat variables correlated with dependent variables

[c]variables not included in the regression

Table 3.11b:

Dependent Variables	R^2	PC1	PC2	PC3	Loc	Sess1	Sess2	Mean Weight	Home Range Size	No. of Captures
		Predictor Variable Beta-Coefficients								
Station Captures	.12	.20				-.28	-.27	▬[c]	▬	▬
Station Individuals	.17	.22				-.37	-.33	▬	▬	▬
Block Captures	.43	.17		.21		-.62	-.58	▬	▬	▬
Block Individuals	.48	.25				-.65	-.59			
Home Range Size 1[a]	ns*	▬[c]	▬	▬		▬	▬		▬	
Home Range Size 2[b]	.53		.35	-.53	▬	▬	▬	-.47	▬	
Female Overlap 1[a]	.45	▬	▬	▬	.39	▬	▬	-.30[m]	.41	▬
Female Overlap 2[b]	.47		▬			▬	▬		.38[m]	▬
Male Overlap 1[a]	.62	▬	▬	▬	.46	▬	▬		.66	▬
Male Overlap 2[b]	.65		▬			▬	▬		.52	▬
Weight	ns*					▬	▬	▬	▬	▬

m - marginally significant   *not significant   [a]regressions run without habitat variables
[b]regressions run with habitat variables correlated with dependent variable
[c]variables not included in the analysis

of PC1 and session. Both sexes avoid shrubs but use vine/goldenrod areas (positive PC1). There is no significant effect due to grassy or vine/goldenrod associations, and only female block captures suggest that females avoid vines and utilize poison/ivy herbaceous areas more (positive PC3). The negative values for session variables reflect the large increase in the number of individuals by the third session (Table 3.5).

The block regressions explain at least twice as much variation in capture and density data as do the station data (Table 3.11a, b). Most of this increase is explained by the increase in explanatory power of the session variables, and very little due to an increase in the explanatory power of habitat.

HABITAT EFFECTS ON INDIVIDUAL RESPONSES

P. leucopus

Home range regressions were straightforward for male *P. leucopus*. There were no significant predictors of home range size, even though a previous ANOVA (Table 3.7) had found a significant effect of plot location. Overlap of both female and other males was affected mostly by home range size, because larger home ranges overlapped with more neighbours. Increased overlap with females was correlated with home ranges that had shrubby habitat (negative PC1) and not much grassy habitat (positive PC2). There were no significant predictors of male *P. leucopus* weight.

Similar results are noted for female *P. leucopus*, although the initial regressions for home range data were run without habitat variables (Table 3.10 b). There were no significant predictors of home range size. A second regression including habitat variables was not run because no habitat variables were significantly correlated with home range size (Table 3.12).

Fifty-one percent of the variation in female-female overlap was explained in the initial regression by location, session, weight and home range size. There was more overlap in the North than the South plot (Table 3.6), and there was a marginally significant trend of more overlap in session 1 than the other two sessions. The amount of overlap decreased with increasing weight. As with males, overlap increased with increasing home range size, but home range size was not the dominant variable of the equation.

The correlation matrix indicated that PC1 was significantly correlated with female overlap (Table 3.12). In order to add PC1 into the regression, the non-significant variable SESS2 was deleted. The new regression with PC1 explained 76 percent of the variation in female-female overlap, and the best predictor was clearly PC1. All variables significant in the first regression were significant in the second regression except for weight, possibly because it was correlated with PC1 (Table 3.12).

There were no significant predictors of female *P.*

Table 3.12 Significant correlations between habitat variables and home range size, home range overlap and individual weight.

		Pearson's Correlation Coefficient (p-value)			
Species	Sex	Home Range Size	Female Overlap	Male Overlap	Weight
P. leucopus	F PC1		-.69 (.000)		.37 (.067)
	PC2				-.55 (.004)
	PC3				
M. pennsylvanicus	F PC1		.42 (.02)	.46 (.012)	
	PC2	.52 (.004)		.42 (.025)	
	PC3	-.38 (.042)	-.38 (.042)	-.68 (.000)	
M. pennsylvanicus	M PC1	-.35 (.051)			
	PC2	.36 (.045)			
	PC3				

leucopus weight in the initial regression. Two habitat variables were correlated with female weight (Table 3.12), but were not significant predictors of weight when included in the full regression.

M. pennsylvanicus

The home range regressions for male and female *M. pennsylvanicus* contained data from the third session only. The first regression of male home range size was not significant (Table 3.11). Location was deleted from the analysis because it was not a significant predictor of home range size (Tables 3.9, 3.11a), and this allowed all three habitat variables to be entered into the subsequent analysis. This regression indicated that male home range size decreased when the home range contained favourable habitat. For PC1, there was a marginally significant effect for home ranges to be larger when they contained shrubs, and smaller with vine/herbaceous habitat. The effect of PC2 was also marginally significant, suggesting that home range size decreased with increasing grass habitat, and increased with vine/goldenrod. For PC3, vine cover increased home range size and poison ivy/herbaceous habitat decreased it. Home range size also increased significantly with more captures.

Similar patterns were found for home range size in female *M. pennsylvanicus* (Table 3.11b). PC2 and PC3 had the same effects on home range size as for males, but there was no significant effect of PC1. Home range size was smaller for larger individuals (weight effect), but there was no effect of the number of captures on home range size.

For male *M. pennsylvanicus*, male overlap and female overlap were only predicted by home range size (Table 3.11a). No second regressions were performed because no habitat variables were correlated with overlap (Table 3.12).

For females, male overlap and female overlap were both affected by home range size as well as location. Second regressions were performed that included PC1 and PC3, but they were not significant predictors of either male or female overlap when the variation due to other variables was accounted for. Note that PC2 was not included in the male overlap regression despite its significant correlation, because I could not enter any more variables into the equation. I could not make room for the variable by deleting any more variables from the first equation because all the variables left were significant predictors of overlap. For both female and male overlap regressions, the inclusion of the habitat variables resulted in the location effect of the initial regressions becoming non-significant.

Habitat variables could be entered directly into the weight regressions for both sexes, but in both cases the regression was non-significant (Table 3.11a, b).

HABITAT SPATIAL AUTOCORRELATION

Moran's coefficient for PC1 showed that this habitat tended to be more clumped (spatially autocorrelated) in the

North plot (Table 3.13). This was especially evident at the scale of blocks, because there was negative spatial autocorrelation in the South plot, compared to a high positive autocorrelation in the North plot. Coefficients for PC2 were similar between plots, while PC3 was obviously more clumped in distribution in the South plot.

DISCUSSION

Space use in *P. leucopus* and *M. pennsylvanicus* is highly flexible. It varied in response to differences in individual needs, as indicated by the larger home ranges of males than females, and adults than juveniles, although it did not vary in response to individual weight. Some, but not all, individuals adjusted their home ranges in response to habitat heterogeneity (Tables 3.14, 3.15). The effects of habitat heterogeneity were also observed in the collective behaviour of many individuals, as indicated by the relationship between habitat and abundances (Tables 3.14, 3.15). Each of these analyses taken individually offers a different perspective of how the organism views its environment.

NON-HABITAT EFFECTS ON HOME RANGES

As predicted, males had larger home ranges than females for both species, and adult *P. leucopus* had larger home ranges than juveniles. These results alone do not tell us anything about mechanisms, but do indicate the flexibility of home range size.

Table 3.13 Moran's coefficient calculated using all station habitat scores, just interior stations (excluding boundary strip, Fig. 3.2), and block values for habitat. Values approaching positive 1 indicate increasing spatial autocorrelation, while values approaching negative 1 indicate negative spatial autocorrelation.

		Moran's Coefficient		
Plot	Habitat	All Stations	Interior Stations	All Blocks
North	PC1	0.187	0.209	0.406
	PC2	0.206	0.111	-0.094
	PC3	0.105	0.072	0.022
South	PC1	0.125	0.034	-0.240
	PC2	0.223	0.110	0.026
	PC3	0.068	0.203	0.351

Table 3.14 Summary of the effects of habitat on *P. leucopus*. For each significant habitat predictor in the regression equation (Table 3.10), the habitat assumed to be the high quality habitat is listed.

		Significant Habitats		
	R^2	PC1	PC2	PC3
Male *P. leucopus*				
Station Captures	.18	shrub	vine/gol[a]	vine
Block Captures	.32	shrub	vine/gol	vine
Home Range Size	ns*			
Male-Male Overlap	.41			
Female-Male Overlap	.64	shrub	vine/gol	
Female *P. leucopus*				
Station Captures	.13	shrub	vine/gol	vine
Block Captures	.23	shrub	vine/gol	
Home Range Size	ns*			
Female-Female Overlap	.76	shrub		
Female-Male Overlap	.68			

[a] gol = goldenrod *not significant

Table 3.15 Summary of the effects of habitat on *M. pennsylvanicus*. For each significant habitat predictor in the regression equation (Table 3.10), the habitat assumed to be the high quality habitat is listed.

		Significant Habitats		
	R^2	PC1	PC2	PC3
Male *M. pennsylvanicus*				
Station Captures	.17	vine/herb		
Block Captures	.40	vine/herb		
Home Range Size	.46	vine/herb	grass	herb/PI[a]
Male-Male Overlap	.28			
Female-Male Overlap	.46			
Female *M. pennsylvanicus*				
Station Captures	.12	vine/herb		
Block Captures	.43	vine/herb		herb/PI[a]
Home Range Size	.53		grass	herb/PI[a]
Female-Female Overlap	.47			
Female-Male Overlap	.65			

[a] poison ivy

The predicted positive relationship between weight and home range size was not observed, and other studies have failed to find an effect as well (Wauters *et al.* 1994; Tufto *et al.* 1996; Koskela *et al.* 1997). There seems little reason to suspect the logic relating weight to resource needs is wrong, but the relationship may be obscured by other variation in the data.

I predicted that home range size would increase with weight, but found the opposite result for female *M. pennsylvanicus*. The only other study I know of that recorded a weight effect for female *M. pennsylvanicus* found the predicted positive relationship (Bowers *et al.* 1996). Although simplistic, it is often the initial prediction of most researchers that weight affects home range size through its affects on metabolism. I suspect this is the case because of the obvious relationship between the weight and home range size of different mammal species. However, larger animals may also be more dominant in social interactions. Tufto *et al.* (1996) found a marginally negative relationship between weight and home range size in roe deer, and speculated that it was due to an unknown social factor. A possible explanation for my results is that the heavier individuals were pregnant, and some studies have recorded that pregnant individuals have smaller home ranges (*e.g.* Koskela *et al.* 1997; Ostfeld *et al.* 1988). I could not test this hypothesis because I recorded individuals as pregnant on the basis of their weight, which makes it almost certain that I would find a relationship between pregnancy status and weight. However, it is interesting that Tufto *et al.* (1996) recorded the negative relationship after accounting for the reproductive status of the female roe deer.

HABITAT EFFECTS ON COMBINED-INDIVIDUAL RESPONSES

The observed relationships between habitat and abundances were not surprising, because other researchers have demonstrated similar habitat preferences (Beckwith 1954; Morris 1979; Adler 1986; Huntly and Inouye 1987; Cunningham 1990). For *P. leucopus*, both males and females preferred shrubby and vine habitats, and avoided grassy habitat (Table 3.14). For *M. pennsylvanicus*, both males and females avoided shrubby habitat for vine/herbaceous associations, and females showed some preference for poison/ivy herbaceous over vine habitat (Table 3.15).

Documenting density patterns can suggest habitat preferences, but I had hoped that the scale-dependent analyses would suggest some of the underlying costs to habitat selection. However, the prediction that there would be more variation explained at the scale of blocks than stations was only weakly supported. While there was always an increase in R^2 values at the scale of blocks for both species (Tables 3.14, 3.15), only a small proportion of the increase was usually attributable to habitat effects. This suggests that either the costs to habitat selection are not changing with scale, or, what I consider more likely, the costs to avoiding poor habitat are causing substantial variation at both scales in my analysis.

The major result from the scale-dependent, combined-individual responses was that there was not a particularity strong relationship between habitat type and abundances at either spatial scale. At both scales of analysis, poor habitats were often overutilized, and good habitats used less often than expected. While I knew that I was dealing with small scales where habitat preferences would not be expressed as strongly as at larger scales (*e.g.* Morris 1987; Morris 1992), I thought that the large differences between habitat types in this study system would compensate. Apparently they did not.

It is unlikely that the large amount of unexplained variation in abundance was caused because individuals were not particularly good at recognizing habitat heterogeneity. Foraging experiments in a wide variety of small mammal taxa and environments have shown their ability to distinguish between differences in foraging costs in trays of seeds immediately adjacent to each other (*e.g.* Brown 1988; Schmidt and Brown 1996; Morris 1997). A more likely explanation is that the organisms do recognize the habitat variation, but there are other, more important factors affecting abundances at this scale.

The decrease in importance of habitat at small scales was recognized by Morris (1987; 1992), who suggested it was due to travel cost explanation offered above. Bowers (1995) found that small-scale habitat heterogeneity was not nearly as important to chipmunk space use as was the distance from their central burrow. Variation in habitat use at small scales was caused by changes in the costs to foraging with distance from the burrow, which led to changes in the degree of habitat selectivity.

Orians and Wittenberger (1991) did not need to invoke travel costs to explain the lack of importance of small-scale habitat. They found that yellow-headed blackbirds were good at choosing the most productive marshes in which to build nests, but within the marsh they were poor at locating the nests near to patches of peak resource density. They suggested that small-scale heterogeneity in the emergence of aquatic insects, their main food resource, was too difficult to predict months in advance when they built their nest. At the scale of the marsh, though, the birds were able to tell which marshes would be the most productive. They chose nest locations on the basis of what they could predict, overall marsh productivity, and then adjusted foraging effort in the short term to adjust to subsequent spatial and temporal heterogeneity in resources.

This scale of recognition may apply to rodents as well. Habitats can change as different insects become abundant, plants produce fruit and seed, and these changes may be difficult to predict through time. In this case, home range placement may be based on a large-scale assessment of habitat quality where small-scale heterogeneity is relatively unimportant.

In addition, even if the individual could ascertain the suitability of a site, the information may be costly to obtain in terms of time and energy. In the time it takes one individual to assess one location thoroughly for suitability, another individual might be able to assess several sites reasonably well. If individuals do not spend a lot of time gathering information for home range placement, then the information that is gathered will be based on large-scale cues to habitat suitability because they are easily observed. Abundances, in this case, would be related to these large-scale cues and not to small-scale habitat heterogeneity.

HABITAT EFFECTS ON INDIVIDUAL RESPONSES

In my study, average home range sizes varied from around three to nine stations (Table 3.6), within the range of the two spatial scales of the combined-individual analyses (one vs nine stations). It is tempting to suggest that, if habitat does not have a strong effect on combined-individual responses at these scales, then home ranges may not be affected by small-scale habitat variation either. However, even if the initial placement of a home range is based on large-scale heterogeneity, once an individual is established, it has time to learn about the local environment and adjust its behaviour accordingly.

In fact, my data showed that, in three of four analyses, habitat was an important factor affecting individual space use: female *P. leucopus* and both sexes of *M. pennsylvanicus* (Tables 3.14, 3.15). To briefly review, female *P. leucopus* had more female-female overlap in shrubby habitat. There was increased overlap of females by male *P. leucopus* in shrubby and vine/goldenrod habitat (Table 3.14), although I will argue below that this was not due to any change in male distribution. Male *M. pennsylvanicus* reduced home range size as vine/herbaceous, grassy and poison/ivy herbaceous habitats increased (Table 3.15). Female *M. pennsylvanicus* reduced home range size in the presence of grass and poison/ivy herbaceous habitats (Table 3.15).

The prediction that habitats of high quality should reduce home range size was upheld for both sexes of *M. pennsylvanicus*. Habitat quality was inferred from habitats that had positive effects on abundances. Ideally, the columns for the capture regressions in Table 3.15 would contain the same habitats as the home range regressions, which would indicate that high quality habitats are also those that reduce home range size. The columns do not match that well, but in the cases that the abundance regressions do not indicate habitat quality, I have made a best guess at habitat quality. For PC3, I assume that habitat quality is similar for males and females, and that males also prefer poison ivy/herbaceous habitat as was recorded for females (Table 3.15). If this assumption is accepted, then the reduction in home range size with poison ivy/herbaceous habitat is as predicted. Because *M. pennsylvanicus* is always typified in the literature as a grassland species, it is not hard to believe that grassy habitat is high quality, in which case its effect on home range size is as predicted for both sexes.

Although I did not anticipate the possibility, the data for *M. pennsylvanicus* actually suggest the relative importance of population density and resource availability on home range size. In several instances, we know that a given habitat is not associated with an increase in density, because there was no significant effect of the habitat in the abundance regressions (Table 3.15). In those cases, habitat resource availability is the most likely explanation for the change in home range size. Of course, when the habitat was significant in the abundance regressions, I cannot differentiate the density effects from those of resource availability. Interestingly, Fortier and Tamarin (1998) separated the effects of resources and density on home range size, and found that males but not females responded to resources, and both sexes responded to density. I found almost the opposite, because both sexes responded to habitat quality, and evidence suggested it was not always due to changes in density.

The home ranges of female *P. leucopus* also responded to habitat, but not by changes in home range size. Home range overlap with other females increased in favourable, shrubby habitat (Table 3.14). This was in the direction I predicted, because the shrubby habitats had higher densities of females, increased density is expected to increase intruder pressure, and increased intruder pressure should lead to increased overlap. However, the prediction was not upheld for the vine/goldenrod habitat which was also associated with higher densities but with no subsequent effect on overlap.

The only effect of habitat on male *P. leucopus* was an increase in overlap with females in shrubby and vine/goldenrod habitats, and this can be explained entirely by female distributions rather than any change in male space use. Females exhibited increased crowding in shrubby habitats as already discussed, and therefore males would overlap them more. I also pointed out in the results that females showed more avoidance of grassy habitats than males. Thus, males would not encounter many females in the grassy habitat, and this would lead to more female overlap in vine/goldenrod than grassy habitat. The data suggest that males were passive in response to heterogeneity in both habitat quality and the distribution of females.

The story of habitat and home ranges is, up to this point, one of inconsistency. I should stress that, when habitat did affect home ranges, it was always in the direction I predicted, but the inconsistencies arise by looking at what did not happen. Why did male *M. pennsylvanicus* but not male *P. leucopus* respond to habitat quality? Why did female *P. leucopus* respond to one habitat but not to another with an increase in overlap? Why did habitat only affect overlap in female *P. leucopus*, and only home range size in male and female *M. pennsylvanicus*?

Other researchers have made similar predictions to mine using similar logic. They have found that increased habitat quality has either reduced home range size (*P. maniculatus*: Bowers and Smith 1979; Jays: Andrén 1990; roe deer: Tufto *et al.* 1996) or had no effect (red squirrels: Wauters *et al.* 1994). Higher quality habitat has been observed to increase overlap (Ims 1987b; Ostfeld *et al.* 1985), although I suspect that exceptions are hard to find because many other studies have not reported overlap values. None of these researchers offered *a priori* reasons for when these factors should or should not be important, even though they correctly predicted the direction of the effect when it occurred.

There are some areas of research that would likely be profitable in providing answers to when different factors should affect home ranges. I think that we need to examine the individual and interacting effects that density, resource availability and access to mates have on home range size. A possible interaction between density and resources is shown in Fig. 3.4. At low densities, home range size will vary

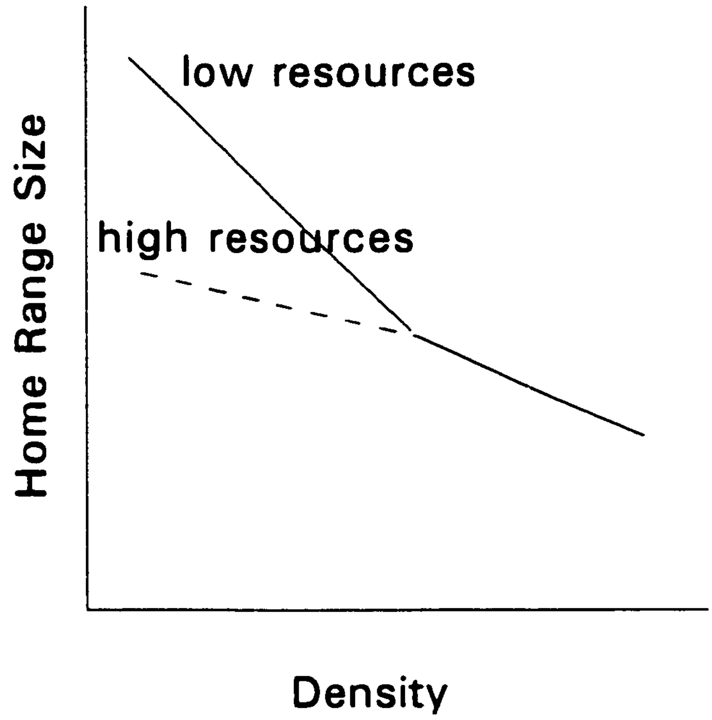

Figure 3.4 Hypothetical relationship between the interacting effects of density and resource availability on home range size. Home ranges are expected to be larger when resources are scarce. However, at high densities, space is limited and home range size constrained to the same value regardless of resource availability.

with resource availability, but at high densities space is so limited that home range size is the same regardless of resource availability (*i.e.* there is no space to expand into). The only way to disentangle the effects of resources and densities would be to observe them at as many different values as possible.

For instance, Fortier and Tamarin (1998) showed no effect of food supplementation at two levels of density for female *M. pennsylvanicus* home ranges, which was in contrast to the effect of habitat in my study. Perhaps, relative to habitat quality in their study, females perceived densities as very high, and therefore did not respond to resources. Relative to habitat quality in my system, densities would have been perceived as low, and therefore females could be more responsive to resources. A similar explanation for why males of only one species responded to habitat would have to take into account the effects of female distributions interacting with changes in male density and resource availability.

There are a growing number of studies that have separated the effects of resources and intruder pressure on home range size, but the results are varied. Intruder pressure appeared more important in sanderlings (Myers *et al.* 1979), grey-sided voles (Wolff and Schauber 1996), female *M. pennsylvanicus* (Fortier and Tamarin 1998), and a pomacentrid reef fish (Norman and Jones 1984). Resources appeared more important for roe deer (Tufto *et al.* 1996) and chipmunks (Mares *et al.* 1982). Mixed results were recorded for male *M. pennsylvanicus* (Fortier and Tamarin 1998), coho salmon (Dill *et al.* 1981), and harriers, although resources were more consistently important in harriers (Temeles 1987). None of these researchers considered the interactions of these factors.

THE RELATIONSHIP BETWEEN INDIVIDUAL AND COMBINED-INDIVIDUAL RESPONSES

As referred to earlier, habitat effects on individual and combined-individual responses would have been perfectly correlated if every habitat that had a positive effect on abundance had a negative effect on home range size. That is, the columns for the abundance regressions and home range size regressions would have contained the same list of habitats (Tables 3.14, 3.15), which would be the case if combined-individual responses are emergent properties of individual responses.

However, in the most extreme example, male *P. leucopus* home ranges were insensitive to habitat variation, despite the fact that their abundances were higher in shrubby and vine habitats (Table 3.14). There were also cases for female *P. leucopus* and both sexes of *M. pennsylvanicus* where habitats that affected home ranges had no effect on abundances, and vice versa. This does not mean that either method for detecting habitat effects is invalid, but clearly they tell us different information about the organism. The problem is confounded because home ranges may respond to many different factors other than habitat.

As Wiens *et al.* (1993) noted, population patterns need not be additive outcomes of individual behaviours, especially if different mechanisms affect populations and individuals. Studies similar to mine have also recorded inconsistent relationships between these levels of organization. Roe deer ranked habitats for foraging within home ranges differently than for placing home ranges (Tufto *et al.* 1996). In the example of Orians and Wittenberger (1991), the lack of correlation between habitat effects at small and large scales in yellow-headed blackbirds was because small scale heterogeneity was unpredictable. A similar study on red-winged blackbirds also found that habitat preferences at small scales were different from those at large scales (Pribil and Picman 1997).

Other examples, relating individual behaviour to populations, use mathematical descriptions of individual movement patterns to predict population responses to spatial heterogeneity (see discussions in Turchin 1991; Wiens *et al* 1993; Lima and Zollner 1996). The simplest models are the well-known diffusion and random-walk models (*e.g.* Skellam 1951; Okubo 1980; Turchin 1991), but tests of the hypotheses are not very common in vertebrates. Stapp and Van Horne (1997) found that shrub density and distribution affected the movements of *P. maniculatus*, but these were only related to population densities over a narrow range of shrub densities. A model examining movements affected by interference and feeding behaviour in oystercatchers was successful at predicting the direction of the effect, but unsuccessful in predicting the magnitude (Goss-Custard *et al.* 1995).

LOCATION EFFECT

One last effect that I have not discussed is the consistent location effect observed in both the abundance and home range regressions for female *P. leucopus*. Densities, home range size and home range overlap were all higher on the North Plot than the South. The favoured habitat of female *P. leucopus* was the shrubby habitat (Table 3.14), but surprisingly there was less shrubby habitat on the North plot (Table 3.4) where female densities were highest. A possible explanation is that the spatial distribution of the shrubby habitat on the North plot was more clumped, or spatially autocorrelated (Table 3.13). Ims *et al.* (1993) suggested that home size and overlap would decrease with fragmentation as fragment size approached the minimum home range size possible. That is, individuals shrink their home range into a fragment that does not allow for either neighbours or spatial overlap. Although I have no objective way to delineate patches of habitat to assess the effects of patch size on home ranges, the best habitat is more fragmented in the South plot at scales similar to home range size.

CONCLUSIONS

Abundances were only weakly correlated with habitat type at both scales of analysis, possibly because abundances were adjusted to larger-scale habitat cues and only secondarily to small-scale habitat heterogeneity. Our understanding of home ranges needs to be taken to a new level. When I did observe effects in this study, they were almost always as predicted, but I could not predict when the effect would occur. There was no consistent relationship between combined-individual and individual responses observed. This may be because initial home range placement, which affects abundances, is in response to large-scale habitat cues, while subsequent changes in home range size and overlap are based on the immediate environment. In order to solve some of the questions that this study raised, the interactions between food supplementation, intruder pressure and access to mates should be investigated using experimental manipulations at different levels of each factor. To relate individual to combined-individual responses will involve understanding the factors that affect home range placement. How do densities and habitat type affect home range placement? How does dispersion of habitat affect home range placement (*e.g.* the location effect I observed)?

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APPENDIX I

A program written in BASIC used to calculate home range size, overlap and habitat composition using capture and habitat data collected at stations.

```
DECLARE SUB findstavscaps ()
DECLARE SUB dataallsta ()
DECLARE SUB findallstations (xcoor2() AS INTEGER, ycoor2() AS
INTEGER, xallsta() AS INTEGER, yallsta() AS INTEGER, Ntotalsta
          AS INTEGER)
DECLARE SUB findstations ()
DECLARE SUB plotmap ()
DECLARE SUB hrcalc (Npts AS INTEGER, hrarea AS SINGLE,
               xcoor2() AS INTEGER, ycoor2() AS INTEGER)
DECLARE SUB findboundarypoints (x AS INTEGER, tempx2() AS
               INTEGER, tempy2() AS INTEGER, wp2 AS INTEGER,
               bounx() AS INTEGER, bouny() AS INTEGER)
DECLARE SUB functionmenu ()
DECLARE SUB bounpoints ()
DECLARE SUB hrsize ()
DECLARE SUB hrsizepoints ()
DECLARE SUB overlap ()
DECLARE SUB habitatcomp ()
DECLARE SUB pauser ()
DECLARE SUB convertxy (a AS STRING, c AS INTEGER)
DECLARE SUB datamenu ()
DECLARE SUB datrawcapture ()
DECLARE SUB datbounpoints ()
DECLARE SUB datallpoints ()
DECLARE SUB datspssconvert ()

COMMON SHARED maxNfixes AS INTEGER
COMMON SHARED Numofrecords AS INTEGER
COMMON SHARED spssfile$, rawfile$, bounfile$
COMMON SHARED hrsizefile$, findstafile$,
     pcscorefile$,hrcompfile$
COMMON SHARED stavscapfile$, hrsizecap$, overlapfile$
COMMON SHARED maxrecords AS INTEGER
CONST pil = 3.141592654#
maxNfixes = 15
maxrecords = 500
DIM SHARED xcoor(maxrecords, maxNfixes)   AS INTEGER
DIM SHARED ycoor(maxrecords, maxNfixes)  AS INTEGER
DIM SHARED recordN(maxrecords) AS INTEGER
DIM SHARED sess(maxrecords)  AS INTEGER
DIM SHARED loca(maxrecords)  AS INTEGER
DIM SHARED sex(maxrecords)  AS INTEGER
DIM SHARED age(maxrecords)  AS INTEGER
DIM SHARED spp(maxrecords)  AS INTEGER
DIM SHARED id(maxrecords)  AS INTEGER
DIM SHARED Ncaps(maxrecords) AS INTEGER
DIM SHARED edge(maxrecords) AS INTEGER
DIM SHARED Nstas(maxrecords) AS INTEGER
DIM SHARED edgetwo(maxrecords) AS INTEGER

'DATA FILE NAMES: For ease of changing, all the data file
```

```
names are
'changed right here, at the beginning of the program.  Not
interactive,
'but it works for me:
spssfile$ = "c:\larry\homerang\raw2m.sav"
    'this is the data from SPSS, see datspssconvert sub
rawfile$ = "c:\larry\homerang\conv2m.dat"
'this is the converted SPSS data, see datspssconvert
sub bounfile$ = "c:\larry\homerang\boun2m.dat"
      'this contains boundary points using all captures, see
bounpoints sub
hrsizefile$ = "c:\larry\homerang\size2m.dat"
hrsizecap$ = "c:\larry\homerang\cvs2m.dat"
findstafile$ = "c:\larry\homerang\sizst2m.dat"
'contains the number of stations within polygon for all
     stations, see findstations sub
pcscorefile$ = "c:\larry\homerang\pcfile.dat"
     'the habitat pc scores,
hrcompfile$ = "c:\larry\homerang\hrcomp2m.dat"
stavscapfile$ = "c:\larry\homerang\cvst2m.dat"
     'the number of stations in polygon vs number of captures,
     see findstavscap sub
overlapfile$ = "c:\larry\homerang\over2m.dat"
     'the overlap of Home ranges

CLS
datamenu

SUB bounpoints
SHARED rec AS INTEGER
SHARED x AS INTEGER
SHARED wp2 AS INTEGER
DIM tempx(maxNfixes) AS INTEGER
DIM tempy(maxNfixes) AS INTEGER
DIM bounx(maxNfixes) AS INTEGER
DIM bouny(maxNfixes) AS INTEGER

'HOW THIS WORKS:
'This algorithm takes the capture data and finds the outer
points that
'form the minimum convex polygon.  To do this, I used angles.
For instance,
'the angle formed between two adjacent outer points and all
other points will
'be smallest for the next outermost point (this is more
obvious with a
'diagram).  The application of this idea obviously involves a
lot more detail
'but thats the basis.
'
'The data used in this section is the capture data, or
"rawfile$".
```

```
'The data file has each line saved in the following order:
'check (-2), number of records, session, location, sex, age,
species, id
'number of captures, edge (1 if HR touches edge, 0 otherwise),
'xy cooridinates, and -1's are inserted as cooridinates if
there aren't
'as many cooridinates as the maxNfixes (which is currently set
to 15).
'    The end of the file is signaled by -9999 alone, on the
last line.

'PRINT "What do you wish to name the file that will contain
          the"
'PRINT "boundary points from each individuals home range?"
'INPUT bounfile$
'bounfile$ = "c:\larry\homerang\boun.tst"
'get rid of the double capture points in the data
OPEN bounfile$ FOR OUTPUT AS #3
FOR rec = 1 TO Numofrecords
  FOR i = 1 TO maxNfixes
    tempx(i) = xcoor(rec, i): tempy(i) = ycoor(rec, i)
    IF xcoor(rec, i) <> -1 THEN
      'Ncaps(rec) = Ncaps(rec) + 1
      IF xcoor(rec, i) = 1 OR xcoor(rec, i) = 9 OR ycoor(rec,
          i) = 1 OR ycoor(rec, i) = 18 THEN edge(rec) = 1

    END IF
  NEXT i
  PRINT "id, numofcaps"; id(rec); Ncaps(rec);
  'pauser
  x = id(rec)
  PRINT #3, USING "#####"; -2; recordN(rec); sess(rec);
     loca(rec);    sex(rec);    age(rec);    spp(rec);
     id(rec);caps(rec); edge(rec); edgetwo(rec);
  PRINT USING "####"; -2; recordN(rec); sess(rec); loca(rec);
     sex(rec);  age(rec);  spp(rec);  id(rec);  Ncaps(rec);
     edge(rec); edgetwo(rec);

  findboundarypoints x, tempx(), tempy(), wp2, bounx(),
     bouny()

  FOR i = 1 TO wp2
    PRINT #3, USING "####"; bounx(i); bouny(i);
    PRINT USING "####"; bounx(i); bouny(i);
  NEXT i
  FOR i = 1 TO maxNfixes - wp2
    PRINT #3, USING "####"; -1; -1;
    PRINT USING "####"; -1; -1;
  NEXT i
  PRINT #3, ""
  PRINT
  'pauser
```

```
NEXT rec
PRINT #3, -9999
CLOSE #3
datamenu
END SUB

SUB convertxy (a AS STRING, c AS INTEGER)
IF a = "a" THEN c = 1
IF a = "b" THEN c = 2
IF a = "c" THEN c = 3
IF a = "d" THEN c = 4
IF a = "e" THEN c = 5
IF a = "f" THEN c = 6
IF a = "g" THEN c = 7
IF a = "h" THEN c = 8
IF a = "i" THEN c = 9
END SUB

SUB dataallsta
REDIM xcoor(maxrecords, 30)
REDIM ycoor(maxrecords, 30)
'findstafile$ = "c:\larry\homerang\finsta.tst"
OPEN findstafile$ FOR INPUT AS #5
INPUT #5, check
rec = 0
DO WHILE check <> -9999
 IF check <> -9999 THEN
   rec = rec + 1
   INPUT #5, recordN(rec), sess(rec), loca(rec), sex(rec),
     age(rec), spp(rec)
   INPUT #5, id(rec), Ncaps(rec), edge(rec), edgetwo(rec),
     Nstas(rec)
   PRINT recordN(rec); sess(rec); loca(rec); sex(rec);
     age(rec); spp(rec);
   PRINT id(rec); Ncaps(rec); edge(rec); Nstas(rec); "  ";

   FOR i = 1 TO Nstas(rec)
     INPUT #5, xcoor(rec, i), ycoor(rec, i)
     PRINT xcoor(rec, i); ycoor(rec, i); "  ";
     IF xcoor(rec, i) = -2 OR ycoor(rec, i) = -2 THEN
       PRINT "Problem with input!"
       STOP
     END IF
   NEXT i
   PRINT
   INPUT #5, check
   IF check <> -2 AND check <> -9999 THEN
     PRINT "Problem with input!"
     PRINT check
     STOP
   END IF
   'pauser
```

```
 END IF
LOOP
Numofrecords = rec
CLOSE #5
functionmenu
END SUB

SUB datamenu
CLS
PRINT "Choose which type of data you wish to use:"
PRINT "  1. Unconverted SPSS (ASCII) file."
PRINT "  2. Raw capture point data."
PRINT "  3. Boundary points."
PRINT "  4. All stations within home range."
PRINT "  5. Quit."
INPUT choice
DO WHILE (choice < 1) OR (choice > 5)
  BEEP
  INPUT choice
LOOP
IF choice = 1 THEN datspssconvert
IF choice = 2 THEN datrawcapture
IF choice = 3 THEN datbounpoints
IF choice = 4 THEN dataallsta
IF choice = 5 THEN PRINT "bye"
END SUB

SUB datbounpoints
REDIM xcoor(maxrecords, maxNfixes) AS INTEGER
REDIM ycoor(maxrecords, maxNfixes) AS INTEGER

'WHATS GOING ON:
'This is simply an input algorithm.  It takes the data from
'bounfile$ and saves it to active variables.  The data are
then
'used in several different ways in the FUNCTIONMENU
sub-routine.


'print "Which file contains the boundary points?"
'input bounfile$
'bounfile$ = "c:\larry\homerang\boun.tst"
OPEN bounfile$ FOR INPUT AS #3
check = -2
rec = 0
DO WHILE check <> -9999
  INPUT #3, check
  'PRINT check
  'pauser
  IF check = -9999 THEN GOTO bottomsub2
  rec = rec + 1
  INPUT #3, recordN(rec), sess(rec), loca(rec), sex(rec),
```

```
     age(rec), spp(rec), id(rec), Ncaps(rec), edge(rec),
     edgetwo(rec)
  PRINT recordN(rec); sess(rec); loca(rec); sex(rec);
     age(rec); spp(rec); id(rec); Ncaps(rec); edge(rec);
  IF check <> -2 OR sess(rec) = -2 OR loca(rec) = -2 OR
     sex(rec) = -2 OR age(rec) = -2 OR spp(rec) = -2 OR
     id(rec) = -2 OR Ncaps(rec) = -2 THEN
    PRINT "Warning: input error into Home range size module!"
    BEEP
    pauser
  END IF
  FOR i = 1 TO maxNfixes
    'PRINT "rec, i"; rec; i
    INPUT #3, xcoor(rec, i), ycoor(rec, i)
    IF xcoor(rec, i) <> -1 THEN PRINT xcoor(rec, i);
     ycoor(rec, i);
    IF xcoor(rec, i) = -2 OR ycoor(rec, i) = -2 THEN
      PRINT "Warning: input error into Home range size
          module!"
      BEEP
      pauser
    END IF
  NEXT i
  PRINT
bottomsub2:
LOOP
Numofrecords = rec
CLOSE #3
functionmenu
END SUB

SUB datrawcapture

'WHATS GOING ON:
'this is simply an input algorithm.  It takes the data from
rawfile$
'and saves it to active variables.  These variables are used
in
'several algorithms that branch from the FUNCTIONMENU
subroutine.
'The rawfile$ contains all the capture points (in order of
capture)
'for an individual during one session.

'REDIM recordN(500) AS INTEGER
'REDIM sess(500) AS INTEGER
'REDIM loca(500) AS INTEGER
'REDIM sex(500) AS INTEGER
'REDIM age(500) AS INTEGER
'REDIM spp(500) AS INTEGER
'REDIM id(500) AS INTEGER
'REDIM xcoor(500, maxNfixes) AS INTEGER
```

```
'REDIM ycoor(500, maxNfixes) AS INTEGER

'rawfile$ = "c:\larry\homerang\temp2.dat"
OPEN rawfile$ FOR INPUT AS #2

rec = 1
DO WHILE check <> -9999
  INPUT #2, check
  IF check <> -9999 THEN
    IF check <> -2 THEN PRINT "check wasn't -2!": pauser
    'PRINT "!rec"; rec; "!";
    INPUT #2, recordN(rec), sess(rec), loca(rec), sex(rec),
     age(rec), spp(rec), id(rec)
    PRINT check; recordN(rec); sess(rec); loca(rec); sex(rec);
     age(rec); spp(rec); id(rec);
    IF recordN(rec) <> rec THEN PRINT : PRINT "Rec <>
     recordN"; rec; recordN: pauser
    Ncaps(rec) = 0
    edge(rec) = 0
    edgetwo(rec) = 1
    FOR i = 1 TO maxNfixes
      INPUT #2, xcoor(rec, i), ycoor(rec, i)
      PRINT xcoor(rec, i); ycoor(rec, i);
      IF xcoor(rec, i) > -1 THEN Ncaps(rec) = Ncaps(rec) + 1
      IF xcoor(rec, i) = 1 OR xcoor(rec, i) = 9 OR ycoor(rec,
          i) = 1 OR ycoor(rec, i) = 18 THEN edge(rec) = 1
      IF (xcoor(rec, i) > 2 AND xcoor(rec, i) < 8) AND
          (ycoor(rec, i) > 2 AND ycoor(rec, i) < 17) THEN
          edgetwo(rec) = 0
    NEXT i
    PRINT
    rec = rec + 1
  END IF
LOOP

Numofrecords = rec - 1
PRINT "All the data is read."
pauser

CLOSE #2
functionmenu
END SUB

SUB datspssconvert
SHARED choose$, col1 AS INTEGER
SHARED colm1$


INPUT "Do you need instructions?", choose$
IF choose$ = "y" THEN
  PRINT "  The part of the program takes an SPSS data file
saved as an"
```

```
  PRINT "ascii file, and converts it into something useful for
this program."
  PRINT "  The ascii file must be in a certain format or it
won't be "
  PRINT "interpreted correctly.  Each line of the data must
represent an"
  PRINT "individual  capture,  and  contain  the  following
information:"
  PRINT  "Session  Number  (1-3),  location  number  (1-2),
sex(1-2), age (1-2), spp (1-?),"
  PRINT  "i.d.  #  (tag  number),  and  finally  the  capture
station."
  PRINT "  The data must be in that order, and within the data
values"
  PRINT " specified, ";
  PRINT "otherwise, error messages will be returned.  Also the
capture"
  PRINT  "station  must  be  a  letter  from  a-i  followed  by  a
number (1-18)"
  PRINT "with no space between the letter and number (e.g.
a18, e7)."
  PRINT "The file must end with a -1 on a separate line (this
marks"
  PRINT "the end of the file)."
  PRINT
  PRINT "Press any Key to continue."

  pauser
  CLS
  PRINT
  PRINT "  The output file puts all the captures for one
individual in one "
  PRINT "session and location on the same line by recording
the i.d. info,"
  PRINT "followed by the x and y cooridinates for each
capture.  You will "
  PRINT "be prompted to input the maximum number of times an
individual"
  PRINT "was captured during a session.  If a given individual
was captured"
  PRINT "less times than the maximum, then the line is filled
up with -1's"
  PRINT "until there are as many stations as the maximum
recorded."
  PRINT "The data is saved in the following order, where
'check' is"
  PRINT "arbitrarily -2, as a checker in the program to make
sure the data is"
  PRINT "inputted/outputted correctly:"
  PRINT "check, record number, session, location, sex, age,
spp, id,"
  PRINT "and then all the x-y cooridinates."
```

```
  PRINT "e.g. -2 55 2 1 1 2 101 5 18 6 18 -1 -1 -1 -1..."
  PRINT "where the '5' is the first x cooridinate, and the
'18'"
  PRINT "is the first y cooridinate."
  PRINT : PRINT
END IF

'choose$ = "n"
'DO WHILE choose$ = "n"
'    INPUT "What is the name of the spss input file?",
spssfile$: PRINT
'   INPUT "What is the name of the output file?", rawfile$:
PRINT
'  PRINT "What is the maximum number of times an individual
was"
'  INPUT "captured during a session?", maxNfixes
'  PRINT : PRINT
'  PRINT "Are these correct?"
'  PRINT " Input file:"; spssfile$
'  PRINT " Output file:"; rawfile$
'  PRINT "Maximum number of captures:"; maxNfixes
'  INPUT choose$
'LOOP
'spssfile$ = "c:\larry\homerang\plsess1.dat"
'rawfile$ = "c:\larry\homerang\temp2.dat"
OPEN spssfile$ FOR INPUT AS #1
OPEN rawfile$ FOR OUTPUT AS #2

'**Start inputting data:
recordN = 0
Ncaps1 = 0
DO WHILE sess1 <> -1
  INPUT #1, sess1
  IF sess1 <> -1 THEN
    INPUT #1, loca1, sex1, age1, spp1, id1
    colm1$ = INPUT$(1, 1)
    row1 = VAL(INPUT$(4, 1))
    convertxy colm1$, col1
    IF sess1 <> sess2 OR loca1 <> loca2 OR id1 <> id2 OR
          recordN = 0 THEN
      IF recordN > 0 THEN
        FOR i = Ncaps1 + 1 TO maxNfixes
          PRINT #2, -1; -1;
          'this fills in data with -1's
          PRINT -1; -1;
        NEXT i
        PRINT #2, " "
        'PRINT #2, Ncaps1
      END IF
      PRINT " "
      recordN = recordN + 1
      PRINT #2, -2; recordN; sess1; loca1; sex1; age1; spp1;
```

```
                    id1; col1; row1;
      PRINT -2; recordN; sess1; loca1; sex1; age1; spp1; id1;
                coll1; row1;
      Ncaps1 = 1
    ELSE
      IF sex1 <> sex2 OR age1 <> age2 OR spp1 <> spp2 THEN
        PRINT
        PRINT "Sex or age has changed for record"; recordN; ",
               capture"; Ncaps1; "."
        pauser
      END IF
      PRINT #2, col1; row1;
      PRINT col1; row1;
      Ncaps1 = Ncaps1 + 1
    END IF
  END IF
  sess2 = sess1: loca2 = loca1: sex2 = sex1: age2 = age1:
  id2 = id1: spp2 = spp1
LOOP
FOR i = Ncaps1 + 1 TO maxNfixes
  PRINT #2, -1; -1;
NEXT i
PRINT #2, " "
PRINT #2, -9999
CLOSE #1: CLOSE #2
CLS
datamenu
END SUB

SUB findallstations (xcoor2() AS INTEGER, ycoor2() AS INTEGER,
     xallsta() AS INTEGER, yallsta() AS INTEGER, Ntotalsta AS
     INTEGER)

'WHATS GOING ON:
'This is an algorithm that branches from two other subs
findstations and
'findstavscaps.  It decides which points are inside the
minimum convex
'polygon (see findstations subroutine description).


Nverts = 0
FOR i = 1 TO maxNfixes
  IF xcoor2(i) > 0 THEN Nverts = Nverts + 1
NEXT i

PRINT "Nverts:"; Nverts

DIM slope(Nverts)
DIM xint(Nverts), yint(Nverts)
DIM direct(maxNfixes) AS INTEGER
minx = 19: miny = 19
```

```
maxx = 0: maxy = 0

FOR i = 1 TO Nverts
  IF xcoor2(i) < minx THEN minx = xcoor2(i)
  IF xcoor2(i) > maxx THEN maxx = xcoor2(i)
  IF ycoor2(i) < miny THEN miny = ycoor2(i)
  IF ycoor2(i) > maxy THEN maxy = ycoor2(i)
NEXT i

'PRINT "minxy,maxxy:"; minx; miny; maxx; maxy

FOR i = 1 TO Nverts
  IF i = Nverts THEN j = 1 ELSE j = i + 1
  deltay = ycoor2(i) - ycoor2(j)
  deltax = xcoor2(i) - xcoor2(j)
  IF deltay <> 0 AND deltax <> 0 THEN
    slope(i) = deltay / deltax
    yint(i) = ycoor2(i) - slope(i) * xcoor2(i)
    xint(i) = -yint(i) / slope(i)
    'PRINT "slope;ycoor2(i);ycoor2(j)"; slope(i); ycoor2(i);
          ycoor2(j)
    IF slope(i) > 0 AND ycoor2(i) > ycoor2(j) THEN direct(i)
          = 1
    IF slope(i) > 0 AND ycoor2(i) < ycoor2(j) THEN direct(i)
          = 0
    IF slope(i) < 0 AND ycoor2(i) > ycoor2(j) THEN direct(i)
          = 0
    IF slope(i) < 0 AND ycoor2(i) < ycoor2(j) THEN direct(i)
          = 1
    'PRINT "y1,y2, direction"; ycoor2(i); ycoor2(j); direct(i)
    'pauser
    '*****
  END IF
  IF deltax = 0 THEN
    slope(i) = 1000
    yint(i) = 1000
    xint(i) = xcoor2(i)
    IF xint(i) = minx THEN direct(i) = 0
    IF xint(i) = maxx THEN direct(i) = 1
    IF xint(i) <> minx AND xint(i) <> maxx THEN
      PRINT "problem with xint not min or max"
      pauser
    END IF
  END IF
  IF deltay = 0 THEN
    slope(i) = 0
    yint(i) = ycoor2(i)
    xint(i) = 1000
    IF yint(i) = miny THEN direct(i) = 0
    IF yint(i) = maxy THEN direct(i) = 1
    IF yint(i) <> miny AND yint(i) <> maxy THEN
      PRINT "Problem with yint not miny or maxy"
```

```
      pauser
    END IF
  END IF
  'PRINT "x,y"; xcoor2(i); ycoor2(i)
  'PRINT "x2,y2"; xcoor2(j); ycoor2(j)
  'PRINT "deltaxy"; deltax; deltay
  'PRINT "slope, yint,xint"; slope(i); yint(i); xint(i)
  'pauser
    '*****
NEXT i
PRINT

l = 0: Ntotalsta = 0
PRINT "Nverts:"; Nverts
FOR i = minx TO maxx STEP 1
FOR j = miny TO maxy STEP 1
  l = l + 1
  criteria = 0: stopper = 0: k = 0
  DO WHILE stopper <> 1 AND k < Nverts
    k = k + 1
    IF slope(k) = 0 THEN
      calc = yint(k)
      actual = j
    END IF
    IF slope(k) = 1000 THEN
      calc = xint(k)
      actual = i
    END IF
    IF slope(k) <> 0 AND slope(k) <> 1000 THEN
      calc = yint(k) + slope(k) * i
      actual = j
    END IF
    'PRINT "xy;calc:actual:direction"; i; j; "  "; calc;
          actual; "  "; direct(k)
    IF (calc + .005 >= actual AND direct(k) = 1) OR (calc -
          .005 <= actual AND direct(k) = 0) THEN
      criteria = criteria + 1
      'PRINT "here!"; criteria;
    ELSE
      'PRINT "stopped"
      stopper = 1
    END IF
  LOOP
  'pauser
  IF criteria = Nverts THEN
    'PRINT "made it to here";
    Ntotalsta = Ntotalsta + 1
    xallsta(Ntotalsta) = i
    yallsta(Ntotalsta) = j
    'PRINT xallsta(Ntotalsta); yallsta(Ntotalsta); "  ";
  END IF
NEXT j
```

```
NEXT i

END SUB

SUB findboundarypoints (x AS INTEGER, tempx2() AS INTEGER,
tempy2() AS INTEGER, wp AS INTEGER, bounxcoor() AS INTEGER,
bounycoor() AS INTEGER)
DIM xcoor2(maxNfixes) AS INTEGER
DIM ycoor2(maxNfixes) AS INTEGER
DIM B(maxNfixes) AS SINGLE
DIM theta(maxNfixes) AS SINGLE
DIM bounpointN(maxNfixes) AS INTEGER
'DIM bounxcoor(maxNfixes) AS INTEGER
'DIM bounycoor(maxNfixes) AS INTEGER

'WHATS GOING ON:
'This   algorithm   branches   from   several   other   subs.
Cooridinates are
'inputed from the other subs, and then this routine chooses
those
'cooridinates which form the outside vertices for a minimum
convex
'polygon.  It does this using angles that is too difficult to
describe
'without using diagrams.  I'll have to draw up a supplementary
'explanation.


FOR i = 1 TO maxNfixes
  xcoor2(i) = 0: ycoor2(i) = 0
  bounxcoor(i) = 0: bounycoor(i) = 0
NEXT i


' FOR i = 1 TO maxNfixes
'   PRINT tempx2(i); tempy2(i)
' NEXT i

Npts1 = 0
FOR i = 1 TO maxNfixes
  IF tempx2(i) <> -1 THEN
    FOR k = 1 TO i - 1
      IF tempx2(i) = xcoor2(k) AND tempy2(i) = ycoor2(k) THEN
GOTO skipout1
    NEXT k
    Npts1 = Npts1 + 1
    xcoor2(Npts1) = tempx2(i)
    ycoor2(Npts1) = tempy2(i)
  END IF
skipout1:
NEXT i
'PRINT "capture, temps"
```

```
'FOR i = 1 TO maxNfixes
'  PRINT x, tempx2(i); tempy2(i), xcoor2(i); ycoor2(i)
'NEXT i
'PRINT "id, Npts1"; id(rec); Npts1
'pauser

IF Npts1 = 1 THEN
             'if there is only one point, you skip
  bounxcoor(1) = xcoor2(1)
             'down past all the angle stuff.
  bounycoor(1) = ycoor2(1)
  wp = 1
  GOTO onepoint
END IF


'choose a starting point
startpt = 0
minx = xcoor2(1)
miny = 0
FOR i = 2 TO Npts1
  IF xcoor2(i) < minx THEN minx = xcoor2(i)
NEXT i
FOR i = 1 TO Npts1
  IF xcoor2(i) = minx AND ycoor2(i) > miny THEN
    miny = ycoor2(i)
    startpt = i
  END IF
NEXT i
IF startpt = 0 THEN PRINT "Didn't choose a starting point!":
'pauser
PRINT
'PRINT "Startpoint:", startpt
bounpointN(startpt) = 1
'pauser

wp = 1
DO WHILE stopper = 0
  'the next if then else chooses the new working points (wp)
and
  'the next working angle points (wap).
  IF wp = 1 THEN
    wpx = xcoor2(startpt): wpy = ycoor2(startpt)
    wapx = xcoor2(startpt): wapy = ycoor2(startpt) - 1.1
  ELSE
    deltax = wpx - xcoor2(minthetaid)
    deltay = wpy - ycoor2(minthetaid)
    IF (deltax = 0) THEN
      IF deltay > 0 THEN wapy = ycoor2(minthetaid) - 1.1
      IF deltay < 0 THEN wapy = ycoor2(minthetaid) + 1.1
      wapx = wpx
    END IF
```

```
    IF (deltay = 0) THEN
      IF deltax > 0 THEN wapx = xcoor2(minthetaid) - 1.1
      IF deltax < 0 THEN wapx = xcoor2(minthetaid) + 1.1
      wapy = wpy
    END IF
    IF (deltax <> 0) AND (deltay <> 0) THEN
      slope = deltay / deltax
      intercept = wpy - (wpx * slope)
      IF (deltax > 0) THEN wapx = xcoor2(minthetaid) - 1.1
      IF (deltax < 0) THEN wapx = xcoor2(minthetaid) + 1.1
      wapy = wapx * slope + intercept
    END IF
    wpx = xcoor2(minthetaid)
    wpy = ycoor2(minthetaid)
  END IF

  'this calculates angles between all points and the wp (which
     forms
  'the vertice between aother point and the wap.)
  FOR i = 1 TO Npts1
    costheta = 0
    a = 0: B(i) = 0: c = 0
    IF (wp <> bounpointN(i)) AND (bounpointN(i) < 2) THEN
      'a,b,c are distances between the points.
      ' The distance between wp and xcoor2 (b(i)) is important
     because
      '  if two points have the same angle, only the farthest
     is chosen
      '  as a boundary point.  Once the distances between the
     points are
      '  known, the Cosine Law can be used to calculate the
     angle.
      'PRINT "wpx,wapx,xcoor2(i)"; wpx; wpy; wapx; wapy;
     xcoor2(i); ycoor2(i)
      a = SQR((wapx - wpx) ^ 2 + (wapy - wpy) ^ 2)
      B(i) = SQR((xcoor2(i) - wpx) ^ 2 + (ycoor2(i) - wpy) ^2)
      c = SQR((wapx - xcoor2(i)) ^ 2 + (wapy - ycoor2(i)) ^ 2)
      costheta = (c ^ 2 - a ^ 2 - B(i) ^ 2) / (-2 * a * B(i))
'The Cosine Law
      'PRINT costheta
      IF (costheta > -.0005) AND (costheta < .0005) THEN
          theta(i) = pil / 2
      IF (costheta > 1 - .0005) AND (costheta < 1 + .0005)
          THEN theta(i) = 0
      IF (costheta > -1 - .0005) AND (costheta < -1 + .0005)
          THEN theta(i) = pil
      IF (costheta >= .0005) AND (costheta <= 1 - .0005) THEN
          theta(i) = ATN(SQR(1 - costheta ^ 2) / costheta)
      END IF
      IF (costheta <= -.0005) AND (costheta >= -1 + .0005)
          THEN
          theta(i) = pil + ATN(SQR(1 - costheta ^ 2) /
```

```
            costheta)
        END IF
        'PRINT "i,theta"; i; theta(i)
      END IF
    NEXT i
    'now the smallest angle must be chosen
    mintheta = 181
    FOR i = 1 TO Npts1
      'PRINT "i, theta(i)"; i; theta(i); xcoor2(i); ycoor2(i)
      IF (wp <> bounpointN(i)) AND (bounpointN(i) < 2) THEN
        IF (theta(i) < mintheta - .0005) THEN
          'PRINT "i,theta(i)"; i; theta(i); xcoor2(i); ycoor2(i)
          mintheta = theta(i)
          minthetaid = i
        END IF
        IF (theta(i) < mintheta + .0005) AND (theta(i) >
            mintheta - .0005) AND B(i) > B(minthetaid) THEN
            minthetaid = i
      END IF
    NEXT i
    'PRINT "Lowest theta:"; theta(minthetaid)
    wp = wp + 1
    ' preparing to go on the the next point
    IF minthetaid <> startpt THEN
      'pauser
      bounpointN(minthetaid) = wp
      ELSE
        stopper = 1
        wp = wp - 1
    END IF
  LOOP

  FOR i = 1 TO Npts1
    IF bounpointN(i) > 0 THEN
      bounxcoor(bounpointN(i)) = xcoor2(i)
      bounycoor(bounpointN(i)) = ycoor2(i)
    END IF
  NEXT i

  'FOR i = 1 TO maxNfixes
  '  PRINT bounxcoor(i); bounycoor(i);
  'NEXT i
  onepoint:

  END SUB

  SUB findstations
  SHARED Nstations AS INTEGER
  DIM tempx(maxNfixes) AS INTEGER
  DIM tempy(maxNfixes) AS INTEGER
  DIM xallsta(100) AS INTEGER
  DIM yallsta(100) AS INTEGER
```

```
'WHATS GOING ON:
'This algorithm is used to measure home range size by counting
the
'number of stations contained within the home range.

'It finds the stations that are contained within the
'minimum convex polygon that is defined by the boundary
points. It was
'a lot f harder than I originally thot to write this
algorithm!
'The method I eventually used was to use the x-y cooridinates
of the
'boundary points to calculate the equations for the lines that
form the
'boundary. Then, the tricky part was that the computer has to
decide if
'the station in question is supposed to be above that line to
be counted "in",
'or below the line to be counted "in". The decision is made,
and then
'each  station is
'is tested to see if it is on the "in" or "out" side for each
line.
'This process is repeated for all
'the lines of the convex polygon, and if the station is "in"
'for each of the lines, it is counted "in" and
'saved to a file, findstafile$.

'The data file is saved in this order, for each line the order
is:
'check (-2), record number, session, location, sex, age,
species, id
'number of captures, edge (1 if HR touches edge of plot, 0
otherwise),
'the number of stations within the polygon,
'and finally the x y cooridinates for the stations within the
polygon.

'  To signal the end of the file, a -9999 is placed alone on
the last
'line of the file.
'NOTE: there are no -1's inserted after the xy cooridinates
because
'the number of stations within a polygon is indeterminate.


'findstafile$ = "c:\larry\homerang\finsta.tst"
OPEN findstafile$ FOR OUTPUT AS #5
FOR rec = 1 TO Numofrecords
  m = 0
  FOR i = 1 TO maxNfixes
    tempx(i) = xcoor(rec, i)
```

```
    tempy(i) = ycoor(rec, i)
    IF xcoor(rec, i) > 0 THEN m = m + 1
  NEXT i
  IF rec > 1 THEN
    REDIM xallsta(100) AS INTEGER
    REDIM yallsta(100) AS INTEGER
  END IF
  Nstations = 0
  IF m > 1 THEN
    findallstations tempx(), tempy(), xallsta(), yallsta(),
Nstations
  ELSE
    xallsta(1) = tempx(1)
    yallsta(1) = tempy(1)
    Nstations = 1
  END IF
  PRINT #5, USING "####"; -2; recordN(rec); sess(rec);
     loca(rec); sex(rec);
  PRINT #5, USING "#####"; age(rec); spp(rec); id(rec);
     Ncaps(rec); edge(rec); edgetwo(rec); Nstations;
  PRINT USING "####"; -2; recordN(rec); sess(rec); loca(rec);
     sex(rec);
  PRINT USING "####"; age(rec); spp(rec); id(rec); Ncaps(rec);
     edge(rec); edgetwo(rec); Nstations;
  i = 1
  DO WHILE xallsta(i) > 0
    IF xallsta(i) > 0 THEN PRINT #5, USING "###"; xallsta(i);
      yallsta(i);
    IF xallsta(i) > 0 THEN PRINT USING "###"; xallsta(i);
      yallsta(i);
    i = i + 1
  LOOP
  PRINT #5, " "
  PRINT
NEXT rec
PRINT #5, -9999
CLOSE #5
datamenu

END SUB

SUB findstavscaps
SHARED Nstations AS INTEGER
SHARED wp AS INTEGER, rec AS INTEGER
DIM tempx(maxNfixes) AS INTEGER
DIM tempy(maxNfixes) AS INTEGER
DIM bounx(maxNfixes) AS INTEGER
DIM bouny(maxNfixes) AS INTEGER
DIM xallsta(100) AS INTEGER
DIM yallsta(100) AS INTEGER
DIM Nstats(maxNfixes) AS INTEGER
```

```
'WHATS GOING ON:
'This algorithm would be used if you wanted to know how the
home range size
'changed as more and more capture points are included.

'See findstations for a description of how the stations within
a
'minimum convex polygon are found.  This algorithm does the
same thing,
'but it does the same thing several times for each individual.
It starts
'with 2 captures, and counts the number of stations in, then
repeats the
'process, each time including a new capture point. That means
that
'it starts with the raw capture data, finds the boundary
points using
'only the first 2 or 3 or etc captures, then finds how many
stations are
'contained within that subset of data.  The data is saved to
'     "stavscapfile$."
'
'Each line in the data file is saved in this order:
'check(-2), record number, session, location, sex, age,
species, id,
'number of captures used to find stations, edge (1 if it
touches the edge, 0 otherwise),
'number of stations in polygon, percent change, and the
cooridinates of each
'station within the polygon.
'At the end of the file, on its own line, a -9999 is placed to
signal
'the end of the file.
'NOTE: there are no -1's in this file as the number of
stations is
'indeterminate.


PRINT "WARNING: THIS SUBROUTINE SHOULD ONLY BE USED IF YOU
HAVE"
PRINT "CHOSEN THE DATA FOR THE 'RAW CAPTURE DATA'."
PRINT "THE PROGRAM WILL WORK IF BOUNDARY POINT FILE IS USED"
PRINT "BUT IT WILL NOT GIVE YOU VERY MEANINGFUL RESULTS!"
PRINT : PRINT
PRINT "Do you wish to continue? (y/n)"
INPUT y$
IF y$ <> "y" THEN datamenu

OPEN stavscapfile$ FOR OUTPUT AS #8
FOR rec = 1 TO Numofrecords
  m = 0
  FOR i = 1 TO maxNfixes
```

```
  IF xcoor(rec, i) > 0 THEN m = m + 1
NEXT i
IF m > 1 THEN
  REDIM Nstats(maxNfixes) AS INTEGER
  FOR caps = 2 TO m
    IF rec > 1 OR caps > 2 THEN
      REDIM xallsta(100) AS INTEGER
      REDIM yallsta(100) AS INTEGER
      REDIM bounx(maxNfixes) AS INTEGER
      REDIM bouny(maxNfixes) AS INTEGER

    END IF
    FOR i = 1 TO caps
      tempx(i) = xcoor(rec, i)
      tempy(i) = ycoor(rec, i)
    NEXT i
    FOR i = caps + 1 TO maxNfixes
      tempx(i) = -1
      tempy(i) = -1
    NEXT i
    findboundarypoints rec, tempx(), tempy(), wp, bounx(),
        bouny()
    'FOR i = 1 TO maxNfixes
    '  PRINT "output:"; bounx(i); bouny(i);
    'NEXT i
    PRINT

    Nstations = 0
    findallstations bounx(), bouny(), xallsta(), yallsta(),
        Nstations
    Nstats(caps) = Nstations
    perchange = 0
    IF caps > 2 THEN perchange = 100 * ((Nstats(caps) /
        Nstats(caps - 1)) - 1)
    'PRINT "Nstations & previous Nstations:   ";
        Nstats(caps); Nstats(caps - 1); perchange

    PRINT #8, USING "####"; -2; recordN(rec); sess(rec);
        loca(rec); sex(rec);
    PRINT #8, USING "#####"; age(rec); spp(rec); id(rec);
        caps; edge(rec); edgetwo(rec); Nstations;
    PRINT #8, USING "#####"; perchange;
    PRINT USING "####"; -2; recordN(rec); sess(rec);
        loca(rec); sex(rec);
    PRINT USING "####"; age(rec); spp(rec); id(rec); caps;
        edge(rec); Nstations; perchange;
    PRINT USING "#####"; perchange;
    i = 1
    DO WHILE xallsta(i) > 0
      IF xallsta(i) > 0 THEN PRINT #8, USING "###";
        xallsta(i); yallsta(i);
      IF xallsta(i) > 0 THEN PRINT USING "###"; xallsta(i);
```

```
          yallsta(i);
        i = i + 1
      LOOP
      PRINT #8, " "
      PRINT
    NEXT caps
  END IF
NEXT rec
PRINT #8, -9999
CLOSE #8
datamenu

END SUB

SUB functionmenu
CLS
'WHATS GOING ON:
'This menu only pops up after you have chosen data from the
DATAMENU sub.
'It allows you to manipulate the data.


PRINT "This screen allows you to choose something to do with
your"
PRINT "data, but remember that you have to have the
appropriate data"
PRINT "opened.  If you would like to change the data, choose
#7 to go"
PRINT "back to the data menu."
PRINT
PRINT
PRINT "What would you like to do with the opened data:"
PRINT "   1) Find boundary points."
PRINT "   2) Calculate home range sizes."
PRINT "   3) Calculate home ranges sizes as a function of the"
PRINT "      number of captures."
PRINT "   4) Calculate the amount of overlap (individuals and
groups)."
PRINT "   5) Calculate habitat composition of the loaded
data."
PRINT "   6) Plot a map."
PRINT "   7) Go back to the data menu."
PRINT "   8) Find all the stations that lie within home
ranges."
PRINT "   9) Number of stations as a function of the number of
captures"
INPUT choice
CLS
IF choice = 1 THEN
  PRINT "YOU MUST HAVE THE 'RAW CAPTURE DATA' FILE OPEN"
  PRINT "TO USE THIS FUNCTION PROPERLY."
  INPUT "Do you wish to go back to the data menu? (y/n)", y$
```

```
  IF y$ = "y" THEN datamenu
  bounpoints
END IF
IF choice = 2 THEN
  PRINT "YOU MUST HAVE THE 'BOUNDARY POINTS DATA' FILE OPEN"
  PRINT "TO USE THIS FUNCTION PROPERLY."
  INPUT "Do you wish to go back to the data menu? (y/n)", y$
  IF y$ = "y" THEN datamenu
  hrsize
END IF
  IF choice = 3 THEN hrsizepoints
IF choice = 4 THEN
  PRINT "YOU MUST HAVE THE 'ALL STATIONS IN HOME RANGE (#4)'
DATA OPEN"
  PRINT "TO USE THIS FUNCTION PROPERLY."
  PRINT
  INPUT "Do you wish to go back to the data menu? (y/n)", y$
  IF y$ = "y" THEN datamenu
  overlap
END IF
IF choice = 5 THEN
  PRINT "YOU MUST HAVE THE 'ALL STATIONS IN HOME RANGE (#4)'
FILE OPEN"
  PRINT "TO USE THIS FUNCTION PROPERLY."
  PRINT
  INPUT "Do you wish to go back to the data menu? (y/n)", y$
  IF y$ = "y" THEN datamenu
  habitatcomp
END IF
IF choice = 6 THEN
  PRINT "YOU MUST HAVE THE 'BOUNDARY POINTS DATA' FILE OPEN"
  PRINT "TO USE THIS FUNCTION PROPERLY."
  PRINT
  INPUT "Do you wish to go back to the data menu? (y/n)", y$
  IF y$ = "y" THEN datamenu
  plotmap
END IF
IF choice = 7 THEN datamenu
IF choice = 8 THEN
  PRINT "YOU MUST HAVE THE 'BOUNDARY POINTS DATA' FILE OPEN"
  PRINT "TO USE THIS FUNCTION PROPERLY."
  PRINT
  INPUT "Do you wish to go back to the data menu? (y/n)", y$
  IF y$ = "y" THEN datamenu
  findstations
END IF

IF choice = 9 THEN findstavscaps
END SUB

SUB habitatcomp
SHARED colm1$
```

```
SHARED coll AS INTEGER

'WHATS GOING ON:

'This subroutine measures the habitat composition of a home
range.

'It does this because by the user loading the file containing
the list
'of stations contained within the home range, then finding the
habitat
'values for that station, and adding them to the total (a
total value
'for pc1,2,&3).

'the pc file should be saved from an spss file in the
following format:
'1. a column of -2's (the check)
'2. the location (1 or 2)
'3. the station (e.g. a13, letters a-i, numbers 1-18)
'4. then the three pc scores.



DIM pc1(2, 9, 18)
DIM pc2(2, 9, 18)
DIM pc3(2, 9, 18)


'pcscorefile$ = "c:\larry\homerang\pcfile.dat"
OPEN pcscorefile$ FOR INPUT AS #6
FOR i = 1 TO 324
  INPUT #6, check
  IF check <> -2 THEN
    PRINT "Check is:"; check
    STOP
  END IF
  INPUT #6, local
  IF local = 0 THEN local = 2
  colm1$ = INPUT$(1, 6)
  row1 = VAL(INPUT$(4, 6))
  convertxy colm1$, coll
  INPUT #6, pc1(local, coll, row1)
  INPUT #6, pc2(local, coll, row1)
  INPUT #6, pc3(local, coll, row1)
  PRINT local; coll; row1; pc1(local, coll, row1); pc2(local,
coll, row1); pc3(local, coll, row1)
NEXT i
CLOSE #6
'hrcompfile$ = "c:\larry\homerang\hrcomp.tst"
OPEN hrcompfile$ FOR OUTPUT AS #7
```

```
FOR rec = 1 TO Numofrecords
  Npts = 0: pc1b = 0: pc2b = 0: pc3b = 0
  i = 1
  DO WHILE xcoor(rec, i) > 0
     IF xcoor(rec, i) > 0 THEN Npts = Npts + 1
     i = i + 1
  LOOP
  FOR i = 1 TO Npts
    pc1b = pc1b + pc1(loca(rec), xcoor(rec, i), ycoor(rec, i))
    pc2b = pc2b + pc2(loca(rec), xcoor(rec, i), ycoor(rec, i))
    pc3b = pc3b + pc3(loca(rec), xcoor(rec, i), ycoor(rec, i))
    PRINT "pc1"; pc1(loca(rec), xcoor(rec, i), ycoor(rec, i))
    PRINT "pc2"; pc2(loca(rec), xcoor(rec, i), ycoor(rec, i))
    PRINT "pc3"; pc3(loca(rec), xcoor(rec, i), ycoor(rec, i))
  NEXT i
  PRINT Nstas(rec), Npts
  PRINT  #7,  USING  "####";  -2;  recordN(rec);  sess(rec);
loca(rec); sex(rec);
  PRINT  #7,  USING  "#####";  age(rec);  spp(rec);  id(rec);
Ncaps(rec); edge(rec); edgetwo(rec); Npts;
  PRINT #7, USING "####.#####"; pc1b; pc2b; pc3b; pc1b / Npts;
pc2b / Npts; pc3b / Npts
  PRINT USING "##"; -2; recordN(rec); sess(rec); loca(rec);
sex(rec);
  PRINT USING "###"; age(rec); spp(rec); id(rec); Ncaps(rec);
edge(rec); Npts;
  PRINT USING "###.####"; pc1b; pc2b; pc3b; pc1b / Npts; pc2b
/ Npts; pc3b / Npts
  'pauser
NEXT rec

CLOSE #6
datamenu
END SUB

SUB hrcalc  (Npts AS INTEGER,  hrarea AS SINGLE,  xcoor2()  AS
INTEGER, ycoor2() AS INTEGER)
'this is based on an equation found in a surveying textbook
that
'calculates area for polygons when the vertices cooridinates
'are known.
'A = 0.5 * [(x2y1 + x3y2 + ... + x1yn) - (x1y2 + x2y3 + ... +
nxy1)]

temparea1 = 0
temparea2 = 0
hrarea = 0
FOR j = 1 TO (Npts - 1)
  temparea1 = temparea1 + xcoor2(j) * ycoor2(j + 1)
  temparea2 = temparea2 + xcoor2(j + 1) * ycoor2(j)
NEXT j
temparea1 = temparea1 + xcoor2(Npts) * ycoor2(1)
```

```
temparea2 = temparea2 + xcoor2(1) * ycoor2(Npts)
PRINT "temparea1&2)"; temparea1; temparea2
'the  156.25  multiplier  is  to  convert  area  from  grid
cooridinates
'into metres squared.
hrarea = -156.25 * (.5 * (temparea2 - temparea1))
PRINT "        area:"; hrarea


END SUB

SUB hrsize
SHARED hrarea AS SINGLE
SHARED Npts AS INTEGER
DIM tempx(maxNfixes) AS INTEGER
DIM tempy(maxNfixes) AS INTEGER
'print "What is the name of the file where you would"
'print "like the home range sizes saved?"
'input hrsizefile$
'hrsizefile$ = "c:\larry\homerang\hrsize.tst"
OPEN hrsizefile$ FOR OUTPUT AS #4
FOR rec = 1 TO Numofrecords
  IF rec > 1 THEN
    REDIM tempx(maxNfixes)
    REDIM tempy(maxNfixes)
  END IF
  Npts = 0
  FOR i = 1 TO maxNfixes
    tempx(i) = xcoor(rec, i): tempy(i) = ycoor(rec, i)
    IF xcoor(rec, i) > -1 THEN Npts = Npts + 1
  NEXT i
  hrcalc Npts, hrarea, tempx(), tempy()
  PRINT #4, USING "####"; -2; recordN(rec); sess(rec);
     loca(rec); sex(rec);
  PRINT #4, USING "#####"; age(rec); spp(rec); id(rec);
     Ncaps(rec); edge(rec); edgetwo(rec);
  PRINT #4, USING "#####.###"; hrarea
  PRINT USING "####"; -2; recordN(rec); sess(rec); loca(rec);
     sex(rec);
  PRINT USING "####"; age(rec); spp(rec); id(rec); Ncaps(rec);
     edge(rec); edgetwo(rec);
  PRINT USING "#####.###"; hrarea
  pauser
NEXT rec

CLOSE #4
datamenu
END SUB

SUB hrsizepoints
SHARED Npts1 AS INTEGER, rec AS INTEGER
SHARED hrarea2 AS SINGLE, wp   AS INTEGER
```

```
DIM tempx(maxNfixes) AS INTEGER
DIM tempy(maxNfixes) AS INTEGER
DIM bounx(maxNfixes) AS INTEGER
DIM bouny(maxNfixes) AS INTEGER

'hrsizecap$ = "c:\larry\homerang\hrszcap.tst"

OPEN hrsizecap$ FOR OUTPUT AS #5

FOR rec = 1 TO Numofrecords
  Npts = 0
  FOR i = 1 TO maxNfixes
    IF xcoor(rec, i) <> -1 THEN Npts = Npts + 1
  NEXT i

  IF Npts > 2 THEN
    FOR i = 2 TO Npts
      PRINT "Input:";
      FOR j = 1 TO i
          tempx(j) = xcoor(rec, j): tempy(j) = ycoor(rec, j)
          bounx(j) = -1: bouny(j) = -1
          PRINT tempx(j); tempy(j); "  ";
      NEXT j
      FOR j = i + 1 TO maxNfixes
        tempx(j) = -1: tempy(j) = -1
        bounx(j) = -1: bouny(j) = -1
        PRINT tempx(j); tempy(j);
      NEXT j
      PRINT
      findboundarypoints rec, tempx(), tempy(), wp, bounx(),
          bouny()
      PRINT "Output:";
      FOR k = 1 TO maxNfixes
        PRINT bounx(k); bouny(k); "  ";
      NEXT k
      PRINT
      'pauser
      Npts1 = 0
      FOR j = 1 TO maxNfixes
        IF bounx(j) > 0 THEN Npts1 = Npts1 + 1
      NEXT j
      PRINT "Npts:"; i;
      hrcalc Npts1, hrarea2, bounx(), bouny()
      'pauser
      PRINT #5, USING "####"; -2; recordN(rec); sess(rec);
          loca(rec); sex(rec);
      PRINT #5, USING "#####"; age(rec); spp(rec); id(rec);
          Ncaps(rec); edge(rec); edgetwo(rec);
      PRINT #5, USING "####"; i;
      PRINT #5, USING "#####.###"; hrarea2
    NEXT i
  END IF
```

```
NEXT rec
CLOSE #5
datamenu
END SUB

SUB overlap

'WHATS GOING ON
'this routine records the home range overlap of individuals
'of the same species.  The amount of overlap is calculated as
the
'number of stations that the species share.  The data used,
therefore,
'is the list of all the stations in the home range (#4 in the
data menu).

'The data is recorded as the total number of stations that the
individual
'overlaps, and then this is broken down into the number of
stations
'overlapped with adult females, juv females, adult males, and
juv males.

'I might later include the number of different individuals
that overlap
'with the target individual.

'Notice that the data are first ordered by stations in hopes
of speeding
'up the routine.

DIM stationrecs(2, 9, 18, 10) AS INTEGER
DIM uniquerecs(200) AS INTEGER


'First order the data:

FOR location = 1 TO 2
FOR r = 1 TO 9
FOR c = 1 TO 18
  i = 0
  FOR rec = 1 TO Numofrecords
    k = 0
    FOR stations = 1 TO Nstas(rec)
      IF loca(rec) = location THEN
      IF xcoor(rec, stations) = r THEN
      IF ycoor(rec, stations) = c THEN
        i = i + 1
        stationrecs(location, r, c, i) = rec
        k = k + 1
      END IF
      END IF
```

```
      END IF
    NEXT stations
  NEXT rec
NEXT c
NEXT r
NEXT location

'Now find the overlap:
OPEN overlapfile$ FOR OUTPUT AS #10

FOR rec = 1 TO Numofrecords
  q = 0
  REDIM uniquerecs(200)
  Nstmad = 0: Nstfad = 0: Nstmjuv = 0: Nstfjuv = 0:
  totalstations = 0
  Nmad = 0: Nfad = 0: Nmjuv = 0: Nfjuv = 0: totalindivs = 0
  FOR stations = 1 TO Nstas(rec)
    PRINT "xy, id", id(rec); xcoor(rec, stations); ycoor(rec,
     stations)
    k = 0
    FOR i = 1 TO 10
      j = stationrecs(loca(rec), xcoor(rec, stations),
          ycoor(rec, stations), i)
      PRINT "sex,age, id"; sex(j); age(j); id(j)
      IF j <> rec AND j > 0 THEN
          IF loca(rec) <> loca(j) THEN BEEP: PRINT "What
          the...?"
          q = q + 1
          'PRINT q
          uniquerecs(q) = j
          IF sex(j) = 1 AND age(j) = 1 THEN
            Nstmad = Nstmad + 1
            k = 1
          END IF
          IF sex(j) = 2 AND age(j) = 1 THEN
            Nstfad = Nstfad + 1
            k = 1
          END IF
          IF sex(j) = 1 AND age(j) = 2 THEN
            Nstmjuv = Nstmjuv + 1
            k = 1
          END IF
          IF sex(j) = 2 AND age(j) = 2 THEN
            Nstfjuv = Nstfjuv + 1
            k = 1
          END IF
      END IF
    'pauser
    NEXT i
    IF k = 1 THEN totalstations = totalstations + 1
NEXT stations
'Now to count the number of individuals
```

```
IF totalstations > 0 THEN
  IF sex(uniquerecs(1)) = 1 AND age(uniquerecs(1)) = 1 THEN
     Nmad = Nmad + 1
  IF sex(uniquerecs(1)) = 2 AND age(uniquerecs(1)) = 1 THEN
     Nfad = Nfad + 1
  IF sex(uniquerecs(1)) = 1 AND age(uniquerecs(1)) = 2 THEN
     Nmjuv = Nmjuv + 1
  IF sex(uniquerecs(1)) = 2 AND age(uniquerecs(1)) = 2 THEN
     Nfjuv = Nfjuv + 1

  FOR i = 2 TO q
    k = 0
    FOR j = 1 TO i - 1
      IF uniquerecs(i) = uniquerecs(j) THEN k = 1
    NEXT j
    IF k = 0 THEN
      IF sex(uniquerecs(i)) = 1 AND age(uniquerecs(i)) = 1
          THEN Nmad = Nmad + 1
      IF sex(uniquerecs(i)) = 2 AND age(uniquerecs(i)) = 1
          THEN Nfad = Nfad + 1
      IF sex(uniquerecs(i)) = 1 AND age(uniquerecs(i)) = 2
          THEN Nmjuv = Nmjuv + 1
      IF sex(uniquerecs(i)) = 2 AND age(uniquerecs(i)) = 2
          THEN Nfjuv = Nfjuv + 1
    END IF
  NEXT i
totalindivs = Nmad + Nfad + Nmjuv + Nfjuv
END IF

PRINT #10, USING "####"; -2; rec; sess(rec); loca(rec);
sex(rec);
PRINT #10, USING "#####"; age(rec); spp(rec); id(rec);
Ncaps(rec); edge(rec); edgetwo(rec); Nstas(rec);
PRINT #10, USING "####"; totalstations; Nstmad; Nstfad;
Nstmjuv; Nstfjuv;
PRINT #10, USING "####"; totalindivs; Nmad; Nfad; Nmjuv; Nfjuv
PRINT USING "####"; -2; rec; sess(rec); loca(rec); sex(rec);
PRINT USING "#####"; age(rec); spp(rec); id(rec); Ncaps(rec);
edge(rec); edgetwo(rec); Nstas(rec);
PRINT USING "####"; totalstations; Nstmad; Nstfad; Nstmjuv;
Nstfjuv;
PRINT "    ";
PRINT USING "####"; totalindivs; Nmad; Nfad; Nmjuv; Nfjuv
'pauser
NEXT rec

BEEP
datamenu
END SUB
```

```
SUB pauser
DO WHILE INKEY$ = ""
LOOP
END SUB

SUB plotmap

anothermap$ = "y"
DO WHILE anothermap$ = "y"
REDIM hrarea(500) AS SINGLE
'hrsizefile$ = "c:\larry\homerang\hrsize.tst"

'OPEN hrsizefile$ FOR INPUT AS #4
'FOR rec = 1 TO Numofrecords
'  FOR j = 1 TO 10
'    INPUT #4, a
'  NEXT j
'  INPUT #4, hrarea(rec)
'NEXT rec
'CLOSE #4
PRINT "You have the following choices:"
PRINT "  1) One map for a session and location with ALL"
PRINT "     individuals on the map."
PRINT "  2) One map but the sexes separated."
choice = 0
DO WHILE choice < 1 OR choice > 2
  INPUT choice
LOOP
IF choice = 1 THEN
  PRINT "Do you want each individual printed separately, with
their"
  PRINT "i.d. and home range size shown (and then cleared
afterwards?)"
  PRINT "y/n"
  INPUT indiv$
ELSE
  indiv$ = "n"
END IF
PRINT
PRINT
INPUT "Which session would you like mapped (1,2,3)?", sessid
PRINT
INPUT "Which location would you like mapped (nor=1,sou=2)?",
locid

CLS

SCREEN 13
WINDOW (100, 0)-(0, 100)
PRINT "Session:"; sessid, "Location: ";
IF locid = 1 THEN PRINT "North" ELSE IF locid = 2 THEN PRINT
```

```
"South"
m = 7
LINE (4, 4)-(46, 91), 13, B

IF choice = 2 THEN LINE (54, 4)-(96, 91), 13, B
FOR rec = 1 TO Numofrecords
  'LINE (4, 4)-(46, 91), 13, B
  FOR i = 1 TO 9
  FOR j = 1 TO 18
    LINE (i * 5 - .1, j * 5 - .1)-(i * 5 + .1, j * 5 + .1),
          13, B
  NEXT j
  NEXT i

  IF choice = 2 THEN LINE (54, 4)-(96, 91), 13, B
  IF sess(rec) = sessid AND loca(rec) = locid THEN
    FOR i = 1 TO maxNfixes
      IF xcoor(rec, i) <> -1 THEN
          IF xcoor(rec, i + 1) = -1 THEN j = 1 ELSE j = i + 1
          IF choice = 2 AND sex(rec) = 1 THEN l = 50 ELSE l=0
          LINE (l + 5 * xcoor(rec, i), 5 * ycoor(rec, i))-(l
               + 5 * xcoor(rec, j), 5 * ycoor(rec, j)), 15
        END IF
      IF xcoor(rec, i) = -1 AND i = 2 THEN
        LINE (l + 5 * xcoor(rec, 1) - .4, 5 * ycoor(rec, 1) -
          .4)-(l + 5 * xcoor(rec, 1) + .4, 5 * ycoor(rec, 1)
          + .4), 15, B
      END IF
      NEXT i
    IF indiv$ = "y" THEN
       LOCATE 5, 20
       PRINT id(rec); hrarea(rec)
       pauser
       CLS
    END IF
  END IF
  IF m < 15 THEN m = m + 1 ELSE m = 7
NEXT rec
INPUT "do you want to map again?"; anothermap$
CLS
LOOP
datamenu


END SUB
```

APPENDIX II

A program written in BASIC used to calculate Moran's coefficient for habitats located in blocks of stations.

```
DECLARE SUB pauser ()
DECLARE SUB blockdata ()
COMMON SHARED totl1pc1
COMMON SHARED totl1pc2
COMMON SHARED totl1pc3
COMMON SHARED totl2pc1
COMMON SHARED totl2pc2
COMMON SHARED totl2pc3
COMMON SHARED meanl1pc1
COMMON SHARED meanl1pc2
COMMON SHARED meanl1pc3
COMMON SHARED meanl2pc1
COMMON SHARED meanl2pc2
COMMON SHARED meanl2pc3

DIM SHARED stanum(3, 6) AS INTEGER
DIM SHARED coeff(18, 18) AS INTEGER
DIM SHARED blockpc1(2, 3, 6)
DIM SHARED blockpc2(2, 3, 6)
DIM SHARED blockpc3(2, 3, 6)


blockdata

totpc1 = 0: totpc2 = 0: totpc3 = 0
FOR loca = 1 TO 2
FOR row = 1 TO 3
FOR col = 1 TO 6
  IF loca = 1 THEN
    totl1pc1 = totl1pc1 + blockpc1(loca, row, col)
    totl1pc2 = totl1pc2 + blockpc2(loca, row, col)
    totl1pc3 = totl1pc3 + blockpc3(loca, row, col)
  END IF
  IF loca = 2 THEN
    totl2pc1 = totl2pc1 + blockpc1(loca, row, col)
    totl2pc2 = totl2pc2 + blockpc2(loca, row, col)
    totl2pc3 = totl2pc3 + blockpc3(loca, row, col)
  END IF
NEXT col
NEXT row
NEXT loca
meanl1pc1 = totl1pc1 / 18
meanl2pc1 = totl2pc1 / 18
meanl1pc2 = totl1pc2 / 18
meanl2pc2 = totl2pc2 / 18
meanl1pc3 = totl1pc3 / 18
meanl2pc3 = totl2pc3 / 18
PRINT "Location 1"
PRINT totl1pc1, totl1pc2, totl1pc3
PRINT meanl1pc1, meanl1pc2, meanl1pc3
```

```
PRINT
PRINT "location2"
PRINT totl2pc1, totl2pc2, totl2pc3
PRINT meanl2pc1, meanl2pc2, meanl2pc3
pauser
FOR i = 1 TO 18
FOR j = 1 TO 18
r1 = FIX((i - 1) / 6) + 1
c1 = i - 6 * (r1 - 1)
r2 = FIX((j - 1) / 6) + 1
c2 = j - 6 * (r2 - 1)
PRINT i; r1; c1, j; r2; c2
'pauser
IF coeff(i, j) = 1 THEN
    covl1pc1 = (blockpc1(1, r1, c1) - meanl1pc1) *
          (blockpc1(1, r2, c2) - meanl1pc1)
    covl2pc1 = (blockpc1(2, r1, c1) - meanl2pc1) *
          (blockpc1(2, r2, c2) - meanl2pc1)
    covl1pc2 = (blockpc1(1, r1, c1) - meanl1pc2) *
          (blockpc2(1, r2, c2) - meanl1pc2)
    covl2pc2 = (blockpc1(2, r1, c1) - meanl2pc2) *
          (blockpc2(2, r2, c2) - meanl2pc2)
    covl1pc3 = (blockpc1(1, r1, c1) - meanl1pc3) *
          (blockpc3(1, r2, c2) - meanl1pc3)
    covl2pc3 = (blockpc1(2, r1, c1) - meanl2pc3) *
          (blockpc3(2, r2, c2) - meanl2pc3)
    totcovl1pc1 = totcovl1pc1 + covl1pc1
    totcovl2pc1 = totcovl2pc1 + covl2pc1
    totcovl1pc2 = totcovl1pc2 + covl1pc2
    totcovl2pc2 = totcovl2pc2 + covl2pc2
    totcovl1pc3 = totcovl1pc3 + covl1pc3
    totcovl2pc3 = totcovl2pc3 + covl2pc3
    'RINT i; j,
    'RINT USING "######.###";
    'pauser
END IF
NEXT j
NEXT i
PRINT "TOTALS: (l1pc1, l2pc1, l1pc2, l2pc2, l1pc3, l2pc3"
PRINT USING "#######.###"; totcovl1pc1; totcovl2pc1;
     totcovl1pc2; totcovl2pc2; totcovl1pc3; totcovl2pc3
FOR r = 1 TO 3
FOR c = 1 TO 6
    totdenl1pc1 = totdenl1pc1 + (blockpc1(1, r, c) -
          meanl1pc1) ^ 2
    totdenl2pc1 = totdenl2pc1 + (blockpc1(2, r, c) -
          meanl2pc1) ^ 2
    totdenl1pc2 = totdenl1pc2 + (blockpc2(1, r, c) -
          meanl1pc2) ^ 2
    totdenl2pc2 = totdenl2pc2 + (blockpc2(2, r, c) -
          meanl2pc2) ^ 2
    totdenl1pc3 = totdenl1pc3 + (blockpc3(1, r, c) -
```

```
            meanl1pc3) ^ 2
        totdenl2pc3 = totdenl2pc3 + (blockpc3(2, r, c) -
            meanl2pc3) ^ 2
    NEXT c
    NEXT r
    PRINT "Denominators:"
    PRINT   USING   "#######.###";   totdenl1pc1;   totdenl2pc1;
    totdenl1pc2; totdenl2pc2; totdenl1pc3; totdenl2pc3
    moranl1pc1 = (18 / 54) * (totcovl1pc1 / totdenl1pc1)
    moranl2pc1 = (18 / 54) * (totcovl2pc1 / totdenl2pc1)
    moranl1pc2 = (18 / 54) * (totcovl1pc2 / totdenl1pc2)
    moranl2pc2 = (18 / 54) * (totcovl2pc2 / totdenl2pc2)
    moranl1pc3 = (18 / 54) * (totcovl1pc3 / totdenl1pc3)
    moranl2pc3 = (18 / 54) * (totcovl2pc3 / totdenl2pc3)
    PRINT "Location 1:"
    PRINT "PC1  ";
    PRINT USING "####.####"; moranl1pc1
    PRINT "PC2  ";
    PRINT USING "##.###"; moranl1pc2
    PRINT "PC3  ";
    PRINT USING "##.###"; moranl1pc3
    PRINT
    PRINT "Location 2:"
    PRINT "PC1  ";
    PRINT USING "##.###"; moranl2pc1
    PRINT "PC2  ";
    PRINT USING "##.###"; moranl2pc2
    PRINT "PC3  ";
    PRINT USING "##.###"; moranl2pc3

    PRINT
    PRINT "bye"

    SUB blockdata

    blockpc1(2, 1, 1) = -2.72
    blockpc1(2, 1, 2) = 3.31
    blockpc1(2, 1, 3) = -.9
    blockpc1(2, 1, 4) = .51
    blockpc1(2, 1, 5) = 1.19
    blockpc1(2, 1, 6) = 1.41
    blockpc1(2, 2, 1) = 3.31
    blockpc1(2, 2, 2) = -3.43
    blockpc1(2, 2, 3) = 2.19
    blockpc1(2, 2, 4) = -5.35
    blockpc1(2, 2, 5) = 4.76
    blockpc1(2, 2, 6) = 1.98
    blockpc1(2, 3, 1) = -9.62
    blockpc1(2, 3, 2) = .14
    blockpc1(2, 3, 3) = -1.81
    blockpc1(2, 3, 4) = -4.9
    blockpc1(2, 3, 5) = -6.67
```

```
blockpc1(2, 3, 6) = .76
blockpc1(1, 1, 1) = -2.26
blockpc1(1, 1, 2) = 2.01
blockpc1(1, 1, 3) = 3.87
blockpc1(1, 1, 4) = 4.66
blockpc1(1, 1, 5) = 5.49
blockpc1(1, 1, 6) = 1.85
blockpc1(1, 2, 1) = -2.33
blockpc1(1, 2, 2) = -3.12
blockpc1(1, 2, 3) = 2.37
blockpc1(1, 2, 4) = 2.7
blockpc1(1. 2, 5) = 4.72
blockpc1(1, 2, 6) = 5.3
blockpc1(1, 3, 1) = -1.47
blockpc1(1, 3, 2) = -7.2
blockpc1(1, 3, 3) = -1.46
blockpc1(1, 3, 4) = -3.04
blockpc1(1, 3, 5) = 5.96
blockpc1(1, 3, 6) = -2.18
blockpc2(2, 1, 1) = 6.68
blockpc2(2, 1, 2) = .15
blockpc2(2, 1, 3) = 6.39
blockpc2(2, 1, 4) = 1
blockpc2(2, 1, 5) = -3.34
blockpc2(2, 1, 6) = -3.42
blockpc2(2, 2, 1) = -3.06
blockpc2(2, 2, 2) = 2.67
blockpc2(2, 2, 3) = 2.91
blockpc2(2, 2, 4) = 3.78
blockpc2(2, 2, 5) = 1.12
blockpc2(2, 2, 6) = .98
blockpc2(2, 3, 1) = 2.39
blockpc2(2, 3, 2) = 9.49
blockpc2(2, 3, 3) = 3.73
blockpc2(2, 3, 4) = .04
blockpc2(2, 3, 5) = 3.84
blockpc2(2, 3, 6) = -2.44
blockpc2(1, 1, 1) = -4.19
blockpc2(1, 1, 2) = -2.24
blockpc2(1, 1, 3) = 3.9
blockpc2(1, 1, 4) = -1.61
blockpc2(1, 1, 5) = -5.36
blockpc2(1, 1, 6) = 1.4
blockpc2(1, 2, 1) = -6.21
blockpc2(1, 2, 2) = -1.04
blockpc2(1, 2, 3) = -1.63
blockpc2(1, 2, 4) = 1.45
blockpc2(1, 2, 5) = -6.48
blockpc2(1, 2, 6) = -4.04
blockpc2(1, 3, 1) = -2.96
blockpc2(1, 3, 2) = -.18
blockpc2(1, 3, 3) = 8.17
```

```
blockpc2(1, 3, 4) = 2.73
blockpc2(1, 3, 5) = -7.59
blockpc2(1, 3, 6) = -7.02
blockpc3(2, 1, 1) = 6.74
blockpc3(2, 1, 2) = 1.38
blockpc3(2, 1, 3) = 5.39
blockpc3(2, 1, 4) = 6.96
blockpc3(2, 1, 5) = 2.45
blockpc3(2, 1, 6) = 1.99
blockpc3(2, 2, 1) = 1.77
blockpc3(2, 2, 2) = -1.69
blockpc3(2, 2, 3) = 1.14
blockpc3(2, 2, 4) = 2.86
blockpc3(2, 2, 5) = .95
blockpc3(2, 2, 6) = 1.7
blockpc3(2, 3, 1) = 2.27
blockpc3(2, 3, 2) = 1.78
blockpc3(2, 3, 3) = 3.02
blockpc3(2, 3, 4) = 1.31
blockpc3(2, 3, 5) = 5.86
blockpc3(2, 3, 6) = 1.82
blockpc3(1, 1, 1) = -3.24
blockpc3(1, 1, 2) = -.57
blockpc3(1, 1, 3) = -10.98
blockpc3(1, 1, 4) = .72
blockpc3(1, 1, 5) = -8.69
blockpc3(1, 1, 6) = -.5
blockpc3(1, 2, 1) = -4.07
blockpc3(1, 2, 2) = -3.18
blockpc3(1, 2, 3) = -2.29
blockpc3(1, 2, 4) = -.38
blockpc3(1, 2, 5) = -3.95
blockpc3(1, 2, 6) = -.92
blockpc3(1, 3, 1) = .46
blockpc3(1, 3, 2) = -5.2
blockpc3(1, 3, 3) = -7.28
blockpc3(1, 3, 4) = -.71
blockpc3(1, 3, 5) = -.91
blockpc3(1, 3, 6) = 3.98

'now find the coefficients
i = 0
FOR r = 1 TO 3
FOR c = 1 TO 6
  i = i + 1
  stanum(r, c) = i
  PRINT r; c; stanum(r, c)
NEXT c
NEXT r
pauser
FOR r = 1 TO 3
FOR c = 1 TO 6
```

```
  a = stanum(r, c)
  'PRINT r + 1, c
  IF r + 1 < 4 THEN coeff(a, stanum(r + 1, c)) = 1
  IF r - 1 > 0 THEN coeff(a, stanum(r - 1, c)) = 1
  IF c + 1 < 7 THEN coeff(a, stanum(r, c + 1)) = 1
  IF c - 1 > 0 THEN coeff(a, stanum(r, c - 1)) = 1
NEXT c
NEXT r
FOR i = 1 TO 18
FOR j = 1 TO 18
  IF coeff(i, j) > 0 THEN PRINT i; j; coeff(i, j)
  IF coeff(i, j) <> coeff(j, i) THEN
    BEEP
    PRINT "coefficientts not equal"; i; j
  END IF
  totcoeff = totcoeff + coeff(i, j)
NEXT j
NEXT i
PRINT "totcoeff:"; totcoeff
pauser

FOR loca = 1 TO 2
FOR r = 1 TO 3
FOR c = 1 TO 6
  PRINT blockpc2(loca, r, c);
NEXT c
PRINT
NEXT r
pauser
PRINT : PRINT
NEXT loca
pauser

END SUB

SUB pauser
DO WHILE INKEY$ = ""
LOOP

END SUB
```

VITA AUCTORIS

NAME: Lawrence A. Heidinga

PLACE OF BIRTH: Winchester, Ontario

YEAR OF BIRTH: 1972

EDUCATION: North Addington Education Centre
1987-1991

Lakehead University, Thunder Bay, Ontario
1991-1995 B.Sc.

University of Windsor, Windsor, Ontario
Anticipated graduation fall 1998.